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DEPARTMENT OF ENERGY AND NATURAL RESOURCES
NATURAL HISTORY SURVEY DIVISION
CHAMPAIGN, ILLINOIS

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Natural History Survey
ILLINOIS
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The Diptera, or True Flies,
of Illinois
I. Tabanidae

L. L. Pechuman
Donald W. Webb
H. J. Teskey

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NATURAL HISTORY SURVEY DIVISION
CHAMPAIGN, ILLINOIS

VOLUME 33, ARTICLE 1
APRIL 1983

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CHAMPAIGN, ILLINOIS

VOLUME 33, ARTICLE 1
APRIL 1983

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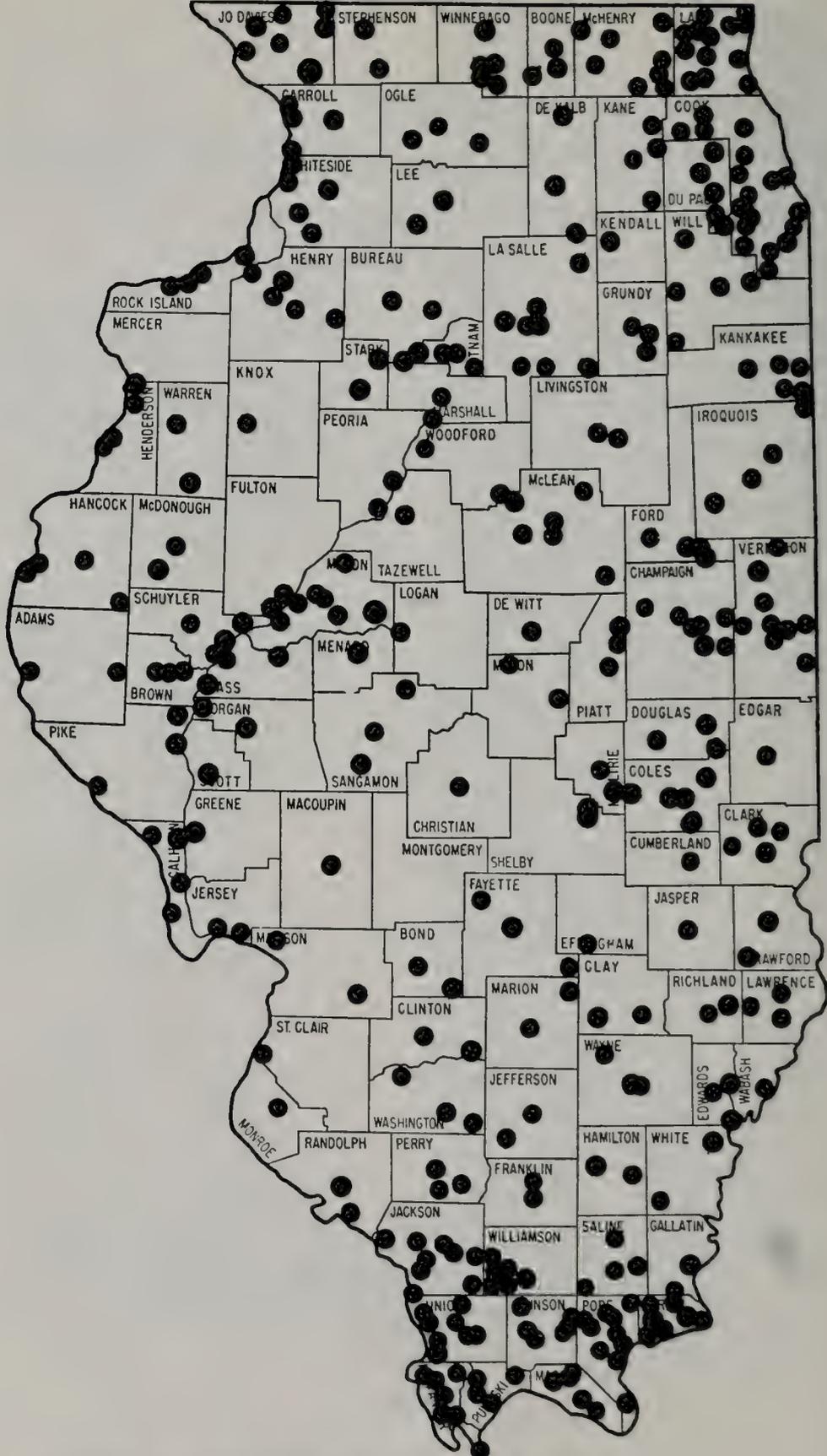
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This report is published by authority of the State of Illinois. It is a contribution from the Section of Faunistic Surveys and Insect Identification of the Illinois Natural History Survey. Dr. L. L. Pechuman is Professor Emeritus, Department of Entomology, Cornell University; Dr. Donald W. Webb is a Taxonomist, Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey; and Dr. H. J. Teskey is in the Diptera Section, Biosystematics Research Institute, Research Branch, Agriculture Canada.

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Frontispiece.—Sites where tabanids have been collected in Illinois.

The Diptera, or True Flies, of Illinois

I. Tabanidae

L. L. Pechuman, Donald W. Webb, and H. J. Teskey

The tabanids, or horse flies and deer flies, are well known to dairy farmers and livestock producers as well as to campers, fishermen, and outdoor enthusiasts as annoying and pain-inflicting inhabitants of most wooded areas of Illinois. These large and persistent flies impart a painful bite and can occur in large enough numbers to make canoeing and hiking virtually impossible.

The tabanid fauna of Illinois has never been studied, although several of the surrounding states have published various reports: Indiana (Burton 1975; Meyer & Sanders 1975), Wisconsin (Roberts & Dicke 1958), Iowa (Richards & Knight 1967), Missouri (Andrews & Wingo 1975), Tennessee (Goodwin 1966), Michigan (Hays 1956), Ohio (Hine 1903), Minnesota (Philip 1931), and Arkansas (Schwardt 1936; Schwardt & Hall 1930). This study is intended to make available in brief form our present knowledge of the tabanids in the central United States, with keys for their determination, and the distribution of those species occurring in Illinois. No attempt is made to give detailed taxonomic descriptions of species. If needed, these can be found for most species in the papers of Brennan (1935) and Stone (1938). Philip (1954, 1955) has keys to all the North American Pangoniinae and Chrysopsinae known at that time. The most recent list of the North American species of Tabanidae is given by Philip (1965).

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have made their collections and data available for this study. Particularly we would like to thank Edward Lisowski for his time, effort, and patience in collecting tabanids throughout Illinois and Drs. Chris Maier, Milton Sanderson, and Gilbert Waldbauer for the Illinois material they have collected over the years.

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Photographs of the wings were provided by Howard Lyons, Department of Plant Pathology, Cornell University. Drawings of the tabanid antennae and the abdominal patterns of *Tabanus* were completed by Miss Donna Baron.

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NATURAL DIVISIONS OF ILLINOIS

In studying the tabanid fauna of Illinois, we placed particular emphasis

on collecting in unique areas within the state. Fig. 1 illustrates the natural divisions of Illinois based upon the features of topography, soil type, bed-rock type, glacial history, and the dis-

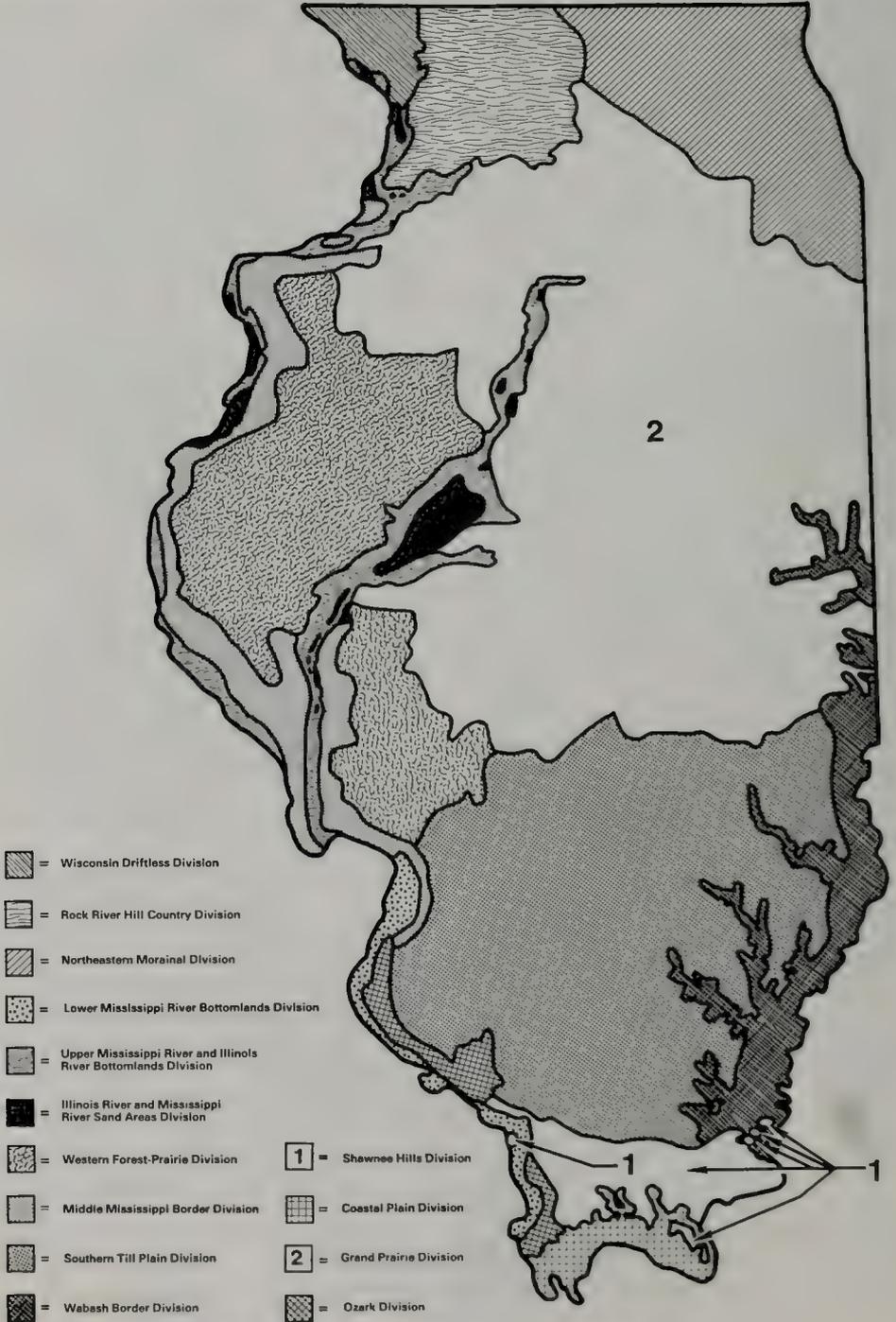


Fig. 1.—The natural divisions of Illinois. (Redrawn from Schwegman 1973)

tribution of native plants and animals (Schwegman 1973).

The Northeastern Morainal Division is the region of most recent glaciation in Illinois. Glacial landforms are common features, including tamarack and sphagnum bogs (Fig. 2) and lakes, fens, marshes and sand terraces (Fig. 3, 4). Boreal tabanids, such as *Chrysops mitis*, *C. sackeni*, *Atylotus bicolor*, *A. woodi*, *Tabanus novaescotiae*, *Hybomitra frontalis*,

and *H. minuscula*, have been collected in Illinois only in this area.

The Wisconsin Driftless Division represents an area of northwestern Illinois that apparently escaped Pleistocene glaciation. The topography is one of rolling hills and great relief, particularly along the interior stream canyons (Fig. 5). Although no species of Illinois tabanids are unique to this area, it is one of the few areas in which



Fig. 2.—Volo Bog: a sphagnum and tamarack bog in Lake County.



Fig. 3.—Illinois Beach State Park: marshes and sand terraces of the Lake Michigan basin, Lake County.

Stonemyia rasa, *Chrysops inda*, and *Tabanus trimaculatus* have been collected in the state.

The Grand Prairie Division forms the largest natural division in Illinois and was formerly a tall-grass prairie,



Fig. 4.—Dead River, Illinois Beach State Park, Lake County.



Fig. 5.—Apple River Canyon State Park: an unglaciated driftless area of Illinois, Jo Daviess County.



Fig. 6.—Siloam Springs State Park: a flood control reservoir, Adams County.



Fig. 7.—LaRue-Pine Hills Ecological Area: part of the Ozark Uplift in Illinois, Union County.



Fig. 8.—Bell Smith Springs Recreational Area: deciduous forest with sandstone cliffs, Pope County.



Fig. 9.—Hayes Creek Canyon: deciduous forest, Pope County.



Fig. 10.—Horseshoe Lake: bald cypress and tupelo swamp, Alexander County.



Fig. 11.—Cache River Swamp, a cypress swamp in Johnson County.

with numerous marshes and prairie potholes. Today it is the most productive agricultural area of Illinois. Numerous species of tabanids have been collected throughout this area.

The Western Forest-Prairie Division is a strongly dissected glacial till plain with many ravines in the level to rolling mesic uplands (Fig. 6). Floodplains are developed along the major streams. Western species of tabanids, such as *Silvius quadrivittatus*, are often collected in this portion of the state.

The Southern Till Plain Division encompasses most of the area of Illinois dissected by the Illinoian Glacial Till Plain south of the Shelbyville Moraine. Both forest and prairie formerly were present although agricultural practices have greatly modified this area. The soils are relatively poor because of their high clay content. Numerous tabanids with very general distribution patterns have been collected throughout this area.

The Wabash Border Division includes the bottomlands of the Wabash River and its major tributaries. Remnants of the eastern deciduous forest containing beeches and tuliptrees are scattered within forest preserves in this portion of eastern Illinois. Malaise traps in a wooded ravine along the Vermilion River collected *Goniops chrysozona*, *Hybomitra sodalis*, and *Tabanus sublongus* in this area of Illinois.

The Ozark Division consists of the Illinois part of the Salem Plateau of the Ozark Uplift. This area is mostly forested (Fig. 7) but contains scattered hill prairies. The division contains many Ozarkian, southern, and southwestern plants and animals that are rare or absent elsewhere in Illinois. *Chrysops pudicus* was collected at several locales in this area but nowhere else in the state.

The Shawnee Hills Division extends across the southern portion of Illinois from the Mississippi River to near the mouth of the Wabash River. This unglaciated hill country is characterized by a high east-west escarpment of sandstone cliffs. Originally this divi-

sion was mostly forested, and considerable forest remains. The topography is very rugged, with many bluffs and ravines (Fig. 8, 9). A variety of tabanids have been collected in this region.

The Coastal Plain Division is a region of swampy forested bottomlands and low clay and gravel hills that is the northernmost extension of the Gulf Coastal Plain Province of North America. Bald cypress (Fig. 10, 11) and tupelo gum swamps are unique features of this division in Illinois. Tabanids such as *Chrysops celatus*, *C. dimmocki*, *C. reicherti*, *C. separatus*, and *Neochrysops globosus* have been collected in Illinois only from this area.

NATURAL HISTORY

Immature Stages

Although extensive work has been done on the biology of many species of tabanids in North America, the work of Teskey (1969), Teskey & Burger (1976), Tidwell (1973), Tidwell & Tidwell (1973), and Goodwin (1972, 1973a, 1973b, 1976a, 1976b) has done much to increase our knowledge of the systematics and biology of the immature stages; these papers should be consulted when identification of the immature stages is required.

Eggs of many species are laid in masses on vegetation above water (Fig. 12-14) or moist ground although logs, rocks, and bridge abutments are also used for this purpose. The egg mass is whitish when freshly laid (Fig. 14) but soon darkens to various shades of brown to jet black, depending on the species. Some species of *Chrysops* lay a single-tiered egg mass (Fig. 14), and *Hybomitra* and *Tabanus* generally have egg masses of more than one tier (Fig. 12).

The larvae of Illinois Tabanidae are relatively well known as a result of work in adjacent areas by Burger (1977), Goodwin (1972, 1973a, 1973b, 1976a, 1976b), Teskey (1969), Teskey & Burger (1976), Tidwell (1973), Tidwell & Tidwell (1973), and others. Larvae of 77 of the 109 species

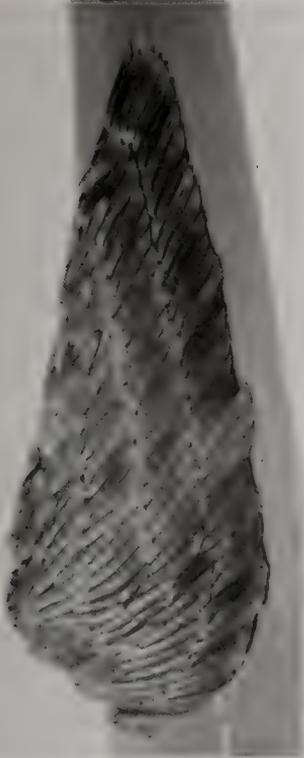


Fig. 12.—A lateral view of a horse fly egg mass.

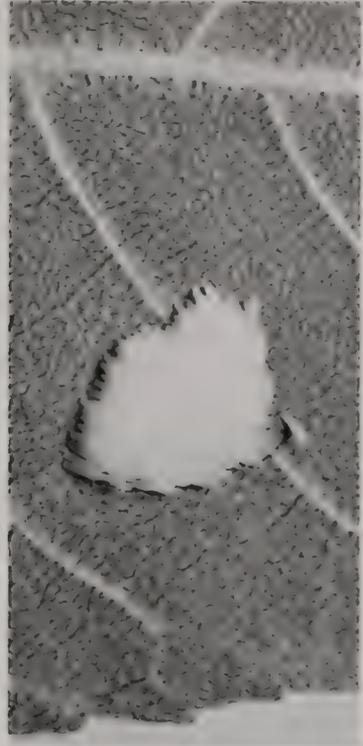


Fig. 14.—Fresh egg mass of *Chrysops moechus*, quite different from those of most species of *Chrysops*.



Fig. 13.—An enlarged view of a deer fly egg mass. Many species of *Chrysops* deposit egg masses of this general type.

recorded or potentially to be found in Illinois have been described. However, because the larvae of 32 species are still unknown, and as some of them are probably very similar to known larvae, great care must be taken in identifying larvae.

Tabanid larvae are distinctive on the bases of the characteristic shape and features of the head capsule, the encircling bands of 3 or 4 pairs of wartlike prolegs on the first 5 or 7 abdominal segments (except in *Goniops*), and in particular, the characteristic features of the posterior spiracles. The elongate, anteriorly tapered head capsule with slender, pointed, usually curved mandibles and the mandibular brush of spines situated dorsolaterally above the base of each mandible is shown in Fig. 77. Such a head capsule is common to all of the Tabanoidea

(Athericidae, Pelecorhynchidae, Rhagionidae, and Tabanidae).

Exposed portions of the posterior spiracles are in the form of a pair of closely appressed vertical linear bars, or a bladelike spine situated at the apex of a short respiratory siphon, or at least a circularly delineated area at the apex of the terminal segment (Fig. 78-80). It is worth noting that the actual site of air exchange is not associated with the bars or spine but rather within a slit at either side of these visible features.

Other features of particular importance in the identification of tabanid larvae are shown in Fig. 87. The extent of pubescence on various aspects of the body is the most important diagnostic feature. Pubescence is normally restricted to the anterior and posterior segmental borders and the posterior margin of the prolegs of a variable number of segments. Such pubescence is referred to as anterior, posterior, and proleg pubescence (Fig. 86). In addition, pubescence may occur in a characteristic configuration midlaterally on the terminal (or anal) segment and as narrow extensions posteriorly from anterior pubescence on one or more thoracic segments and anteriorly from posterior pubescence on the penultimate (preanal) segment. As this pubescence may be extremely pale, proper illumination is the key to accurate interpretation. Combinations of reflected and transmitted light (or backlighting) of varied intensities must be used. In some cases the pubescence may only be seen in profile. It may be necessary to slide mount larval exuviae in glycerine for viewing at high magnification under a compound microscope.

Identifications can be made of living or preserved larvae or of larval exuviae. However, it is necessary to slow the movement of living larvae. This is most easily accomplished by immersing the larvae in ice water. A styrofoam insulating block excavated to hold an individual ice cube contain-

er is ideal for use under a stereoscopic microscope. A wire window screen platform wedged at half the depth of the container serves to support the larva and to prevent the ice in the lower half from floating. Preserved larvae and exuviae can be viewed while they are immersed in the preserving fluid in shallow dishes.

The larval stages of most species live under moist conditions, varying from aquatic habitats to moist soils and from rapidly flowing streams to stagnant ponds. Some species are found only in sphagnum bogs (Fig. 2). The larvae of some species live in relatively dry soil and others in rotten wood. Some species show great tolerance of variation in larval habitat.

The larvae of many species of *Tabanus* and *Hybomitra* are known to be carnivorous, but the food requirements of the various species of *Chrysops* are unknown.

The larvae of most species look much alike to the casual observer. They are usually white, but may be brownish or greenish, tapering at each end (Fig. 85-91). The larvae of *Goniops chrysocoma* is bottle shaped (Fig. 81). The larvae of some species have dark bands (Fig. 203). When full grown, the larvae of many species move to drier situations to pupate. As far as is known, all species overwinter as larvae.

The pupae are brown or straw colored with a row of stiff spines encircling the apical third of each abdominal segment. At the apex of the abdomen are 6 stout, sharply pointed projections forming the pupal aster. The pupal stage requires from 1 to 3 weeks, depending on the species and the temperature.

Under Illinois conditions, most species have one generation a year. There is some evidence, however, that *Tabanus lineola* and *T. similis* may occasionally develop from egg to adult in one season. Some individuals of *T. atratus* and other large *Tabanus* species may take 2 or 3 years to complete their development. The emergence of the

males of a given species normally is slightly in advance of the main emergence of the females.

Habits of Adults

Most female horse flies and deer flies suck blood and attack both humans and animals. The males, which do not suck blood, are generally collected from flowers or foliage. Tabanids of both sexes frequently rest on paths and roads, especially those in wooded areas (Fig. 8, 9, 10, 11). *Hybomitra difficilis*, *H. microcephala*, and *Tabanus sulcifrons* have a decided proclivity for such situations. The females often enter buildings in considerable numbers and tend to congregate at windows since they are attracted to light. Both sexes of many species occasionally come to lights at night, and almost all males of *Tabanus punilus* and *T. sackeni* have been taken at lights.

Tabanids are most active on warm sunny days when there is no wind. A slight drop in temperature or a sudden breeze greatly reduces the number of attacking females. There are exceptions to this rule, however; Pechuman (1972) reported, being attacked by *Chrysops moechus* after dark and by *C. indus* at uncomfortably cool temperatures. Some species are normally crepuscular or nocturnal; these include *Tabanus sackeni* and probably *T. sublongus*.

Moving objects and dark objects seem to be most subject to attack. Pechuman (1972) noted that predominantly dark cattle in a herd usually have the most horse flies feeding on them.

Although the immature stages of most tabanids inhabit wet or moist conditions, adults are often numerous some distance from breeding areas.

Natural Enemies

There is an extensive but scattered literature on the natural enemies of tabanids, but the following discussion is restricted to those applying to Illinois species.

Adults are preyed upon by birds,

dragonflies (Odonata), robber flies (Asilidae), and wasps of the genera *Vespula*, *Crabro*, and *Bembix*. *Crabro monticola* and some species of *Bembix* provision their nests with quantities of tabanids, but the populations of these wasps do not seem to be large enough to have any appreciable effect on tabanid populations. Adult tabanids are found in spider webs, but this is not common except at windows inside barns.

Larvae and pupae are parasitized by Hymenoptera of the families Diapriidae and Pteromalidae and by Diptera of the families Bombyliidae and Tachinidae, but these seem to do little toward reducing populations. Teskey (1969) reports that only 2 percent of the larvae he collected were parasitized although in specific localities the percentage might be higher. On one occasion, in an area where there were numerous egg masses of *Chrysops moechus*, Pechuman (1972) noted that many freshly hatched larvae became entangled and died in webs of tetranychid mites on the leaves. Shore birds feed to some extent on tabanid larvae.

Parasitism of eggs by the hymenopterous families Trichogrammatidae and Scelionidae is apparently common.

The cannibalistic habits of *Hybomitra* and *Tabanus* larvae are suspected to have a greater effect on larval populations than do predators and parasites.

Economic Importance

Because of their medical and veterinary importance, both by direct injury and by the transmission of disease organisms, the economic importance of horse flies and deer flies has received wide attention (Webb & Wells 1924; Philip 1931; Anthony 1962; Jamnback 1969).

Tabanids are vectors of several diseases of man and animals caused by such organisms as viruses (equine infectious anemia, vesicular stomatitis, hog cholera, California encephalitis), bacteria (anthrax, tularemia), rickett-

sia or rickettsia-like organisms (Q fever, anaplasmosis), trypanosomes (surra, mal de caderas, murrina), and filarial worms (loiasis, elaeophorosis), which have been discussed in Anthony (1962), Jones & Anthony (1964), DeFoliart et al. (1969), Wright et al. (1970), and Tidwell et al. (1972).

Most of these disease organisms are transmitted mechanically. Since tabanid bites are painful, the host makes an effort to dislodge the biting fly, and since tabanids are nervous and alert feeders, they are easily disturbed. When dislodged, the fly returns to the attack but may select a nearby host. If the first host has disease organisms in its blood, some of these adhering to the proboscis may be injected into the blood of the second host. Although some of the diseases mentioned are present in Illinois, only anaplasmosis is reasonably common, occurring in the spring and fall in southern Illinois.

The biological transmission of the filarioid parasite *Elaeophora schneideri* to deer, elk, and domestic sheep by various species of *Tabanus* and *Hybomitra* has been reported by Hibler et al. (1969, 1970, 1971).

Control

Little of a positive nature can be said about the control of horse flies and deer flies. Applications of insecticides to restricted areas have been of little value, and applications over wide areas have been only moderately effective while increasing the danger to nontarget organisms. Insecticides have given more successful control of the larvae than of adults, but damage to other organisms has been even greater (Jamnback & Wall 1959).

Repellents for use on livestock have shown some promise, but their effects are of short duration. The standard repellents commercially available for human use, and effective for mosquitoes and black flies, are generally useless as deer fly repellents. In fact, the shiny appearance of the skin after using them may even attract the flies.

Natural enemies show little promise

as controls, although mass releases of egg parasites would be expected to cause some population reduction.

Sudden changes in water level are destructive to some species, and manipulation of water levels has been fairly effective in Connecticut (Anderson & Kneen 1969). However, such manipulation is not often possible. Drainage reduces the available breeding areas for many species, but it may actually increase larval habitats for such species as *Tabanus quinquevittatus*.

On farms with small ponds and seepage areas, most emergent vegetation can be removed to reduce oviposition sites significantly. Egg laying is thus concentrated on the small amount of vegetation remaining, and this can be destroyed with its load of egg masses. However, this procedure is not practical for large bodies of water and swamps.

The most promising method of control, at least in limited areas, is the use of trapping devices. Shining black panels covered with sticky substance and baited with dry ice are quite effective for *Tabanus*. Canopy traps of the general type described under *Collection and Preservation* (Fig. 17) and box traps are used in the coastal areas of several states to reduce tabanid populations on beaches and golf courses. In New York canopy traps are used on stud farms and are regarded as successful. Pechuman (1972) used such a trap near a swimming pool where horse flies were attacking swimmers, and the resulting reduction in flies was dramatic.

COLLECTION AND PRESERVATION

Horse flies and deer flies can be collected in the situations mentioned under *Habits of Adults*. Females can be taken as they attack animals and humans, from windows in buildings, and from cars parked with open windows. Both sexes can be collected from flowers, by sweeping vegetation with an insect net, from roads in wooded areas, and from lights at night. Some species of wasps of the genera

Crabro and *Bembix* capture tabanids to provision their nests, and excellent specimens of both sexes can be obtained by capturing the wasps as they approach their nests or by digging out the nests. Males of certain species can be collected as they hover along roads or in clearings, and other males can be found at dawn on exposed rocks in elevated situations. Collecting larvae and rearing adults from them will pro-

more selective and the catch is largely restricted to horse flies. Unlike the Malaise trap, it rarely collects male specimens. The canopy is shining black plastic below and transparent plastic above, with the bottom about 60 cm from the ground. A shining black sphere (a beach ball painted glossy black) about 60 cm in diameter is suspended about 30 cm from the ground by a cord. The color and its

Fig. 15.—Horizontal Malaise trap used in collecting tabanids.

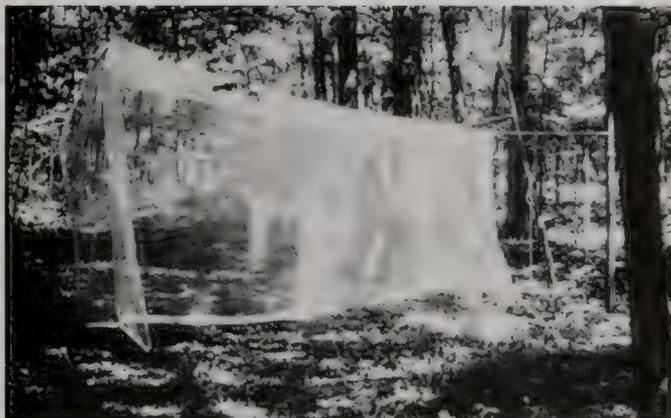


Fig. 16.—Free-standing Malaise trap used in collecting tabanids.

duce about equal numbers of both sexes.

The use of traps will yield large numbers of specimens. Traps used in obtaining material for this paper were of three types. The Malaise trap is placed to form a barrier that intercepts the flight of tabanids and other insects. Two different types of Malaise traps were used during this study (Fig. 15, 16). The canopy trap (Fig. 17) is

reflection, and possibly heat from the canopy and sphere, and the movement of the sphere attract horse flies under the canopy; many of these then fly upward and are caught in a collection apparatus. Such a device can be a simple plastic or wire dome with an inverted funnel within it to prevent escape of the specimens; this type of collecting head is usually used when control is the main object. A some-



Fig. 17.—Canopy trap used in collecting tabanids.

Fig. 18.—One type of collecting head used with a canopy trap.



what more complicated device (Fig. 18) produces better quality specimens for study. If dry ice or another source of carbon dioxide is placed near the top of the canopy, the catch is increased considerably.

Horse flies and deer flies are easily preserved, but the specimens must be of good quality. They should be pinned through the right side of the thorax on the day of collection; no further treatment is necessary. All, of course, should carry the usual locality label with date of collection and collector's name. A second label with host, ecological situation, and a diagram of the eye pattern (which disappears shortly after death) is helpful.

Flies not pinned when fresh rarely

make good specimens for study. If these are moistened so they can be pinned, much of the body pattern, often important for species determination, may be destroyed. Specimens preserved in alcohol have the same disadvantage. Reasonably good specimens can be mounted from alcohol if they are placed overnight in cellosolve, transferred for about an hour to xylene, and then pinned. Specimens mounted directly from alcohol are almost worthless.

Pinned specimens that are dirty or greasy can be cleaned by immersion in ethyl acetate for several hours.

Techniques for collecting and rearing the immature stages of tabanids have been described by Teskey (1962, 1969).

CLASSIFICATION

Horse flies and deer flies belong to the family Tabanidae, which is world-wide in distribution and comprises more than 3,000 described species. The most modern classification on a worldwide basis is that of Mackerras (1954), and for North America that of Philip (1957, 1965).

The family is divided into three subfamilies and each subfamily into tribes; not all tribes are represented in Illinois. A listing by subfamily and tribe of the genera found or likely to be found in Illinois follows.

Species found in Illinois

PANGONIINAE:

Pangoniini	
<i>Stonemyia</i>	1
Scionini	
<i>Goniops</i>	1

CHRYSOPSINAE:

Bouvieromyiini	
<i>Merycomyia</i>	
Chrysopsini	
<i>Chrysops</i>	30
<i>Silvius</i>	1
<i>Neochrysops</i>	1

TABANINAE:

Diachlorini	
<i>Diachlorus</i>	
<i>Chlorotabanus</i>	
Haematopotini	
<i>Haematopota</i>	
Tabanini	
<i>Atylotus</i>	3
<i>Leucotabanus</i>	1
<i>Tabanus</i>	35
<i>Hybomitra</i>	9
<i>Hamatabanus</i>	1

TAXONOMIC CHARACTERS

Distinctive structural characters are few in the Tabanidae, and most of them are confined to the head and its appendages. Chaetotaxy, so useful in many groups of Diptera, cannot be used, since macrochaetae are not present. Since distinguishing structural characters are few, much dependence is placed on ground color and pilosity, and these must be used with caution on partly denuded specimens.

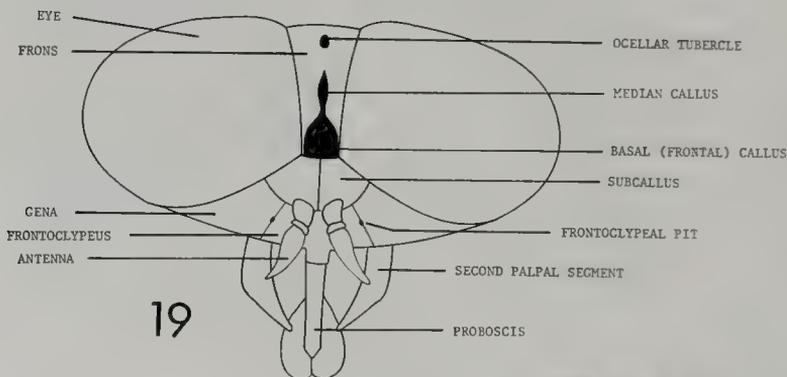
Some characters of the head are restricted to females, requiring the use of separate keys to the males of *Chrysops*, *Hybomitra*, and *Tabanus*. Since males do not attack man or animals, they are much less common in collections than females; the male of several North American species is still unknown. Males are easily recognized by the contiguous eyes.

With Fig. 19–22 as guides, most of the characters used in the keys can be readily understood.

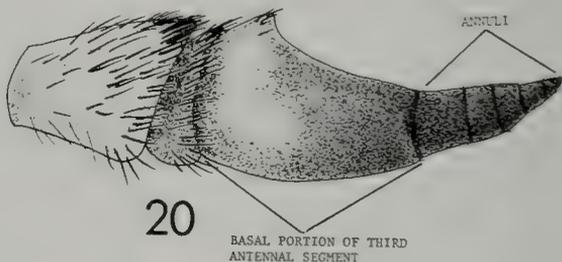
KEY TO GENERA OF TABANIDAE

Adults

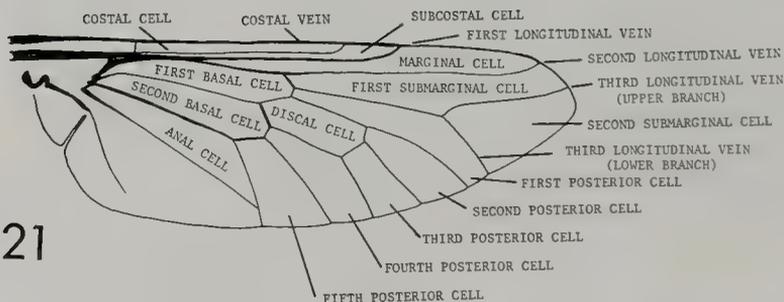
1. Hind tibiae with 2 apical spurs2
 Hind tibiae without apical spurs7
2. Third segment of antenna with 8 distinct annuli (Fig. 23, 24).....3
 Third segment of antenna with 5 or fewer distinct annuli (Fig. 26)4
3. Eyes of female with upper inner angles acute; frons broader than width of eye; wings with dark pattern (Fig. 37)**Goniops**
 Eyes of female normal; frons narrower than width of eye; wings hyaline (Fig. 36)**Stonemyia**
4. Third antennal segment with rather broad basal plate, 2 or 3 annuli (Fig. 25); first antennal segment only slightly longer than wide, total length of antennae equal to or shorter than thickness of head; large species with very small tibial spurs**Merycomyia**
 Third antennal segment with rather narrow basal plate, 4 annuli (Fig. 26); first antennal segment usually at least twice as long as wide, total length of antennae greater than thickness of head; hind tibial spurs pronounced5
5. Abdomen globose, wider than thorax, with 2 rows of dark spots; wings rather evenly fumose (Fig. 74).....**Neochrysops**
 Abdomen slender, variously marked or unpatterned; wings only rarely evenly fumose6
6. Wings with isolated clouds (Fig. 73); second antennal segment not more than half length of first (Fig. 27)**Silvius (Griseosilvius)**
 Wings with dark crossband or traces of such band; first 2 antennal segments subequal (Fig. 26).....**Chrysops**
7. First antennal segment distinctly longer than wide (Fig. 29); frons of female widened below, broader than high; wing with gray maculations (Fig. 76)**Haematopota**



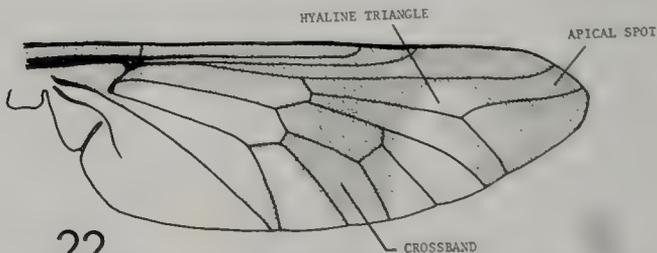
19



20

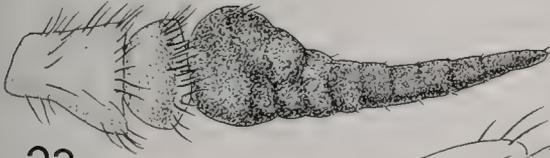


21



22

Fig. 19-22.—Head, antenna, wings. 19. *Hybomitra illota*, anterior view of head. 20. *Hybomitra illota*, antenna. 21. *Hybomitra illota* wing (markings not shown). 22. *Chrysops* sp. wing.



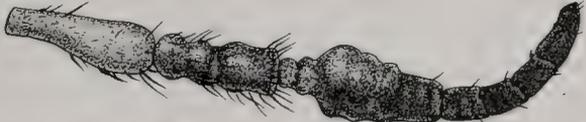
23 STONEMYIA



24 GONIOPS



25 MERYCOMYIA



26 CHRYSOPS



27 SILVIUS



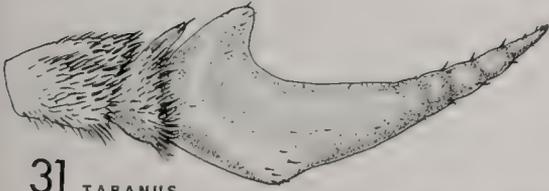
28 DIACHLORUS



29 HAEMATOPOTA



30 HAMATABANUS



31 TABANUS

Fig. 23-31.—Antennae. 23. *Stonemyia*. 24. *Goniops*. 25. *Merycomyia*. 26. *Chrysops*. 27. *Silvius*. 28. *Diachlorus*. 29. *Haematopota*. 30. *Hamatabanus*. 31. *Tabanus*.

- First antennal segment usually scarcely longer than wide; frons of female higher than broad; wing pattern, if any, not as above8
8. Third antennal segment with no dorsal angle (Fig. 28); frons of female narrow, median callus a narrow line; wings with dark pattern (Fig. 75); eyes bare; no ocellar tubercle; fore tibiae swollen; basicosta (subepaulets) bare**Diachlorus**
Without this combination of characters.....9
9. Ocelli small but distinct; frons narrow; frontal callus narrow, ridgelike, well removed from eyes**Leucotabanus**
No ocelli, but ocellar tubercle may be present; frons and callosities, if present, variable but not ridgelike10
10. Basicostae (subepaulets) bare or nearly so; abdomen green, unpatterned (pale yellow in older dried specimens); frontal callosities lacking; eyes bare**Chlorotabanus**
Basicostae with macrotrichia similar in appearance and density to those on costal vein; abdomen unicolorous or patterned, never green; frontal callosities present or absent; eyes bare or hairy11
11. Third antennal segment with hooklike projection from basal plate reaching nearly to base of annulate portion (Fig. 30); eyes sparsely hairy in female, densely haired in male**Hamatabanus**
Third antennal segment rarely with projection (Fig. 31); if present, eyes bare.....12
12. Vertex with distinct bare ocellar tubercle in female, male with elevated anteriorly shining tubercle; eyes hairy in most species.....**Hybomitra**
Vertex without ocellar tubercle; if elevated tubercle present in male, then completely pollinose; eyes bare or hairy13
13. Frons of female with frontal callosities absent or reduced to 1 or 2 small oval spots well separated from eyes; eyes hairy, heavily so in males, often yellow or pale brown in dried specimens**Atylotus**
Frons at least with broad basal callus; eyes hairy or bare, usually blackish in dried specimens**Tabanus**
- dominal segments with prolegs (Fig. 82-112, 190-218, 261-270)2
2. Three pairs of prolegs on each of first 7 abdominal segments, a pair dorsally, laterally, and ventrally (Fig. 82-110).....3
Four pairs of prolegs, including an additional ventrolateral pair, on each of first 7 abdominal segments (Fig. 111, 112; 190-218; 261-270)5
3. Body surface, except respiratory siphon, almost or completely covered with a dense, short pubescence.....4
Body surface with large bare areas; pubescence restricted to anterior or posterior margin or posterior border of prolegs of 1 or more segments.....**Chrysops** (separate key)
4. Pubescence completely covers body surface, conspicuously mottled with dark and pale areas (Fig. 109). Third antennal segment shorter than second. Respiratory siphon length equal to or only slightly longer than its basal diameter**Chlorotabanus crepuscularis**
Pubescence absent from narrow posterior band on most segments, not conspicuously mottled (Fig. 110). Third antennal segment longer than second segment. Respiratory siphon length about twice as long as its basal diameter**Diachlorus ferrugatus**
5. Respiratory siphon comprises distal ends of 2 opposed sclerotized plates between which tracheal trunks terminate in a protrusible spiracular spine (Fig. 80). Inconspicuous and incomplete striations present only laterally on segments**Merycomyia whitneyi**
Respiratory siphon always membranous and lacks sclerotized plates, tracheal trunks sometimes terminating in a spiracular spine. Striations present or absent on abdominal segments.....6
6. Respiratory siphon shorter than its basal diameter. Integumental striations extremely fine on all aspects of body, usually visible only under high magnification; striations spaced at approximately 5 μm **Haematopota rara**
If respiratory siphon shorter than its basal diameter, then striations more widely spaced, usually at more than 20 μm7
7. Respiratory siphon very short, projecting no more than half its basal diameter. Anal segment usually shorter than its greatest diameter, hemispherical (Fig. 111, 112). Striations uniformly spaced on all aspects of body.....8
Respiratory siphon ranges from slightly shorter (Fig. 196, 197) to about four times longer than its basal diameter. Anal segment usually somewhat attenuated posteriorly toward respiratory siphon (Fig. 190-218, 261-270). Striations normally absent from dorsal and

Larvae

1. Body pear shaped. Integument opaque and roughened. All segments with an annular ring of small tubercles or crenulate frills (Fig. 81)**Goniops chrysocoma**
Body elongate, more or less cylindrical. Integument membranous and transparent, usually with longitudinal striations on some aspect of most segments, or integument entirely covered by short, dense pubescence. Some ab-

ventral surfaces of at least prothorax, and more widely spaced dorsally and ventrally than laterally on other segments9

8. Pubescence encircles anterior three-quarters of prothorax and broadly encircles posterior half of anal segment so that anal ridges and base of respiratory siphon are covered by enlarged pubescent area (Fig. 111). Inhabits wet soil on banks of streams and rivers**Silvius quadrivittatus**

Pubescence encircles little more than anterior quarter of prothorax and restricted to narrow annulus around base of respiratory siphon and vestiture of anal ridges on anal segment so that pubescence on anal ridges is separated from that encircling base of respiratory siphon (Fig. 112). Inhabits decaying wood and tree holes**Leucotabanus annulatus**

9. Midlateral surfaces of anal segment lack pubescent markings. Striations present on dorsal and ventral surfaces of all abdominal segments, or if absent, pubescence restricted, at most, to a prothoracic annulus and to the anal ridges**Hybomitra** (separate key)

Either median lateral surfaces of anal segment with pubescent markings, or striations absent or poorly developed on dorsal or ventral surface or on both surfaces abdominal segments**Tabanus, Atylotus** (separate key)

TAXONOMIC TREATMENT

In this paper a list of the localities where each species in Illinois was collected is omitted. Instead, the Illinois distribution is shown on separate maps for most of the species. Localities are listed for those species collected at five or fewer sites in Illinois. A map of the North American distribution of each species is provided.

In the brief description that precedes the discussion of each species, the average size of individuals is given. Characters given for the male include only those showing obvious differences from those of the female.

Stonemyia Brennan

The species of this genus are not known to suck blood; they are found on flowers and resting on the ground in openings in wooded areas. None of the species is common. Nothing is

known of the biology of Nearctic species.

Until this genus was erected, the species under consideration were placed in various genera, most commonly in *Pangonia* and *Buplex*.

KEY TO SPECIES OF STONEMYIA

- 1. Yellowish species, including antennae and legs**isabellina**
- Brown species; abdominal tergites with grayish hind margins.....**rasa**

Stonemyia isabellina (Wiedemann)

Silvius isabellina Wiedemann (1828:112). Type-locality: North America.

Pangonia pigra Osten Sacken (1875:367). Type-locality: Kentucky, Bee Spring.

Moderate size (12 mm); yellow; wing membrane very faintly tinted, costal cell yellow.

This species was originally described in the genus *Silvius* and for many years was unrecognized, the specific name *pigra* being used.

The immature stages of this species are not known.

S. isabellina is an eastern species, extending from Georgia to the southern tip of New York and west to western Kentucky (Fig. 32). As yet this species has not been collected in Illinois although specimens have been examined from western Kentucky and Ohio.



Fig. 32.—Distribution of *Stonemyia isabellina* in North America.

Stonemyia rasa (Loew)

Pangonia rasa Loew (1869:5). Type-locality: northern Wisconsin.

Moderate size (12.5 mm); dark brown; abdominal tergites with grayish

hind margins; legs reddish brown; wing membrane faintly tinted, costal cell yellow (Fig. 36).

The immature stages of this species are unknown.

In Illinois adults have been collected from late July to early August.

S. rasa is a northeastern species, extending from northern Georgia to southern Quebec and west to Minnesota and Illinois (Fig. 33). In Illinois this species has been collected only in the northern part of the state.



Fig. 33.—Distribution of *Stonemyia rasa* in Illinois and North America.

Goniops Aldrich

Goniops chrysocoma (Osten Sacken)

Pangonia chrysocoma Osten Sacken (1875:368). Type-locality: New York (lectotype).

Goniops hippoboscoides Aldrich (1892:237). Type-locality: Pennsylvania, Jeannette.

Stout species (12 mm); yellowish; eyes with upper inner angles acute; frons broader than width of eye; wings (Fig. 37) with dark pattern. Male brownish; abdominal tergites with pale bands on hind margins.

This is the only species in this genus, and neither sex is likely to be confused with any other tabanid. They are stout-bodied insects, 10–15 mm long, with the fore part of the wings infuscated.

The eggs are laid on the underside of tree leaves above damp ground in wooded areas. The female normally remains with the eggs until they hatch, and when disturbed makes a loud buzzing sound. The larvae (Fig. 81) are found in the lower layers of deep leaf mold and in damp soil (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early May and have been collected until early July.

G. chrysocoma is a northeastern species, extending from Georgia to Vermont and southwest to Arkansas (Fig. 34). This species has been collected at only three localities in eastern and southern Illinois.

Illinois records.—Jackson County, Makanda; Pope County, Dixon Springs Agricultural Experiment Station (1.5 miles S Glendale); Vermilion County, Forest Glen Forest Preserve (5 miles SE Westville).



Fig. 34.—Distribution of *Goniops chrysocoma* in North America.

Merycomyia Hine

Merycomyia whitneyi (Johnson)

Tabanus whitneyi Johnson (1904:15). Type-locality: New York.

Merycomyia mixta Hine (1912:516). Type-locality: Georgia, Bainbridge.

Merycomyia geminata Hine (1912:515). Type-locality: Connecticut, Lyme.

Large size (21 mm); brownish; first antennal segment only slightly longer than wide (Fig. 25); flagellum with two or three annuli; abdomen with large white patch indented above on fourth tergite, two white spots on fifth tergite; wing membrane tinted with brown, deeper toward front margin, base, and along veins; costal cell yellowish brown; hind tibiae with very small apical spurs. Male easily associated with female.

The larvae have been collected from organic material under a meter of water, from sandy clay mud in the marginal region of a small lake, from moss along the edge of a pool, and from silt along a stream (Pechuman 1972; Teskey 1969; Tidwell 1973).

M. whitneyi is a southeastern species, extending from central Florida to Maine and west to Indiana and Alabama, with a disjunct population in southern Ontario (Fig. 35). As yet this species has not been collected in Illinois although the Indiana record was collected in a county adjacent to Illinois.



Fig. 35.—Distribution of *Merycomyia whitneyi* in North America.

Chrysops Meigen

This genus includes the common deer flies with dark wing markings. The eyes are bright green and gold with dark markings. The bright colors and dark markings disappear from the eyes shortly after death. The deer flies are annoying pests of man but probably are of less importance as pests of livestock than the larger *Tabanus* and *Hybomitra* species.

They are most abundant in wooded

areas but are also found in many other surroundings. Adult deer flies first appear in early April in Illinois and have been collected until mid-September. The main flight season of each species is short, rarely over 2 weeks; nevertheless, specimens may be found throughout the season.

The males of all species of *Chrysops* (except *C. sequax tau*) found or likely to be found in Illinois are known. In several species, however, the male is known from only a single or very few specimens.

To aid in identification, Fig. 38–72 illustrate the wing patterns of the various species of *Chrysops* found in the central states. All of these wing photographs are of females; all are at the same magnification.

KEY TO SPECIES OF CHRYSOPS

Females

1. Apical spot (Fig. 42) dilutely extended around wing reducing hyaline triangle to subhyaline area not reaching hind margin of wing; large brown species; first antennal segment swollen; little or no trace of abdominal markings **brunneus**
Without this combination of characters 2
2. Wing pattern extremely faint, almost obsolete, only costal cell obviously darkened; rather small, dark species, with yellow on abdomen not in form of stripes **fulvistigma**
Wing pattern distinct even in rare cases where wing membrane tinted rather than hyaline 3
3. Apex of wing beyond crossband hyaline (Fig. 44) 4
Apex of wing beyond crossband infuscated, apical spot present (Fig. 50) 11
4. Second basal cell hyaline (Fig. 44); frontoclypeus without median pollinose stripe 5
Second basal cell at least half infuscated (Fig. 45); frontoclypeus with median pollinose stripe 6
5. Bare integument runs from ocellar area to occiput uninterrupted by pollinose areas; sublateral thoracic stripes distinct **calvus**
Bare integument of ocellar area interrupted by pollinose band; sublateral thoracic stripes indistinct **niger**
6. Abdomen entirely dark, sometimes with indefinite pattern of grayish pollinose areas 7

- Abdomen with pale areas on at least first 2 abdominal segments.....10
- 7. Fifth posterior cell with hyaline area at base (Fig. 45)8
- Fifth posterior cell infuscated at base (Fig. 47)9
- 8. Crossband reaches hind margin of wing rather broadly, outer margin quite straight or slightly bowed (Fig 45); hyaline spot at base of fifth posterior cell large, distinct.....**carbonarius**
- Crossband usually not broadly reaching hind margin of wing, outer margin irregular (Fig. 40); hyaline spot at base of fifth posterior cell usually not clear-cut, sometimes almost obsolete**ater**
- 9. Pleura with yellow to orange-red pile; crossband broadly reaches hind margin of wing (Fig. 47).....**cincticornis**
- Pleura with grayish or pale yellowish pile; crossband narrowly or not reaching hind margin of wing (Fig. 59)**mitis**
- 10. Wing picture pale (Fig. 48); pleura with gray pile; no median abdominal triangle (occasional specimens of *C. mitis* have small reddish spots laterally at base of abdomen but wing picture is dark).....**cuclux**
- Wing picture dark (Fig. 51); pleura with yellow or orange pile; median abdominal triangle present.....**excitans**
- 11. Frontoclypeus with pollinose stripe or projection below antennae12
- Frontoclypeus without pollinose stripe or projection15
- 12. Abdomen completely black**separatus**
- Abdomen with yellow and black pattern13
- 13. First basal and costal cells lightly infuscated to nearly hyaline (Fig. 71); abdomen black with middorsal yellow stripe, often shorter lateral stripes**upsilon** (in part)
- First basal and costal cells heavily infuscated (Fig. 53); abdomen yellow with black pattern14
- 14. Frontoclypeus black, rarely yellow; abdominal markings not in form of stripes.....**frigidus**
- Frontoclypeus yellow; abdomen with 4 black stripes.....**sequax tau**
- 15. First basal cell completely infuscated (Fig. 57), rarely subhyaline toward apex16
- First basal cell always at least half hyaline, sometimes almost entirely so.....26
- 16. Wing pattern pale buffy brown (Fig. 57); first basal cell subhyaline toward apex; wing membrane tinted; hyaline triangle nearly reaches second longitudinal vein; apical spot narrow, entering only upper corner of second submarginal cell.....**luteopennis**
- Wing pattern dark brown to black (Fig. 60); apical spot broad, occupying nearly half to all of second submarginal cell.....17
- 17. Hyaline triangle small but clear, distinct, restricted to apices of second and third posterior cells (Fig. 60)**moechus**
- Hyaline triangle extends toward costal margin beyond second posterior cell (Fig. 41)18
- 18. Hyaline triangle reaches and sometimes crosses second longitudinal vein, sometimes upper portion tinted so that it is indistinct, often narrow and crescent shaped (Fig. 41)19
- Hyaline triangle does not extend much beyond bifurcation, not crescent shaped22
- 19. Frontal callus yellow**beameri**
- Frontal callus black or deep brown20
- 20. Yellowish species with abdomen conspicuously black striped21
- Fuscous species; abdomen with pale median line, occasionally traces of pale lateral lines**dacne**
- 21. Abdomen with 2 prominent submedian black stripes; sublateral stripes absent on tergites 1 and 2, sometimes 3; hyaline triangle rounded at apex (Fig. 63)**pikei**
- Abdomen with 4 complete black stripes; hyaline triangle pointed apically (Fig. 68)**sequax sequax**
- 22. Abdomen with 4, more or less complete, dark longitudinal stripes23
- Abdomen not striped or with fewer than 4 stripes25
- 23. Most of fifth posterior cell infuscated (Fig. 72); scutellum yellow**vittatus**
- Fifth posterior cell almost entirely hyaline (Fig. 38); scutellum dark, with or without paler apex and/or sides.....24
- 24. Apical spot nearly fills second submarginal cell (Fig. 38); abdomen with 2 central stripes, rarely joined on second segment; frontal callus usually yellow, sometimes brown or black**aberrans**
- Apical spot only half fills second submarginal cell (Fig. 69); abdomen with 2 central stripes, usually joined on second segment; frontal callus usually black, sometimes brownish, rarely yellowish**striatus**
- 25. Apical spot fills most of second submarginal cell, extends into first and sometimes second posterior cell, is usually connected with crossband by

- streak of infuscation in first posterior cell (Fig. 58); abdomen with 2 stripes, sometimes reduced to faint lines or enlarged to cover most of abdomen on each side of yellow stripe; scutellum usually with considerable yellow **macquarti**
- Apical spot fills only about half of second submarginal cell, does not extend farther (Fig. 56); abdomen not striped; scutellum dark **indus**
- 26(15). Apical spot narrow, including at most only extreme apex of second submarginal cell (Fig. 66) 27
- Apical spot broad, entering second submarginal cell over at least one-third of upper branch of third longitudinal vein (Fig. 70) 30
27. Apical spot, just beyond where it leaves crossband, slightly wider than marginal cell (Fig. 66); frontal callus usually yellow, often bordered with black or brown, occasionally black 28
- Apical spot at base narrower than or just as wide as marginal cell (Fig. 39); frontal callus normally black 29
28. Second abdominal segment with black spot almost joining that on first segment; second and third sternites with black sublateral spots; robust species **sackeni**
- Second abdominal segment with black spot usually not attaining anterior margin of segment, second and third sternites without sublateral spots; more slender species **puadicus** (in part)
29. Apical spot very narrow, more dilute than crossband (Fig. 39); front little convergent at vertex. Abdomen with pale markings usually grayish or dull yellow; second abdominal segment with black triangles, one on each side of dark median marking, triangles may or may not be connected with latter by dark band along posterior margin of segment **aestuans**
- Apical spot varies from one-half to full width of marginal cell, same density as crossband (Fig. 43); front somewhat convergent at vertex. Abdomen with pale yellow markings, often quite bright; second abdominal segment with dark median marking which may have projections along posterior margin of segment that do not form lateral triangles **callidus**
30. Blackish species with middorsal yellow (occasionally grayish) abdominal stripe, often with shorter sublateral stripes 31
- Abdomen with different pattern, showing more yellow 32
31. Infuscation of costal cell distinctly paler than crossband (Fig. 71); apical spot often nearly fills second submarginal cell **upsilon** (in part)
- Costal cell same color as crossband (Fig. 70); apical spot variable but rarely fills more than half of second submarginal cell **univittatus**
32. Hyaline triangle distinctly crosses second longitudinal vein, nearly separating apical spot from crossband (Fig. 54) 33
- Hyaline triangle, at most, reaches second longitudinal vein (Fig. 61) 34
33. Second abdominal segment with black inverted V or pair of oblique spots **geminatus**
- Second abdominal segment entirely yellow **impunctus**
34. Abdomen with 4 rows of spots, but lateral spots on second segment may be reduced or absent; median figure on second abdominal segment an inverted V; scutellum and frontal callus normally dark, but latter sometimes brownish **montanus**
- Abdomen normally without 4 rows of spots 35
35. Hyaline triangle reaches second longitudinal vein (Fig. 64) **puadicus** (in part)
- Hyaline triangle does not reach second longitudinal vein (Fig. 50) 36
36. Abdominal markings black, median marking of second segment usually reaches anterior margin; frontal callus normally black, sometimes yellow; usually at least basal portion of hind femora black **dimmocki**
- Abdominal markings brown, often quite pale, median marking of second abdominal segment rarely attains anterior margin; frontal callus yellow; hind femora yellow, pale brown, or mahogany 37
37. Thorax greenish gray with fuscous stripes; outer margin of crossband sinuous (Fig. 46) **celatus**
- Thorax yellow brown with dark brown stripes; outer margin of crossband concave, straight, or sinuous 38
38. Second abdominal segment with dark median marking, reaching only about halfway across segment, leaving an anterior greenish yellow area; outer margin of crossband sinuous (Fig. 65); legs usually rather uniform mahogany color **reicherti**
- Second abdominal segment with dark median marking, reaching across about two-thirds of segment, pale anterior area without greenish tinge; outer margin of crossband usually straight or somewhat concave (Fig. 52); legs yellow or pale brownish **flavidus**

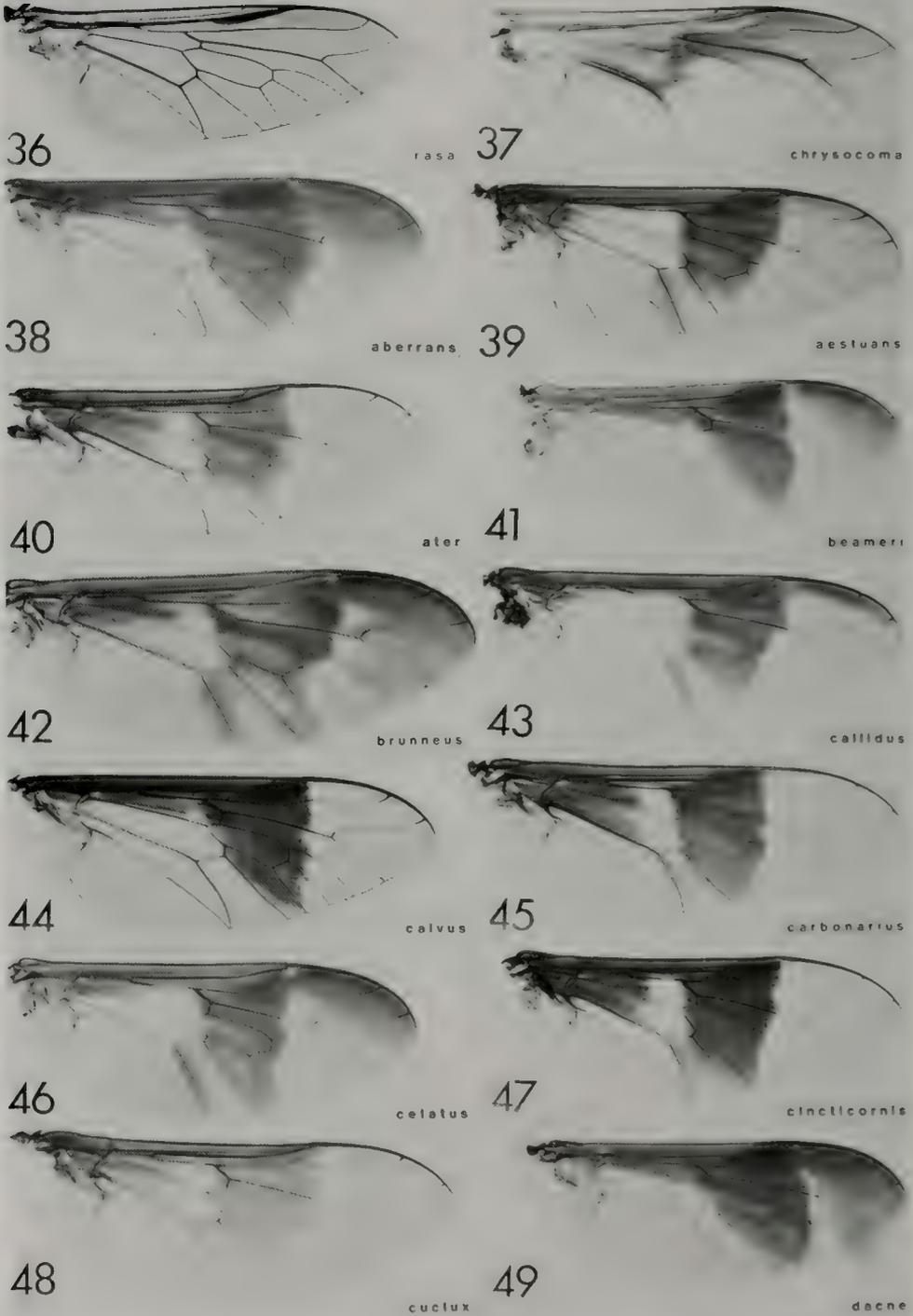


Fig. 36-49.—Wing patterns. 36. *Stonemyia rasa*. 37. *Goniops chrysocoma*. 38. *Chrysops aberrans*. 39. *C. aestuans*. 40. *C. ater*. 41. *C. beameri*. 42. *C. brunneus*. 43. *C. callidus*. 44. *C. calvus*. 45. *C. carbonarius*. 46. *C. celatus*. 47. *C. cincticornis*. 48. *C. cuclux*. 49. *C. dacne*.



Fig. 50-63.—Wing patterns. 50. *Chrysops dimmocki*. 51. *C. excitans*. 52. *C. flavidus*. 53. *C. frigidus*. 54. *C. geminatus*. 55. *C. impunctus*. 56. *C. indus*. 57. *C. luteopennis*. 58. *C. macquarti*. 59. *C. mitis*. 60. *C. moechus*. 61. *C. montanus*. 62. *C. niger*. 63. *C. piket*.

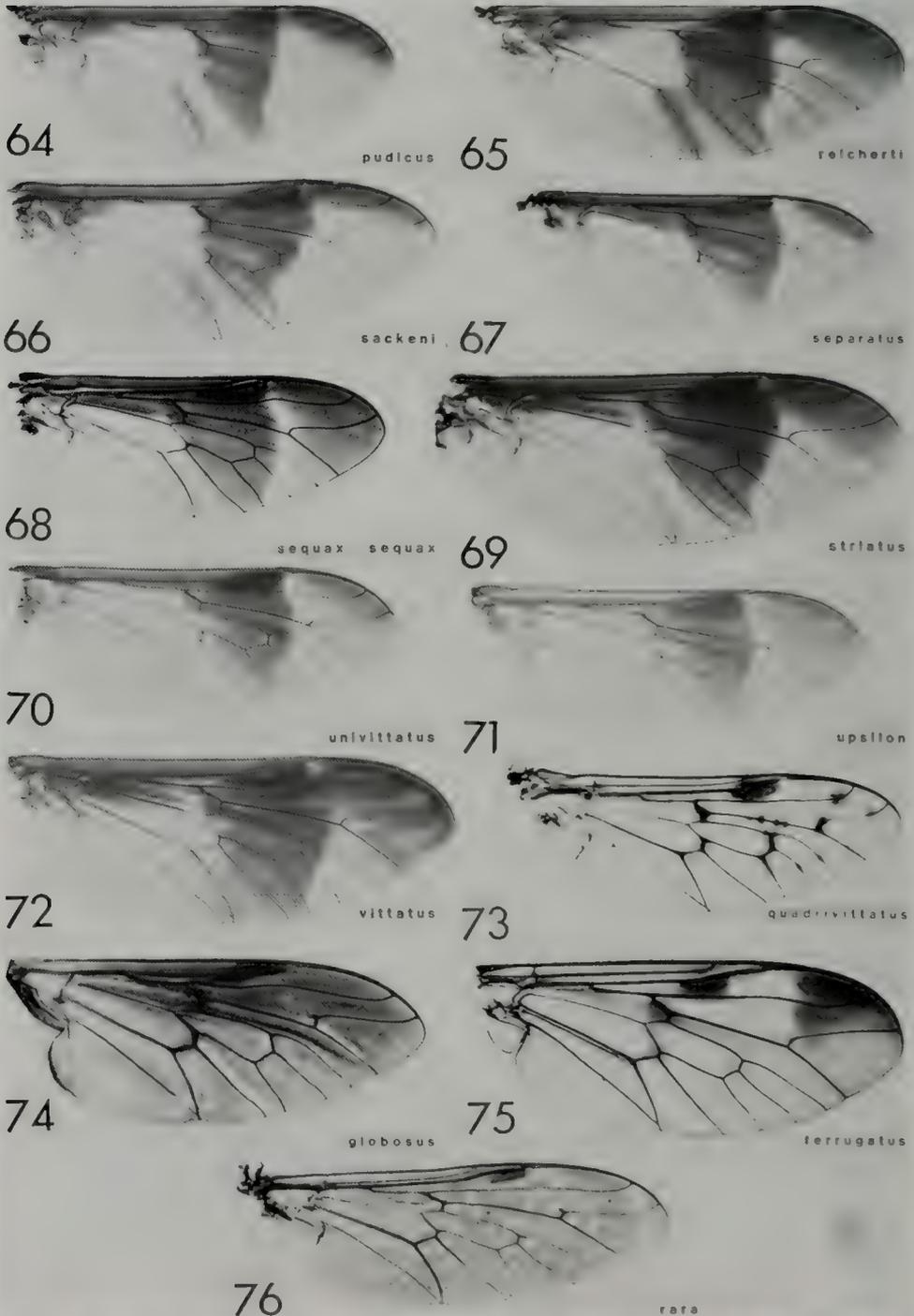


Fig. 64-76.—Wing patterns. 64. *Chrysops pudicus*. 65. *C. reicherti*. 66. *C. sackeni*. 67. *C. separatus*. 68. *C. sequax sequax*. 69. *C. striatus*. 70. *C. univittatus*. 71. *C. upsilon*. 72. *C. vittatus*. 73. *Silvius quadrivittatus*. 74. *Neochrysops globosus*. 75. *Diachlorus ferrugatus*. 76. *Haematopota rara*.

Males

1. Wing pictures pale brown to evanescent yellow; frontoclypeus with pollinose triangle or pollinose stripe below antennae.....2
Wing picture dark brown to black, usually latter; frontoclypeus with or without pollen (if large species with brown wing pattern, swollen scapes, and indefinite abdominal pattern, see couplet 16).....4
2. Wing with obvious apical spot; frontoclypeus yellow with pollinose area in form of equilateral triangle below antennae**luteopennis**
If apical spot present, it is fine line along costal border or an indefinite darkening of apical area; frontoclypeus black with pollen in form of stripe.....3
3. Wing pattern distinct; abdomen with pale area restricted to lateral margins of first 2 tergites; legs black.....**cuclux**
Wing pattern very faint; abdomen with yellow sublateral and median spots on first 2 tergites; first 2 sternites mostly yellow; legs with considerable yellow**fulvistigma**
4. Apex of wing beyond crossband hyaline, sometimes with vague cloud.....5
Apex of wing infuscated beyond crossband so that apical spot present12
5. Frontoclypeus wholly black with midfacial pollinose stripe, which begins below antennae runs at least halfway to oral margin.....6
Frontoclypeus mostly yellow without midfacial pollinose stripe.....11
6. Abdomen completely black7
First 2 abdominal segments with small reddish or yellowish spots sublaterally**excitans** (in part)
7. Fifth posterior cell with hyaline area at base8
Fifth posterior cell infuscated at base9
8. Outer margin of crossband straight or slightly evenly bowed; crossband usually reaches hind margin of wing in fourth and fifth posterior cells in full intensity; hyaline area at base of fifth posterior cell large, sharply defined.....**carbonarius**
Outer margin of crossband usually bowed or irregular; crossband does not usually reach wing margin in full intensity; hyaline area at base of fifth posterior cell without clearly defined margin; apical area of wing sometimes dilutely infuscated**ater**
9. Crossband broad, distinctly reaches hind margin of wing; outer margin of crossband usually straight**cincticornis**
Crossband narrow, does not reach or indistinctly reaches hind margin of wing; outer margin of crossband usually irregular10
10. Beard with many yellow hairs; yellow hairs frequently mixed with black hairs of thorax, legs, and abdomen; sometimes with traces of abdominal markings**excitans** (in part)
Beard wholly black; rarely with pale hairs on body or traces of pale abdominal markings**mitis**
11. Thoracic stripes, especially sublateral ones, fairly distinct, rarely with spot at bifurcation of third longitudinal vein**calvus**
Thoracic stripes obsolete; often with spot at bifurcation of third longitudinal vein**niger**
12. Frontoclypeus with midfacial pollinose stripe.....13
Frontoclypeus without such stripe.....15
13. Abdomen entirely black**separatus**
Abdomen with pale markings14
14. Abdomen black with narrow yellowish middorsal line, occasionally similar shorter sublateral lines; hyaline triangle approaches costal margin at least as subhyaline streak**upsilon**
Abdomen otherwise marked, often with considerable yellow; hyaline triangle does not reach beyond bifurcation**frigidus**
15. Abdomen completely black; hyaline triangle restricted to apices of second and third posterior cells**moechus**
Abdomen not wholly black; hyaline triangle not as above.....16
16. Brown species with no definite abdominal pattern although dark markings may be indicated by dark shadows; hyaline triangle indicated by clear area along edge of crossband, does not usually extend beyond center of third posterior cell; first antennal segment considerably swollen**brunneus**
Blackish or yellowish species; wing pattern clear-cut; hyaline triangle open at hind margin of wing; if otherwise, first antennal segment not swollen.....17
17. Black species; abdomen with yellowish median longitudinal stripe, occasionally with similar abbreviated stripe on each side; hyaline triangle crosses second longitudinal vein; apical spot rarely occupies more than half of second submarginal cell, often less**univittatus**
Without above combination of characters18
18. Apical spot very little broader at apex than at origin, crossing upper branch of third longitudinal vein at apex, occupying very little of second submarginal cell.....19

- Apical spot considerably broadened toward apex, crossing at least half of upper branch of third longitudinal vein21
19. Hyaline triangle does not reach second longitudinal vein.....**sackeni**
Hyaline triangle reaches or crosses second longitudinal vein20
20. Second abdominal segment with sublateral black triangles which join median figure along posterior border of segment; fourth posterior cell usually hyaline at apex, fifth posterior cell with considerable infuscation, especially basally; pale markings grayish yellow; apical spot very narrow....**aestuans**
Second abdominal segment without sublateral black triangles; fourth posterior cell usually entirely infuscated, fifth posterior cell often mostly hyaline; pale markings yellow**callidus**
21. Abdomen yellow and black; large black figure of second abdominal segment broadly joined to black figure of first segment; median yellow markings on tergites 3 and 4 do not reach anterior border of segments; apical spot occupies one-half to two-thirds of second submarginal cell22
Without above combination of characters24
22. Fore coxae black; hyaline triangle does not reach beyond bifurcation**indus**
Fore coxae yellow; hyaline triangle extends beyond bifurcation23
23. Abdomen with 4 rows of black spots, middorsal rows joining anteriorly on segments 2-4; apical spot fills about half of second submarginal cell.....**montanus**
Abdominal pattern not in form of rows or spots**dimmocki**
24. Apical spot fills half or less of second submarginal cell.....25
Apical spot fills all or nearly all of second submarginal cell, sometimes extending into first posterior cell or beyond26
25. Thorax yellow in ground color with brown stripes; legs yellow**flavidus**
Thorax greenish gray with fuscous stripes; legs variable.....**pudicus**
26. Outer margin of crossband sinuous; apical spot nearly surrounds hyaline triangle; basal half of first posterior cell and basal third of second basal cell infuscated; base of second abdominal segment often with greenish cast; legs pale mahogany; thorax ground color brownish.....**reicherti**
Without above combination of characters27
27. Basal cells never more than half infuscated, often almost entirely hyaline28
At least first basal cell more than half infuscated, often entirely so30
28. Hyaline triangle does not cross second longitudinal vein**celatus**
Hyaline triangle crosses second longitudinal vein29
29. Second abdominal segment with 2 oblique spots, frequently joined to form inverted V in center of segment.....**geminatus**
Second abdominal segment completely yellow or with traces of dark markings at posterior margin.....**impunctus**
30. Hyaline triangle reaches or nearly reaches second longitudinal vein (if subhyaline beyond bifurcation of third longitudinal vein, predominantly black species with pale abdominal markings reduced)31
Hyaline triangle scarcely extends beyond bifurcation of third longitudinal vein; predominantly yellowish species with dark abdominal markings34
31. Blackish species with reduced pale abdominal markings.....**dacne**
Yellow species with black abdominal markings32
32. Frontoclypeus and cheeks mostly yellow; second basal cell hyaline**beameri**
Frontoclypeus with large black spot on each side, cheeks with considerable black; second basal cell at least partly infuscated33
33. No sublateral spots on first and second abdominal tergites; second basal cell rarely more than half infuscated; hyaline triangle rounded at apex**pikei**
Sublateral stripes cross first 2 abdominal tergites; second basal cell largely infuscated with subhyaline area near apex; hyaline triangle pointed at apex**sequax**
34. Abdomen with median yellow stripe, longitudinal black band on each side; lateral margins of segments narrowly yellow**macquarti**
Abdomen yellow with 4 more or less complete rows of black spots35
35. Ground color of thorax and scutellum yellow; fifth posterior cell heavily infuscated with hyaline area at base.....**vittatus**
Ground color of thorax grayish olive, scutellum sometimes with some yellow; fifth posterior cell usually hyaline or subhyaline, sometimes infuscated36
36. Apical spot completely fills second submarginal cell; sublateral rows of abdominal spots about as dark as median rows**aberrans**
Apical spot does not completely fill second submarginal cell; sublateral

rows of abdominal spots paler than median rows**striatus**

Larvae

1. Respiratory spine absent (Fig. 82-90)2
 Respiratory spine present (Fig. 78, 91-108)10
2. Pubescence diffusely covers all of last 3 or 4 segments, but densest near their midlengths. Larva very slender, with long prolegs. Respiratory siphon approximately five times as long as its basal diameter (Fig. 82)**moechus**
 Distinct nonpubescent areas on last 3 segments. Respiratory siphon no more than four times as long as its basal diameter3
3. Anterior pubescent annuli on prothorax and mesothorax broad, covering at least one-half and one-third lengths of segments, respectively, without posterior projections (Fig. 83-85)8
 Thoracic annuli narrower, usually with posterior projections although these may be short (Fig. 86-90)4
4. Lateral pubescent projections from prothoracic annulus expanded apically (Fig. 86-88). Living larva greenish5
 Lateral pubescent projections from prothoracic annulus, if present, tapered (Fig. 89, 90). Living larva usually creamy white7
5. Posterior pubescence on preanal segment separated into dorsal and ventral portions, dorsal portion connected by narrow strip to adjacent proleg pubescence. Proleg pubescence encircles at least first 4 abdominal segments (Fig. 86, 87)6
 Posterior pubescence encircles preanal segment but not connected to adjacent proleg pubescence (although slight projections from posterior and proleg pubescence dorsolaterally on this segment suggest an ancestral connection). Proleg pubescence restricted to border of dorsal prolegs on all but first abdominal segment (Fig. 88).....**ater**
6. Proleg and posterior pubescences on preanal segment broadly connected dorsolaterally, leaving only small dorsal area clear. Similar but narrower connections usually present ventrolaterally on this segment and dorsolaterally on preceding ninth segment (Fig. 86)**cuclux**
 Proleg and posterior pubescences narrowly connected only dorsolaterally on preanal segment (Fig. 87)**carbonarius**
7. Pubescent projections from thoracic annuli absent. Proleg and posterior pubescent annuli on preanal segment with narrow connections dorsolateral-

ly. Pubescence encircles posterior two-thirds of anal segment, broadly connected to pubescence on anal ridges (Fig. 89)**macquarti**

- Pubescent projections from thoracic annuli present though often short and inconspicuous. Proleg and posterior pubescences on preanal segment essentially absent. Posterior pubescence absent from anal segment (Fig. 90).....**frigidus**
8. Striations absent laterally on all segments**geminatus**
 Striations present laterally on all segments9
9. Anterior pubescence encircles first 3 or 4 abdominal segments. Posterior pubescent annulus on anal segment with dorsolateral and lateral pointed projections from its anterior margin on each side, sometimes with small isolated spot between and anterior to these projections (Fig. 85)**vittatus**
 Anterior pubescence encircles only first abdominal segment, interrupted at least laterally on remainder. Posterior annulus on anal segment with only dorsolateral pointed projections and somewhat isolated pubescent spot anteroventral to this projection (Fig. 84)**pikei**
10. Preanal segment with proleg and posterior pubescences broadly joined dorsally, ventrally, and laterally, leaving small clear areas only dorsolaterally and ventrolaterally (Fig. 91)**montanus**
 Preanal segment with proleg and posterior pubescences not joined.....11
11. Anterior pubescent annuli on pro- and mesothorax wide, covering approximately one-half to one-third length of segments; prothoracic annulus lacks posterior pubescent projections (Fig. 92-94).....12
 Anterior pubescent annuli on thoracic segments narrower with posterior pubescent projections laterally (Fig. 95-98)14
12. Posterior pubescence encircles seventh abdominal segment. Anterior pubescence encircles first 5 abdominal segments (Fig. 92).....**sequax**
 Posterior pubescence either absent on seventh abdominal segment or restricted to small lateral spot. Anterior pubescence encircles no more than first abdominal segment13
13. Pubescence present, though very pale, on anterior margin of first 7 abdominal segments (Fig. 93).....**niger**
 Pubescence absent from first 7 abdominal segments (Fig. 94)**calvus**

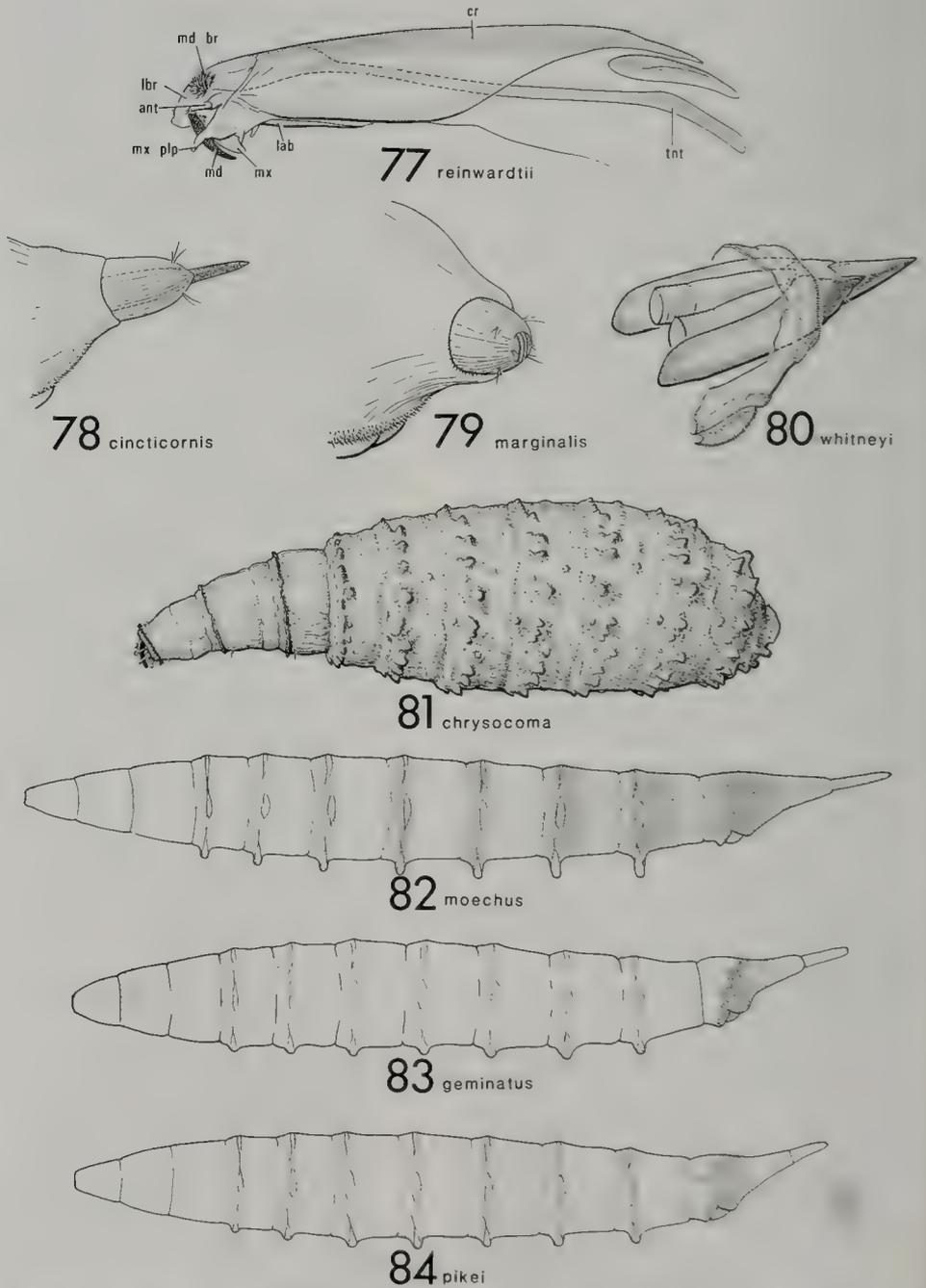


Fig. 77-84.—Head capsule. 77. *Tabanus reinwardtii*. Respiratory siphons. 78. *Chrysops cincticornis*. 79. *Tabanus marginalis*. 80. *Merycomyla whitneyi*. Larva. 81. *Goniops chrysocoma*. 82. *Chrysops moechus*. 83. *C. geminatus*. 84. *C. pikei*. Abbreviations: ant, antenna; cr, cranium; lab, labium; lbr, labrum; md, mandible; md br, mandibular brush; mx, maxilla; mx plp, maxillary palp; tnt, tentorial arm.

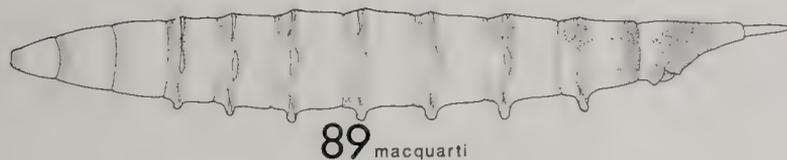
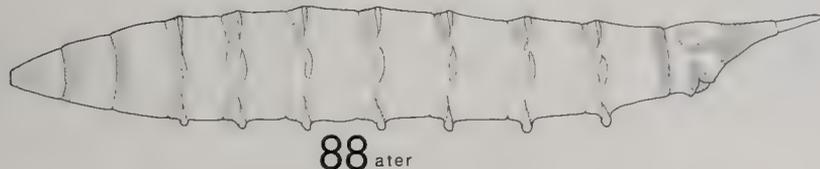
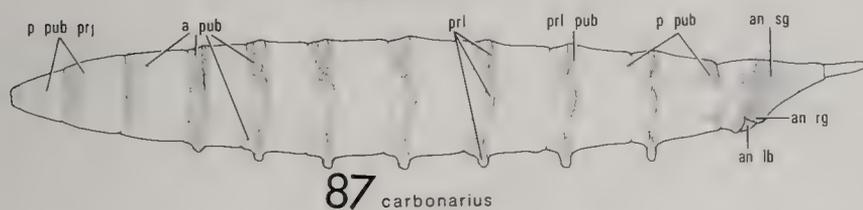
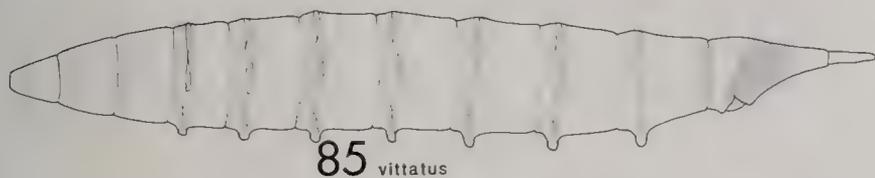


Fig. 85–91.—Larvae. 85. *Chrysops vittatus*. 86. *C. cuclux*. 87. *C. carbonarius*. 88. *C. ater*. 89. *C. macquarti*. 90. *C. frigidus*. 91. *C. montanus*. Abbreviations: a pub, anterior pubescence; an sg, anal segment; an lb, anal lobe; an rg, anal ridge; p pub, posterior pubescence; p pub prj, posterior pubescent projection; prl, proleg; prl pub, proleg pubescence; resp sph, respiratory siphon; resp spn, respiratory spine.



92 sequax



93 niger



94 calvus



95 celatus



96 flavidus



97 univittatus



98 reicherti

Fig. 92-98.—Larvae. 92. *Chrysops sequax*. 93. *C. niger*. 94. *C. calvus*. 95. *C. celatus* 96. *C. flavidus*. 97. *C. univittatus*. 98. *C. reicherti*.



99 dimmocki



100 indus



101 callidus



102 aestuans



103 cincticornis



104 striatus



105 sackeni

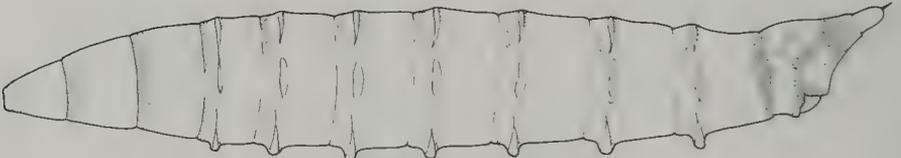
Fig. 99-105.—Larvae. 99. *Chrysops dimmocki*. 100. *C. indus*. 101. *C. callidus*. 102. *C. aestuans*. 103. *C. cincticornis*. 104. *C. striatus*. 105. *C. sackeni*.



106 brunneus



107 aberrans



108 excitans



109 crepuscularis



110 ferrugatus



111 quadrivittatus



112 annulatus

Fig. 106-112.—Larvae. 106. *Chrysops brunneus*. 107. *C. aberrans*. 108. *C. excitans*. 109. *Chlorotabanus crepuscularis*. 110. *Diachlorus ferrugatus*. 111. *Silvius quadrivittatus*. 112. *Leucotabanus annulatus*.

14. Prothoracic annulus with single broad posterior pubescent projection on each side, as if area between usual paired projections were filled with pubescence (Fig. 95, 97)15
 Prothoracic annulus with paired pubescent projections on each side17
15. Posterior pubescence on anal segment extends forward dorsally at least three-quarters length of segment (Fig. 95, 96)16
 Posterior pubescence on anal segment extends forward dorsally little more than half length of segment (Fig. 97)**univittatus, upsilon**
16. Pubescence covers about nine-tenths of anal segment; only narrow encircling band on its anterior margin clear. Posterior pubescent annulus of preanal segment with distinct anterior projections laterally (Fig. 95).....**celatus**
 Pubescence on anal segment less extensive, covering approximately three-quarters of segment. Posterior pubescence on preanal segment restricted to lateral surfaces, without anterior projections (Fig. 96).....**flavidus**
17. Lateral pubescent projections from prothoracic annulus either expanded apically (Fig. 99, 100) or basally broad where leaving annulus (Fig. 98)18
 Lateral pubescent projections from prothoracic annulus slender, tapered (Fig. 103, 108).....20
18. Pubescence absent from posterior margin of abdominal segment 7 (Fig. 98)**reicherti**
 Pubescence encircles posterior margin of abdominal segment 719
19. Patch of pubescence dorsolaterally on anal segment closely proximal to, or continuous with, pubescence on anterior border of same segment (Fig. 100).....**indus**
 Patch of pubescence dorsolaterally on anal segment forming tonguelike anterior projection of posterior annulus (Fig. 99).....**dimmocki**
20. Anterior pubescence encircles only first abdominal segment (Fig. 103, 108).....21
 Anterior pubescence encircles first 3-5 abdominal segments (Fig. 101, 102, 104-107)23
21. Proleg pubescence on segments 5 to 10 greatly reduced, as evidenced by its not traversing spaces between prolegs. Posterior pubescent annulus on anal segment not united to pubescence on anal ridges (Fig. 108).....**excitans**
 Proleg pubescence encircles segments 5 to 10. Posterior pubescent annulus on anal segment united to pubescence on anal ridges at least ventrally (Fig. 103, 104).....22
22. Posterior pubescence on preanal segment with single short anterior projection midlaterally (Fig. 104).....**striatus**
 Posterior pubescence on preanal segment with four short anterior projections midlaterally (Fig. 103).....**mitis, cincticornis**
23. Posterior pubescent annulus on anal segment extends forward dorsally over at least half length of segment, usually broadly connected to pubescence on anal ridges (Fig. 101, 102).....24
 Posterior pubescent annulus on anal segment extends forward dorsally less than half length of segment, its connection to anal ridge pubescence, if present, usually only on ventral surface (Fig. 104-107)25
24. Posterior pubescent annulus on anal segment extends forward dorsally only half length of segment, usually enclosing clear nonpubescent areas ventrolaterally behind anus (Fig. 102)**aestuans**
 Posterior pubescent annulus on anal segment usually extends forward dorsally more than half length of segment, only occasionally enclosing clear areas ventrolaterally (Fig. 101) ..**callidus**
25. Posterior pubescent annulus on anal segment lacks any direct ventral connection with pubescence on anal ridges, although narrow connection may exist through lateral club-shaped projections from posterior annulus. Anterior pubescence encircles first 4 or 5 abdominal segments (Fig. 106, 107).....26
 Posterior pubescent annulus on anal segment connected ventrally to pubescence on anal ridges or shows vestiges of ventrolateral connections. Anterior pubescence encircles first 2 or 3 abdominal segments (Fig. 105)**sackeni**
26. Anal segment with lateral club-shaped pubescent projection from posterior annulus and paired oval dorsolateral patches of pubescence, lower one being larger (Fig. 107)**aberrans**
 Anal segment with midlateral pubescent bar not connected to posterior annulus, several small pubescent spots dorsolaterally (Fig. 106)**brunneus**

Chrysops aberrans Philip

Chrysops aberrans Philip (1941:122). Type-locality: Minnesota, Ramsay County. Moderate size (8 mm); yellow and black; frontoclypeus shining yellow; frontal callus usually yellow, sometimes brown or black; thorax greenish in ground color; scutellum dark; black stripes on abdomen, median pair rarely joining on second tergite; apical

spot broad (Fig. 38), usually nearly filling second submarginal cell; hyaline triangle does not reach second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing; first basal cell infuscate; second basal cell hyaline; fifth posterior cell mostly hyaline. Male with yellow areas reduced; second basal cell largely infuscated.

C. aberrans is often confused with *C. striatus*. The two species are much alike and often fly together but can be distinguished by the characters given in the key. Although the frontal callus is typically yellow, some populations run rather heavily to individuals with the callus brown or black.

The larvae (Fig. 107) are most commonly collected from mud or sand at the edges of ponds and lakes but have also been taken from a variety of other semiaquatic habitats (Pechuman 1972; Teskey 1969).

This species is most commonly collected in and near cattail swamps. In Illinois adults appear in late June and have been collected until late August.

Its peak abundance is from mid-July to mid-August.

C. aberrans is an east-central species, extending from New Jersey to Nova Scotia and west to Minnesota and Iowa, with a possible disjunct population in Nebraska (Fig. 113). In Illinois this species is found in the northern two-thirds of the state (Fig. 113).

Chrysops aestuans Wulp

Chrysops aestuans Wulp (1867:135). Type-locality: Wisconsin.

Chrysops moerens Walker (1848:201).

Type-locality: Nova Scotia.

Moderate size (8.5 mm); black; frontoclypeus shining yellow; frontal callus black; abdomen with gray or yellowish gray markings not in form of stripes, black triangles on second abdominal segment, one on each side of median dark marking, triangles may or may not be connected with latter by dark band along posterior margin of segment; apical spot narrow, reaching extreme apex of second submarginal cell; hyaline spot (Fig. 39) broad, extending apically toward costal margin beyond second longitudinal vein; crossband saturate, covering discal cell, usually not reaching hind margin of wing; both basal cells hyaline, fifth posterior cell infuscate basally. Male generally darker; both basal cells partly infuscated.

C. aestuans belongs in a difficult taxonomic group, which includes *C. callidus*, *C. dimmocki*, *C. pudicus*, *C. sackeni*, and some rarer forms. However, most specimens can be separated by the characters given in the key.

The larvae (Fig. 102) have been found in marshes bordering large bodies of water. The eggs are laid on emergent vegetation, often over rather deep water (Pechuman 1972; Teskey 1969). This species is normally collected near large bodies of water. In Illinois adults appear in early June and have been collected through mid-August.

C. aestuans is widespread across the central United States and Canada, extending from Nova Scotia to British

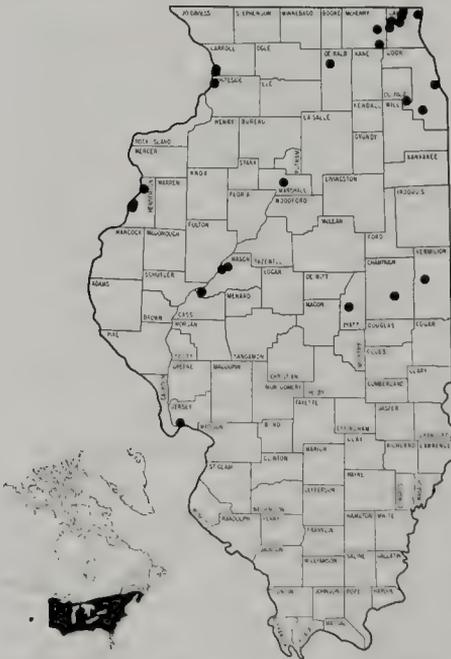


Fig. 113.—Distribution of *Chrysops aberrans* in Illinois and North America.



Fig. 114.—Distribution of *Chrysops aestuans* in Illinois and North America.

Columbia and Oregon (Fig. 114). In Illinois this species is found in various parts of the northern two-thirds of the state, particularly in Lake County (Fig. 114).

Chrysops ater Macquart

Chrysops ater Macquart (1850:344). Type-locality: Newfoundland.

Chrysops carbonarius nubiapex Philip (1955:92). Type-locality: New York, Little Valley.

Chrysops fugax Osten Sacken (1875:375). Type-locality: Maine, Norway (lectotype).

Moderate size (8 mm); black; abdomen entirely black; no apical spot but occasionally a trace of infuscation in apical area; hyaline spot covers apical third of wing (Fig. 40); crossband covers discal cell, often not reaching hind margin of wing, outer margin usually irregular; both basal cells more than half infuscated; fifth posterior cell with distinct to vague hyaline area at base. Male with both basal cells at least three-fourths infuscated; frequently with apical infuscation but not a distinct apical spot.

Previously, this species had been synonymized with *C. carbonarius*. The less intensely infuscated and less extensive crossband with an irregular outer margin and the less clear-cut hyaline area at the base of the fifth posterior cell separate most specimens of *C. ater* from *C. carbonarius*.

The triple-tiered egg mass is deposited on tree leaves or other vegetation overhanging ponds or portions of streams where the water is barely in motion. The larvae (Fig. 88) are found in mud and organic matter along streams (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early June and have been collected until early July.

C. ater is a widespread species, extending from Virginia to Newfoundland and west to Alberta and Utah, with a disjunct population in Alaska (Fig. 115). It is conceivable that this species extends from Alberta to Alaska. In Illinois this species is known only from three northern records.

Illinois Records.—Ogle County, 1 mile N Polo; Stephenson County, 2 miles S Orangeville; Winnebago County, 4 miles NW Durand.



Fig. 115.—Distribution of *Chrysops ater* in North America.

***Chrysops beameri* Brennan**

Chrysops beameri Brennan (1935:265).
Type-locality: Kansas, Comanche County.

Moderate size (8 mm); yellow and black; frontoclypeus shining yellow; frontal callus yellow; thorax yellow to greenish yellow in ground color; abdomen with black stripes, 4 stripes of about equal intensity or central stripes only slightly accentuated; apical spot broad but usually only barely reaching first posterior cell (Fig. 41); hyaline triangle reaches second longitudinal vein, apex pointed; crossband covers discal cell, narrowed posteriorly but reaches hind margin of wing; first basal cell infuscated; second basal cell hyaline; fifth posterior cell hyaline. Male similar to female, including wing characters; first basal cell completely infuscated; second basal cell completely hyaline.

This species is in a taxonomic group with *C. hinei* and can be confused with paler specimens of *C. hinei*. The characters in the key are generally sufficient to separate these two species.

The larvae of *C. beameri* are unknown.

This species is widespread in the eastern and southern United States, extending from northern Florida to New Jersey and west to Kansas and eastern Texas (Fig. 116). As yet this species has not been collected in Illinois although specimens have been examined from western Indiana and eastern Missouri. This species is a late season flyer and is not often collected.



Fig. 116.—Distribution of *Chrysops beameri* in North America.

***Chrysops brunneus* Hine**

Chrysops brunneus Hine (1903:34). Type-locality: Ohio, Sandusky.

Rather large (9 mm); brown; frontoclypeus shining yellow; first antennal segment swollen; abdominal pattern obsolete, sometimes with dark shadows and faint pale median triangles; apical spot broad (Fig. 42), continues around wing, joining crossband by lightly infuscated area along hind margin; hyaline triangle isolated, not reaching second longitudinal vein; crossband broad, covering discal cell, reaching posterior margin of wing, and joining with extended apical spot; both basal cells partly infuscated; fifth posterior cell diffusely infuscated. Male differs from female only in sex characters.

C. brunneus is a rather distinctive species, and the characters in the key readily separate it from other species.

Like the larvae of some other species of *Chrysops*, *brunneus* larvae apparently may live in either fresh or brackish water habitats. The single known larva was taken between the



Fig. 117.—Distribution of *Chrysops brunneus* in Illinois and North America.

basal portion of the leaves of *Spartina* in a salt marsh (Goodwin 1976a).

In Illinois adults of this species appear in mid-June and have been collected until late August.

C. brunneus is a central and eastern species, extending along the Atlantic coast states from Florida to New York, west to Texas, then north through the central states, and northeast into southern Ontario and into upstate New York along Lake Ontario (Fig. 117). In Illinois this species has most often been collected in the northeast, with a single record from Union County in southern Illinois (Fig. 117).

Chrysops callidus Osten Sacken

Chrysops callidus Osten Sacken (1875: 379). Type-locality: Illinois (lectotype).

Moderate size (8 mm); black and yellow; frontoclypeus shining yellow; front somewhat convergent at vertex; pale markings of abdomen yellow (sometimes quite bright), markings not in form of stripe, dark median markings of second abdominal segment may have projections along posterior margin of segment but these projections do not form lateral triangles; apical spot narrow (Fig. 43), varies from one-half width to full width of marginal cell; hyaline triangle broad, rounded apically, just reaching or barely crossing second longitudinal vein; cross-band covers discal cell, narrowed posteriorly but reaches hind margin of wing; both basal cells hyaline; fifth posterior cell infuscated basally. Male with pale markings less extensive; both basal cells partly infuscated.

C. callidus belongs in a difficult taxonomic group, which includes *C. aestuans*, *C. dimmocki*, *C. pudicus*, *C. sackeni*, and some rarer forms. However, most specimens can be separated by the characters given in the key.

The larvae (Fig. 101) are found in a variety of situations, including mud on the shores of ponds and slow-moving streams, wet organic material, and around the roots of plants growing at the water's edge. Larvae have also been

collected under as much as 1 m of water as far as 10 m from the shoreline. The flat, one-layered egg masses are found only over water. These masses, which shortly after oviposition become dark and shining, are laid along the edges of creeks and ponds on emergent vegetation, but none are found on similar adjacent growth over mud. Since these egg masses are often quite abundant and noticeable, this selectivity is striking (Jones & Bradley 1923; Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults of this species appear in early April and have been collected until late August. Its peak abundance is from mid-June until late July.

C. callidus is an eastern and central species, extending from Florida to Maine and west to South Dakota and Texas (Fig. 118). This species is widespread throughout Illinois (Fig. 118). It is active and aggressive and causes considerable annoyance to man and livestock.



Fig. 118.—Distribution of *Chrysops callidus* in Illinois and North America.

***Chrysops calvus* Pechuman & Teskey**

Chrysops calvus Pechuman & Teskey (1967:645). Type-locality: New York, Allegany State Park.

Moderate size (8.5 mm); blackish; frontoclypeus without median pollinose stripe; central area of vertex bare, uninterrupted by pollinose band; sub-lateral thoracic stripes bright, distinct; no apical spot except in some specimens as narrow line along costal border (Fig. 44); no hyaline triangle; cross-band saturate, black, covers discal cell, reaching hind margin of wing; first basal cell infuscated; second basal cell hyaline; fifth posterior cell hyaline. Male wing with both basal cells largely infuscated. Face with considerable yellow in both sexes.

This species until recently (Pechuman & Teskey 1967) was included with *C. niger* but may be separated by the characters given in the key. Teskey (1969) has shown the larva of *C. calvus* to be separable from that of *C. niger*.

Larvae (Fig. 94) were taken from saturated clay soil on the banks of a pool in a flood channel of a brook (Teskey 1969).

C. calvus is an eastern and north-central species, extending from Georgia to Nova Scotia and west to Minnesota and northern Ontario. A disjunct population is present in the panhandle of Florida (Fig. 119). As yet this species has not been collected in Illinois although specimens have been examined from southeastern Wisconsin.

***Chrysops carbonarius* Walker**

Chrysops carbonarius Walker (1848:203).

Type-locality: Nova Scotia.

Moderate size (8.5 mm); black; frontoclypeus with median pollinose stripe; abdomen entirely dark; no apical spot or hyaline triangle (Fig. 45); crossband broad, covers discal cell, not tapered posteriorly, reaches hind margin of wing, outer margin straight or slightly bowed; both basal cells more than half infuscated; fifth posterior cell with clear-cut hyaline area at base. Male with both basal cells at least three-fourths infuscated; hyaline area at base of fifth posterior cell clear-cut, as in female.

This species is very similar to *C. ater* although specimens can be readily separated by the characters given in the key.



Fig. 119.—Distribution of *Chrysops calvus* in North America.



Fig. 120.—Distribution of *Chrysops carbonarius* in North America.

The larvae (Fig. 87) have been found in saturated mud on the banks of streams and ponds (Pechuman 1972; Teskey 1969).

C. carbonarius is primarily an eastern species, extending from northern Florida to Nova Scotia and west to Wisconsin and Louisiana (Fig. 120). As yet this species has not been collected in Illinois although specimens have been examined from central Wisconsin.

Chrysops celatus Pechuman

Chrysops celatus Pechuman (1949:82).

Type-locality: New Jersey, Medford Lakes.

Moderate size (8.5 mm); yellowish brown; frontoclypeus shining yellow; frontal callus yellow; thorax greenish gray with fuscous stripes; abdomen with dark brown or blackish markings not in form of stripes, median marking of second abdominal segment rarely attains anterior margin; apical spot broad (Fig. 46), covering more than half of second submarginal cell; hyaline triangle does not reach second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing, outer margin usually sinuate; basal half of first basal cell infuscate; second basal cell hyaline; basal half of fifth posterior cell infuscate; hind femora yellow. Male easily associated with female.

This species was treated as a subspecies of *C. flavidus* (Pechuman 1957), but its separation at the specific level is justified by the lack of intergrades with *flavidus*. This fact is further con-

firmed by Teskey (1969), who found the larvae of the two forms to be distinct.

The larvae (Fig. 95) have been found in sand and mud at the edges of ponds and lakes and in highly organic boglike situations (Pechuman 1972; Teskey 1969; Tidwell 1973).

This species has been collected only once in Illinois in late July.

C. celatus is a southeastern species, extending from Florida to Massachusetts and west to eastern Texas (Fig. 121). A disjunct population occurs in northern Indiana, Ohio, and southern Michigan and Ontario.

Illinois Records.—Johnson County, Little Black Slough Nature Preserve, 4 miles SW Vienna.

Chrysops cincticornis Walker

Chrysops cincticornis Walker (1848:201).

Type-locality: unknown.

Chrysops celer Osten Sacken (1875:376).

Type-locality: Massachusetts (lectotype).

Rather large (9 mm); black; frontoclypeus with median pollinose stripe; pleura with yellow to orange-red pile; abdomen entirely dark; no apical spot or hyaline triangle (Fig. 47); crossband broad, covering discal cell, broadly reaching hind margin of wing; both basal cells with basal half infuscate; fifth posterior cell infuscate at base. Male lacks orange pleural pile of female; anal area of wing dilutely infuscate.

Earlier workers discussed this species as *C. celer*, subsequently synonymized under *cincticornis*. The females are distinctive from other Illinois species of *Chrysops* because of the orange-red pile on the thoracic pleura.

The larvae (Fig. 103) are found in the muddy edges of ponds and streams. The egg mass is brown and in several layers, much like a *Tabanus* egg mass (Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults of this species appear in mid-May and can be collected until late July. Most specimens have



Fig. 121.—Distribution of *Chrysops celatus* in North America.



Fig. 122.—Distribution of *Chrysops cincticornis* in Illinois and North America.

been collected around the margins of lakes and bogs in Lake and McHenry counties.

C. cincticornis is a central and eastern species, extending from Georgia to Nova Scotia and west to Minnesota and eastern Texas (Fig. 122). Two disjunct records are known from North Dakota. In Illinois (Fig. 122) this species has been collected only in the northern half of the state.

Chrysops cuclux Whitney

Chrysops cuclux Whitney (1879:35). Type-locality: New Hampshire, Milford.

Moderate size (8 mm); black; frontoclypeus with median pollinose stripe; pleura with gray pile; abdomen with pale grayish yellow area laterally near base, no median abdominal triangles; no apical spot or hyaline triangle (Fig. 48); crossband broad, pale, covering discal cell, generally reaching hind margin of wing although very pale in this area; basal half of both basal cells infusate, pale. In male, pale area of abdomen smaller than in female.

This species is similar to *C. excitans* although the wing picture is distinctly

paler and abdomen has no middorsal pale markings.

The larvae (Fig. 86) are known from wet mud along streams and occasionally from pond margins (Pechuman 1972; Teskey 1969).

C. cuclux is a northeastern species, extending from Georgia to Nova Scotia and west to Wisconsin (Fig. 123). A disjunct population has been examined from northwestern Ontario. As yet this species has not been collected in Illinois although specimens have been examined from southeastern Wisconsin and northwestern Indiana.



Fig. 123.—Distribution of *Chrysops cuclux* in North America.

Chrysops dacne Philip

Chrysops dacne Philip (1955:99). Type-locality: Georgia, Clarke County.

Moderate size (7.5 mm); dark brown; frontoclypeus shining yellow; no pale stripe above wing base; abdomen often with narrow pale median line, rarely with obsolete sublateral lines; apical spot very broad (Fig. 49), covering all of second submarginal cell; hyaline triangle narrow, not clearly reaching second longitudinal vein; crossband broad, covering discal cell, broadly reaching hind margin of wing; first

basal cell completely infuscated; second basal cell hyaline; fifth posterior cell hyaline; hind legs predominately yellow or brown. Male with hyaline areas of wing somewhat tinted.

For many years this species was called *C. lugens*, but the name *lugens* should be used for another form. This species resembles *C. parvulus* although the yellowish hind legs and the extension of the apical spot into the first posterior cell readily separate *C. dacne* from *parvulus*.

Immature stages are unknown.

C. dacne is a southern and eastern species, extending from northern Florida to Massachusetts and west to eastern Texas (Fig. 124). This species is reported in the literature from the southwesternmost county of Michigan although this specimen has not been examined. As yet this species has not been collected in Illinois.



Fig. 124.—Distribution of *Chrysops dacne* in North America.

Chrysops dimmocki Hine

Chrysops dimmocki Hine (1905:393). Type-locality: Massachusetts, Longmeadow.

Moderate size (8 mm); black and yellow; frontoclypeus shining yellow; frontal callus normally black but sometimes yellow; abdominal markings not in form of stripes, median marking of second abdominal segment usually reaches anterior margin; apical spot broad (Fig. 50), covering apical half of second submarginal cell; hyaline triangle broad, not reaching second longitudinal vein; crossband broad, covering discal cell, narrowing posteriorly but generally reaching hind margin of



Fig. 125.—Distribution of *Chrysops dimmocki* in North America.

wing; both basal cells hyaline; fifth posterior cell with basal margin infuscate; at least basal portion of hind femora black. Male with both basal cells partly infuscated.

This species resembles both *C. celatus* and *C. flavidus*, but the characters in the key suffice to separate *C. dimmocki* from both of these species.

The larvae (Fig. 99) have been collected in organic substrates in swamps as well as in mud and sand at the edges of ponds (Pechuman 1972; Teskey 1969; Tidwell 1973).

Adults of this species have been collected only twice in Illinois in mid-May and late June.

C. dimmocki is a southeastern species, extending from southern Florida to New Hampshire and west to eastern Texas (Fig. 125). Two disjunct populations are present in the central states, one in southern Illinois and western Tennessee, the other in Ohio and northwestern Pennsylvania.

Illinois Records.—Massac County, Unionville; Union County, Pine Hills Recreational Area.

Chrysops excitans Walker

Chrysops excitans Walker (1850:72). Type-locality: Nova Scotia, Cape Breton Island.

Chrysops lubalis Harris (1925:68). Nomen nudum.

Large species (10 mm); black; frontoclypeus with median pollinose stripe; pleurae with dense yellowish pile; abdomen with yellow area laterally near base, usually with median triangles on

second, third, and sometimes fourth tergites; no apical spot or hyaline triangle (Fig. 51); crossband broad, covering discal cell, not reaching hind margin of wing; both basal cells with basal half infuscate; fifth posterior cell with basal half infuscate. Male much darker than female, with pale abdominal markings reduced or obsolete.

This species resembles *C. cuclux*, but the much darker wing picture and the presence of yellowish pile on the thoracic pleurae and pale middorsal abdominal markings readily identify this species.

The larvae (Fig. 108) are found in mud and organic habitats along the edges of pools, ponds, and lakes (Pechuman 1972; Teskey 1969).

C. excitans is a northern species, extending from Virginia to Labrador and west to California and Alaska (Fig. 126). In Illinois this species has been collected once in late June 1892.

Illinois Records.—Lake County, Grass Lake.



Fig. 126.—Distribution of *Chrysops excitans* in North America.

Chrysops flavidus Wiedemann

Chrysops flavidus Wiedemann (1821:55).
Type-locality: Georgia, Savannah.

Chrysops canifrons Walker (1848:197).

Type-locality: Florida.

Chrysops pallidus Bellardi (1859:73).

Type-locality: Mexico.

Moderate size (8.5 mm); yellow and brown; frontoclypeus shining yellow; frontal callus yellow; thorax yellow with brown stripes; abdomen with brown markings not in form of stripes; apical spot broad (Fig. 52), covering apical half of second submarginal cell; hyaline triangle broad, not reaching second longitudinal vein; crossband broad, covering discal cell, narrowed posteriorly, reaching hind margin of wing; both basal cells somewhat infuscate at base; fifth posterior cell with basal half infuscate; hind femora yellow, sometimes brownish at base. Male differs from female only in sex characters.

This species resembles *C. celatus*, and was previously considered a subspecies of *flavidus*. The characters designated in the key will separate these two species.

The larvae (Fig. 96) have been taken from ponds, streams, and marshes (Jones & Bradley 1923; Pechuman 1972; Teskey 1969; Tidwell 1973).



Fig. 127.—Distribution of *Chrysops flavidus* in Illinois and North America.

In Illinois adults appear in late May and have been collected until early September.

C. flavidus is a widely distributed species, extending from the southern tip of Florida to Massachusetts, west to Missouri and northeastern Mexico, and to Cuba and the Bahamas (Fig. 127). In Illinois this species has been collected in the southern two-thirds of the state (Fig. 127).

***Chrysops frigidus* Osten Sacken**

Chrysops frigidus Osten Sacken (1875: 384). Type-locality: New York, Sharon Springs (lectotype).

Chrysops canadensis Kröber (1926:277). Type-locality: Ontario, Ottawa.

Moderate size (7.5 mm); black and orange; frontoclypeus black with median pollinose stripe; thorax and pleurae with yellow pile; color pattern of abdomen variable, sometimes almost completely black or almost completely orange yellow, but pattern never in form of longitudinal stripes; apical spot broad (Fig. 53), broadly united with crossband, covers entire upper branch of third longitudinal vein; hyaline triangle does not extend beyond third longitudinal vein; crossband broad, covering discal cell, not reaching hind margin of wing; both basal cells partly infuscated; fifth posterior cell with basal half infuscate; legs often with considerable yellow, hind tibiae never completely black. Male with infuscation in both basal cells greater than that in female.

This species is rather distinct from other species of *Chrysops*, having a yellow pile on the thorax and pleurae. The characters in the key readily separate this species.

The larvae (Fig. 90) are usually found in mossy substrates in bogs and swamps and along streams and ponds (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early June and can be collected until late July.

C. frigidus is a northern species, extending from New York to Labrador and west to British Columbia (Fig. 128).



Fig. 128.—Distribution of *Chrysops frigidus* in North America.

In Illinois the species is restricted to the northeast corner of the state.

Illinois Records.—Lake County, Chain O'Lakes State Park, Volo Bog Nature Preserve, Antioch; McHenry County, Moraine Hills State Park (3 miles S McHenry).

***Chrysops fulvistigma* Hine**

Chrysops fulvistigma Hine (1904:55). Type-locality: North Carolina, Raleigh.

Small size (7 mm); yellow and black; frontoclypeus black, occasionally with a short median pollinose stripe; thorax dark, nearly black, with gray pollen; abdomen yellow at base, black at apex, basal segment with large median black spot, second segment with two contiguous black triangles, their bases reaching posterior margin; wing pattern extremely faint. Male easily associated with female by abdominal markings and nearly obsolete wing pattern; frontoclypeus with pollinose stripe reaching half way to oral margin.

The nearly obsolete wing pattern easily separates this species from any other *Chrysops* likely to be found in Illinois.

Immature stages are unknown.

C. fulvistigma is a southeastern species,



Fig. 129.—Distribution of *Chrysops fulvistigma* in North America.

extending from the western panhandle of Florida to New Jersey and west to eastern Texas (Fig. 129). As yet this species has not been collected in Illinois.

Chrysops geminatus Wiedemann

Chrysops geminatus Wiedemann (1828: 205). Type-locality: unknown.

Chrysops fallax Osten Sacken (1875:392). Type-locality: New York, Tarrytown (lectotype).

Small to moderate size (7 mm); black and yellow; frontoclypeus shining yellow; abdominal marking usually not in form of stripes, but black markings occasionally reduced, appearing as broken rows of spots; apical spot broad (Fig. 54), nearly separated from crossband, covering nearly all of second submarginal cell; hyaline triangle large, extends well beyond second longitudinal vein; crossband broad, covering most of discal cell, narrowed posteriorly, reaching hind margin of wing; both basal cells hyaline; fifth posterior cell hyaline. Male with some dilute infuscation in both basal cells.

The larvae (Fig. 83) have been found in wet soil, plant debris, and moss along streams and ponds and in wet soil under trees (Pechuman 1972; Teskey 1969).

In Illinois adults appear from late June to early July.

C. geminatus is an eastern and southern species, extending from the panhandle of Florida to Maine and west to Arkansas and Wisconsin (Fig. 130). In Illinois this species has been collect-



Fig. 130.—Distribution of *Chrysops geminatus* in Illinois and North America.

ed in the northeastern third of the state (Fig. 130).

Chrysops impunctus Kröber

Chrysops impunctus Kröber (1926:301).

Type-locality: Ontario, Port Stanley.

Small to moderate size (7.5 mm); yellow and black; frontoclypeus yellow; thorax greenish with black stripes; abdomen with basal two segments yellow, remaining segments black, segments 3 and 4 with median yellow stripe; apical spot broad (Fig. 55), covering nearly all of second submarginal cell, nearly separated from crossband; hyaline triangle large, extending well beyond second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing; first basal cell with basal infuscation; second basal cell hyaline; fifth posterior cell diffusely infuscate. Male easily associated with female; yellow stripe on abdominal segments 3 and 4 is broader than that in most females.

This species was previously considered a subspecies of *C. geminatus*.

Both sexes of this species are distin-

guished from other Illinois *Chrysops* by the two completely yellow basal abdominal segments. Occasional specimens of *geminatus* have the spots on the second segment reduced to a vague shadow in the center of the segment. Rarely, specimens of *impunctus* show a trace of a dark marking on the second tergite, but it is at the apex of the segment.

Immature stages are unknown.

In Illinois adults appear in mid-June and have been collected until late July.

C. impunctus is an eastern and southern species, extending from Louisiana to Delaware and west to Illinois (Fig. 131). This species has been collected in long series from Vermilion County, Illinois.

Illinois Records.—Douglas County, Walnut Point State Park (5 miles SE Hindsboro); Vermilion County, Kickapoo State Park, Forest Glen Forest Preserve (5 miles SE Westville), 2.8 miles E Oakwood.



Fig. 131.—Distribution of *Chrysops impunctus* in North America.

Chrysops indus Osten Sacken

Chrysops indus Osten Sacken (1875:383).

Type-locality: New York, Cayuga Lake.

Chrysops pilumnus Kröber (1926:278).

Type-locality: Ontario, Jordan.

Moderate size (8 mm); yellow and black; frontoclypeus shining yellow; frontal callus black; scutellum dark; abdomen with median row of rather large yellow triangles, hind margin of tergites narrowly yellow, lateral margins broadly yellow; apical spot broad

(Fig. 56), extending into second submarginal cell; hyaline triangle does not reach second longitudinal vein; cross-band broad, covering discal cell, reaching hind margin of wing; first basal cell infuscate; second basal cell hyaline; fifth posterior cell almost completely infuscate; apical half of anal cell infuscate. Male with black areas much more extensive than in female; both basal cells and fifth posterior cell almost completely infuscated.

This species resembles *C. macquarti* in appearance, but the dark scutellum and the abdomen without stripes readily separate these two species.

The larvae (Fig. 100) have been found in mud and in plant debris and moss in a variety of semiaquatic habitats (Pechuman 1972; Teskey 1969).

In Illinois adults appear in late May and have been collected until late July.

C. indus is a northern and eastern species, extending from Virginia to Maine and west to Manitoba (Fig. 132). The range of this species may extend into Georgia. In Illinois this species has been collected in the northern part of the state (Fig. 132).



Fig. 132.—Distribution of *Chrysops indus* in Illinois and North America.

Chrysops luteopennis Philip

Chrysops luteopennis Philip (1936c:159).

Type-locality: Minnesota, Anoka County, Moore's Lake.

Moderate size (8 mm); dull yellow and black; frontoclypeus yellow, some specimens with small triangle of pollen below antennae; frontal callus yellow, darkened above (in one specimen callus wholly dark brown); black median stripes of abdomen joined on second tergite, sublateral stripes do not reach anterior margin of second tergite; wing membrane lightly tinted, pattern pale brown, not covering all of discal cell; hyaline triangle does not quite reach second longitudinal vein (Fig. 57). Male similar to female, but wing membrane, especially in anal area, more heavily tinted; apical spot slightly broader; triangular pollinose area on frontoclypeus reaches halfway to level of frontoclypeal pits.

The combination of a tinted wing membrane and brown wing pattern which does not completely cover the discal cell should separate this species from any other likely to be found in Illinois.

The larva of this species is unknown.

C. luteopennis is a rarely collected species of *Chrysops* known from only five localities in the north-central states and in southern Ontario (Fig. 133). Eventually it may be found in Illinois near Lake Michigan.



Fig. 133.—Distribution of *Chrysops luteopennis* in North America.

Chrysops macquarti Philip

Chrysops macquarti Philip (1961:161).

Type-locality: Maryland, Catonsville.

Moderate size (7.5 mm); yellow and black; frontoclypeus shining yellow; frontal callus black or dark brown; thorax greenish gray in ground color; scutellum usually with considerable yellow; abdomen with yellow median stripe between two black stripes of varying width, laterally yellow; apical spot very broad (Fig. 58), extending into second posterior cell; hyaline triangle does not reach second longitudinal vein; crossband broad, covers discal cell, narrows posteriorly but reaches hind margin of wing; first basal cell infusate; second basal cell hyaline; fifth posterior cell hyaline. Male generally darker than female with broader black abdominal stripes and often dark scutellum; second basal cell half or more infuscated.

This species resembles *C. indus* but is smaller and can be readily separated from *indus* by the characters in the key.

The larvae (Fig. 89) are usually found in saturated soils bordering sluggish streams (Pechuman 1972; Teskey 1969).

In Illinois adults appear in mid-June and have been collected until early August.



Fig. 134.—Distribution of *Chrysops macquarti* in Illinois and North America.

C. macquarti is a widespread eastern species, extending from northern Florida to Maine and west to Wisconsin and Louisiana (Fig. 134). In Illinois this species is rare, having been collected from only five localities (Fig. 134).

Chrysops mitis Osten Sacken

Chrysops mitis Osten Sacken (1875:374).

Type-locality: Canada, Hudson Bay (lectotype).

Large species (9.5 mm); black; frontoclypeus with median pollinose stripe; pleura with grayish or pale yellowish pile; abdomen entirely dark; no apical spot or hyaline triangle (Fig. 59); crossband broad, covering discal cell, narrowly or not at all reaching hind margin of wing; basal half of both basal cells infuscate; base of fifth posterior cell infuscate. Male with considerable dilute infuscation in anal area of wing.

This species is close to *C. ater* in general appearance, and some specimens can scarcely be differentiated. The characters in the key will generally separate these two species.

The egg mass is in three tiers, resembling those of *C. ater* and *C. cincticornis*. The larvae (similar to Fig.

103) have been collected on the edges of ponds and streams and in swamps, usually in a highly organic substrate (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early June and have been collected only until the middle of June.

C. mitis is a northern species, extending from New York to Labrador and west to Idaho and Alaska (Fig. 135). In Illinois this species is restricted to the northeast corner of the state.

Illinois Records.—Kankakee County, Wichert; Lake County, Antioch, Sand Lake.

Chrysops moechus Osten Sacken

Chrysops moechus Osten Sacken (1875:387). Type-locality: District of Columbia (lectotype).

Moderate size (7.5 mm); yellow and black; frontoclypeus shining yellow; frontal callus usually black; thorax greenish in ground color; black markings of abdomen usually in form of stripes; apical spot very broad (Fig. 60), covering first posterior cell; hyaline triangle extremely small but regular in outline; crossband broad, covering discal cell, extending to hind margin of wing; first basal cell infuscate; second basal cell hyaline; fifth posterior cell mostly hyaline. Male black; wings almost entirely infuscated except for small hyaline triangle.

The body pattern of this species is variable, the black abdominal stripes of some specimens being reduced to a series of dashes; in others the stripes are extensive and the entire insect appears quite dark. This species is very distinctive from other species of *Chrysops*, particularly in the wing pattern.

Eggs are laid on the underside of leaves of trees overhanging streams, sometimes many feet above the water. Pechuman (1972) observed oviposition only over moving water. The egg mass is unusual in that the individual eggs are deposited almost at right angles to the leaf (Fig. 14) and do not overlap each other as is usual in *Chrysops* egg masses (Fig. 12, 13). The larvae (Fig. 82) have been collected in wet mud, often un-



Fig. 135.—Distribution of *Chrysops mitis* in North America.



Fig. 136.—Distribution of *Chrysops moechus* in Illinois and North America.

der water, along streams (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early June and have been collected until early August. The male is black and is rather frequently collected from leaves of trees overhanging streams (Pechuman 1972).

C. moechus is an eastern species, extending from the Florida panhandle to Maine and west to Minnesota and Louisiana (Fig. 136). In Illinois (Fig. 136) this species has been collected in the northeastern third of the state and in Pope County in southern Illinois.

Chrysops montanus Osten Sacken

Chrysops montanus Osten Sacken (1875: 382). Type-locality: New York, Catskill Mountain House (in Greene County).

Moderate size (8 mm); black and yellow; frontoclypeus shining yellow; frontal callus normally dark but sometimes brownish; scutellum normally dark; abdomen with geminate black spot, often with sublateral black spot on second tergite, and four rows of

spots on third, fourth, and fifth tergites; apical spot variable but usually broad, covering most of second submarginal cell (Fig. 61); hyaline triangle large, reaching second longitudinal vein; cross-band broad, covering discal cell, reaching hind margin of wing; first basal cell partly infusate; second basal cell nearly hyaline; fifth posterior cell partly infusate. Male with yellow areas usually much reduced; both basal cells partly infuscated.

Some specimens lack the small black lateral spots on the second abdominal segment or have them much reduced. The size and shape of the apical spot is also subject to considerable variation.

The larvae (Fig. 91) have been collected in sand and organic material on the edges of ponds and lakes (Pechuman 1972; Teskey 1969).

In Illinois adults appear in late May and have been collected until late August.

C. montanus is an eastern and north-central species, extending from southern Florida to New Brunswick and west to Manitoba and eastern Texas (Fig. 137). This species has been col-



Fig. 137.—Distribution of *Chrysops montanus* in Illinois and North America.

lected infrequently in southern and northern Illinois (Fig. 137).

Chrysops niger Macquart

Chrysops niger Macquart (1838:165).

Type-locality: North America.

Moderate size (7.5 mm); black; frontoclypeus without median pollinose stripe; bare area of vertex interrupted by pollen; sublateral thoracic stripes dull or obsolete; apical spot and hyaline triangle absent (Fig. 62); crossband broad, covering discal cell, narrowed posteriorly, reaching hind margin of wing; first basal cell infusate; second basal cell hyaline; fifth posterior cell hyaline. Male with both basal cells largely infusate. Face with considerable yellow in both sexes.

The combination of a hyaline second basal cell, saturate crossband, and largely yellow face separates this species and its sibling species, *C. calvus*, from other dark *Chrysops*. It is separated from *calvus* by the characters in the key. Some specimens have a small spot at the bifurcation of the third longitudinal vein. The anal area of the wing is sometimes dilutely infusate.

The larvae (Fig. 93) seem tolerant of many conditions and have been collected from such varied situations as stagnant mud and plant debris on the edge of a pool, mud on the banks of a small brook, wet soil under trees, sphagnum bogs, and the shores of lakes (Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults appear in early April and have been collected until late June.

C. niger is an eastern and central species, extending from northern Florida to Nova Scotia and west to Minnesota and eastern Texas (Fig. 138). In Illinois this species is found throughout the state (Fig. 138).

Chrysops pikei Whitney

Chrysops pikei Whitney (1904:205). Type-locality: Missouri, Pike County.

Rather small size (7 mm); yellow and black; frontoclypeus shining yellow; frontal callus black; thorax greenish yellow in ground color; abdomen with black stripes, sublateral ones quite short; apical spot broad (Fig. 63), extending into first posterior cell; hyaline triangle reaches second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing; first basal cell infusate; second basal cell hyaline; fifth posterior cell partly infusate. Male with second basal cell partly infusate.

This species is rather distinctive and is readily separated from other species by the characters given in the key.

The egg mass is in more than one tier, resembling a small *Tabanus* egg mass. The larvae (Fig. 84) are found in debris and in the banks of ponds and streams (Jones & Bradley 1924; Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults appear in mid-May and have been collected until early September.

C. pikei is a southeastern and central species, extending from northern Florida to Virginia and west to South Dakota and eastern Texas (Fig. 139). Disjunct



Fig. 138.—Distribution of *Chrysops niger* in Illinois and North America.



Fig. 139.—Distribution of *Chrysops pikel* in Illinois and North America.

populations are found in southwestern South Dakota and southern Florida. This species is widespread throughout Illinois (Fig. 139).

Chrysops pudicus Osten Sacken

Chrysops pudicus Osten Sacken (1875: 381). Type locality: Massachusetts (lectotype).

Moderate size (7.5 mm); black and yellow; frontoclypeus shining yellow; frontal callus yellow or fuscous; dark spot under scutellum; abdominal markings not in form of stripes; apical spot covers apical third of second submarginal cell; hyaline triangle broad, usually reaching second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing; both basal cells hyaline; fifth posterior cell hyaline (Fig. 64); hind femora usually dark at base. Male with both basal cells partly infuscated.

C. pudicus belongs to the group which includes *C. callidus*, *C. sackeni*, and *C. dimmocki* and may be separated from them by the characters given in the key; the apical spot of *pudicus* is sub-

ject to some variation but is always wider than it is in *callidus* and usually falls between those of *sackeni* and *dimmocki*.

Larvae have been taken from wet soil along a roadside ditch (Pechuman 1972).

In Illinois adults appear in early May and have been collected until mid-September.

C. pudicus is a southeastern species, extending from southern Florida to Massachusetts and west to Illinois and eastern Texas (Fig. 140). Disjunct populations have been examined from Wisconsin, Michigan-Indiana, New York-Ontario, and Nova Scotia. In Illinois this species is found in the southern fourth of the state (Fig. 140).



Fig. 140.—Distribution of *Chrysops pudicus* in Illinois and North America.

Chrysops reicherti Fairchild

Chrysops reicherti Fairchild (1937:60). Type-locality: Florida, Jefferson County, Monticello.

Large size (9.0 mm); yellow and brown; frontoclypeus shining yellow; thorax grayish brown with fuscous stripes; abdomen pale grayish brown,

tergites 2–6 with lateral brown band; apical spot broad (Fig. 65), covering second submarginal cell; hyaline triangle does not reach second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing; first and second basal cells partly infuscate; fifth posterior cell infuscate. Male with apical spot more extensive, often nearly surrounding hyaline triangle, which may be reduced to pale band or series of spots; both basal cells infuscated on most of basal half.

This species is related to *flavidus* but can be readily separated from *flavidus* by the characters given in the key.

Larvae (Fig. 98) have been collected from wet mud and organic debris in ponds and small lakes (Goodwin 1972; Tidwell 1973).

In Illinois adults appear in mid-July and have been collected until late August.

C. reicherti is a southeastern species, extending from southern Florida to Delaware and west to Illinois and eastern Texas (Fig. 141). In Illinois this species has been collected only in the

southernmost part of the state (Fig. 141).

Chrysops sackeni Hine

Chrysops sackeni Hine (1903:42). Type-locality: Ohio, Sandusky.

Moderate size (8.5 mm); black and yellow; frontoclypeus shining yellow; frontal callus usually yellow, often bordered with black or brown, occasionally black; abdominal markings not in form of stripes, black spot on second segment nearly joins with that on first segment, second and third sternites with black sublateral spots; apical spot narrow (Fig. 66), extending partly into second submarginal cell, at its origin slightly wider than marginal cell; hyaline triangle broad, not reaching second longitudinal vein; crossband broad, covering discal cell, not reaching hind margin of wing; both basal cells hyaline; fifth posterior cell partly infuscate. Male usually with pale markings less extensive; both basal cells partly infuscated.

C. sackeni often flies with *C. callidus*, and occasional specimens are difficult



Fig. 141.—Distribution of *Chrysops reicherti* in Illinois and North America.



Fig. 142.—Distribution of *Chrysops sackeni* in Illinois and North America.

to separate from that species. In cases of doubt, the shape of the frontal callus is usually the best character to inspect; the callus of *C. callidus* is narrow and black, whereas in *C. sackeni* it is higher in proportion to its width and is often yellow or brown.

The larvae (Fig. 105) have been collected in mud on the edges of permanent and temporary ponds, along stream margins, in swamps, and in organic material on the edge of salt marshes (Pechuman 1972; Teskey 1969). The egg mass resembles that of *C. callidus*.

In Illinois adults appear in mid-June and have been collected until mid-September.

C. sackeni is a northeastern and north-central species, extending from Delaware to Maine and west to Iowa and Manitoba (Fig. 142). A disjunct population has been examined from western Nebraska. In Illinois this species has been collected in the northeastern part of the state (Fig. 142).

***Chrysops separatus* Hine**

Chrysops separatus Hine (1907:228). Type-locality: North Carolina, Raleigh.

Moderate size (8 mm); thorax, abdomen, and frontoclypeus black, the latter with broad pollinose stripe extending three-fourths its length; first basal cell wholly infuscated (Fig. 67), second basal cell clear; apical spot not joined to crossband. Male has both basal cells and discal cell outlined in black with centers clear; pollinose stripe of frontoclypeus extends to oral margin.

No other wholly black *Chrysops* likely to be found in Illinois has the combination of an apical spot and a pollinose stripe on the frontoclypeus.

The larva of this species is unknown.

In Illinois adults have been collected only during mid-May.

C. separatus is a southeastern species, extending from Georgia to Maryland and west to Illinois and northeastern Mississippi, with an apparently disjunct population extending from southwestern Mississippi to eastern Texas and



Fig. 143.—Distribution of *Chrysops separatus* in North America.

Oklahoma (Fig. 143). In Illinois this species is known only from the southern third of the state.

Illinois Records.—Perry County, Du Quoin; Pope County, 4 miles NNW Golconda, Lusk Creek (3 miles SE Eddyville).

***Chrysops sequax sequax* Williston**

Chrysops sequax sequax Williston (1887: 133). Type-locality: western Kansas.

Moderate size (8.0 mm); yellow and black; frontoclypeus shining yellow with large black spot on each side; thorax grayish green in ground color with dark stripes; abdomen yellow with black stripes; apical spot broad (Fig. 68), covering all of second submarginal cell; hyaline triangle reaches second longitudinal vein; crossband broad, covering discal cell, reaching hind margin of wing; first basal cell completely infuscate; second basal cell hyaline; fifth posterior cell partly infuscate along lateral margins. Male with black abdominal stripes broader than in female; second basal cell infuscate; fifth posterior cell infuscate.

C. sequax resembles the related species *C. beameri* and *C. pikei*, but the characters used in the key usually present no difficulty. Rarely *sequax* has a brown or yellowish frontal callus, and in this case it may be separated from *beameri* by the large black spots flanking the frontoclypeus.

The larvae (Fig. 92) have been collected from soft, slimy muck on the margin of a livestock watering pond (Teskey & Burger 1976).



Fig. 144.—Distribution of *Chrysops sequax sequax* in Illinois and North America.

In Illinois adults appear at the beginning of July and have been collected until early September.

C. sequax sequax is a central subspecies, extending from Louisiana to Pennsylvania and west to western South Dakota (Fig. 144). A disjunct population has been examined from Georgia and Alabama. In Illinois this subspecies is widely distributed throughout the state (Fig. 144).

***Chrysops sequax tau* Philip**

Chrysops sequax tau Philip (1955:113).

Type-locality: Illinois, Golconda.

Moderate size (8.0 mm); this form is separated from the nominate form by the presence of a narrow, sometimes broken, stripe of pollen on the frontoclypeus; there is also a tendency for the apical spot to be less extensive and for the frontal callus to be partly brown or yellowish. Specimens and biological studies probably will be needed to determine the true status of *tau*. The male is unknown.

The larva of this subspecies is unknown.

In Illinois adults appear in late July



Fig. 145.—Distribution of *Chrysops sequax tau* in North America.

and have been collected until early August.

C. sequax tau is an east-central subspecies, extending in a narrow band from Virginia west to Missouri and Arkansas (Fig. 145). In Illinois this subspecies has been collected only in the southeastern part of the state.

Illinois Records.—Lawrence County, Red Hills State Park; Pope County, Golconda, Lusk Creek.

***Chrysops striatus* Osten Sacken**

Chrysops striatus Osten Sacken (1875: 391). Type-locality: (lectotype, no locality data).

Moderate size (8.0 mm); yellow and black; frontoclypeus shining yellow; frontal callus usually black or brown, thorax greenish in ground color; abdomen with black stripes, median pair usually united on second tergite; apical spot broad (Fig. 69), usually covering only about half of second submarginal cell; hyaline triangle does not reach second longitudinal vein; cross-band broad, covering discal cell, narrowed posteriorly but reaches hind margin of wing; first basal cell infusate; second basal cell hyaline; fifth posterior cell mostly hyaline. Male with yellow areas reduced; second basal cell largely infuscated.

This species often flies with *C. aberrans*, which it resembles, but the two forms can be separated by the characters given in the key.

Larvae (Fig. 104) have been collected from mud on the edge of streams. They are probably found also in the

cattail swamps where adults are common (Pechuman 1972; Teskey 1969).

In Illinois adults appear in late June and have been collected until mid-July.

C. striatus is a north-central and north-eastern species, extending from Massachusetts to Maine and west to Manitoba (Fig. 146). In Illinois this species has been collected in four counties in the northeast corner of the state (Fig. 146).



Fig. 146.—Distribution of *Chrysops striatus* in Illinois and North America.

Chrysops univittatus Macquart

Chrysops univittatus Macquart (1855:56).

Type-locality: Maryland, Baltimore.

Chrysops wiedemanni Kröber (1926:267).

Type-locality: (syntypes from several localities in Canada and the United States).

Chrysops fraternus Kröber (1926:328).

Type-locality: unknown.

Rather small size (7 mm); black or dark brown; frontoclypeus shining yellow, often blackish laterally, abdomen with median yellowish stripe, sometimes similar shorter sublateral stripes; apical spot broad and nearly separated from crossband (Fig. 70); hyaline tri-

angle almost reaches anterior margin of wing; crossband broad, covering most of discal cell, narrowed posteriorly but reaches hind margin of wing; both basal cells and fifth posterior cell hyaline. Male with first basal cell infuscated.

Pechuman (1957) called this species *C. wiedemanni* Kröber. Since that time it has been shown (Philip 1961) that the correct name is *univittatus*, and the species called *univittatus* by various workers before 1961 is now known as *C. macquarti* Philip. The name *C. obsoletus* has also been applied to *univittatus*, but this name properly belongs to a quite unrelated species.

The body coloration of *C. univittatus* is extremely variable. The abdominal pattern varies from three distinct yellow stripes to only a trace of a median stripe.

Larvae (Fig. 97) have been found in wet soil and plant debris along both sluggish and swift streams, in mud on the shores of ponds and lakes, and in marshes (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early



Fig. 147.—Distribution of *Chrysops univittatus* in Illinois and North America.

May and have been collected until late August.

C. univittatus is an eastern and central species, extending from the panhandle of Florida to New Brunswick and west to Minnesota and Louisiana (Fig. 147). This is an abundant and widespread species in Illinois (Fig. 147).

Chrysops upsilon Philip

Chrysops upsilon Philip (1950a:458). Type-locality: Georgia, Millen.

Moderate size (8 mm); black and yellow; frontoclypeus brown with yellow in center and short median pollinose stripe; frontal callus black; thorax grayish green in ground color; scutellum dark; abdomen dark brown to black with broad yellow median stripe and short sublateral stripes; apical spot broad (Fig. 71), covering most of the second submarginal cell; hyaline spot generally does not reach second longitudinal vein except as subhyaline streak; crossband broad, covering discal cell, reaching hind margin of wing; infuscation of costal cell paler than that of crossband; both basal cells and fifth posterior cell hyaline. Male with pollinose stripe on frontoclypeus more extensive than in female, often reaching nearly to oral margin; first basal cell infuscated.

Among Illinois *Chrysops*, *upsilon* is likely to be confused only with *C. univittatus*, which lacks pollen on the frontoclypeus; in cases where the pollen is indistinct, the best character for separation is the color of the costal cell, which is paler than the crossband in *upsilon*.

Larvae are unseparable from those of *C. univittatus*.

In Illinois adults appear in early June and have been collected until mid-September.

C. upsilon is a southeastern species, extending from the panhandle of Florida to Delaware and west to Illinois and eastern Texas (Fig. 148). In Illinois this species has been collected in the southern part of the state (Fig. 148).



Fig. 148.—Distribution of *Chrysops upsilon* in Illinois and North America.

Chrysops vittatus Wiedemann

Chrysops vittatus Wiedemann (1821:56).

Type-locality: North America.

Chrysops areolatus Walker (1848:197).

Type-locality: New York.

Chrysops lineatus Jaenicke (1867:334).

Type-locality: Illinois.

Chrysops ornatus Kröber (1926:328).

Type-locality: Ontario, Jordan.

Moderate size (8 mm); yellow and black; frontoclypeus shining yellow; frontal callus yellow; thorax yellow in ground color; scutellum yellow; abdomen with black stripes; apical spot broad (Fig. 72), covering second submarginal cell; hyaline triangle does not reach second longitudinal vein; crossband very broad, covering discal cell, reaching hind margin of wing; first basal cell infuscate; second basal partly infuscate; fifth posterior cell largely infuscated. Male with yellow areas reduced; second basal cell largely infuscated.

This species is rather distinctive from other species of *Chrysops* and is readily separated by the characters in the keys.

The larvae (Fig. 85) have been col-

lected in wet soil and plant debris from the edges of streams, ponds, and lakes, as well as from saturated soil under trees (Pechuman 1972; Teskey 1969).

In Illinois adults appear in mid-June and have been collected until late August.

C. vittatus is an eastern and central species, extending from northern Florida to Nova Scotia and west to North Dakota and Eastern Texas (Fig. 149). This species is abundant and widely distributed throughout Illinois (Fig. 149).



Fig. 149.—Distribution of *Chrysops vittatus* in Illinois and North America.

Silvius Meigen
***Silvius quadrivittatus* (Say)**

Chrysops quadrivittatus Say (1823:33).
Type-locality: near the Rocky Mountains.

Moderate size (8 mm); grayish species; basal callus diamond shaped; wings (Fig. 73) clear with small but distinct spots on crossveins, bifurcation and subapically on second longitudinal (R_{2+3}), both branches of third

longitudinal (R_4 and R_5), and both branches of fourth longitudinal (M_1 and M_2) veins, occasionally some subapical spots obsolete; legs mostly yellow; abdomen with four rows of dark spots. Male similar, but abdomen with yellowish cast.

Larvae (Fig. 111) have been found in damp silty soil overlain by grass and vegetable debris on the steep banks of desert rivers (Burger 1977).

In Illinois adults appear in mid-June and have been collected until mid-August.

S. quadrivittatus is a central and southwestern species, extending from Mississippi to Illinois and west to Montana, California, and Mexico (Fig. 150). In Illinois this species has been collected only in the western part of the state (Fig. 150).



Fig. 150.—Distribution of *Silvius quadrivittatus* in Illinois and North America.

Neochrysops Walton
***Neochrysops globosus* Walton**

Neochrysops globosus Walton (1918:192).
Type-locality: Maryland, Cabin John Bridge.

This genus is based on one rarely collected species.

Small size (8.5 mm); frontal callus large, oval, dark brown; frontoclypeus yellow with dark spot on each side and triangular area of pollen below antennae; antennae slender and elongate; thorax yellow with three shining black stripes, center one extending onto scutellum; wing (Fig. 74) rather uniformly infuscated with spur on an indication of one at bifurcation of third longitudinal vein; abdomen yellow, globose, wider than thorax, with double row of large black spots on tergites 1–5 with stiff black hairs laterally, especially heavy on segments 3 and 4. Male holoptic, closely resembles female; abdomen less globose, scarcely wider than thorax; frontoclypeus with yellow pollinose stripe reaching half way to oral margin. The male has previously been unknown, but the only specimen seen from Illinois was a male.

The globose abdomen and other characters mentioned here and in the key to genera distinguish this species from any other Illinois tabanid.

The immature stages are unknown, and little is known about the habits of this species.

In Illinois adults have been collected only in early June.

N. globosus is a rare species, collected mostly as single specimens in Maryland, Delaware, Alabama, Mississippi, Tennessee, and Illinois (Fig. 151).

Illinois records.—Pulaski County, Wetaug.



Fig. 151.—Distribution of *Neochrysops globosus* in North America.

Diachlorus Osten Sacken
Diachlorus ferrugatus (Fabricius)

Chrysops ferrugatus Fabricius (1805:111).

Type-locality: Carolina.

Tabanus americanus Palisot de Beauvois (1819:222). Type-locality: United States. Name preoccupied (Forster 1771).

Diabasis ataenia Macquart (1838:156).

Type-locality: Carolina.

Chrysops approximans Walker (1848:198).

Type-locality: Florida.

Chrysops convergens Walker (1848:198).

Type-locality: Honduras.

Tabanus rondanii Bellardi (1859:68).

Type-locality: Mexico.

Moderate size (8 mm); yellowish brown; first antennal segment scarcely longer than wide; third antennal segment without dorsal angle; median callus a narrow line; eyes bare; ocellar tubercle absent; frons higher than broad; abdomen yellowish, caudal segments brown; basicosta bare; wings pale brown; apical spot broad, dark brown; fore tibiae swollen; hind tibiae without apical spurs. The male is readily associated with the female.

Larvae (Fig. 110) have been found associated with root mats of woody plants in shaded areas (Jones & Anthony 1964) in swamps and bogs and at the edges of lakes and streams.

Diachlorus ferrugatus is a southeastern species, extending from Florida to New Jersey and west to eastern Texas, with a disjunct population in northeast Indiana (Fig. 152). It is also found in



Fig. 152.—Distribution of *Diachlorus ferrugatus* in North America.

Yucatan, Central America, and Grand Bahama Island. As yet this species has not been collected in Illinois although specimens have been examined from Indiana.

Chlorotabanus Lutz
Chlorotabanus crepuscularis
 (Bequaert)

Tabanus crepuscularis Bequaert (1926: 234). Type-locality: United States.

Tabanus flavus Macquart (1834:200). Type-locality: United States. Name preoccupied (Wiedemann 1828).

Stout species (12 mm); yellowish (green when alive); frontal callosity absent; thorax and abdomen uniformly greenish yellow; wings hyaline, several crossveins with narrow brown margins; hind tibiae without spurs. Males similar to females except for sexual differences.

This species is readily separated from other species of tabanids by its uniform yellowish color in pinned specimens.

Larvae (Fig. 109) have usually been found along the edges of ponds and slow moving streams and in floating vegetation in open water (Tidwell 1973). Wilson (1969) collected larvae from the forest floor.

C. crepuscularis is a southeastern species, extending from Florida to Delaware and west to central Texas (Fig. 153). As yet this species has not been collected in Illinois although specimens have been examined from western Tennessee.



Fig. 153.—Distribution of *Chlorotabanus crepuscularis* in North America.

Haematopota Meigen
Haematopota rara Johnson

Haematopota rara Johnson (1912:182).

Type-locality: Pennsylvania, Folsom.

Moderate size (8 mm); slender gray species; frons wider than high, with narrow callus across its entire width, a velvety black spot on each side directly above callus; eyes essentially bare; first antennal segment enlarged, shining; wings gray with white maculations (Fig. 76). Male with distinctly hairy eyes but easily associated with female on characters of the antennae and wing.

This species, with the white wing maculations, is not likely to be confused with any other species which may be found in Illinois.

The immature stages of this species are unknown; adults have been taken frequently in sphagnum bogs, and such situations may also be a favored larval habitat.

H. rara is an eastern species with several disjunct populations from eastern Tennessee to Cape Breton Island (Fig. 154). As yet it has not been collected in Illinois although specimens have been examined from Ohio.



Fig. 154.—Distribution of *Haematopota rara* in North America.

Atylotus Osten Sacken

At least four species of this genus are found in Illinois. All of them are small or moderately sized hairy insects of little economic importance. Considerable variation is exhibited in *Atylotus*, and the determination of some specimens to the specific level is sometimes difficult.

KEY TO SPECIES OF ATYLOTUS

Females

- 1. Frons with 2 small rounded callosities **woodi**
- Frons without callosities 2
- 2. Pleural hairs bright yellow; basal plate of antennae about as broad as long **bicolor**
- Pleural hairs gray; basal plate variable, slender to broad 3
- 3. Abdomen with whitish hairs; frons of moderate width; basal plate of antennae almost as broad as long; palpi short, thick, abruptly tapering to point; eye in life usually with diagonal band **ohioensis**
- Abdomen with mostly yellow hairs; frons rather narrow; basal plate of antennae never as broad as long; palpi not especially thick or abruptly tapered; no band on eye in life **thoracicus**

Males

- 1. Postocular fringe very short, not recurved forward over upper eye margins **woodi**
- Postocular fringe long, recurved over eyes 2
- 2. Pleural hairs bright yellow **bicolor**
- Pleural hairs gray 3
- 3. Abdomen with hairs mostly whitish; sometimes with median patches of black hairs and some sublateral yellowish hairs; basal plate of antennae broad; eye in life usually with diagonal band **ohioensis**
- Abdomen with hairs mostly yellow; basal plate of antennae rather narrow; no eye band in life **thoracicus**

A key to the larval stages is incorporated within the key to the larval stages of *Tabanus*.

Atylotus bicolor (Wiedemann)

Tabanus bicolor Wiedemann (1821:46).

Type-locality: North America.

Tabanus fulvescens Walker (1848:171).

Type-locality: Massachusetts and unknown (cotypes).



Fig. 155.—Distribution of *Atylotus bicolor* in Illinois and North America.

Tabanus reficeps Macquart (1855:55).

Type-locality: Maryland, Baltimore.

Small to moderate size (11 mm); yellow or light orange; abdomen with median, indefinitely outlined dark area; wings hyaline, costal cell hyaline or pale yellow; eyes hairy. Male eye facets differentiated; eyes hairy.

Larvae (Fig. 218) have been collected from such diverse habitats as the muddy banks of ponds and streams, sphagnum bogs, wet sod, and sod in salt marshes (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early July and have been collected until late July.

A. bicolor is a northern species, extending from the District of Columbia to Maine and west to Alberta (Fig. 155). In Illinois this species has been collected in the two northeastern counties, and a single record exists from Havana, Mason County (Fig. 155).

Atylotus ohioensis (Hine)

Tabanus ohioensis Hine (1901:28). New name for *pruinosis* Hine (1900).

Tabanus pruinosus Hine (1900:248).

Name preoccupied (Bigot 1892).

Type-locality: Ohio.

Small size (9 mm); grayish black; abdomen often grayish laterally on first 2 tergites; wings hyaline, costal cell sometimes faintly tinged with yellow; eyes hairy. Male eye facets differentiated; abdomen laterally often more extensively pale than in female; eyes hairy.

Although of minor importance, *A. ohioensis* attacks man and animals. It attacks man around the head, much as do several species of *Chrysops*.

Larvae (Fig. 216) have been collected in saturated pasture sod, seepage areas, and moss along streams (Pechuman 1972; Teskey 1969).

In Illinois adults appear in late June and have been collected until early July.

A. ohioensis is a northern species, extending from Pennsylvania to Alberta (Fig. 156). This species has been collected at only two localities in north-central Illinois.

Illinois Records.—Bureau County, Princeton; Woodford County, Spring Bay.



Fig. 156.—Distribution of *Atylotus ohioensis* in North America.

Atylotus thoracicus (Hine)

Tabanus thoracicus Hine (1900:248). Type-locality: New York, Oswego.

Small size (10 mm); dull yellowish; abdomen with median indefinitely outlined dark area, which is broader posteriorly; wings hyaline, costal cell pale yellow; eyes hairy. Male eye facets differentiated; eyes hairy.

Although not a common species, *A. thoracicus* is sometimes found in rather

large numbers in sphagnum bogs, and males are as commonly collected as females. The flight is weak, and when disturbed, this species rarely flies more than a few yards. There are no records of *A. thoracicus* biting.

Larvae (Fig. 215) have been found in open areas of a sphagnum bog mat (Teskey 1969).

In Illinois adults appear in mid-July and have been collected until late July.

A. thoracicus is a northern species, extending from Delaware to Nova Scotia and west to Wisconsin (Fig. 157). In Illinois this species has been collected at a single locality.

Illinois Records.—Iroquois County, Iroquois County Conservation Area (3 miles NE Beaverville).



Fig. 157.—Distribution of *Atylotus thoracicus* in North America.

Atylotus woodi Pechuman

Atylotus woodi Pechuman (1981:2). Type-locality: Ontario, Wellington County, Puslinch Township.

Moderate size (10.5 mm); grayish yellow; eye with fine short hairs; frons with two rounded calli well separated from each other and from frontal margins; femora and tibiae yellow; abdomen with broad dark median longitudinal stripe, yellowish laterally. Male

easily associated with female; hairs on upper occipital margin short, not recurved over eyes.

The presence of frontal calli in the female and the short nonrecurved hairs of the upper occipital margin in the male separate this species from all other *Atylotus* known from Illinois.

Larvae (Fig. 217) have been found in a marl bog (Teskey 1969, species C).

In Illinois adults have been collected only once, which was in early August.

A. woodi is a northern species, extending from Ontario to northern Illinois and southern Wisconsin (Fig. 158). This species has been collected at only a single locality in northeastern Illinois.

Illinois Records.—Lake County, Cedar Lake.



Fig. 158.—Distribution of *Atylotus woodi* in North America.

Leucotabanus Lutz

Leucotabanus annulatus (Say)

Tabanus annulatus Say (1823:32). Type-locality: Missouri

Moderate size (11 mm); frons very narrow; small basal callus continued dorsally as slender line; ocellar tubercle present; abdomen brownish with pale bands. Male superficially quite dif-

ferent from female; thorax and abdomen with long white hairs; upper eye facets enlarged, distinctly divided from smaller lower facets.

This species is crepuscular and probably nocturnal. On occasion it will attack cattle in numbers at dusk.

The larvae (Fig. 112) are found in rot holes in trees, in decaying logs, and less commonly in soil beneath forest litter (Tidwell 1973).

In Illinois adults appear in early July and have been collected until mid-August.

L. annulatus is a southeastern and central species, extending from southern Florida to Delaware and west to Kansas and eastern Texas (Fig. 159). In Illinois this species is collected only in the southern third of the state (Fig. 159).

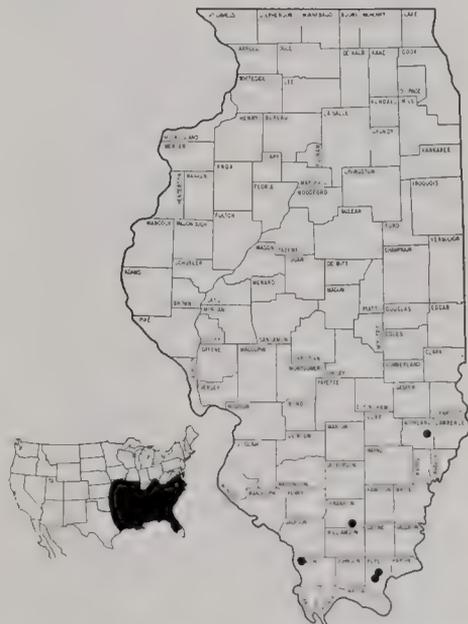


Fig. 159.—Distribution of *Leucotabanus annulatus* in Illinois and North America.

Tabanus Linnaeus

The present restriction of the genus *Tabanus* is discussed under the genus *Hybomitra*.

Tabanus includes some of the largest flies in Illinois although some species are quite small. Some major pests of man, livestock, and wildlife are in this genus. Serious pests of livestock in-

- low; face and pleurae yellow haired
.....**fulvulus**
- Third antennal segment usually entirely orange yellow; femora pale, sometimes darkened at base; palpi white; face and pleurae pale haired
.....**pallidescens**
21. Frons very narrow, at least 5 times as high as width at base22
Frons not over 4.5 times as high as wide, usually broader23
22. Frons widened above; basal plate of antennae very narrow, over twice as long as greatest width.....**sackeni**
Frons essentially parallel sided; basal plate of antennae broad, never more than one and one half times as long as greatest width**wilsoni**
23. Second palpal segment much swollen basally¹; median abdominal stripe broad**sagax**
Second palpal segment not very swollen basally; median abdominal stripe narrow24
24. Pale markings of abdomen yellowish brown, sublateral spots touch hind margins of segments (Fig. 169); frons over 3.5 times as high as wide**sublongus**
Pale markings of abdomen grayish, sublateral spots small, separated from hind margins; frons not more than 3.5 times as high as wide**longus**
- 25(13). Second abdominal segment with no pale median spot but occasionally two small sublateral spots (Fig. 170); fore tibiae distinctly bicolored; thorax white pollinose.....**trimaculatus**
Second abdominal segment with pale median spot (Fig. 171, 174)26
26. Abdomen with both median and sublateral spots (Fig. 171-177).....27
Abdomen without sublateral spots although abdomen may be paler laterally35
27. Wings with large brown spots not confined to crossveins and bifurcation; sublateral pale spots of abdomen usually confined to tergites 4-6 (Fig. 171).....**venustus**
Spots on wings, if present, confined to crossveins and bifurcation; sublateral pale spots usually on tergite 2 (Fig. 174-176)28
28. Bifurcation with dark spot; grayish species.....29
Bifurcation without dark spot; coloration variable30
29. Median and sublateral spots broadly joined along posterior margins of abdominal segments (Fig. 172); frons narrow; basal callus higher than wide.....**cymatophorus**
Median and sublateral spots narrowly or not at all joined along posterior margins of abdominal segments (Fig. 173); frons broad, basal callus almost square**reinwardtii**
30. Small species, usually 12 mm or less; frons widened above; costal cell hyaline31
Large species, usually 13 mm or more, differing in at least one other character from above33
31. Median callus large; palpi not swollen basally or sharply pointed; eyes in life with 2 purple bands.....**pumilus**
Median callus slender; palpi swollen basally but with apex acute; eyes in life unicolorous or with single purple band32
32. Eyes unicolorous in life**sparus sparus**
Eyes with single purple band**sparus milleri**
33. First antennal segment swollen above; sides of subcallus usually with few hairs.....**fairchildi**
First antennal segment not swollen above; sides of subcallus without hairs34
34. Sublateral white abdominal spots considerably larger than small median triangles, usually reaching anterior border of second and third segments (Fig. 177)**marginalis**
Median abdominal triangles relatively larger, sublateral spots smaller, rarely extending to anterior border of segments**vivax**
- 35(26). Second abdominal segment with pale spot distinctly smaller than spots on third and fourth segments (Fig. 178, 179); scutellum with pale pile; fore tibiae unicolorous36
Second abdominal segment with pale spot not markedly smaller than those on segments 3 and 4 (Fig. 184-186).....38
36. Abdomen black with very small median triangles (Fig. 178)**superjumentarius**
Abdomen usually brownish, at least in part; median triangles large (Fig. 179)37
37. Genae, pleurae, venter pale haired.....**molestus molestus**
Genae, pleurae, venter brown haired....**molestus mixis**
38. Bifurcation with no spot39
Bifurcation with conspicuous spot43
39. Wings with smoky tinge; costal cell dark yellow; abdomen with median triangles small or obsolete (Fig. 160, 180); large species, 19-25 mm40
Wings hyaline; costal cell hyaline or slightly tinted; abdomen with median triangles conspicuous (Fig. 181); smaller species, 11-19 mm41

¹Some specimens of *orbicallus* with inconspicuous hairs on the eye will key to this point; such specimens may be distinguished from *sagax* by the narrow, almost obsolete, pale median abdominal triangles and the frons, which is distinctly widened above.

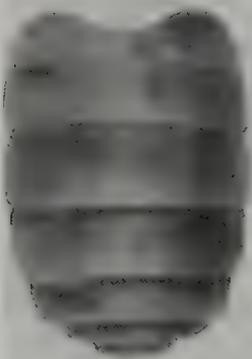
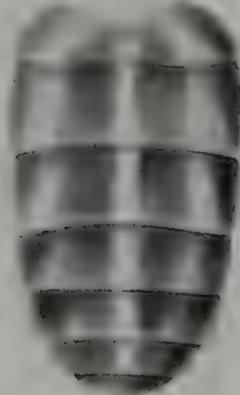
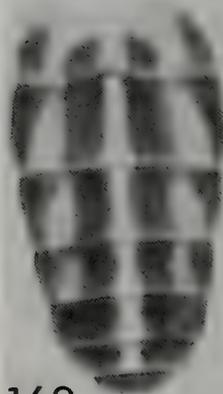
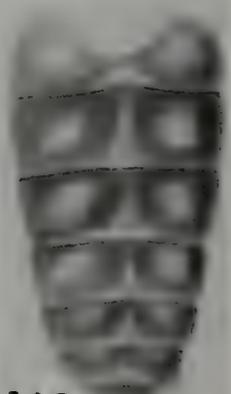
160 *calens*161 *lineola*162 *similis*163 *subsimilis*164 *quinquevittatus*165 *mularis*166 *fulvulus*167 *pallidescens*168 *sackeni*

Fig. 160-168.—Abdominal patterns. 160. *Tabanus calens*. 161. *T. lineola*. 162. *T. similis*. 163. *T. subsimilis*. 164. *T. quinquevittatus*. 165. *T. mularis*. 166. *T. fulvulus*. 167. *T. pallidescens*. 168. *T. sackeni*.



169 *sublongus*



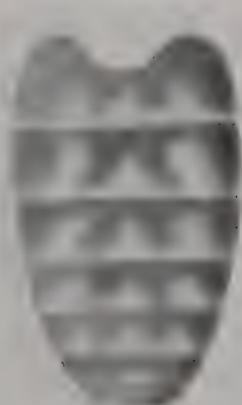
170 *trimaculatus*



171 *venustus*



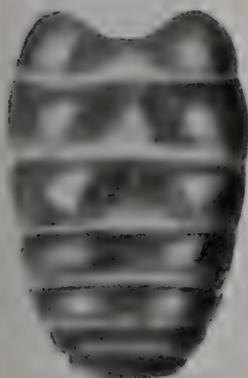
172 *cymatophorus*



173 *reinwardtii*



174 *pumillus*



175 *sparus sparus*



176 *fairchildi*



177 *marginalis*

Fig. 169–177.—Abdominal patterns. 169. *Tabanus sublongus*. 170. *T. trimaculatus*. 171. *T. venustus*. 172. *T. cymatophorus*. 173. *T. reinwardtii*. 174. *T. pumillus*. 175. *T. sparus sparus*. 176. *T. fairchildi*. 177. *T. marginalis*.

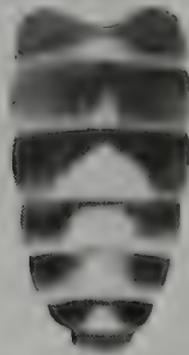
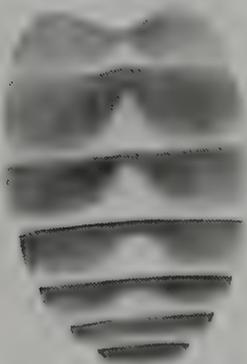
178 *superjumentarius*179 *molestus*180 *novaescotiae*181 *nigripes*182 *petiolatus*183 *melanocerus*184 *sulcifrons*185 *turbidus*186 *equalis*

Fig. 178-186.—Abdominal patterns. 178. *Tabanus superjumentarius*. 179. *T. molestus*. 180. *T. novaescotiae*. 181. *T. nigripes*. 182. *T. petiolatus*. 183. *T. melanocerus*. 184. *T. sulcifrons*. 185. *T. turbidus*. 186. *T. equalis*.

40. Fore tibiae unicolorous; median abdominal triangles obsolete, arising from faint posterior bands (Fig. 160)

.....**calens** (in part)

Fore tibiae bicolored; abdominal triangles small but distinct, not arising from bands (Fig. 180)

.....**novaesotiae**

41. Tibiae unicolorous, fore tibiae may be slightly paler at base; first posterior cell slightly or not at all narrowed at margin; subcallus thinly pollinose or denuded; usually under 15 mm

.....**nigripes**

At least fore tibiae bicolored; first posterior cell much narrowed, closed at margin or petiolate; subcallus pollinose; larger species, 15–19 mm.....42

42. Frons over 6 times as high as width at base; hind tibiae uniformly yellowish white, barely darkened at apex; second abdominal segment with median triangle usually crossing segment, joining spot on first segment (Fig. 182); first posterior cell usually closed, frequently petiolate

.....**petiolatus**

Frons less than 6 times as high as wide; hind tibiae often extensively dark toward apex; second abdominal segment with median triangle rarely crossing segment (Fig. 183); first posterior cell may be open or closed, rarely petiolate

.....**melanocerus**

43(38). Fore tibiae bicolored, basally pale with pale hair

.....44

Fore tibiae unicolorous, occasionally

base somewhat brownish with orange hair

.....45

44. Frons narrow (Fig. 189), 5 times or more as high as wide; first posterior cell normally petiolate, sometimes closed at margin

.....**limbatinevris**

Frons moderately wide (Fig. 187), averaging 4.5 times as high as wide; first posterior cell normally open although often narrowed at margin.....

.....**sulcifrons**

45. Costal cell yellow; frons 6 times as high as width at base, distinctly widened above; antennae usually wholly orange.....

.....**turbidus**

Costal cell hyaline or faintly tinted; frons about 4.5 times as high as wide, scarcely widened above; basal plate of third antennal segment partly black

.....**equalis**

Males¹

1. Eyes hairy

.....2

Eyes bare

.....7

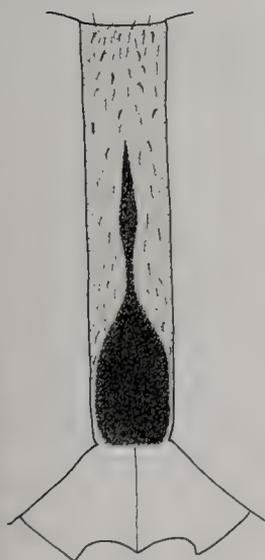
2. Upper eye facets considerably enlarged, occupying about three-fourths of total eye area; abdomen with parallel-sided median longitudinal stripe and similar more irregular sublateral stripes

.....**subsimilis subsimilis**

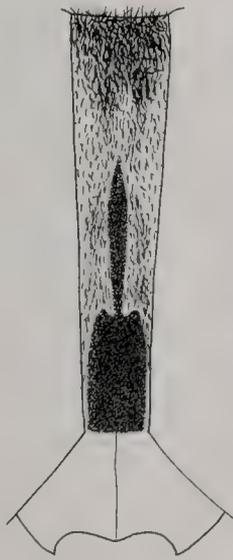
Eye facets all of one size or upper facets slightly enlarged; abdomen otherwise marked

.....3

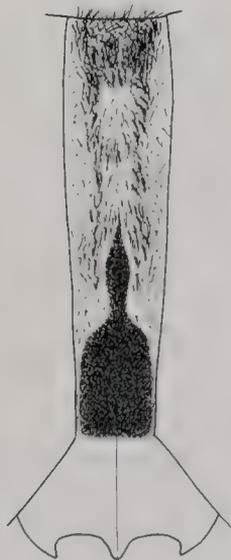
¹The male has not been recognized for *Tabanus longus*.



187 **sulcifrons**



188 **abdominalis**



189 **limbatinevris**

Fig. 187–189.—Frontes. 187. *Tabanus sulcifrons*. 188. *T. abdominalis*. 189. *T. limbatinevris*.

3. Bifurcation and crossveins of wing with distinct brown spots**reinwardtii**
No spots on wings4
4. All femora black; first antennal segment swollen above; hair on eyes sparse
Femora brown, sometimes with dusky shadows; first antennal segment not swollen; hair on eyes abundant5
5. Dorsal margin of occiput and vertex with dense fringe of white hair; palpi large and stout, less than twice as long as greatest thickness; pale median markings of abdomen obsolete
Dorsal margin of occiput and vertex with fringe of long dark hairs, recurved forward; palpi either very small or about 2.5 times as long as greatest thickness; pale median markings of abdomen distinct6
6. Basal plate of antennae rather slender, about 2 times as long as greatest width**quaesitus**
Basal plate broader, about 1.5 times as long as wide.....**exilipalpis**
- 7(1). Abdomen unicolorous or with narrow indistinct pollinose bands.....8
Abdomen with median markings14
8. Frontal triangle denuded and shining; third antennal segment with rather long tooth; black species with heavily infuscated wings**atratus atratus**
Frontal triangle pollinose, differs in at least one other character from the above.....9
9. Bifurcation without distinct spot10
Bifurcation with distinct spot or wing mostly black11
10. Wing dilutely infuscated, costal cell darker, hind tibial fringe black
Wing hyaline, costal cell deep yellow; hind tibial fringe orange**calens** (in part)
Wing dilutely infuscated**americanus**
11. Genae gray.....**proximus**
Genae brown to black12
12. Lower margin of area of large facets of eye somewhat sinuate, at lowest point about on level with top of antennal pits.....**subniger**
Lower margin of large facets more nearly straight, somewhat higher than antennal pits13
13. Integument of thoracic dorsum brown, contrasting with black abdomen; wing membrane, except for spots, rather uniformly dilutely infuscated.....**stygius**
Integument of thoracic dorsum dark brown to black, usually contrasting but slightly with black abdomen; apex of wing, except for spots, almost hyaline.....**nigrescens**
- 14(7). Abdomen broadly orange laterally with conspicuous black median spots; pale median spots absent or obsolete; large and small eye facets little differentiated; femora black; wings spotted, first posterior cell often narrowed at wing margin15
Abdomen with pale median markings; differs in at least one other character from the above.....16
15. Thorax with lavender tint, narrowly and inconspicuously striped; second palpal segment slender, 3 times as long as thick; all tibiae essentially unicolorous.....**gladiator**
Thorax brown, broadly and conspicuously striped; second palpal segment about twice as long as thick; all tibiae distinctly paler at base.....**abdominalis**
16. Abdomen with longitudinal stripe which may or may not be somewhat widened at posterior margins of segments17
Abdomen with median markings that do not form uninterrupted stripe.....26
17. Spots forming median abdominal stripe parallel sided; sublateral spots similar but often more irregular, rarely broken into roundish spots18
Median spots widened at posterior margin of each segment so that stripe not parallel sided; sublateral spots usually roundish.....21
18. Prescutal lobe usually paler than mesonotum; annulate portion of third antennal segment usually shorter than basal plate; costal cell usually hyaline19
Prescutal lobe usually concolorous with mesonotum; annulate portion of third antennal segment as long as or longer than basal plate; costal cell infuscated20
19. Scutellum and thorax dark gray to black, concolorous; hind femora usually dark.....**lineola**
Scutellum reddish, sometimes faintly, on posterior margin; hind femora usually reddish (if scutellum partly reddish, upper eye facets enlarged, and femora dark, see *subsimilis*, couplet 2.).....**similis**
20. Palpi and pleurae yellow pollinose
Palpi, face, and pleurae white or gray pollinose**mularis**
21. Upper eye facets not much larger than lower facets22
Upper eye facets much larger than lower facets.....23
22. Hair and pollen of face, mesonotum, and pleurae yellow.....**fulvulus**
Pollen of face and pleurae gray, hairs gray to pale yellow; hairs of mesono-

- tum mixed gray and black.....**wilsoni**
23. Third antennal segment entirely orange; long hairs on dorsum of thorax yellow**pallidescens**
Third antennal segment with at least annuli dark; long hairs on dorsum of thorax black to gray24
24. Costal cell hyaline; short recumbent hairs of thoracic dorsum gray; sublateral abdominal spots gray**sackeni**
Costal cell tinted; short hairs of thorax often yellowish; sublateral abdominal spots usually yellow or with yellowish tint.....25
25. Median abdominal stripe broad; face below eyes with many black hairs, beard yellowish white; second palpal segment stout, yellow brown with many black hairs**sagax**
Median abdominal stripe narrow; face with almost no black hairs, beard pale gray; second palpal segment relatively slender, pale yellowish white with few black hairs.....**sublongus**
- 26(16). Frontal triangle bare, somewhat protuberant; abdominal triangles sometimes indistinct; small chunky species usually under 13 mm**nigripes**
Frontal triangle pollinose.....27
27. Abdomen with median spots or triangles, at least some segments with sublateral spots28
Abdomen with median spots or triangles; no distinct sublateral spots although some segments may be paler laterally35
28. First antennal segment swollen above; third antennal segment entirely black; eyes sometimes with sparse hairs.....**fairchildi** (in part)
First antennal segment not swollen; third antennal segment variable; eyes bare.....29
29. Wing with distinct spots on bifurcation, crossveins or with irregular maculations30
Wing without spots although very faint spot may be present on bifurcation31
30. Wing with brown maculations not confined to bifurcation and crossveins; white bands of tergites 2-4 nearly obliterate median and sublateral spots but spots distinct on tergite 5.....**venustus**
Wing spots confined to bifurcation and crossveins; abdomen otherwise marked**cymatophorus**
31. Fore tibiae entirely black; sublateral abdominal spots very large, often crossing second and third segments; third antennal segment black**marginalis**
Fore tibiae paler at base; sublateral spots smaller; third antennal segment rarely entirely black32
32. Moderate-sized species, 14-15 mm; second palpal segment yellow brown, about twice as long as wide; median triangles fairly large, sometimes crossing segment; sublateral spots reach posterior margin on at least second segment; anterior portion of wing somewhat tinted.....**vivax**
Small species, usually under 11 mm; second palpal segment whitish, less than twice as long as thick; median triangles small, never crossing segment; sublateral spots small, rarely reaching posterior margins of segments; wing entirely hyaline.....33
33. Tibiae same color as reddish brown to brown femora or slightly paler basally; antennae yellowish, often with annulate portion somewhat darker; basal plate 2.5 to 3 times as long as wide; occipital tubercle prominent, often projecting above level of eyes**pumilus**
Tibiae distinctly paler than dark femora except apex of fore tibia, which is dark; antennae uniformly dull brownish; basal plate about twice as long as wide; occipital tubercle inconspicuous, compressed, usually not reaching level of eyes34
34. Eye in life without stripes**sparus sparus**
Eye in life with single purple stripe**sparus milleri**
- 35(27). Pale spot on second abdominal segment much smaller than those on third and fourth segments, or absent....36
Pale spot on second abdominal segment not markedly smaller than those on two following segments39
36. Abdomen blackish with large white triangles not arising from bands on tergites 3-5; fore tibiae bicolored**trimaculatus**
Without this combination of characters....37
37. Abdominal triangles very small, not arising from bands; scutellum concolorous with thorax; area of large eye facets occupies about half of total eye area, sharply demarcated.....**superjumentarius**
Abdominal triangles moderate in size, often arising from bands; scutellum white pollinose, contrasting with dark thorax; area of large facets occupies about two-thirds of total area, not sharply demarcated.....38
38. Face and cheeks gray pollinose; abdominal spots arise from pale bands, which may cover posterior half of third and fourth segments; venter with wide gray bands**molestus molestus**
Face and cheeks mostly brown pollinose; abdominal bands, if present, very narrow on dorsum and venter**molestus mixis**

39. No spot at bifurcation40
 Bifurcation with conspicuous spot43
40. Little differentiation in size of eye facets, line of demarcation indistinct; large species (over 20 mm) with very small median triangles, dark yellow legs and antennae**calens** (in part)
 Large eye facets distinctly set off from small facets; size not over 20 mm, usually less; third antennal segment at least partly dark41
41. Larger species (20 mm); abdomen with median black stripe on which pale median triangles superimposed; femora chestnut brown**novaesotiae**
 Smaller species (16–17 mm); pale median abdominal triangles not on black stripe; femora dark brown to black42
42. Median triangle crosses second abdominal segment; hind tibiae usually completely pale; large facets occupy about half of eye area**petiolatus**
 Median triangle does not cross second abdominal segment; hind tibiae darkened at apex; large eye facets occupy about two-thirds of total eye area**melanocerus**
43. Legs rather uniformly yellowish to dark brown, fore tibiae not paler at base44
 Legs with femora darker than tibiae, fore tibiae paler at base45
44. Third antennal segment usually wholly yellow; costal cell yellow, veins outlined in brown; upper eye facets much enlarged**turbidus**
 Third antennal segment partly black; costal cell hyaline or pale yellow, veins not at all or only vaguely outlined; upper eye facets only moderately enlarged**equalis**
45. Lower margin of upper eye facets straight or curved upward; first antennal segment yellow to brown; inner surface of hind tibia usually with many yellow hairs; first posterior cell clearly narrowed at wing margin.....**limbatinevris**
 Lower margin of upper eye facets usually curved downward, giving sinuate appearance or, if straight or curved upward, first antennal segment dark; inner surface of hind tibia mostly dark haired; first posterior cell rarely much narrowed at wing margin**sulcifrons**
- Respiratory spine absent6
3. Prothoracic annulus with single broad caudal projection laterally as if area between usual paired projections were filled with pubescence (Fig. 199, 200)....4
 Prothoracic annulus with 2 narrow caudal projections laterally (Fig. 201, 202)....5
4. Posterior pubescence present on all abdominal segments as well as metathorax; lateral club-shaped pubescent extension of posterior annulus on anal segment connected to pubescence on anal ridges (Fig. 199).....**stygius**
 Posterior pubescence present on no more than last 4 or 5 abdominal segments; lateral club-shaped pubescent extension of posterior annulus on anal segment separated from pubescence on anal ridges (Fig. 200)**proximus**
5. Posterior pubescent annulus on preanal segment with 4 rather long anterior projections laterally, dorsolateral projection connected to, or almost to, adjacent pubescent annulus bordering proleg; proleg pubescence extensive, extending between dorsal, lateral, and ventrolateral prolegs (Fig. 201)**gladiator**
 Dorsolateral projection anteriorly from posterior pubescent annulus or preanal segment well separated from adjacent proleg pubescence; proleg pubescence narrowly borders only prolegs, does not extend between dorsal, lateral, and ventrolateral prolegs (Fig. 202)**nigrescens**
6. Respiratory siphon about 4 times as long as its basal diameter; third antennal segment as long as second; posterior pubescence on anal segment forms dorsal patch, does not encircle segment (Fig. 191)**pumilus**
 Respiratory siphon no more than about twice as long as its basal diameter; third antennal segment shorter than second; posterior pubescence on anal segment, if present, not restricted to dorsal surface7
7. Prolegs relatively long, with strong apical crochets (Fig. 192); larvae live in fast-flowing streams**fairchildi**
 Prolegs lacking crochets8
8. Pubescence absent from first 7 abdominal segments, apart from normal proleg spination; respiratory siphon approximately twice as long as its basal diameter (Fig. 193–195).....9
 Pubescence present at least anteriorly on one or more of first 7 abdominal segments or, if pubescence faint and not easily seen, respiratory siphon less than twice as long as its basal diameter12
9. Pubescent markings usually restricted to small spot on each median lateral sur-

Key to Larvae of *Tabanus* and *Atylotus*

1. Pubescence covers entire body surface (Fig. 190); mature larvae approximately 50 mm long**americanus**
 Pubescence does not completely cover body, restricted to anterior or posterior margins or bordering prolegs on one or more segments, sometimes almost absent2
2. Respiratory spine present (Fig. 199–202).....3

- face of anal segment (Fig. 193), occasionally indistinct patches present on posterior margin of this segment and anterior margin of meso and metathorax.....**marginalis, vivax**
- Pubescence either absent or differently distributed on midlateral surface of anal segment, broadly encircling posterior margin of anal segment and sometimes present on lateral anterior margin of meso or metathorax or both.....10
10. Pubescent markings on midlateral surface of anal segment either in form of curved band extending between anal ridge pubescence and posterior annulus or as several small patches tracing such a route (Fig. 194).....11
- Midlateral surface of anal segment without pubescent markings (Fig. 195).....**nigripes**
11. Very closely spaced striations present only laterally on all abdominal segments.....**petiolatus**
- Striations absent from all aspects of first 7 abdominal segments (Fig. 194).....**melanocerus**
12. Midlateral surface of anal segment with at most 1 minute pubescent spot, often bare; respiratory siphon shorter than its basal diameter; anterior pubescence encircles none of abdominal segments (Fig. 196–198).....13
- Midlateral surface of anal segment with pubescent markings more extensive; respiratory siphon usually longer, but if short, anterior pubescence encircles first abdominal segment and usually more segments.....15
13. Narrow pubescent annulus encircles posterior margin of preanal segment; anterior margins of first 7 abdominal segments with progressively smaller areas of pubescence (Fig. 196, 197).....14
- Posterior pubescence absent from preanal segment; anterior pubescence on abdominal segments restricted to no more than first 2 segments (Fig. 198).....**sackeni**
14. Anterior pubescent annuli on pro- and mesothorax with caudal projections laterally extending two-thirds and one-half length of segments, respectively, (Fig. 197).....**molestus**
- Anterior pubescent annuli on pro- and mesothorax lacking or with very short caudal projections (Fig. 196).....**fulvulus, pallidescens, wilsoni**
15. All segments ornately marked with dark pubescence; anterior pubescence on meso- and metathorax and proleg pubescence on abdominal segments united laterally with posterior pubescence on same segment by 1–4 pairs of narrow pubescent bands; pubescent annuli border prolegs with short caudal projections middorsally (Fig. 203).....**atratus**
- Pattern and color of pubescence variable, but anterior and proleg pubescence not connected to posterior pubescence on same segment, no distinct caudal projections of proleg pubescence dorsally.....16
16. Prothoracic annulus with single broad caudal projection laterally, as if area between usual paired projections were filled with pubescence (Fig. 204–208).....17
- Prothoracic pubescent annulus with 2 caudal projections laterally (Fig. 209–218).....21
17. Anal segment and respiratory siphon each longer than its basal diameter.....18
- Anal segment and respiratory siphon each about equal in length to its basal diameter.....20
18. Posterior pubescence present only on anal and preanal segments and encircles these segments (Fig. 204).....**superjumentarius**
- Posterior pubescence encircles all abdominal segments.....19
19. Anal segment dorsolaterally with 4 patches of pubescence arranged in shape of reclining Y (Fig. 205).....**reinwardtii**
- Anal segment with only 2 patches of pubescence dorsolaterally (Fig. 206).....**trimaculatus**
20. Body creamy white; posterior pubescence encircles at least posterior 5 segments; midlateral surface of anal segment with dorsal extension of anal ridge pubescence curving posteriorly, almost reaching posterior pubescent annulus (Fig. 207).....**novaescotiae**
- Body light brown to beige; posterior pubescence encircles no more than posterior 4 segments; dorsal extension of anal ridge pubescence with short apical nipple directed toward but widely separated from posterior annulus (Fig. 208).....**lineola**
21. Pubescence laterally on anal segment comprising narrow dorsal extension of anal ridge pubescence with 2 caudal projections from it midlaterally and dorsolaterally and with no isolated pubescent spots (Fig. 213–216); length of respiratory siphon equal to or shorter than its basal diameter; striations usually complete on dorsal and ventral surfaces of abdominal segments.....22
- Pubescence, if present laterally on anal segment, does not form such a figure, usually with isolated pubescent spots; respiratory siphon usually longer than its basal diameter; striations usually incomplete on dorsal and ventral aspects of abdominal segments.....26

190 *americanus*191 *pumilus*192 *fairchildi*193 *marginalis*194 *melanocerus*195 *nigripes*196 *fulvulus*

Fig. 190-196.—Larvae. 190. *Tabanus americanus*. 191. *T. pumilus*. 192. *T. fairchildi*. 193. *T. marginalis*. 194. *T. melanocerus*. 195. *T. nigripes*. 196. *T. fulvulus*.

197 *molestus*198 *sackeni*199 *stygius*200 *proximus*201 *gladiator*202 *nigrescens*203 *atratus*

Fig. 197-203.—Larvae. 197. *Tabanus molestus*. 198. *T. sackeni*. 199. *T. stygius*. 200. *T. proximus*. 201. *T. gladiator*. 202. *T. nigrescens*. 203. *T. atratus*.

204 *superjumentarius*205 *reinwardtii*206 *trimaculatus*207 *novaescotiae*208 *lineola*209 *similis*210 *limbatinevris*

Fig. 204–210.—Larvae. 204. *Tabanus superjumentarius*. 205. *T. reinwardtii*. 206. *T. trimaculatus*. 207. *T. novaescotiae*. 208. *T. lineola*. 209. *T. similis*. 210. *T. limbatinevris*.

211 *sulcifrons*212 *calens*213 *quinquevittatus*214 *sparus*215 *thoracicus*216 *ohioensis*217 *woodi*

Fig. 211–217.—Larvae. 211. *Tabanus sulcifrons*. 212. *T. calens*. 213. *T. quinquevittatus*. 214. *T. sparus*. 215. *Atylotus thoracicus*. 216. *A. ohioensis*. 217. *A. woodi*.



218 bicolor

Fig. 218.—*Atylotus bicolor* larva.

22. Midlateral caudal projection from lateral pubescent figure on anal segment united with posterior annulus; mature larvae 12–15 mm long (Fig. 214)
*sparus*
 Midlateral caudal projection from lateral pubescent figure on anal segment separated from posterior annulus; mature larvae 16–25 mm long23
23. Posterior pubescence present on abdominal segments 2–8 and encircles last 3 or 4 segments (Fig. 215, 216)24
 Posterior pubescence present on abdominal segments 5–8 and usually encircles only last 2 segments (Fig. 213).....
*quinquevittatus*
24. Anterior pubescence on meso- and metathorax interrupted dorsally and ventrally (Fig. 217)*Atylotus woodi*
 Anterior pubescence encircles meso- and metathorax25
25. Pubescence pale; anterior pubescence encircles abdominal segments 1–7; caudal projections from prothoracic annulus slender and tapered (Fig. 215)*Atylotus thoracicus*
 Pubescence moderately dark; anterior pubescence encircles abdominal segments 1–5; lateral caudal projections from prothoracic annulus expanded posteriorly (Fig. 216)..*Atylotus ohioensis*
26. Posterior pubescence present on all abdominal segments, encircles at least last 4 segments27
 Posterior pubescence present on no more than last 4 segments, encircles no more than last 3 segments (Fig. 212, 218)29
27. Anal segment and respiratory siphon longer than their greatest diameters, latter about 1.5 times longer28
 Anal segment and respiratory siphon about equal in length to their greatest diameters (Fig. 209)
*similis, subsimilis*
28. Anterior pubescence encircles first 7 abdominal segments (Fig. 210).....
*limbatinevris*
 Anterior pubescence encircles first 3 or 4 abdominal segments (Fig. 211).....
*sulcifrons*
29. Posterior pubescence encircles last 3 abdominal segments; meso- and metathoracic annuli with caudal projections (Fig. 212)*calens*
 Posterior pubescence encircles only last 2 abdominal segments; meso- and metathoracic annuli lack slender caudal projections (Fig. 218)
*Atylotus bicolor*

Tabanus abdominalis Fabricius

Tabanus abdominalis Fabricius (1805:96).

Type-locality: Carolina.

Fairly large (20.75 mm); orange and black; frons very narrow, averaging slightly over six times as high as width at base, slightly widened above (Fig. 188); second palpal segment so densely covered with short black hair that segment appears black; wing tinted with dark spots and dark yellow costal cell; first posterior cell may be slightly open at margin, closed, or short petiolate; femora deep black with black hairs; tibiae orange at base, black toward apex; abdomen orange with black median spots, which may have indistinct pale triangles superimposed, or all spots may be nearly obsolete so entire abdomen appears orange; venter orange yellow. Male easily associated with female, except that first posterior cell moderately narrowed or wide open; upper eye facets only slightly differentiated from lower facets; eyes bare.

This species has had other species confused with it, and literature records should be used with caution. A discussion of the taxonomy of *T. abdominalis* may be found under *T. limbatinevris*.

The larva is unknown. The larva of *T. abdominalis* described by Goodwin (1973b) apparently is that of *T. limbatinevris*.

In Illinois adults appear in mid-July and have been collected until September.

T. abdominalis ranges from Texas to Florida and north to Virginia and Kentucky. In Illinois it has been collected only in the southern third of the state, and this seems to mark the northern extent of its range (Fig. 219).



Fig. 219.—Distribution of *Tabanus abdominalis* in Illinois and North America.

Tabanus americanus Forster

Tabanus americanus Forster (1771:100).

Type-locality: Virginia and New York.

Tabanus plumbeus Drury (1773:2). Type-

locality: Virginia and New York.

Tabanus ruficornis Fabricius (1775:789).

Type-locality: America.

Tabanus limbatus Palisot de Beauvois (1806:54). Type-locality: United States.

Large (24 mm); reddish brown; subcallus not denuded; palpi pale to reddish brown; eye bare; wing hyaline with dark brown costal cell; abdomen with narrow pale bands on hind margins of segments. Male eye facets distinctly differentiated; eyes bare.

This species is the largest horse fly in North America, sometimes reaching a length of 30 mm.

Larvae (Fig. 190) have been found

in decaying logs and along margins of ponds as well as in the moist areas of the forest floor (Tidwell 1973).

In Illinois adults appear in late June and have been collected until late July.

T. americanus is a southeastern species, extending from the southern tip of Florida to New Hampshire and west to eastern Texas (Fig. 220) with a disjunct, and possibly not permanent, distribution in southern Ontario and Michigan. In Illinois this species is only found in the southern third of the state (Fig. 220).



Fig. 220.—Distribution of *Tabanus americanus* in Illinois and North America.

Tabanus atratus atratus Fabricius

Tabanus atratus Fabricius (1775:789).

Type-locality: America.

Tabanus americanus Drury (1773:2).

Type-locality: New York.

Tabanus niger Palisot de Beauvois (1806:54). Type-locality: Pennsylvania.

Tabanus validus Wiedemann (1828:113).

Type-locality: Pennsylvania, Philadelphia.

Large (24 mm); black, subcallus denuded; eye bare; wing uniformly dark brown to black; abdomen some-

times with a whitish or bluish bloom. Male eye facets distinctly differentiated; eyes bare.

The eggs are laid on grass or leaves over marshy areas or streams and also on concrete bridge abutments. The larvae (Fig. 203), which can be found throughout the year, live in moist earth or in water and seem to tolerate a wide range of moisture conditions (Jones & Bradley 1923; Pechuman 1972; Teskey 1969; Tidwell 1973). The life cycle is usually completed in 1 year, but some individuals require 2 years and possibly more.

In Illinois adults appear in late May and have been collected until early September.



Fig. 221.—Distribution of *Tabanus atratus* in Illinois and North America.

T. atratus atratus is a widely distributed species, extending from the southern tip of Florida to Maine and west to North Dakota and into the north-eastern corner of Mexico (Fig. 221). In Illinois this species has been collected throughout the state (Fig. 221).

Tabanus calens Linnaeus

Tabanus calens Linnaeus (1758:601).

Type-locality: America.

Tabanus giganteus De Geer (1776:226).

Type-locality: Pennsylvania.

Tabanus lineatus Fabricius (1781:455).

Type-locality: America.

Tabanus pallidus Palisot de Beauvois (1809:100). Type-locality: United States.

Tabanus bicolor Macquart (1847:37).

Type-locality: South Carolina. Name preoccupied (Wiedemann 1821).

Tabanus coesiofasciatus Macquart (1855:52). Type-locality: Maryland, Baltimore.

Large (24 mm); subcallus not denuded; palpi pale to reddish brown; eyes bare; thorax brown with indistinct reddish lines; wing pale yellowish with costal cell darker; abdomen blackish, sometimes with faint, pale, median triangles (Fig. 160). Male eye facets show little differentiation and line of demarcation not distinct; pale median triangles of abdomen, when

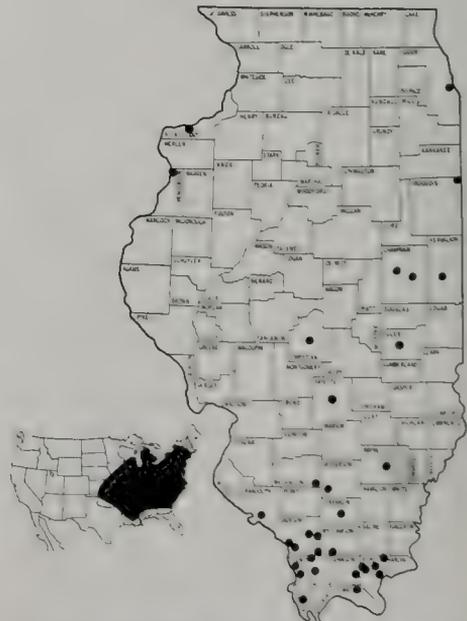


Fig. 222.—Distribution of *Tabanus calens* in Illinois and North America.

present, usually larger than in female; eyes bare.

This species name was unrecognized for many years, and generally was called *T. giganteus* De Geer. However, Linnaeus's name seems to be correctly associated with this species (Philip 1952).

Larvae (Fig. 212) have been collected in damp pasture sod (Teskey 1969).

In Illinois adults appear in mid-July and have been collected until mid-September. Although this species flies throughout the day, most activity is at dusk, when large numbers may suddenly appear and attack animals and humans. The males hover at dusk.

T. calens is an eastern and central species, extending from Georgia to Massachusetts and west to Arkansas (Fig. 222). In Illinois this species is collected throughout the state (Fig. 222).

Tabanus cymatophorus Osten Sacken

Tabanus cymatophorus Osten Sacken (1876:444). Type-locality: Kentucky, Mammoth Cave.
Rather large (19 mm); brownish gray

with three rows of abdominal spots, which are confluent along hind margins (Fig. 172); frons narrow, 4.5 times as high as wide; wings with brown spots on crossveins and bifurcation; pleural hairs and beard white. Male easily associated with female; upper eye facets enlarged, occupying about two-thirds of eye area, distinctly set off from small facets.

A larva (Jones & Bradley 1924) has been taken from the margins of a shallow pool.

In Illinois adults appear in early July and have been collected until late August.

T. cymatophorus is a southeastern species, extending from Mississippi to Maryland and west to Texas (Fig. 223). In Illinois this species has been collected only in the southern part of the state (Fig. 223).

Tabanus equalis Hine

Tabanus equalis Hine (1923:205). Type-locality: Kansas, Jackson County.

Tabanus uniformis Hine (1917:270). Type-locality: Kansas, Jackson County.
Name preoccupied (Ricardo 1911).

Large size (20 mm); brownish with rather faint wing spots on crossveins and bifurcation; costal cell hyaline or somewhat tinted; fore tibiae uniform in color; abdomen with median row of gray triangles, sometimes indistinct (Fig. 186). Male readily associated with female; upper eye facets moderately enlarged, cover about two-thirds of eye area.

Schomberg & Howell (1955) found the larvae to be terrestrial. They were present up to a depth of 10 cm in well drained, grass covered soil in the shade of trees. The adults are most abundant at dusk, and males hover at that time. Males have frequently been taken at lights at night.

In Illinois adults appear in mid-April and have been collected until late July.

T. equalis is a central species, extending from Louisiana to southern Indiana



Fig. 223.—Distribution of *Tabanus cymatophorus* in Illinois and North America.

and west to Kansas and Texas (Fig. 224). In Illinois this species is widespread in the southern two-thirds of the state (Fig. 224).

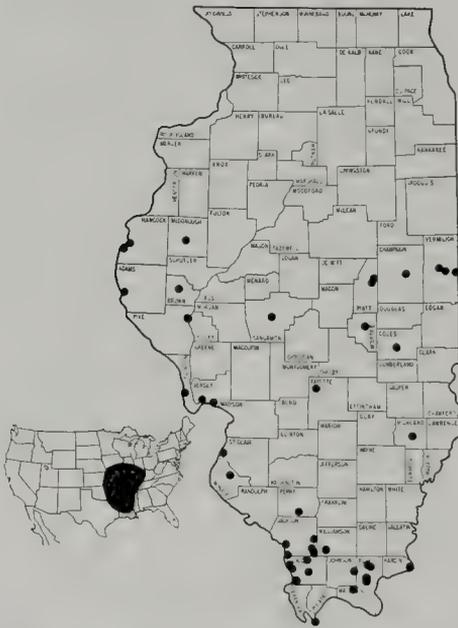


Fig. 224.—Distribution of *Tabanus equalis* in Illinois and North America.

Tabanus exilipalpis Stone

Tabanus exilipalpis Stone (1938:54). Type-locality: South Carolina, Beaufort.

Rather small (11.5 mm); eye with very short, sparse pile; palpi very slender, slightly thickened at base; basal plate of antenna rather broad with distinct angle; frons narrow, 4 times as high as width at base; beard white; wings hyaline, including costal cell; legs yellowish brown; abdomen dark brown with pale median stripe, which widens at apex of each segment, segments 2–5 with round pale sublateral spots. Male with densely pilose eyes; occipital border with long black hairs recurved anteriorly; eye facets essentially one size.

The hair on the eyes of females may easily be overlooked, but the combination of slender palpi, the median stripe on the abdomen, and rounded sublateral spots will separate this species from

most other species likely to be found in Illinois.

The larva and biology of this species are unknown.

T. exilipalpis is a central and southern species, extending from Alabama north to western Kentucky, apparently with a disjunct population along the coast of South Carolina (Fig. 225). As yet this species has not been collected in Illinois although specimens have been examined from western Kentucky.



Fig. 225.—Distribution of *Tabanus exilipalpis* in North America.

Tabanus fairchildi Stone

Tabanus fairchildi Stone (1938:63). Type-locality: New York, Taghkanic, near Ithaca.

Moderate size (14 mm); blackish brown; antennae black, with first segment swollen above; sides of subcallus with few hairs laterally; eyes bare or with short, scattered hairs; thorax does not strongly contrast with abdomen; wing hyaline; bifurcation of third longitudinal vein without a dark spot; abdomen with 3 rows of pale spots (Fig. 176). Male eye facets somewhat differentiated, but line of demarcation not distinct; eyes often with short, scattered hairs but sometimes apparently bare.

This species was long confused with *T. vivax*, and most references to that species before 1938 actually refer to *T. fairchildi*. It is not commonly netted in the field and does not seem to be a serious pest of livestock.

The larvae (Fig. 192) differ from most tabanids in that they occur in

swiftly flowing streams. The eggs are placed on projecting stones or logs in riffles, and often many females deposit their eggs on the same object, resulting in the accumulation of several hundred egg masses. The larvae are found under stones, often in the swiftest part of the stream. They probably pupate in mud on the edge of the stream (Pechuman 1972; Teskey 1969; Tidwell 1973). Tidwell (1973) also reports finding larvae beneath a layer of moss on a partially submerged log in a beaver dam.

In Illinois adults appear in early June and have been collected until late July.

T. fairchildi is a widespread species, extending from the panhandle of Florida to Maine and west to Kansas and Oklahoma (Fig. 226). This species has been collected only infrequently in Illinois.

Illinois Records.—Pope County, Herod, Lusk Creek; Vermilion County, Oakwood.



Fig. 226.—Distribution of *Tabanus fairchildi* in North America.

***Tabanus fulvulus* Wiedemann**

Tabanus fulvulus Wiedemann (1828:153).

Type-locality: America.

Tabanus fulvofrater Walker (1848:181).

Type-locality: Illinois.

Tabanus mutatus Walker (1850:23). Type-locality: United States.

Moderate size (14 mm); yellowish to orange; palpi yellow; frons very narrow and widened above; third antennal segment moderately broad, orange, annuli black; eyes bare; thoracic dorsum

without stripes; wing hyaline, costal cell colored; abdomen with yellow median line of large contiguous triangles and sublateral yellow spots (Fig. 166). Male eye facets differentiated but not markedly so; eyes bare.

Larvae (Fig. 196) have been taken from well drained, leaf covered soils of a mixed pine-hardwood forest in Louisiana (Tidwell & Tidwell 1973).

In Illinois adults appear in early June and have been collected until early September.

T. fulvulus is a southern and central species, extending from southern Florida to Long Island, New York and west to Wisconsin and Oklahoma (Fig. 227). In Illinois this species has been collected in the southern two-thirds of the state (Fig. 227).



Fig. 227.—Distribution of *Tabanus fulvulus* in Illinois and North America.

***Tabanus gladiator* Stone**

Tabanus gladiator Stone (1935:12). Type-locality: South Carolina, Charleston.

Large size (23 mm); orange brown with lavender thorax; frons very narrow, slightly widened above; palpi long, straplike, each with truncate apex; cos-

tal cell deep yellow, brown spots on crossveins and bifurcation; first posterior cell narrowed at margin; all femora black; abdomen orange brown, somewhat darker in center. Male easily associated with female; upper eye facets scarcely enlarged, line of demarcation indistinct; black median areas of abdomen more evident than in female.

Larvae (Fig. 201) have been collected in the upper 2 cm of mud and organic debris at the margins of small ponds or lakes (Goodwin 1973b).

T. gladiator is a southeastern species, extending from southern Florida to Maryland and west to eastern Texas (Fig. 228). As yet this species has not been collected in Illinois although specimens have been examined from western Kentucky.



Fig. 228.—Distribution of *Tabanus gladiator* in North America.

Tabanus limbatinevis Macquart

Tabanus limbatinevis Macquart (1847:32).

Type-locality: unknown (stated by Macquart to be Tasmania).

Tabanus abdominalis Osten Sacken (1876: 434), not Fabricius (1805:96). Misidentification.

Fairly large (19.5 mm); reddish brown; frons rather narrow, averaging $5\frac{1}{3}$ times as high as width at base, slightly widened above (Fig. 189); second palpal segment yellowish with short black hair; wing tinted, with dark spots and yellow costal cell; first posterior cell normally petiolate, occasionally closed at margin or narrowly open; femora black to brown, usually with mixture of black and yellow hairs; fore

tibiae pale yellow on basal one-third to one-half, balance of segment black or brown; middle and hind tibiae yellow, somewhat darker near apex; abdomen dull reddish brown with middorsal row of pale triangles; venter dark yellow with trace of dark median markings. Male lacks diagnostic characters of narrower frons and petiolate first posterior cell, which separate the female from *T. sulcifrons*; line of demarcation setting off larger upper eye facets straight or slopes slightly upward; in most *sulfifrons*, line sinuate and slopes downward before bending upward along lateral margins of eyes. A dark form of *T. sulcifrons* (which may be a distinct species) has eye structures similar to those of *limbatinevis*, but all I [Pechuman] have seen have the first two antennal segments dark brown or black rather than the yellow or yellow-brown of *limbatinevis*; also in this form the length of the second palpal segment is 2 to 2.37 times its greatest thickness, while in *limbatinevis* the length is 1.8 to 1.9 times the greatest thickness.

Tabanus limbatinevis has not been recognized as a distinct species since it was described. Macquart thought his specimen came from Tasmania, but Philip (1959:208) recognized the type in the British Museum (Natural History) as Nearctic and placed it as a synonym of *abdominalis* Fabricius. At the same time he mentioned that the two syntypes of *abdominalis* in the Paris Museum were the form "with bright orange abdomens and reduced median spots, plus closed cell R₅." This finding was confirmed by Osten Sacken (1878), who also saw Fabricius' types.

Earlier, however, Osten Sacken (1876) had redescribed as *abdominalis* a smaller, browner form. In 1878, apparently after seeing Fabricius' types, he stated that his original redescription was based on "a small and very abnormally colored specimen. . ." Through the kindness of Mrs. Margaret K. Thayer we were able to study Osten Sacken's material in the Museum of Comparative

Zoology. One specimen had a note on the pin in Osten Sacken's handwriting which said, "Specimen from which I made my first description of *T. abdominalis*. It is very doubtfully one; may be a *T. exul* with an adventitiously closed cell!" This specimen closely matches the type of *T. limbatinevris* kindly lent to us by Mr. J. E. Chainey of the British Museum (Natural History). Osten Sacken's other specimens from Kentucky on which his subsequent redescription of *abdominalis* was based (1878) are *abdominalis*.

For additional confirmation, we sent one specimen each of *limbatinevris* and *abdominalis* to Dr. L. Tsacas, Museum National d'Histoire Naturelle, Paris, for comparison with the types of *abdominalis*. In a number of characters, the specimen of the species we are calling *abdominalis* matched Fabricius' types. The type-specimen of *abdominalis* has the first posterior cell closed at the margin in the left wing and short petiolate in the right wing, according to Dr. Tsacas. The cooperation of Dr. Tsacas in this investigation is greatly appreciated.

Workers subsequent to Osten Sacken included *limbatinevris* with *abdominalis* or *sulcifrons*. Based on a number of specimens with his determination label, Stone (1938) placed *limbatinevris* with *sulcifrons*. Numerous specimens of the

three species involved were studied, and a summary of this study is given in Table 1.

The larvae (Fig. 210) described as *T. abdominalis* (Goodwin 1973b) have been collected along the margin of a slough in the upper 2–5 cm of mud just at the water line.

In Illinois adults appear in early July and have been collected until late August, with most collections in August.



Fig. 229.—Distribution of *Tabanus limbatinevris* in Illinois and North America.

Table 1.—Comparison of body length, frons ratio, and first posterior cell in *Tabanus abdominalis*, *T. limbatinevris*, and *T. sulcifrons*.

	Length ^a (mm)			Frons Ratio ^a			First Posterior Cell ^b (Percent)		
	Range	Median	Mean	Range	Median	Mean	Petiolate	Closed	Narrowly ^c Open
abdominalis	18.25–23.00	20.77	20.75	5.50–6.91	6.15	6.16	24	22.5	53.5
limbatinevris	15.6–22.00	19.6	19.4	4.50–6.56	5.33	5.35	91	5	4
sulcifrons	16.2–22.60	20.0	19.9	3.83–5.83	4.50	4.46	1.2	1	3.8 ^d

^aBased on 78 specimens each of *limbatinevris* and *sulcifrons* and 35 of *abdominalis*.

^bBased on 164 specimens of *limbatinevris*, 96 of *abdominalis*, and 547 of *sulcifrons*.

^c"Narrowly open" is defined as being narrowed to the extent that in most cases examination with a hand lens is necessary to determine if the cell is open or closed. Since the condition of the first posterior cell occasionally varies in a single specimen, these figures are based on a count of individual wings.

^dThe remaining 94 percent are somewhat narrowed or wide open.

The North American range of *T. limbata* is shown in Fig. 229. In New England it seems to be confined largely to coastal areas. It is rather widely distributed in Illinois (Fig. 229), but the bulk of the records are from the more southern counties.

***Tabanus lineola* Fabricius**

Tabanus lineola Fabricius (1794:369).

Type-locality: North America.

Moderate size (13 mm); yellowish, brown, or nearly black; frons narrow, distinctly widened above; median callosus slender; eyes bare; annulate portion of third antennal segment usually shorter than basal portion; scutellum entirely dark; prescutal lobes usually paler than mesonotum; wing hyaline; hind femora mostly dark; abdomen with pale median stripe and variable sublateral stripes (Fig. 161). Male eye facets distinctly differentiated; eyes bare.

Specimens collected in Illinois are generally of the melanistic form of this species.

Larvae (Fig. 208) have been collected from a wide variety of habitats,

including moist forest soil, margins of ponds and streams, wooded swamps, and bogs (Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults appear in early June and have been collected until mid-September.

T. lineola is a widespread east-central species, extending from Cuba to southern Quebec and west to South Dakota and southern Texas (Fig. 230). In Illinois this species is widespread throughout the state (Fig. 230).

***Tabanus marginalis* Fabricius**

Tabanus marginalis Fabricius (1805:99).

Type-locality: North America.

Tabanus nivosus Osten Sacken (1876: 445). Type-locality: New Jersey.

Moderate size (13 mm); blackish brown; first antennal segment not swollen above; sides of subcallus without hairs; eyes bare; wing hyaline; bifurcation of third longitudinal vein without brown spot; abdomen with three rows of pale spots, median row being much smaller than sublateral rows (Fig. 177). Male eye facets distinctly differentiated; sublateral abdominal spots of even



Fig. 230.—Distribution of *Tabanus lineola* in Illinois and North America.



Fig. 231.—Distribution of *Tabanus marginalis* in North America.

greater extent than those of female; eyes bare.

Larvae (Fig. 193) have been found in a wide range of saturated freshwater habitats (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early August.

T. marginalis is a northern species, extending from northeastern Georgia to Cape Breton, Nova Scotia, and west in a narrow band to British Columbia and Colorado (Fig. 231). This species has been collected only once in Illinois in 1906.

Illinois Records.—Lake County, Sun Lake.

Tabanus melanocerus Wiedemann

Tabanus melanocerus Wiedemann (1828:122). Type-locality: Kentucky.

Moderate size (17 mm); dark brown to blackish; subcallus pollinose; eyes bare; thorax does not contrast strongly with abdomen; wing hyaline or tinged faintly yellowish, costal cell sometimes yellow; first posterior cell much narrowed, sometimes closed at wing margin; bifurcation of third longitudinal vein without brown spot; fore tibiae pale, dark at apex; abdomen with median row of pale triangles and tergites with narrow, sometimes obsolete, pale bands on hind margins (Fig. 183). Male eye facets distinctly differentiated; eyes bare.

Larvae (Fig. 194) have been taken from mud and organic debris at the edges of streams, ditches, and lakes



Fig. 232.—Distribution of *Tabanus melanocerus* in North America.

(Pechuman 1972; Teskey 1969; Tidwell 1973).

T. melanocerus is a southern and eastern species, extending from southern Florida to Massachusetts and west to Oklahoma and Texas (Fig. 232). As yet this species has not been collected in Illinois although specimens have been examined from western Kentucky.

Tabanus molestus molestus Say

Tabanus molestus molestus Say (1823:31).

Type-locality: Missouri.

Atylotus tenessensis Bigot (1892:660).

Type-locality: Tennessee.

Fairly large (19 mm); dark brown with dorsum of thorax, including scutellum, white pollinose except for small dark spot just anterior of scutellum; legs rather uniformly dark brown; wing spots on crossveins and bifurcation distinct but rather faint; pale median spot on second tergite smaller than those on tergites 3 and 4 (Fig. 179). Male eye facets enlarged, sharply set off; dorsum of thorax dark brown except scutellum, which is white haired and pollinose as in female; abdomen with median triangles expand-

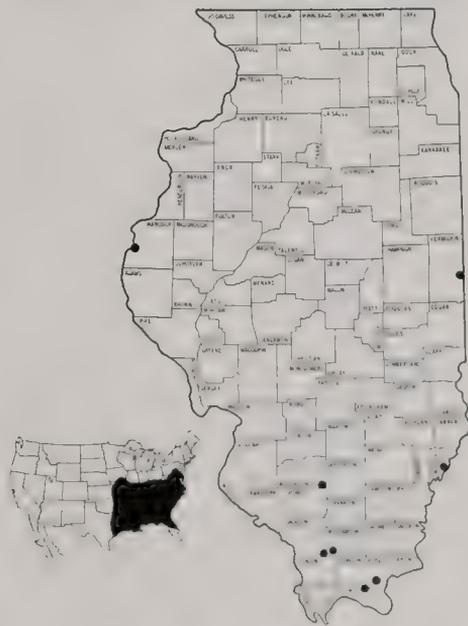


Fig. 233.—Distribution of *Tabanus molestus molestus* in Illinois and North America.

ed more extensively laterally than in female.

Tidwell (1973) found the larvae (Fig. 197) beneath moss on banks of streams well above the high-water mark, and Thompson et al. (1978) report a larva from the shoreline of a slough.

In Illinois adults appear in early June and have been collected until late August.

T. molestus molestus is a southeastern subspecies, extending from central Florida to New York and west to Iowa and eastern Texas (Fig. 233). This subspecies has been collected infrequently in the southern half of Illinois (Fig. 233).

Tabanus mularis Stone

Tabanus mularis Stone (1935:15). Type-locality: Louisiana, Baton Rouge.

Rather small (11 mm); palpi, cheeks, and beard white; costal cell dark yellow to brown, rest of wing hyaline; abdomen blackish with yellow median parallel sided stripe, indefinite orange brown near lateral margins of tergites. Male colored essentially like female; upper eye facets enlarged, line of demarcation distinct.

The larva of this species has not been recognized. See the discussion under *Tabanus quinquevittatus*.

In Illinois adults appear in mid-June and have been collected until mid-August.

T. mularis is a central and southeastern species, extending from the panhandle of Florida to Maryland and west to Missouri and eastern Texas (Fig. 234). In Illinois this species has been collected in the southern two-thirds of the state (Fig. 234).

Tabanus nigrescens Palisot de Beauvois

Tabanus nigrescens Palisot de Beauvois (1809:100). Type-locality: United States.

Large size (22 mm); black; subcallus not denuded; palpi dark brown to black; facial setae black; eyes bare; mesonotum dark brown; wing pale yellowish with dark spots, dark costal cell, deeper color in basal cells and base of discal cell. Male eye facets distinctly differentiated; thorax often with brownish tinge; eyes bare.

Larvae (Fig. 202) have been collected from the margin of a beaver pond (Tidwell 1973) and from mud on edges of marshes, lakes, and small woodland streams (Goodwin 1973b).

In Illinois adults appear in late July.

T. nigrescens is a widespread eastern species, extending from Georgia to Massachusetts and west to Minnesota and Louisiana (Fig. 235). This species has been collected only twice in Illinois.

Illinois Records.—Cook County, Willow Springs; Vermilion County, Forest



Fig. 234.—Distribution of *Tabanus mularis* in Illinois and North America.



Fig. 235.—Distribution of *Tabanus nigrescens* in North America.

Glen Forest Preserve (5 miles SE Westville).

Tabanus nigripes Wiedemann

Tabanus nigripes Wiedemann (1821:25).

Type-locality: Georgia, Savannah.

Tabanus coffeatus Macquart (1847:39).

Type-locality: Pennsylvania, Philadelphia.

Small to moderate size (12 mm); blackish brown; subcallus thinly pollinose or partly denuded; eyes bare; thorax does not contrast strongly with abdomen; wings hyaline, occasionally with traces of spots and yellow costal cell; first posterior cell slightly or not at all narrowed at margin; bifurcation of third longitudinal vein without brown spot; tibiae unicolorous although fore tibiae may be slightly paler at base; abdomen with median row of pale triangles, tergites with narrow pale bands on hind margins (Fig. 181). Male eye facets distinctly differentiated; frontal triangle prominent, denuded; eyes bare.

Larvae (Fig. 195) have been found in acidic sphagnum bogs and boglike areas (Teskey 1969) and at the margin of a small pond in a mixed pine-hardwood region (Tidwell 1973).

T. nigripes is a widespread central and eastern species, extending from southern Florida to New Hampshire and west to Minnesota and the panhandle of Texas (Fig. 236). This species has been collected only once in Illinois.

Illinois Records.—McHenry County, Algonquin.



Fig. 236.—Distribution of *Tabanus nigripes* in North America.

Tabanus novaescotiae Macquart

Tabanus novae-scotiae Macquart (1847: 40). Type-locality: Nova Scotia.

Tabanus actaeon Osten Sacken (1876: 443). Type-locality: Massachusetts (lectotype).

Fairly large size (20 mm); reddish brown with thorax sometimes fuscous; eyes bare; thorax does not strongly contrast with abdomen; wing hyaline or faintly tinged with yellow, especially in costal cell; bifurcation of third longitudinal vein without brown spot; basal half of fore tibia yellowish; abdomen with median dark longitudinal band, which may be broad and distinct or nearly obsolete, and median row of pale triangles (Fig. 180). Male eye facets distinctly differentiated; eyes bare.

For many years this species went under the name *Tabanus actaeon*, and much of the older literature is under this name.

Larvae (Fig. 207) have been found in sphagnum moss (Teskey & Burger 1976).

In Illinois adults appear in early September.

T. novaescotiae is a northeastern species, extending from the mountains



Fig. 237.—Distribution of *Tabanus novaescotiae* in North America.

of Virginia and West Virginia to Cape Breton, Nova Scotia and west to Minnesota (Fig. 237). This species has been collected only once in Illinois.

Illinois Records.—Lake County, 2 miles NW Fox Lake.

Tabanus orbicallus Philip

Tabanus orbicallus Philip (1936a:157).

Type-locality: Kansas, Gove County.

Moderate size (14 mm); grayish; eye hair short, sometimes indistinct; frons broad, widened above; legs rather uniformly yellow; wings, including costal cell, hyaline; median line of abdomen with dark band, on which are poorly indicated pale triangles, yellow-brown area on each side of median band. Male eyes densely pilose; upper eye facets only slightly enlarged; abdomen much like that of female, but yellow-brown area less extensive.

The larva and biology of this species are unknown.

T. orbicallus is a west-central species, extending from western Illinois to South Dakota and Kansas (Fig. 238) with a disjunct record of a specimen from Indiana.

Illinois Records.—Henderson County, Big River State Park (4 miles S Keithsburg).



Fig. 238.—Distribution of *Tabanus orbicallus* in North America.

Tabanus pallidescens Philip

Tabanus pallidescens Philip (1936b:150).

Type-locality: Mississippi, Blue Mountain.

Moderate size (14 mm); yellowish; frons very narrow, widened above; antennae yellow, annulate portion some-

times a little darker, basal plate broad; palpi white or pale yellow; beard, pleura white haired; legs uniformly yellow, hind femora sometimes with darker shadows; median stripe of abdomen with series of contiguous triangles (Fig. 167). Male readily associated with female; basal plate narrower than in female; upper eye facets much enlarged, occupying two-thirds of eye area, sharply set off from small lower facets.

The larvae (as in *fulvulus*, Fig. 196) have been taken from well drained leaf covered soils and from ruts in an old logging road in a mixed pine-hardwood forest in Louisiana (Tidwell & Tidwell 1973).

In Illinois adults appear in early June and have been collected until early August.

T. pallidescens is a southeastern species, extending from northern Florida to southern New Jersey and west to Kansas and eastern Texas (Fig. 239). This species has been collected infrequently in the southern half of Illinois (Fig. 239).



Fig. 239.—Distribution of *Tabanus pallidescens* in Illinois and North America.

Tabanus petiolatus Hine

Tabanus petiolatus Hine (1917:270). Type-locality: Louisiana, Lecompte.

Tabanus yulenus Philip (1950b:243).

Type-locality: Louisiana, Triumph.

Moderate size (16 mm); brownish; frons very narrow, slightly widened above; first posterior cell usually petiolate, sometimes closed or, rarely, narrowly open; fore tibiae bicolored; hind tibiae pale yellow, slightly darkened at extreme apex; abdomen with conspicuous row of pale triangles, which usually cross each segment; on tergite 2 pale triangle expanded anteriorly, joins pale spot on tergite 1 to form hourglass shaped marking (Fig. 182). Male similar to female, but first posterior cell narrowly open; upper eye facets enlarged, line of demarcation distinct.

Larvae have been collected in leaf mold on the banks of a stream and in moss (Teskey 1969).

In Illinois adults appear in late August.

T. petiolatus is a southeastern species, extending from southern Florida to New Jersey and west to southern Illinois and eastern Texas (Fig. 240). This species has been collected only once in Illinois.

Illinois Records.—Johnson County, Little Black Slough Nature Preserve (4 miles SW Vienna).



Fig. 240.—Distribution of *Tabanus petiolatus* in North America.

Tabanus proximus Walker

Tabanus proximus Walker (1848:147).

Type-locality: United States, St. Louis.

Tabanus benedictus Whitney (1904:206).

Type-locality: Missouri, Pike County.

Large size (24 mm); blackish brown with whitish bloom on unicolorous abdomen; frons very narrow, slightly widened above; face, cheeks gray pollinose; antennae orange; palpi dark brown; wing with yellowish tint, costal cell much darker yellow, bifurcation and crossveins with dark spots; first posterior cell narrowly open or closed. Male similar to female; first posterior cell open; upper eye facets enlarged with line of demarcation distinct; small facets extend in band around margin of eye to vertex.

Larvae (Fig. 200) have been collected most often terrestrially in the moist floodplain soils of large rivers (Tidwell 1973) or from the margin of a slough (Jones & Bradley 1924). Schwardt (1936) found egg masses on tree leaves over a moist pasture and at the border of a small swamp.

In Illinois adults appear in mid-July and have been collected until early September.

T. proximus is a central and southern species, extending from the panhan-



Fig. 241.—Distribution of *Tabanus proximus* in Illinois and North America.

dle of Florida to Maryland and west to Illinois and eastern Texas (Fig. 241). In Illinois this species has been collected from the western and southern parts of the state (Fig. 241).

Tabanus pumilus Macquart

Tabanus pumilus Macquart (1838:150).
Type-locality: Carolina.

Small size (9.5 mm); dark brown to grayish black; median callus subquadrate; second palpal segment rather slender, apex not sharply pointed; frons somewhat widened above; eyes bare; wing hyaline; thorax does not contrast strongly with abdomen, abdomen with row of faint median triangles, roundish sublateral spots (Fig. 174). Male eye facets distinctly differentiated; occipital tubercle conspicuous; eyes bare.

Larvae (Fig. 191) have been collected from saturated, highly or totally organic habitats in bogs and swamps and along streams (Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults appear in mid-May and have been collected until mid-July.

T. pumilus is an eastern and southern species, extending from central Florida to Maine and west to Iowa and

eastern Texas (Fig. 242). This species is widespread throughout Illinois (Fig. 242).

Tabanus quinquevittatus Wiedemann

Tabanus quinquevittatus Wiedemann (1821:34). Type-locality: Georgia, Savannah.

Tabanus costalis Wiedemann (1828:173).
Type-locality: Kentucky.

Tabanus vicarius Walker (in part) (1848:187). Type-locality: North America.

Tabanus manifestus Walker (1850:41).
Type-locality: unknown.

Tabanus baltimorensis Macquart (1855:54).
Type-locality: Maryland, Baltimore.

Moderate size (12.5 mm); yellowish; frons with sides essentially parallel; pollen on head yellow; palpi yellow; annulate portion of third antennal segment usually longer than basal portion; eyes bare, in life with single purple band; thorax bright yellow pollinose; prescutal lobe concolorous with rest of mesonotum; wing hyaline with dark yellow costal cell; abdomen with yellow median stripe bordered with black, lateral margins usually yellowish (Fig. 164). Male eye facets distinctly differentiated; eyes bare.

This species is referred to in much of the earlier literature as *T. costalis* and less extensively as *T. vicarius*. It can be distinguished from related species by the yellowish color, which includes the palpi and pleurae, and by the deep yellow tint of the costal cell.

Schwardt (1936) obtained numerous egg masses in the laboratory from what he called *Tabanus costalis* Wiedemann. The egg masses were of two kinds, probably indicating a difference in egg mass form of two species, since his reared specimens were a mixture of *T. mularis* and *T. quinquevittatus*. He noted that the larvae were not cannibalistic, as were those of other species with which he was working, and suggested that this was part of the reason the adults were so numerous. Presumably his comments apply to both species.

Larvae (Fig. 213), unlike those of most species of Tabanidae, are usually

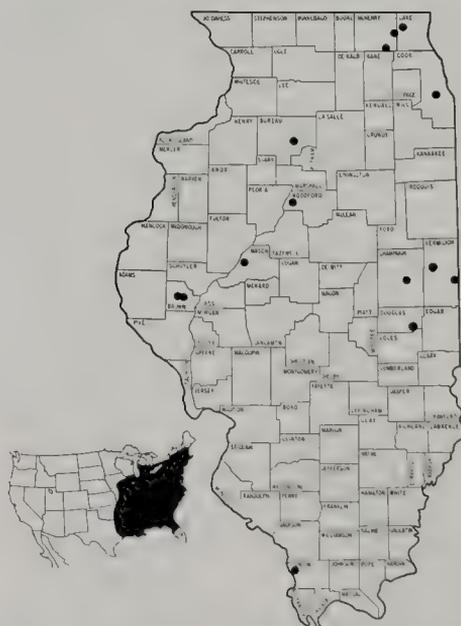


Fig. 242.—Distribution of *Tabanus pumilus* in Illinois and North America.

found in relatively dry situations. Moist, but not wet, pastures and hayfields seem to be preferred, but larvae must have considerable tolerance to variations in moisture, since they have been collected in dry, cultivated fields and in mud along the margins of brooks (Pechuman 1972; Teskey 1969). The large populations of this species probably result from this ability to breed in diverse situations.

In Illinois adults appear at the first of July and have been collected until early September.

T. quinquevittatus is a widespread central and eastern species, extending from the southern tip of Florida to southern Quebec and west to Colorado (Fig. 243). This species is widespread throughout all of Illinois (Fig. 243).



Fig. 243.—Distribution of *Tabanus quinquevittatus* in Illinois and North America.

Tabanus reinwardtii Wiedemann

Tabanus reinwardtii Wiedemann (1828: 130). Type-locality: Pennsylvania.

Tabanus erythrotelus Walker (1850:25).

Type-locality: North America.

Moderate size (17 mm); grayish black; basal callus large and shining; frons broad and essentially parallel sided; eyes bare or with short, scattered hairs;

thorax does not strongly contrast with abdomen; wing spotted with brown; bifurcation of third longitudinal vein with brown spot; abdomen with gray median triangles, larger pale sublateral spots (Fig. 173). Male eye facets somewhat differentiated, but line of demarcation not distinct; eyes hairy.

Larvae (Fig. 205) are found in mud along streams and ponds, usually in situations where the water is cool and the area shaded (Pechuman 1972; Teskey 1969; Tidwell 1973).

In Illinois adults appear in early July and have been collected until mid-August.

T. reinwardtii is a northern species, extending from northern Georgia to southern Quebec and west to Montana and Alberta (Fig. 244) with a disjunct population on Cape Breton, Nova Scotia. In Illinois this species has been collected widely over the northern half of the state (Fig. 244).



Fig. 244.—Distribution of *Tabanus reinwardtii* in Illinois and North America.

Tabanus sackeni Fairchild

Tabanus sackeni Fairchild (1934:141). Type-locality: Kentucky, Cumberland Gap.

Moderate size (13.5 mm); brownish; frons narrow, widened above; palpi white; third antennal segment very slender; eyes bare; wing hyaline; abdomen with pale median line of contiguous triangles and pale sublateral spots, which rarely reach hind margins of tergites (Fig. 168). Male eye facets distinctly differentiated; pale sublateral spots often reach hind margins of tergites; eyes bare.

This species is crepuscular and probably nocturnal as well; many individuals of both sexes have been collected at light. Nothing is known of its biology.

Larvae (Fig. 198) have been collected 10–15 cm deep in well drained soil on a hillside in a hardwood forest in Arkansas (Goodwin 1976b).

In Illinois adults appear in late June and have been collected until late September.

T. sackeni is a northeastern species, extending from Georgia to New Hampshire and west to Kansas and Arkansas (Fig. 245). This species has been collected in southern Illinois and in a band across north-central Illinois (Fig. 245).



Fig. 245.—Distribution of *Tabanus sackeni* in Illinois and North America.

Tabanus sagax Osten Sacken

Tabanus sagax Osten Sacken (1876:452).

Type-locality: Illinois (lectotype).

Atylotus baal Townsend (1895:58). Type-locality: Virginia, Dixie Landing.

Tabanus dawsoni Philip (1931:105). Type-locality: Minnesota, Itasca Park.

Moderate size (14 mm); orange brown; frons parallel sided, quite broad; third antennal segment variable but usually slender, dark orange with annuli black; second palpal segment swollen; eyes bare; wing hyaline; abdomen with median line of contiguous triangles, rather indistinct sublateral spots. Male eye facets distinctly differentiated; eyes bare.

This species is rather uncommon throughout its range, and it may be a crepuscular species like *T. sackeni*.

The larvae and biology of this species are unknown.

In Illinois adults appear at the end of July and have been collected until mid-September.

T. sagax is an eastern species, extending from North Carolina to Massachusetts and west to Minnesota and Missouri (Fig. 246). This species has only been collected three times in Illinois from the northern part of the state.

Illinois Records.—Carroll County, Savanna; Lake County, Fox Lake; McHenry County, Algonquin.



Fig. 246.—Distribution of *Tabanus sagax* in North America.

Tabanus similis Macquart

Tabanus similis Macquart (1850:335).

Type-locality: unknown (stated by Macquart to be Tasmania).

Tabanus scutellaris Walker (1850:27).

Type-locality: North America.

Moderate size (13 mm); brownish to almost black; frons rather broad, widened above; median callus somewhat broadened; eyes bare; annulate portion of third antennal segment usually shorter than basal portion; scutellum reddish brown at tip; wing hyaline; prescutal lobe usually paler than mesonotum; hind femora reddish; abdomen with pale median stripe and sublateral stripes (Fig. 162). Male eye facets differentiated, but size difference small, line of demarcation often indistinct; general color usually brownish; eyes normally bare, sometimes with few scattered hairs.

Larvae (Fig. 209) have been found in a variety of semiaquatic habitats along streams and ponds and at the edges of marshes and bogs. They are also found in damp sod and relatively dry agricultural land; this terrestrial environment may be this species' more common habitat (Pechuman 1972).

In Illinois adults appear in mid-May and have been collected until mid-August.

T. similis is a widespread species, extending from New Jersey to Nova Scotia and west to British Columbia and California (Fig. 247). In Illinois this species is found throughout the state (Fig. 247).

***Tabanus sparus sparus* Whitney**

Tabanus sparus sparus Whitney (1879:38).

Type-locality: New Hampshire, Milford.

Small size (10 mm); grayish black; median callus very narrow; second palpal segment swollen at base and sharply pointed; frons narrow, widened above; eyes bare, unicolorous in life; thorax does not strongly contrast with abdomen; wing hyaline; abdomen with row of small median triangles and oval sublateral spots, which often reach hind margins of segments (Fig. 175). Male eye facets distinctly differentiated; occipital tubercle inconspicuous, usually laterally compressed; eyes bare.

Larvae (Fig. 214) have been collected from cranberry bogs and along the boggy margins of streams (Teskey 1969).

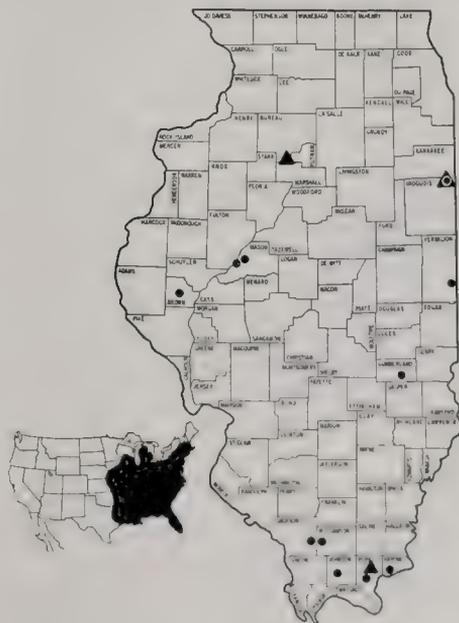


Fig. 247.—Distribution of *Tabanus similis* in Illinois and North America.

Fig. 248.—Distribution of *Tabanus sparus sparus* (triangles) and *T. sparus milleri* (circles) in Illinois and North America.

In Illinois adults appear in mid-June and have been collected until late July.

T. sparus (including the subspecies *sparus* and *milleri*) is a widespread eastern species, extending from the tip of Florida to New Hampshire and west to Wisconsin, Kansas, and eastern Texas (Fig. 248). This subspecies has been collected only twice in Illinois. However, the record from Pope County is doubtful, as it is based on a dried specimen on which no eye bands were evident when it was relaxed.

Illinois Records.—Iroquois County, Iroquois County Conservation Area (4 miles NE Beaverville); Pope County, Lusk Creek.

Tabanus sparus milleri Whitney

Tabanus sparus milleri Whitney (1914: 344). Type-locality: Florida.

No characters have been found to separate dried specimens of this subspecies from *T. sparus sparus*. However, living specimens and dried specimens which have been moistened have a diagonal purple band on the eye, whereas in *T. sparus sparus* the eye has no band. The similar-appearing *T. pumilus* has two diagonal bands across the eye in life.

The larvae have been collected in matted roots of grasses and in muck at the edge of a pond (Hays & Tidwell 1967).

In Illinois adults appear in early June and have been collected until late July.

The Nearctic distribution of this subspecies is included within the distribution of *T. sparus* (Fig. 248). In Illinois this subspecies has been collected widely in the southern half of the state (Fig. 248).

Tabanus stygius Say

Tabanus stygius Say (1823:33). Type-locality: Arkansas.

Large species (22 mm); frons brown, rather narrow; palpi dark brown to black; subcallus not denuded; eyes bare; thorax with grayish white pile; wing yellowish with dark spots; costal cell

deep yellow; abdomen black. Male eye facets distinctly differentiated; pile of thorax dark brown; third antennal segment dark orange; eyes bare.

The egg masses are laid on aquatic plants, chiefly *Sagittaria*, growing in shallow water. The larvae (Fig. 199) are found in muddy banks of ponds and streams (Pechuman 1972; Teskey 1969; Tidwell 1973), and Wilson (1969) reports finding larvae in a relatively dry forest floor in Louisiana. It often takes 2 years for this species to complete its life cycle.

In Illinois adults appear in early June and have been collected until early August.

T. stygius is a widespread eastern species, extending from southern Florida to Maine and west to Colorado and eastern Texas (Fig. 249). Although infrequently collected in Illinois, this species is found throughout the state (Fig. 249).



Fig. 249.—Distribution of *Tabanus stygius* in Illinois and North America.

Tabanus sublongus Stone

Tabanus sublongus Stone (1938:74). Type-locality: Maryland, Plummer Island.

Moderate size (13 mm); dark orange brown; third antennal segment moderately slender; second palpal segment not very swollen basally; frons about four times as high as width at base, parallel sided; eyes bare; wing hyaline; abdomen with median line of contiguous pale triangles, grayish yellow to orange sublateral spots, which usually reach hind margins of segments (Fig. 169). Male eye facets distinctly differentiated; eyes bare.

The larva and biology of this species are unknown.

In Illinois adults appear at the beginning of July and have been collected until early September.

T. sublongus is a central and eastern species, extending from Georgia to New York and west to Kansas and eastern Texas (Fig. 250). Although infrequently collected in Illinois, this species is fairly widespread throughout the state (Fig. 250).



Fig. 250.—Distribution of *Tabanus sublongus* in Illinois and North America.

***Tabanus subniger* Coquillett**

Tabanus subniger Coquillett (1906:48).
Type-locality: Illinois, Lake Forest.

Tabanus nigricans Johannsen (1935:15), not Wiedemann (1828:157). Misidentification.

Large species (23 mm); frons broad, gray, narrowed above, notched at vertex; palpi dark brown to black; subcallus not denuded; eye bare; thorax with grayish white pile; wings pale yellowish with dark spots, costal cell yellow; abdomen black. Male eye facets distinctly differentiated; pile of thorax dark brown; third antennal segment dark brown or black; eyes bare.

This large species superficially resembles *T. stygius*, but is easily distinguished by the characters given in the key.

A single larva of this species was taken from a pond at Ithaca, New York. The larva and pupa of this specimen are keyed by Johannsen (1935) to *Tabanus nigricans*.

In Illinois adults have only been collected from late June to early July.

In spite of its large size and conspicuous appearance, *T. subniger* is a rarely collected northeastern species, extending from New Jersey to New York and west to Illinois (Fig. 251). This species has been collected twice in northeastern Illinois.

Illinois Records.—Cook County, Stickney; Lake County, Lake Forest.



Fig. 251.—Distribution of *Tabanus subniger* in North America.

***Tabanus subsimilis* Bellardi**

Tabanus subsimilis Bellardi (1859:66).
Type-locality: Mexico.
Tabanus vittiger schwardti Philip (1942:29).
Type-locality: Tennessee, Knoxville.

Moderate size (14 mm); dark brown to blackish; frons rather broad, usually slightly bowed in center, slightly widened above; eyes bare; wings hyaline; scutellum reddish at tip, sometimes obscurely so; coxae, fore and hind femora blackish; middle femora and occasionally other femora may be somewhat paler toward apex; abdomen with median and sublateral stripes, latter rather irregular, offset between tergites 2 and 3 (Fig. 163). Male with upper eye facets enlarged, distinctly set off from lower small facets, occupying almost three-fourths of total eye area; eyes hairy.

The larvae have been found in mud along the edges of streams and ponds and in seepage areas (Pechuman 1973). Thompson (1975) found the larvae in compost, flower beds, and lawn turf and suggests that this is an adaptive species, which may breed predominately in upland situations.

In Illinois adults appear in early May and have been collected until mid-October. This is the longest period of emergence observed for an Illinois species, suggesting the possibility of more than one generation per year.



Fig. 252.—Distribution of *Tabanus subsimilis* in Illinois and North America.

T. subsimilis is a widespread species, extending from southern Mexico to New Jersey and west to southern California (Fig. 252). In Illinois this species is common and widespread (Fig. 252).

Tabanus sulcifrons Macquart

Tabanus sulcifrons Macquart (1855:53) (as *fulcifrons*). Type-locality: Maryland, Baltimore.

Tabanus variegatus Fabricius (1805:95). Type-locality: North America. Name preoccupied (De Geer 1776).

Tabanus tectus Osten Sacken (1876:436). Type-locality: Pennsylvania, Doubling Gap.

Tabanus exul Osten Sacken (1878:558). Type-locality: Maryland, Pennsylvania, New Jersey, District of Columbia.

Fairly large size (20 mm); reddish brown; frons moderately wide, 4.5 times as high as wide (Fig. 187); eyes bare; thorax does not strongly contrast with abdomen; wing somewhat tinted, with dark spots and dark yellow costal cell; bifurcation of third longitudinal vein with brown spot; first posterior cell normally open although often narrowed at margin; fore tibiae pale at base; abdomen with median row of pale rather broad triangles, hind margins of tergites with pale bands that broaden laterally (Fig. 184). Male eye facets distinctly differentiated; eyes bare.

Because of its large size and capacity for blood, this species is occasionally a serious pest. It is most abundant when the other economically important species are gone for the season or on the decline. The adults of both sexes are frequently seen resting on country roads in considerable numbers; when disturbed, the females follow automobiles, even at fairly rapid speeds. They are active until dark and sometimes are found around lights.

The egg masses have been found on small branches of trees well away from water, and larvae (Fig. 211) have been collected in dry and in slightly moist soil as well as at the edges of ponds in saturated mud and plant debris (Pechu-

Tabanus quinquelineatus Macquart (1834:200). Type-locality: Georgia.
Tabanus apicalis Walker (1848:176).

Type-locality: unknown. Name pre-occupied.

Moderate size (16 mm); eyes bare; thorax with grayish white pile; wing nearly hyaline except for dark costal cell and dark spots; basal half of fore tibia white; abdomen dark with median white triangles on third, fourth, and fifth segments, occasionally two small sublateral white spots on the second segment (Fig. 170). Male eye facets distinctly differentiated; eyes bare.

The egg masses are deposited on vegetation along the edges of ponds and slow streams, and the larvae (Fig. 206) are found in organic mud and decaying vegetation near water (Pechuman 1972; Tidwell 1973; Goodwin 1973b). Larvae have also been found in rotting logs (Pechuman 1972).

In Illinois adults appear in late May and have been collected until early September.

T. trimaculatus is a widespread species, extending from northern Florida to Rhode Island and west to Nebraska

and central Texas (Fig. 255). In Illinois this species is found throughout the state (Fig. 255).

Tabanus turbidus Wiedemann

Tabanus turbidus Wiedemann (1828:124).

Type-locality: Kentucky.

Large size (22 mm); brown; frons very narrow, widened above; antennae, palpi, legs reddish brown; wings with brown spot on bifurcation and cross-veins, most veins margined with brown; costal cell yellow; first posterior cell wide open; abdomen brown with a row of sometimes indistinct pale triangles (Fig. 185). Male readily associated with female; annulate portion of third antennal segment sometimes slightly darkened; legs a little darker than in female, abdominal spots larger and more conspicuous; upper eye facets enlarged but not sharply set off from smaller facets.

The larva is unknown. The adults are largely crepuscular and nocturnal.

In Illinois adults appear in mid-July and have been collected until late August.

T. turbidus is a southeastern species, extending from central Florida to South Carolina and west to southern Illinois and western Arkansas (Fig. 256). This species has been collected in Illinois only in the south.

Illinois Records.—Alexander County, 4 miles ESE McClure; Johnson County, 0.2 mile E Grantsburg; Union County, LaRue-Pine Hills Ecological Area (4 miles N Wolf Lake), Union County Conservation Area (2 miles SE Ware).

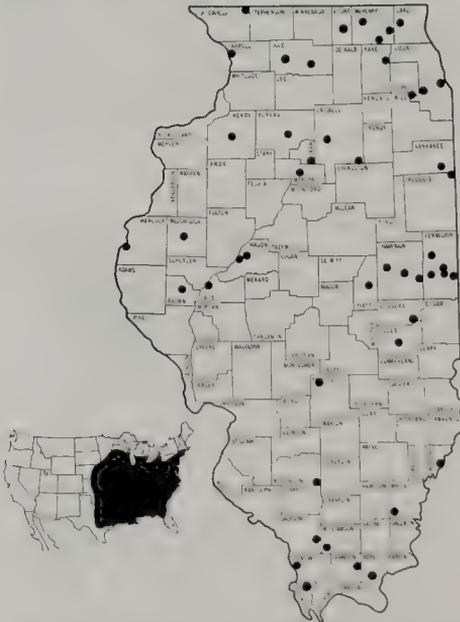


Fig. 255.—Distribution of *Tabanus trimaculatus* in Illinois and North America.



Fig. 256.—Distribution of *Tabanus turbidus* in North America.

Tabanus venustus Osten Sacken

Tabanus venustus Osten Sacken (1876: 444). Type-locality: Texas, Dallas.

Moderate size (16 mm); brown; wings variegated with brown areas not confined to bifurcation and crossbands; abdomen with white median triangles, small sublateral spots on tergites 3–6 (Fig. 171). Male easily associated with female by its variegated wings but differs in having a brown thoracic dorsum except for white pollinose scutellum; abdominal pale areas much more extensive than in female, formed by running together of median and sublateral spots to form pale posterior bands on tergites 2–4; upper eye facets somewhat enlarged but not clearly set off from small facets.

Larvae of *T. venustus* have been collected on the banks of streams and spring-fed ponds (Schwardt 1936). Thompson et al. (1978) collected a larva at the margin of a small pond.

In Illinois adults appear in late June and have been collected until early September.

T. venustus is a south-central species,

extending from Louisiana to southwestern Ohio and west to Nebraska and central Texas (Fig. 257). In Illinois this species has been infrequently collected (Fig. 257).

Tabanus vivax Osten Sacken

Tabanus vivax Osten Sacken (1876:446).

Type-locality: New York, Trenton Falls.

Tabanus arborealis Stone (1935:14). Type-locality: Vermont, Rutland.

Moderate size (14.5 mm); dark brown, sometimes with reddish cast and sometimes nearly black; vertex slightly depressed or flat; frons about 3.5 times as high as wide; last antennal annulus black; first antennal segment not swollen above; sides of subcallus without hairs; eyes bare; thorax does not strongly contrast with abdomen; wing hyaline often with yellowish tinge anteriorly; abdomen with three rows of pale spots, median triangle on second segment does not reach anterior margin. Male eye facets distinctly differentiated, lower facets curve upward in band separating large facets laterally from eye margin; eyes bare.

This species is not commonly col-

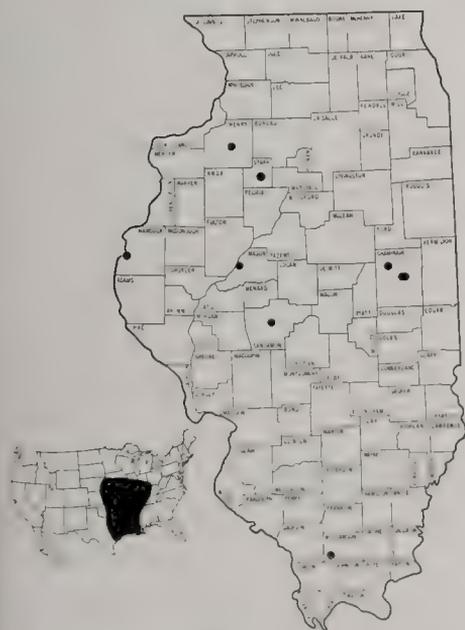


Fig. 257.—Distribution of *Tabanus venustus* in Illinois and North America.



Fig. 258.—Distribution of *Tabanus vivax* in North America.

lected. For many years it was confused with what is now called *T. fairchildi*, and most records earlier than 1938 actually refer to *fairchildi*.

Larvae (as in *marginalis*, Fig. 193) have been found in pasture sod at the edge of a permanently wet area and in boglike areas bordering streams (Pechuman 1972; Teskey 1969).

T. vivax is a northeastern species, extending from West Virginia to Labrador and west to Wisconsin (Fig. 258). As yet this species has not been collected in Illinois although specimens have been examined from southern Wisconsin.

Tabanus wilsoni Pechuman

Tabanus wilsoni Pechuman (1962:66).

Type-locality: Arkansas, Arkansas County, Arkansas River.

Moderate size (14 mm); brown; frons very narrow, sometimes slightly widened above; first two antennal segments and rather broad basal plate of third segment dark yellow, annulate portion black; palpi white; dorsum of thorax brown, contrasting with gray pollinose, white haired pleurae; wings with faint yellowish tint, darker in costal cell; coxae, fore and hind femora mostly dusky; pale median band of abdomen narrow, widening at apex of each segment; sublateral spots small, roundish, yellow brown. Male similar to female, but basal plate of antennae narrower, pleural hairs with yellowish tint, sublateral abdominal spots more extensive; upper eye facets not greatly



Fig. 259.—Distribution of *Tabanus wilsoni* in North America.

enlarged but line of demarcation distinct.

Larvae (as in *fulvulus*, Fig. 196) have been found in relatively dry soil in a bottomland hardwood forest in Louisiana (Tidwell & Tidwell 1973).

T. wilsoni is a south-central species, extending in a narrow band from Louisiana to western Kentucky (Fig. 259). As yet this species has not been collected in Illinois although specimens have been examined from western Kentucky.

Hamatabanus Philip

Hamatabanus carolinensis (Macquart)

Tabanus carolinensis Macquart (1838:149).

Type-locality: Carolina.

Tabanus scitus Walker (1848:181). Type-locality: Georgia.

Tabanus hirtioculatus Macquart (1855:53).

Type-locality: Maryland, Baltimore.

Tabanus cerastes Osten Sacken (1876:462). Type-locality: Kentucky, Bee Spring.

Large, stout (14 mm); brownish; eyes sparsely pilose; subcallus pollinose; frons higher than wide; third antennal



Fig. 260.—Distribution of *Hamatabanus carolinensis* in Illinois and North America.

segment with extended dorsal angle (Fig. 30); abdomen with three rows of pale spots; wings hyaline to pale brown; hind tibiae without apical spurs, sublateral ones on second abdominal tergite frequently reaching entirely across segment. Male readily associated with female but eyes more obviously hairy.

The larva is unknown.

In Illinois adults appear at the beginning of June and have been collected until early July.

H. carolinensis is a southeastern species, extending from northern Florida to Maryland and west to Missouri and Louisiana (Fig. 260). In Illinois this species is found only in the southern part of the state (Fig. 260).

KEY TO SPECIES OF HYBOMITRA

Females

1. Black species with first 3 abdominal segments mostly bright orange **cincta**
Abdomen otherwise marked 2
2. Subcallus denuded, shining 3
Subcallus pollinose 6
3. Subcallus swollen; whole of face below eyes denuded, shining; small species with dark wing markings **hinei**
Subcallus normal; face below eyes not shining 4
4. Abdomen broadly orange brown laterally, median black area constricted on third segment; all crossveins spotted with brown **lasiophthalma**
Abdomen not broadly orange brown laterally, if paler laterally, median dark area on third segment not constricted 5
5. Eye apparently bare; basal portion of third antennal segment narrow; abdomen brownish, faintly reddish brown laterally with median row of indistinct whitish triangles **difficilis**
Eye hairy; basal portion of third antennal segment stout **lurida**
6. Abdomen broadly orange brown laterally; basal plate and usually annulate portion of antennae orange; palpi stout; frons about 5 times as high as width at base, widened above **epistates**
Without this combination of characters 7
7. Bifurcation with distinct spur vein
..... **tetrica hirtula**
No spur vein at bifurcation 8
8. Abdomen black with median row of distinct white triangles, no sublateral spots **sodalis**

- Abdomen otherwise marked 9
9. Second palpal segment slender, scarcely thickened at base 10
Second palpal segment stout, especially at base 12
10. Femora, except bases of hind femora, brown; sides of abdomen reddish brown; second palpal segment extremely slender; third antennal segment practically without dorsal excision **minuscula**
Femora usually black, if brown, sides of abdomen without considerable orange brown 11
11. Prescutal lobe black; hair of palpi uneven **astuta**
Prescutal lobe pale; hair of palpi short, lying smoothly against segment **pechumani**
12. Bifurcation with distinct spot; third antennal segment stout **illota**
Bifurcation without distinct spot; third antennal segment more slender 13
13. Legs nearly uniformly brownish, rarely femora somewhat darker; third antennal segment very slender; prescutal lobe black **microcephala**
Femora black or grayish; third antennal segment not especially slender; prescutal lobe rarely black **frontalis**

Males

1. Stiff hairs along midline between eyes **difficilis**
No stiff hairs along midline between eyes 2
2. Black species with first 3 abdominal segments mostly bright orange **cincta**
Abdomen otherwise marked 3
3. Small dark species with gray, protuberant frontal triangle; genae black, somewhat shining; dark cloud on wing near stigma **hinei**
Differing in one or more characters from above 4
4. Crossveins and bifurcation with distinct dark spots; abdomen laterally broadly orange **lasiophthalma**
Wings hyaline, tinted, or with dark spot only at bifurcation 5
5. Abdomen black, obscurely reddish laterally with no distinct sublateral spots; conspicuous row of white median triangles **sodalis**
Abdomen otherwise marked 6
6. Small species, not over 12 mm, with very slender second palpal segment; sides of abdomen broadly dark orange, but first segment usually completely black; third segment with very shallow dorsal excision **minuscula**
Species usually over 12 mm, but if smaller, second palpal segment stout, dorsal excision distinct 7

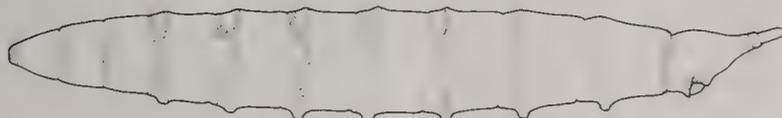
261 *microcephala*262 *lasiophthalma*263 *epistates*264 *frontalis*265 *hinei*266 *minuscula*267 *cincta*

Fig. 261–267.—Larvae. 261. *Hybomitra microcephala*. 262. *H. lasiophthalma*. 263. *H. epistates*. 264. *H. frontalis*. 265. *H. hinei*. 266. *H. minuscula*. 267. *H. cincta*.



268. *lurida*



269. *pechumani*



270. *sodalis*

Fig. 268-270.—Larvae. 268. *Hybomitra lurida*. 269. *H. pechumani*. 270. *H. sodalis*.

9. Posterior pubescence absent from anal segment (Fig. 268); tracheal trunks swollen to about 0.7 mm wide in preanal segment, abruptly tapered at level of first abdominal segment.....***lurida***
 Posterior pubescence present, although often indistinct, on anal segment (Fig. 269, 270); tracheal trunks slender (0.4 mm wide in preanal segment) and rather gradually tapered anteriorly10
10. Pubescence very pale, usually encircling anterior margin of first abdominal segment and posterior margin of anal segment (Fig. 269); living larva light green.....***pechumani***
 Pubescence moderately pigmented, at least on thoracic segments, absent laterally on anterior margin of first abdominal segment, vestigial on posterior margin of anal segment (Fig. 270); living larva pale brown***sodalis***

rows of grayish triangles; prescutal lobes dark; wings hyaline, costal cell pale yellow. Male eye facets scarcely differentiated; pale abdominal markings with orange cast; eyes hairy.

***Hybomitra astuta* (Osten Sacken)**

Tabanus astutus Osten Sacken (1876: 471). Type-locality: New Hampshire, White Mountains.

Moderate size (14 mm); brownish black; eyes hairy; second palpal segment slender, scarcely thickened at base; palpal hairs long, uneven, semi-erect; subcallus pollinose; abdomen with three



Fig. 271.—Distribution of *Hybomitra astuta* in North America.

This species is related to *H. pechumani* although they can be readily separated by the characters given in the keys.

The larva is unknown.

H. astuta is a northern species, extending from New York to Labrador and west to Alaska (Fig. 271). As yet this species has not been collected in Illinois although specimens have been examined from northern Wisconsin.

Hybomitra cincta (Fabricius)

Tabanus cinctus Fabricius (1794:366).

Type-locality: Virginia.

Moderate to large size (19 mm); black with orange band covering most of first three tergites; eyes practically bare; subcallus partly denuded; wing with dark yellow tint. Male eye facets little differentiated; eyes hairy.

It is not likely that this species, with its brilliant yellow or orange band on the abdomen, will be confused with any other species in the central states.

Larvae (Fig. 267) have been found under stones in streams (Pechuman 1972; Teskey & Burger 1976).

H. cincta is a southern and eastern species, extending from Louisiana and the panhandle of Florida north to Maine and west to the upper portion of Michigan (Fig. 272). As yet this species has not been collected in Illinois although specimens have been examined from western Kentucky.



Fig. 272.—Distribution of *Hybomitra cincta* in North America.

Hybomitra difficilis (Wiedemann)

Tabanus difficilis Wiedemann (1828:165).

Type-locality: unknown.

Moderate size (13 mm); dark brown; subcallus denuded; eyes almost bare;

basal portion of third antennal segment narrow; abdomen rather broad with median row of inconspicuous pale triangles, obscurely reddish laterally; wings hyaline with yellow costal cell. Male eye facets scarcely differentiated; row of stiff black hairs stands erect between eyes; frontal triangle grayish; eyes almost bare.

For many years this species was known as *carolinensis*, but Macquart's name belongs to another species. It is rarely common enough to be a pest, but occasionally is abundant in local areas. Under such circumstances it attacks wild and domestic animals and humans indiscriminately. It is an early season form.

In spite of the abundance of this species in some areas, the immature stages remain unknown.

In Illinois adults have been collected only in mid-June.

H. difficilis is an eastern and central species, extending from northern Florida to Massachusetts and west to Wisconsin and Arkansas (Fig. 273). This species has been collected only once in eastern Illinois.

Illinois Records.—Vermilion County, Forest Glen Forest Preserve (5 miles SE Westville).



Fig. 273.—Distribution of *Hybomitra difficilis* in North America.

Hybomitra epistates (Osten Sacken)

Tabanus epistates Osten Sacken (1878:555). Type-locality: Canada, Northwest Territories, Fort Simpson.

Tabanus socius Osten Sacken (1876:467). Type-locality: Canada, Northwest Territories, Fort Simpson. Name preoccupied (Walker 1848).

Moderate size (14 mm); brownish; second palpal segment rather swollen; subcallus pollinose; frons about five times as high as width at base, widened above; basal portion of third antennal segment mostly orange, about two-thirds as wide as long; eyes hairy. Male eye facets scarcely differentiated; eyes hairy.

Larvae (Fig. 263) are usually found in wet moss in swamps (Pechuman 1972; Teskey 1969).

In Illinois adults appear in mid-June and have been collected until mid-July.

H. epistates is a northern species, extending from Delaware to Nova Scotia and west to Oregon and Alaska (Fig. 274). In Illinois this species is collected only in the northern half of the state (Fig. 274).



Fig. 274.—Distribution of *Hybomitra epistates* in Illinois and North America.

Hybomitra frontalis (Walker)

Tabanus frontalis Walker (1848:172).

Type-locality: Nova Scotia, Cape Breton.

Tabanus incisus Walker (1850:26). Type-locality: Nova Scotia.

Tabanus septentrionalis Loew (1858:592). Type-locality: Labrador.

Tylostypia labradorensis Enderlein (1925:363). Type-locality: Labrador.

Tabanus canadensis Curran (1927:82).

Type-locality: Manitoba, Winnipegosis.

Moderate size (14 mm); blackish brown to yellowish; eyes hairy; subcallus pollinose; second palpal segment stout, especially at base; prescutal lobe rarely black; abdomen with faint grayish or yellowish median triangles, yellowish, reddish, or gray sublateral spots, which may or may not reach hind margins of tergites; wing hyaline, costal cell tinged with yellow; femora black or grayish. Male eye facets slightly differentiated but line of demarcation indistinct; sublateral abdominal spots usually larger, more reddish than in female, sometimes forming broad sublateral band; eyes hairy.

Pechuman (1957) treated this species as two subspecies. Intergrades between the two forms are found frequently. Although McAlpine (1961) has characterized a number of morphs, Pechuman believes them all to belong to a single species.

Larvae (Fig. 264) have been collected from wet moss in swamps (Teskey 1969).



Fig. 275.—Distribution of *Hybomitra frontalis* in Illinois and North America.

In Illinois adults appear in late June and have been collected until late July.

H. frontalis is a northern species, extending from Vermont to Labrador and west to Colorado and Alaska (Fig. 275). In Illinois this species has only been collected from the northeast part of the state (Fig. 275).

***Hybomitra hinei* (Johnson)**

Tabanus hinei Johnson (1904:15). Type-locality: New Jersey, Merchantville.

New name for *politus* Johnson (1900:325).

Theriopectes politus Johnson (1900:325).

Name preoccupied in *Tabanus* (Walker 1871). Type-locality: New Jersey, Merchantville.

Small to moderate size (11 mm); subcallus swollen, denuded, shiny; eyes with short hair; abdomen shining black with orange laterally; wing tinted with yellow, dark, poorly defined band in vicinity of discal cell, costal cell dark yellow. Male eye facets little differentiated; frontal triangle prominent, grayish; eyes hairy.

Larvae (Fig. 265) have been found in moss and partly decayed organic material around roots of shrubs and along banks of ponds, lakes, streams, and ditches (Pechuman 1972; Teskey 1969).

H. hinei is an eastern coastal species, extending from South Carolina to New Hampshire with several disjunct populations in New York, Ontario, Michigan, Wisconsin, and Indiana (Fig. 276). As yet this species has not been collected in Illinois although specimens have been examined from Indiana and Wisconsin.



Fig. 276.—Distribution of *Hybomitra hinei* in North America.

***Hybomitra illota* (Osten Sacken)**

Tabanus illota Osten Sacken (1876:469).

Type-locality: Hudson Bay Territory (lectotype).

Moderate size (13 mm); brownish black; subcallus pollinose; eyes hairy; second palpal segment stout, especially at base; third antennal segment stout; abdomen with faint median triangles, gray or yellowish gray sublateral spots; wings hyaline with pale yellow costal cell and faint brownish spots. Male eye facets scarcely differentiated; sublateral spots larger than in female, usually more yellowish; eyes hairy.

The larvae are found in organic debris and moss on the edges of ponds and swamps and in sphagnum bogs (Pechuman 1972; Teskey 1969).

In Illinois adults appear in late May and have been collected until mid-July.

H. illota is a northern species, extending from New York to the Gaspé Peninsula and west to Washington and southern Alaska (Fig. 277). In Illinois this species is collected only in the northeast corner of the state.

Illinois Records.—Cook County, Palos Hills; Du Page County, Argonne National Laboratories; Lake County, Volo.



Fig. 277.—Distribution of *Hybomitra illota* in North America.

Hybomitra lasiophthalma (Macquart)

Tabanus lasiophthalmus Macquart (1838:147). Type-locality: Carolina.

Tabanus punctipennis Macquart (1847:39). Type-locality: Pennsylvania, Philadelphia.

Tabanus notabilis Walker (1848:166). Type-locality: New York and Georgia.

Tabanus fretus Stone (1938:154). Type-locality: Connecticut, Lyme.

Tabanus guttiferus Harris (1925:70). *Nomen nudum*.

Tabanus redactus Walker (1850:66). Type-locality: unknown.

Moderate size (14 mm); brownish; subcallus denuded, shiny; eyes hairy; basal callus shiny, protuberant; abdomen broadly orange brown laterally; wings hyaline or faintly tinted, with conspicuous dark spots, yellow costal cell. Male eye facets little differentiated; frontal triangle grayish; eyes hairy.

The eggs are laid on various plants over moist ground; the egg mass is small and shining black, resembling a drop of tar on the leaf. Larvae (Fig. 262) are found in moist or wet sod, sphagnum bogs, and marshes (Pechu-

man 1972; Teskey 1969). Wilson (1969) collected larvae from a relatively dry forest floor.

In Illinois adults appear in mid-April and have been collected until mid-July.

H. lasiophthalma is a wide-ranging species, extending from Georgia to southern Quebec and west to eastern Texas and British Columbia (Fig. 278). In Illinois this species is distributed throughout the state (Fig. 278).

Hybomitra lurida (Fallén)

Hybomitra lurida Fallén (1817:5). Type-locality: Scandia.

Tabanus metabola McDunnough (1922:239). Type-locality: Alberta, Nordegg.

Moderate size (13 mm); brownish black; subcallus denuded, shiny; eyes hairy; third antennal segment stout; abdomen with faint median triangles, yellowish sublateral spots on second, third, and fourth tergites; wings hyaline with dark yellow costal cell, faint brownish spots, and a tendency for veins toward bases of wings to be outlined in yellowish brown. Male eye facets scarcely differentiated; thorax and abdomen rather shiny; eyes hairy.

Previously, this species had been



Fig. 278.—Distribution of *Hybomitra lasiophthalma* in Illinois and North America.



Fig. 279.—Distribution of *Hybomitra lurida* in North America.

reported as *H. metabola*. However, it has been shown (Pechuman & Stone 1968) that it is the same as the Old World *lurida*, and this name has priority.

Larvae (Fig. 268) are most commonly found in sphagnum bogs, but have also been taken in moss in swamps, ditches, and marshes (Teskey 1969).

H. lurida is a widespread northern species, extending from Massachusetts to northern Labrador and west to Colorado and Alaska (Fig. 279). This species has been collected only once in Illinois.

Illinois Records.—McHenry County, Algonquin.

Hybomitra microcephala (Osten Sacken)

Tabanus microcephalus Osten Sacken (1876:470). Type-locality: New Hampshire, White Mountains.

Moderate size (14 mm); grayish black; subcallus pollinose; third antennal segment very slender; second palpal segment stout, especially at base; eyes hairy; prescutal lobe black; abdomen with three rows of grayish or pinkish gray spots, which are largest on second tergite; wings hyaline with yellow-

ish costal cell and tendency for veins to be outlined in pale yellow; legs uniformly brown or reddish. Male eye facets scarcely differentiated; sublateral abdominal spots often reddish; eyes hairy.

Larvae (Fig. 261) have been collected from a well-decayed log (Teskey & Burger 1976).

H. microcephala is a northeastern species, extending from South Carolina to southern Quebec and west to Manitoba (Fig. 280). As yet this species has not been collected in Illinois although specimens have been examined from Wisconsin and Ohio.

Hybomitra minuscula (Hine)

Tabanus minusculus Hine (1907:226).

Type-locality: Maine, Orono; New York, Oswego; Massachusetts, Springfield; Canada.

Small to moderate size (11 mm); rather shining blackish brown; subcallus pollinose; second palpal segment very slender; third antennal segment practically without dorsal excision; eyes hairy; abdomen with considerable orange brown laterally; wings tinted, with tendency for veins to be outlined in deeper



Fig. 280.—Distribution of *Hybomitra microcephala* in North America.



Fig. 281.—Distribution of *Hybomitra minuscula* in North America.

tint, costal cell yellow. Male eye facets scarcely differentiated; eyes hairy.

Larvae (Fig. 266) are found in sphagnum (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early August.

H. minuscula is a northeastern species, extending from Virginia to northern Labrador and west to Wisconsin (Fig. 281). This species has been collected only once in Illinois.

Illinois Records.—Lake County, Cedar Lake.

Hybomitra pechumani
Teskey & Thomas

Hybomitra pechumani Teskey & Thomas (1979:346). Type-locality: Ontario, Alfred.

Moderate size (11 mm); palpi slender; eyes sparsely pilose; prescutal lobe reddish or brown; wings hyaline with dark yellow costal cell; abdomen with median row of gray triangles, larger sublateral pale spots. Male with upper eye facets enlarged, line of demarcation distinct; eyes densely pilose; sublateral pale abdominal markings sometimes pinkish; integument subshining.



Fig. 282.—Distribution of *Hybomitra pechumani* in North America.

Most records in the literature of *typhus* Whitney refer to this species. However, the name *typhus* properly belongs to a less commonly collected species (Teskey & Thomas 1979).

Larvae (Fig. 269) are found in wet moss in sphagnum bogs, in swamps, and at the edges of ponds and lakes (Teskey 1969, as *H. typhus*).

H. pechumani is a wide-ranging northern species, extending from northern Georgia to Labrador and west to Idaho, British Columbia, and the Northwest Territories (Fig. 282). As yet this species has not been collected in Illinois although specimens have been examined from central Wisconsin and Ohio.

Hybomitra sodalis (Williston)

Tabanus sodalis Williston (1887:139).

Type-locality: Connecticut.

Tabanus aestivalis Harris (1925:70). Nomen nudum.

Moderate size (15 mm); blackish; subcallus pollinose; basal portion of third antennal segment partly darkened; eyes with fine inconspicuous hairs; abdomen black with median row of grayish white triangles; wings tinted, especially anteriorly, costal cell dark yellow. Male eye facets scarcely differentiated; sides of abdomen usually tinted with orange brown; eyes hairy.

Pechuman (1957) considered this species as a subspecies of *trispila* Wiedemann, but it has been shown (Pechuman 1960) that two sibling species are involved. They can be separated by the basal portion of the third antennal segment, which is partly black in *sodalis* and entirely orange in *trispila*.

Larvae (Fig. 270) have been found in wet soil near the edges of streams, in seepage areas, in moss in woodland swamps, and in relatively dry sod (Pechuman 1972; Teskey 1969).

In Illinois adults appear in early July and have been collected until late July.

H. sodalis is a northeastern species, extending from northern Georgia to New Brunswick and west to Minnesota (Fig. 283). In Illinois this species



Fig. 283.—Distribution of *Hybomitra sodalis* in Illinois and North America.

has been collected at several localities in the northern half of the state (Fig. 283).

***Hybomitra tetrica hirtula* (Bigot)**

Therioptectes hirtula Bigot (1892:641).

Type-locality: Washington Territory.

Moderate size (15 mm); blackish; palpi white, rather stout at base; beard white; frons rather wide, widened above; prescutal lobe brown; bifurcation with spur vein; abdomen with three rows of gray spots, sublateral ones sometimes with reddish tinge. Male readily associated with female by spur vein at bifurcation; upper eye facets scarcely differentiated; beard with some dark hairs.

Collecting in 1979 at the sole recorded locality in Illinois did not produce this species, and since Illinois is well out of its known range, it is possible that the specimens here recorded have an erroneous locality label.

The immature stages are unknown. In Illinois adults have been collected in early July.

H. tetrica hirtula is a western species, extending from Colorado to Manitoba and west to British Columbia and California, with a disjunct record in Illinois (Fig. 284). This subspecies has been collected only once in Illinois.

Illinois records.—Ogle County, White Pines Forest State Park (7 miles W Oregon).



Fig. 284.—Distribution of *Hybomitra tetrica hirtula* in North America.

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Volume 32, Article 2.—Primary Insect Types in the Illinois Natural History Survey Collection, Exclusive of the Collembola and Thysanoptera. Donald W. Webb. July 1980. 138 p., index.

Volume 32, Article 3.—The Genera of Nearctic Therevidae. Michael E. Irwin and Leif Lyneborg. November 1980. 85 p., index.

Volume 32, Article 4.—The Lake Sangchris Study: Case History of an Illinois Cooling Lake. R. Weldon Larimore and John A. Tranquilli, eds. August 1981. 459 p., index.

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VOLUME 33, ARTICLE 2
APRIL 1983

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This report is printed by authority of the State of Illinois. It is a contribution from the Section of Faunistic Surveys and Insect Identification.

An Annotated Bibliography of the Illinois Herpetological Literature, 1960-1980, and An Updated Checklist of Species of the State

Michael A. Morris, Richard S. Funk, and Philip W. Smith

This bibliography has been compiled to provide a source of titles for those seeking literature dealing with the herpetofauna of Illinois that has appeared since the publication of "The Amphibians and Reptiles of Illinois" (Smith 1961). We believe that this bibliography includes all taxonomically and distributionally pertinent papers, published from 1960 to September 1980, having reference to Illinois populations. Papers are listed alphabetically by author and numbered consecutively.

Following the List of Titles is an updated Checklist of Species, also numbered consecutively. Subspecies names are not given since they are virtually unchanged since 1961. The name or name combination used by Smith (1961) appears in brackets immediately after each entry when his name usage differs from that listed here. Only species that are, or were, native to and represented by specimens from Illinois are listed. However, following the List of Titles is a list of extralimital species that now are not considered to be, or to have been, a regular part of the Illinois fauna.

The List of Titles and the Checklist of Species are cross-referenced. Thus, the List of Titles indicates which species each reference cites, and the Checklist of Species indicates which references treat each species. A few other annotations have been included when appropriate.

Titles 137 and 231 in the List of Titles, because of their general nature, have not been indexed in the species

checklist. A question mark preceding a title number indicates that the paper may refer to that species, but the specific identity is somewhat uncertain. For example, titles 112, 202, and 205 could refer to either *Hyla chrysoscelis* or *H. versicolor* or to both species.

All amphibians and reptiles are reduced in numbers in Illinois to some degree. A few of those known in the state prior to 1961 (*Pseudemys concinna*, *Clemmys guttata*, *Thamnophis sauritus*, and *Nerodia fasciata*) may now be extirpated, but some species (e.g., *Hemidactylum scutatum*, *Scaphiopus holbrooki*, *Gastrophryne carolinensis*, *Scincella lateralis*, and *Clonophis kirtlandi*) have been found to have more extensive ranges within the state than were known in 1961, even though they are less common now than then. The papers cited in the following List of Titles will help the user to determine the present status of each species of amphibian and reptile known to occur, or to have occurred, in Illinois.

We are indebted to Doris Sublette, former librarian at the Illinois Natural History Survey, for her generous aid in searching titles; to Ronald A. Brandon, Southern Illinois University at Carbondale, and Lauren E. Brown, Illinois State University, for reviewing the manuscript; and to Shirley McClell-

Michael A. Morris, Department of Zoology, Southern Illinois University at Carbondale; Richard S. Funk, Department of Zoology, The Ohio State University, Columbus; and Philip W. Smith, Taxonomist, Emeritus, Illinois Natural History Survey, Champaign.

lan, associate editor at the Illinois Natural History Survey, for the final editing.

LIST OF TITLES

1. Ackerman, K. 1975. Rare and endangered vertebrates of Illinois. Bureau of Environmental Science, Illinois Department of Transportation. 50 p. Species: 1, 2, 6, 10, 12, 14, 20, 24, 26, 29, 38, 39, 41, 42, 43, 47, 48, 60, 62, 66, 70, 75, 76, 92, 93, 97, and *Cemophora coccinea*.
2. Altig, R. 1967. Food of *Siren intermedia nettingi* in a spring-fed swamp in southern Illinois. American Midland Naturalist 77: 239-241. Species: 19.
3. Andersen, F. L., and N. D. Levine. 1961. *Tritrichomonas batrachorum* in a hog-nosed snake. Journal of Parasitology 47: 877-878. Species: 71.
4. Anderson, D. R., D. W. Duszynski, and W. C. Marquardt. 1968. Three new coccidia (Protozoa: Telosporae) from kingsnakes, *Lampropeltis* spp., in Illinois, with a redescription of *Eimeria zamenis* Phisalix, 1921. Journal of Parasitology 54: 577-581. Species: 72, 73.
5. Anderson, J. D. 1967a. *Ambystoma texanum*. Catalogue of American Amphibians and Reptiles: 37.1-37.2. Species: 7.
6. ———. 1967b. *Ambystoma opacum*. Catalogue of American Amphibians and Reptiles: 46.1-46.2. Species: 4.
7. ———. 1967c. *Ambystoma maculatum*. Catalogue of American Amphibians and Reptiles: 51.1-51.4. Species: 3.
8. Anonymous. 1966. Collecting rarity. Chicago Herpetological Society Bulletin 1(5): 32. Species: 84.
9. Applegate, R. D. 1974. Some notes on the nest of the midland painted turtle (*Chrysemys picta marginata* Agassiz). Chicago Herpetological Society Bulletin 9: 42. Species: 45.
10. ———. 1975. A range extension of the eastern box turtle (*Terrapene carolina*) in Illinois. Illinois State Academy of Science Transactions 68: 17. Species: 52.
11. ———, and C. W. Zimbleman. 1978. Herpetofauna of the Dixon Springs Agricultural Center and vicinity, Pope County, Illinois. Chicago Herpetological Society Bulletin 13: 72-74. Species: 3, 4, 7, 8, 9, 11, 12, 13, 16, 17, 21, 22, 23, 27, 28, 30, 31, 33, 34, 37, 38, 40, 44, 45, 46, 52, 55, 56, 57, 58, 59, 62, 64, 65, 66, 72, 73, 74, 77, 79, 80, 86, 87, 91, 94, 95.
12. Ashton, R. E. 1976. Endangered and threatened amphibians and reptiles in the United States. Society for the Study of Amphibians and Reptiles Herpetological Circular 5. v + 65 p. Species: 1, 2, 6, 10, 12, 14, 16, 20, 24, 26, 29, 38, 39, 41, 42, 48, 60, 66, 70, 75, 76, 78, 92, 93, 97, 98.
13. Axtell, C. B. 1976. Comparisons of morphology, lactate dehydrogenase, and distribution of *Rana blairi* and *Rana utricularia* in Illinois and Missouri. Illinois State Academy of Science Transactions 69: 37-48. Species: 32, 37.
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16. ———. 1973. Field behavior of the six-lined racerunner in Peoria County. Peoria Academy of Science Proceedings 6: 23. Species: 61.
17. Behler, J. L., and F. W. King. 1979. The Audubon Society field guide to North American reptiles and amphibians. Alfred A. Knopf, New York. 719 p. Descriptions and ranges of all species occurring in Illinois.
18. Benton, M. J. 1980a. Geographic variation in the garter snakes (*Thamnophis sirtalis*) of the north-central United States, a multivariate study. Zoological Journal of the Linnean Society 68: 307-323. Species: 91.
19. ———. 1980b. Geographic variation and the validity of subspecies names for the eastern garter snake, *Thamnophis sirtalis*. Chicago Herpetological Society Bulletin 15: 57-69. Species: 91.
20. Best, L. B. 1978. Field sparrow reproductive success and nesting ecology. Auk 95: 9-22. Species: 64, 72, 89, 98.
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270. ———. 1973. *Masticophis flagellum*. Catalogue of American Amphibians and Reptiles: 145.1-145.4. Species: 75.
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277. Ziomek, J. J. 1974. Notes on the spring activity of amphibians in the Palos Hills area of Swallow Cliff and Crooked Creek Woods, Cook County, Illinois. Chicago Herpetological Society Bulletin 9: 10-11. Species: 2, 3, 27, 30.

CHECKLIST OF SPECIES

AMPHIBIA

Caudata

Cryptobranchidae

1. *Cryptobranchus alleganiensis* (Daudin) [*Cryptobranchus a. alleganiensis*], hellbender: 1, 12, 17, 58, 61, 65, 75, 118, 132, 192, 225, 226.

Ambystomatidae

2. *Ambystoma laterale* Hallowell, blue-spotted salamander: 1, 12, 17, 58, 61, 75, 120, 121, 141, 145, 196, 202, 225, 226, 238, 252, 253, 254, 255, 266, 277.

3. *Ambystoma maculatum* (Shaw), spotted salamander: 7, 11, 17, 28, 58, 61, 132, 145, 196, 202, 205, 216, 225, 226, 274, 277.

4. *Ambystoma opacum* (Gravenhorst), marbled salamander: 6, 11, 17, 28, 58, 61, 132, 188, 202, 205, 225, 226.

5. *Ambystoma platineum* (Cope), silvery salamander [Not recognized as a valid species in 1961 and not then known in Illinois]: 75, 89, 120, 121, 176, 266.

6. *Ambystoma talpoideum* (Holbrook), mole salamander: 1, 12, 17, 28, 54, 58, 61, 75, 89, 120, 121, 132, 205, 223, 225, 226, 266.

7. *Ambystoma texanum* (Matthes), smallmouth salamander: 5, 11, 17, 25, 28, 33, 58, 61, 94, 112, 132, 135, 168, 185, 198, 205, 221, 225, 226, 248, 251, 273.

8. *Ambystoma tigrinum* (Green) [*Ambystoma t. tigrinum*], tiger salamander: 11, 17, 21, 27, 28, 31, 35, 37, 58, 61, 82, 98, 112, 116, 130, 132, 196, 202, 205, 225, 226, 235.

Salamandridae

9. *Notophthalmus viridescens* (Rafinesque) [*Notophthalmus v. louisianensis*], eastern newt: 11, 17, 30, 34, 37, 58, 61, 112, 132, 152, 196, 202, 205, 221, 225, 226, 260.

Plethodontidae

10. *Desmognathus fuscus* (Green) [*Desmognathus f. conanti*], dusky salamander: 1, 12, 17, 32, 33, 58, 61, 70, 75, 120, 121, 132, 180, 198, 205, 225, 226, 266, 272.

11. *Eurycea bislineata* (Green) [*Eurycea b. rivicola*], two-lined salamander: 11, 17, 58, 61, 75, 89, 118, 132, 160, 219, 225, 226, 240.

12. *Eurycea longicauda* (Green) [*Eurycea l. longicauda* and *E. l. melanopleura*], longtail salamander: 1, 11, 12, 17, 58, 61, 75, 89, 118, 122, 132, 193, 205, 221, 222, 225, 226, 236, 237, 240, 244.

13. *Eurycea lucifuga* Rafinesque, cave salamander: 11, 17, 32, 33, 58, 61, 69, 72, 75, 89,

118, 119, 132, 155, 193, 205, 221, 222, 225, 226, 237.

14. *Hemidactylium scutatum* (Schlegel), four-toed salamander: 1, 12, 17, 58, 61, 75, 91, 140, 189, 196, 202, 216, 225, 226, 234, 266.

15. *Plethodon cinereus* (Green) [*Plethodon c. cinereus*], redback salamander: 17, 58, 61, 89, 108, 111, 169, 180, 196, 202, 225, 226, 227, 245, 272.

16. *Plethodon dorsalis* Cope, zigzag salamander: 11, 12, 17, 58, 61, 69, 75, 108, 109, 110, 118, 132, 136, 151, 193, 205, 221, 222, 225, 226, 243, 244, 245.

17. *Plethodon glutinosus* (Green) [*Plethodon g. glutinosus*], slimy salamander: 11, 17, 58, 61, 69, 107, 108, 118, 132, 202, 205, 221, 222, 225, 226, 236, 240, 244.

Proteidae

18. *Necturus maculosus* (Rafinesque) [*Necturus m. maculosus*], mudpuppy: 17, 38, 58, 61, 105, 116, 132, 157, 196, 202, 205, 225, 226.

Sirenidae

19. *Siren intermedia* Le Conte [*Siren i. nettingi*], lesser siren: 2, 17, 39, 54, 58, 61, 64, 68, 96, 132, 150, 157, 171, 180, 188, 193, 202, 205, 221, 225, 226.

Salientia

Pelobatidae

20. *Scaphiopus holbrookii* (Harlan), eastern spadefoot toad: 1, 12, 17, 29, 45, 58, 61, 75, 205, 225, 226, 241, 262, 266.

Bufonidae

21. *Bufo americanus* Holbrook [*Bufo a. americanus* and *B. a. charlesmithi*], American toad: 11, 14, 17, 21, 41, 52, 53, 58, 61, 73, 112, 118, 132, 148, 183, 196, 200, 202, 205, 213, 221, 222, 225, 226, 240.

22. *Bufo woodhousei* Girard [*Bufo w. fowleri*], Fowler's toad: 11, 17, 21, 41, 52, 58, 61, 73, 118, 130, 132, 133, 141, 188, 196, 200, 202, 205, 212, 221, 222, 225, 226, 236, 240.

Hylidae

23. *Acris crepitans* Baird [*Acris c. blanchardi*], northern cricket frog: 11, 17, 21, 52, 58, 61, 101, 102, 103, 112, 116, 118, 132, 188, 196, 202, 205, 221, 225, 226, 240, 275.

24. *Hyla avivoca* Viosca [*Hyla a. avivoca*], bird-voiced treefrog: 1, 12, 17, 52, 58, 61, 75, 80, 89, 120, 121, 132, 205, 225, 226, 229, 266.

25. *Hyla chrysoscelis* Cope, Cope's gray treefrog

[Not recognized as a valid species in 1961 and not then known in Illinois]: 17, 44, 58, 61, 80, 104, ?112, 129, 196, ?202, ?205, 225.

26. *Hyla cinerea* (Schneider), green treefrog: 1, 12, 17, 52, 58, 61, 75, 80, 89, 95, 117, 132, 205, 225, 226, 266.

27. *Hyla crucifer* Wied [*Hyla c. crucifer*], spring peeper: 11, 17, 21, 47, 52, 58, 61, 80, 116, 118, 132, 141, 188, 196, 202, 205, 225, 226, 240, 248, 277.

28. *Hyla versicolor* Le Conte [*Hyla v. versicolor*], gray treefrog: 11, 17, 21, 44, 52, 58, 61, 80, 95, ?112, 116, 118, 129, 132, 188, 196, 199, ?202, ?205, 225, 226, 240.

29. *Pseudacris streckeri* Wright and Wright [*Pseudacris s. illinoensis*], Strecker's chorus frog: 1, 12, 14, 17, 45, 50, 51, 58, 61, 75, 89, 115, 118, 120, 121, 171, 225, 226, 228, 230, 266.

30. *Pseudacris triseriata* (Wied) [*Pseudacris t. triseriata* and *P. t. feriarum*], striped chorus frog: 11, 14, 17, 21, 50, 52, 58, 61, 82, 112, 116, 132, 141, 188, 196, 202, 205, 225, 226, 248, 275, 277.

Ranidae

31. *Rana areolata* Baird and Girard [*Rana a. circulosa*], crawfish frog: 11, 17, 58, 61, 89, 118, 132, 188, 225, 226.

32. *Rana blairi* Mecham, Littlejohn, Oldham, Brown, and Brown, plains leopard frog [*Rana p. pipiens* X *sphenocephala*; *R. blairi* not yet described in 1961]: 13, 14, 17, 21, ?36, 42, 43, ?52, 61, ?112, 153, 173, 194, 225.

33. *Rana catesbeiana* Shaw, bullfrog: 11, 17, 21, 52, 58, 61, 89, 112, 116, 118, 132, 139, 188, 196, 202, 205, 225, 226, 240, 246, 275.

34. *Rana clamitans* Latreille [*Rana c. melanota*], green frog: 11, 17, 21, 52, 58, 61, 116, 118, 125, 126, 127, 128, 130, 132, 196, 202, 205, 225, 226, 240.

35. *Rana palustris* Le Conte, pickerel frog: 17, 21, 58, 61, 196, 202, 205, 214, 215, 225, 226, 266.

36. *Rana pipiens* Schreber [*Rana p. pipiens*], northern leopard frog: 17, ?36, 42, 43, 48, 58, 61, 116, 173, 194, 196, 202, 225, 226, 275.

37. *Rana sphenocephala* Cope [*Rana p. sphenocephala*], southern leopard frog: 11, 13, 14, 17, ?36, 42, 43, 48, ?52, 58, 61, 118, 130, 132, ?138, 173, ?188, 194, 205, 225, 226, 240.

38. *Rana sylvatica* Le Conte [*Rana s. sylvatica* and *R. s. cantabrigensis*], wood frog: 1, 11, 12, 17, 21, 58, 61, 75, 89, 149, 180, 196, 202, 205, 225, 226, 240, 266.

Microhylidae

39. *Gastrophryne carolinensis* (Holbrook) [*Gastrophryne c. carolinensis*], eastern narrowmouth toad: 1, 12, 17, 58, 61, 75, 81, 89, 118, 120, 121, 180, 190, 225, 226, 266.

REPTILIA

Testudines

Chelydridae

40. *Chelydra serpentina* (Linnaeus) [*Chelydra s. serpentina*], snapping turtle: 11, 17, 21, 26, 51, 58, 61, 63, 88, 112, 116, 132, 166, 185, 188, 196, 202, 205, 222, 224, 226, 240, 275.

41. *Macrochelys temmincki* (Troost), alligator snapping turtle: 1, 12, 17, 21, 58, 61, 75, 88, 93, 205, 226.

Kinosternidae

42. *Kinosternon flavescens* (Agassiz) [*Kinosternon f. spooneri*], yellow mud turtle: 1, 12, 17, 21, 51, 58, 61, 75, 88, 89, 121, 124, 130, 165, 166, 167, 218, 226, 230, 266.

43. *Kinosternon subrubrum* (Lacépède) [*Kinosternon s. subrubrum* X *hippocrepis*], eastern mud turtle: 1, 17, 51, 58, 61, 75, 88, 123, 132, 166, 202, 224, 226.

44. *Sternotherus odoratus* (Latreille) [*Sternotherus odoratus*], stinkpot: 11, 17, 21, 58, 61, 63, 88, 106, 116, 132, 166, 168, 188, 196, 202, 205, 221, 222, 224, 226.

Emydidae

45. *Chrysemys picta* (Schneider) [*Chrysemys p. marginata* and *C. p. belli*], painted turtle: 9, 11, 17, 21, 51, 58, 61, 63, 86, 88, 112, 116, 118, 130, 132, 134, 159, 166, 172, 188, 196, 202, 205, 226, 250, 275.

46. *Pseudemys scripta* (Schoepff) [*Pseudemys s. elegans*], pond slider: 11, 17, 21, 58, 61, 63, 88, 90, ?106, 132, 166, 168, 188, 196, 202, 205, 222, 226, 230, 260.

47. *Pseudemys floridana* (Le Conte) X *P. concinna* (Le Conte) [*Pseudemys f. hoyi* X *P. c. hieroglyphica*], hieroglyphic slider: 1, 17, 58, 61, 75, 88, 226, 266.

48. *Clemmys guttata* (Schneider), spotted turtle: 1, 12, 17, 58, 61, 63, 75, 87, 88, 196, 202, 226, 266.

49. *Emydoidea blandingi* (Holbrook), Blanding's turtle: 17, 58, 61, 63, 75, 88, 112, 142, 166, 196, 202, 226, 230, 260, 266.

50. *Graptemys geographica* (Lesueur), map turtle: 17, 21, ?51, 58, 61, 63, 88, 116, 164, 166, 196, 202, 226.

51a. *Graptemys kohni* (Bauer), Mississippi map turtle [Not recognized as a valid species in 1961]: 17, 58, 61, 63, 88.

51b. *Graptemys pseudogeographica* (Gray), false map turtle: 17, ?51, 55, 58, 61, 63, 88, 90, 116, 118, 157, 162, 163, 166, 205, 226, 230.

52. *Terrapene carolina* (Linnaeus) [*Terrapene c. carolina*], eastern box turtle: 10, 11, 17, 21, 58, 61, 63, 84, 85, 88, 89, ?106, 118, 131, 132, ?146, 185, 188, 202, 205, 222, 226, 236, 240.

53. *Terrapene ornata* (Agassiz) [*Terrapene o.*

ornata], ornate box turtle: 17, 21, 49, 58, 61, 88, 89, 120, 121, 130, 170, 188, 202, 226, 261.

Trionychidae

54. *Trionyx muticus* Lesueur [*Trionyx m. muticus*], smooth softshell turtle: 17, 58, 61, 88, 166, 226, 230, 263, 264.

55. *Trionyx spiniferus* Lesueur [*Trionyx s. spinifer*], spiny softshell turtle: 11, 17, 21, 58, 61, 63, 88, 112, 116, 132, 166, 196, 202, 205, 226, 230, 240, 263, 265.

Sauria

Iguanidae

56. *Sceloporus undulatus* (Latreille) [*Sceloporus u. hyacinthinus*], eastern fence lizard: 11, 17, 58, 61, 118, 132, 188, 205, 221, 226, 236, 240.

Scincidae

57. *Eumeces fasciatus* (Linnaeus), five-lined skink: 11, 17, 49, 58, 61, 118, 132, 161, 188, 196, 202, 205, 216, 221, 222, 226, 236, 240.

58. *Eumeces laticeps* (Schneider), broadhead skink: 11, 17, 58, 61, 118, 132, 161, 185, 188, 195, 205, 226, 240.

59. *Scincella lateralis* (Say) [*Scincella laterale*], ground skink: 11, 17, 21, 40, 58, 61, 114, 118, 130, 132, 188, 205, 221, 226, 236, 237, 240.

Anguidae

60. *Ophisaurus attenuatus* Cope [*Ophisaurus a. attenuatus*], slender glass lizard: 1, 12, 17, 58, 61, 75, 89, 112, 113, 116, 120, 121, 180, 185, 196, 202, 226, 266.

Teiidae

61. *Cnemidophorus sexlineatus* (Linnaeus) [*Cnemidophorus s. sexlineatus*], six-lined racerunner: 14, 15, 16, 17, 21, 51, 58, 61, 89, 118, 120, 121, 130, 132, 185, 196, 202, 226, 240.

Serpentes

Colubridae

62. *Carphophis amoenus* (Say) [*Carphophis a. helenae* and *C. a. vermis*], worm snake: 1, 11, 17, 57, 58, 61, 118, 132, 154, 205, 222, 226, 236.

63. *Clonophis kirtlandi* (Kennicott) [*Natrix kirtlandi*], Kirtland's water snake: 17, 21, 49, 56, 58, 61, 75, 112, 114, 154, 171, 178, 185, 196, 202, 226, 230, 247, 248, 249.

64. *Coluber constrictor* Linnaeus [*Coluber c. flaviventris*], racer: 11, 17, 20, 21, 58, 61, 74, 112, 118, 132, 154, 188, 196, 202, 205, 210, 221, 222, 226, 236, 240, 271.

65. *Diadophis punctatus* (Linnaeus) [*Diadophis p. amyi*, *D. p. edwardsi*, and *D. p. stictogenys*], ringneck snake: 11, 17, 21, 58, 61, 89, 118, 132,

154, 205, 221, 222, 226.

66. *Elaphe guttata* (Linnaeus) [*Elaphe g. emoryi*], corn snake: 1, 11, 12, 17, 29, 58, 61, 75, 89, 120, 121, 171, 226, 239, 266.

67. *Elaphe obsoleta* (Say) [*Elaphe o. obsoleta* and *E. o. spiloides*], rat snake: 17, 21, 58, 61, 67, 74, 77, 100, 112, 132, 154, 182, 188, 196, 202, 205, 210, 216, 221, 222, 226, 240.

68. *Elaphe vulpina* (Baird and Girard) [*Elaphe v. vulpina*], fox snake: 17, 21, 46, 58, 61, 77, 79, 112, 154, 157, 158, 196, 202, 210, 226.

69. *Farancia abacura* (Holbrook) [*Farancia a. reinwardti*], mud snake: 17, 58, 61, 75, 89, 132, 154, 205, 224, 226, 266.

70. *Heterodon nasicus* Baird and Girard [*Heterodon n. nasicus*], western hognose snake: 1, 12, 17, 21, 51, 58, 61, 75, 89, 97, 120, 121, 154, 171, 226, 232, 266.

71. *Heterodon platyrhinos* Latreille, eastern hognose snake: 3, 17, 21, 58, 61, 67, 71, 77, 79, 116, 132, 154, 184, 188, 196, 202, 205, 220, 226, 259.

72. *Lampropeltis calligaster* (Harlan) [*Lampropeltis c. calligaster*], prairie kingsnake: 4, 11, 17, 20, 21, 24, 58, 61, 62, 112, 130, 132, 154, 158, 168, 171, 188, 205, 216, 226.

73. *Lampropeltis getulus* (Linnaeus) [*Lampropeltis g. holbrooki* and *L. g. niger*], common kingsnake: 4, 11, 17, 23, 58, 61, 71, 77, 118, 132, 154, 182, 205, 226, 240.

74. *Lampropeltis triangulum* (Lacépède) [*Lampropeltis t. triangulum* and *L. t. sypila*], milk snake: 11, 17, 21, 58, 61, 77, 79, 82, 112, 116, 132, 154, 180, 196, 202, 205, 226, 230, 267.

75. *Masticophis flagellum* (Shaw) [*Masticophis f. flagellum*], coachwhip snake: 1, 12, 17, 58, 61, 75, 89, 120, 121, 226, 266, 269, 270.

76. *Nerodia cyclopion* (Duméril and Bibron) [*Natrix c. cyclopion*], green water snake: 1, 12, 17, 58, 61, 75, 89, 96, 205, 226, 266.

77. *Nerodia erythrogaster* (Forster) [*Natrix e. flavigaster* and *N. e. neglecta*], plainbelly water snake: 11, 17, 58, 61, 96, 132, 154, 171, 180, 188, 201, 205, 222, 226.

78. *Nerodia fasciata* (Linnaeus) [*Natrix sipedon confluens*], southern water snake: 12, 17, 58, 60, 61, 75, 89, 226, 266.

79. *Nerodia rhombifera* (Hallowell) [*Natrix r. rhombifera*], diamondback water snake: 11, 17, 21, 58, 61, 96, 132, 154, 171, 188, 205, 224, 226.

80. *Nerodia sipedon* (Linnaeus) [*Natrix s. sipedon* and *N. s. pleuralis*], northern water snake: 11, 17, 21, 56, 58, 60, 61, 279, 96, 112, 116, 118, 132, 154, 186, 188, 196, 202, 205, 217, 221, 222, 226, 236.

81. *Ophedrys aestivus* (Linnaeus), rough green snake: 17, 58, 61, 74, 118, 132, 154, 188, 205, 226.

82. *Ophedrys vernalis* (Harlan) [*Ophedrys v. blanchardi*], smooth green snake: 17, 21, 58, 61, 92, 112, 154, 196, 202, 226, 260, 276.

83. *Pituophis melanoleucus* (Daudin) [*Pituophis m. sayi*], bullsnake: 17, 21, 58, 61, 75, 83, 89, 99, 112, 143, 144, 154, 157, 202, 226, 246.

84. *Regina grahami* Baird and Girard [*Natrix grahami*], Graham's crayfish snake: 8, 17, 58, 61, 75, 112, 154, 185, 196, 202, 226, 259, 275.

85. *Regina septemvittata* (Say) [*Natrix septemvittata*], queen snake: 17, 21, 58, 61, 66, 75, 77, 89, 116, 154, 186, 196, 202, 226.

86. *Storeria dekayi* (Holbrook) [*Storeria d. wrightorum*], brown snake: 11, 17, 21, 58, 61, 74, 77, 112, 116, 154, 175, 177, 188, 196, 202, 205, 221, 226, 242.

87. *Storeria occipitomaculata* (Storer) [*Storeria o. occipitomaculata*], redbelly snake: 11, 17, 21, 58, 61, 112, 116, 132, 154, 185, 196, 202, 205, 226.

88. *Thamnophis proximus* (Say) [*Thamnophis sauritus proximus*], western ribbon snake: 17, 21, 49, 58, 61, 112, 188, 196, 202, 205, 206, 207, 208, 226.

89. *Thamnophis radix* (Baird and Girard) [*Thamnophis r. radix*], plains garter snake: 17, 20, 21, 58, 61, 76, 82, 112, 143, 144, 154, 157, 158, 174, 179, 181, 182, 196, 202, 226, 248.

90. *Thamnophis sauritus* (Linnaeus) [*Thamnophis s. sauritus* X *proximus*], eastern ribbon snake: 17, 58, 61, 202, 206, 207, 209, 226, 266.

91. *Thamnophis sirtalis* (Linnaeus) [*Thamnophis s. sirtalis* and *T. s. semifasciata*], common garter snake: 11, 17, 18, 19, 21, 22, 58, 61, 74, 78, 82, 116, 118, 132, 182, 186, 188, 196, 202, 205, 216, 226, 230, 240, 275.

92. *Tantilla gracilis* Baird and Girard [*Tantilla g. hallowelli*], flathead snake: 1, 12, 17, 29, 58, 61, 75, 89, 120, 121, 171, 205, 226, 266.

93. *Tropidoclonion lineatum* (Hallowell) [*Tropidoclonion l. lineatum*], lined snake: 1, 12, 17, 49, 58, 61, 75, 116, 154, 226, 232, 233.

94. *Virginia valeriae* Baird and Girard [*Virginia v. elegans*], smooth earth snake: 11, 17, 21, 58, 61, 74, 118, 132, 154, 180, 187, 197, 205, 221, 222, 226, 230, 240.

Crotalidae

95. *Agkistrodon contortrix* (Linnaeus) [*Agkistrodon contortrix mokeson*], copperhead: 11, 17, 58, 61, 74, 79, 89, 118, 132, 147, 154, 156, 204, 205, 226, 236, 237, 240.

96. *Agkistrodon piscivorus* (Lacépède) [*Agkistrodon p. leucostomus*], cottonmouth: 17, 58, 61, 74, 79, 89, 96, 120, 121, 132, 154, 204, 205, 221, 222, 226.

97. *Crotalus horridus* Linnaeus [*Crotalus h. horridus*], timber rattlesnake: 1, 12, 17, 21, 58, 59, 61, 74, 75, 79, 89, 118, 132, 154, 191, 204, 205, 226, 257, 258, 266.

98. *Sistrurus catenatus* (Rafinesque) [*Sistrurus c. catenatus*], massasauga: 12, 17, 20, 58, 61, 75, 77, 79, 112, 154, 196, 202, 203, 204, 226, 258, 266.

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DEPARTMENT OF ENERGY AND NATURAL RESOURCES

NATURAL HISTORY SURVEY DIVISION
CHAMPAIGN, ILLINOIS

VOLUME 33, ARTICLE 3
SEPTEMBER 1985

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ILLINOIS
Natural History Survey
BULLETIN

**125 Years
of Biological Research
1858–1983:
A Symposium**

STATE OF ILLINOIS
DEPARTMENT OF ENERGY AND NATURAL RESOURCES

NATURAL HISTORY SURVEY DIVISION
CHAMPAIGN, ILLINOIS

VOLUME 33, ARTICLE 3
SEPTEMBER 1985

STATE OF ILLINOIS

EXECUTIVE DEPARTMENT

Proclamation

WHEREAS, the Illinois State Natural History Society was organized in Bloomington in 1858, and has evolved into the highly respected Illinois State Natural History Survey of the Department of Energy and Natural Resources, now located in Urbana; and

WHEREAS, Dr. Paul G. Risser currently heads the staff of 200 which includes nationally acclaimed scientists; and

WHEREAS, the Natural History Survey's work has received national recognition in the areas of insect control, fish and pond management, floricultural disease control, game species, waterfowl, and periodic reports on endangered animal species; and

WHEREAS, the Natural History Survey has brought world-wide recognition to the State of Illinois and information of immeasurable value to Illinoisans on both the history and the future of the flora and fauna in the state,

THEREFORE, I, James R. Thompson, Governor of the State of Illinois, proclaim September 24, 1983, as NATURAL HISTORY SURVEY DAY in Illinois, in celebration of its 125th anniversary.

In Witness Whereof, I have hereunto set my hand and caused the Great Seal of the State of Illinois to be affixed.

Done at the Capitol in the City of Springfield, this SEVENTH day of SEPTEMBER, in the Year of Our Lord one thousand nine hundred and EIGHTY-THREE, and of the State of Illinois the one hundred and SIXTY-FIFTH



Jim Edgar
SECRETARY OF STATE

James R. Thompson

GOVERNOR



ILLINOIS NATURAL HISTORY SURVEY 125TH ANNIVERSARY CELEBRATION

SYMPOSIUM

274 Medical Sciences Building
University of Illinois, Urbana, IL
(Open to the public – no charge)

Morning Session

Moderator – Dr. F. A. Bazzaz, Head
Department of Plant Biology
University of Illinois, U-C

- 9:00 Opening. Dr. P. G. Risser, Chief,
INHS
- 9:05 A host plant is more than its
chemistry. Dr. D. H. Janzen,
Professor of Biology, University
of Pennsylvania, Philadelphia
- 9:55 Plant kairomones and insect
pest control. Dr. R. L. Metcalf,
Professor of Biology and Research
Professor of Entomology, Univer-
sity of Illinois, Urbana-Cham-
paign, and Principal Scientist,
INHS
- 10:25 Break

- 10:35 Early contributions of insect
toxicology to the evolution of en-
vironmental toxicology. Dr. A.
S. Felsot, Associate Entomolo-
gist, Section of Economic Ento-
mology, INHS
- 11:05 Biotic and abiotic stresses as
primary and predisposing fac-
tors affecting Illinois trees. Drs.
D. F. Schoeneweiss, D. Neely,
and E. B. Himelick, Plant
Pathologists, Section of Botany
and Plant Pathology, INHS
- 11:35 Summary. Dr. C. E. Eastman,
Associate Entomologist, and Dr.
M. Kogan, Entomologist, Sec-
tion of Economic Entomology,
INHS
- 11:45 Adjournment

LUNCHEON

12:00–1:45 PM
Illini Union Rooms B and C
University of Illinois, Urbana, IL
(Open to the public by reservation)

Recognition of
Friends of the Illinois Natural History Survey

Luncheon Address

“Long-term Biological Research in a Rapidly Changing Environment”
by

Dr. Lorin I. Nevling, Jr., Director
Field Museum of Natural History
Chicago, IL

Afternoon Session

Moderator – Dr. J. E. King, Head
Scientific Sections
Illinois State Museum
Springfield, IL

- 2:15 Opening. Dr. P. G. Risser, Chief,
INHS
- 2:20 Lake Tahoe: a microcosm for the
study of change. Dr. C. R.
Goldman, Director of the Lake
Tahoe Research Group, Division
of Environmental Studies,
University of California, Davis
- 3:05 A comparison of the embryonic
development of northern,
Florida, and reciprocal F_1
hybrid largemouth bass in dif-
ferent thermal environments.
Dr. D. P. Philipp, Associate
Aquatic Biologist, and Ms. C.
Kaminski, Junior Technical
Assistant, Section of Aquatic
Biology, INHS, and Dr. G. S.

Whitt, Professor of Genetics and
Development, University of Il-
linois, Urbana-Champaign, and
Research Affiliate, INHS

- 3:35 Break
- 3:45 Evolution of reproductive
behavior in percid fishes. Dr. L.
M. Page, Ichthyologist, Section
of Faunistic Surveys and Insect
Identification, INHS
- 4:15 Wind drift and migration of
thrushes: a telemetry study. Mr.
W. W. Cochran, Associate
Wildlife Specialist, Section of
Wildlife Research, INHS, and
Mr. C. G. Kjos, Fish and
Wildlife Biologist, U.S. Fish and
Wildlife Service, Department of
the Interior, Fort Snelling, MN
- 4:45 Summary. Dr. J. R. Karr, Pro-
fessor of Ecology, Ethology, and
Evolution, University of Il-
linois, Urbana-Champaign
- 4:55 Adjournment

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This paper is published by authority of the State of Illinois and is a contribution from various staff members and guest speakers who made presentations on the occasion of the Survey's 125th anniversary year.

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ACKNOWLEDGMENTS

The Illinois Natural History Survey celebrated its 125th anniversary in 1983 by hosting a series of special events for its friends and staff. Two of them were the 125th Anniversary Symposium and Luncheon held on 24 September 1983 at Urbana, and the contents of this commemorative bulletin are based on the papers and summary comments presented at those two functions. The proclamation from Governor James R. Thompson, recognizing the importance of the Survey to the people of Illinois (Frontispiece), was read at the luncheon.

The papers contributed to the symposium were selected on the basis of recommendations solicited from the staffs of the Survey's research sections: Aquatic Biology, Botany and Plant Pathology, Economic Entomology, Faunistic Surveys and Insect Identification, and Wildlife Research. The papers presented by Survey staff members do not adequately reflect either past or present programs in toto, i.e., they are indicative, not definitive.

Each manuscript was subjected to rigorous review by the editorial committee and by at least 2 of 17 anonymous, non-Survey scientists. To these people and our colleagues, R. W. Larmore and W. G. Ruesink, comembers with us on the symposium program committee, we are grateful for quietly supporting us in the preparation of this publication. We also thank several members of the Survey's supportive staff, A. K. Adams, P. L. Duzan, R. J. Korb, L. L. Le Mere, S. H. McClellan, B. A. Nelson, S. J. Peratt, J. A. Sanders, E. L. Steger, B. P. Sweeney, and M. L. Williamson, who spared no effort in helping us to complete this volume. Finally, special thanks are due to F. A. Bazzaz, former Head, Department of Plant Biology, University of Illinois, Urbana-Champaign, and J. E. King, Head, Scientific Section, Illinois State Museum, Springfield, who served as moderators of the morning and afternoon symposium sessions, respectively.

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An Introduction to the Symposium

Paul G. Risser

The Natural History Society of Illinois was proposed to the State Teacher's Association in December 1857 and was organized on 30 June 1858, thus beginning the 125 years celebrated by this symposium volume. The society subsequently became the Illinois State Laboratory of Natural History, which was combined with the State Entomologist's Office in 1917 and renamed the Illinois Natural History Survey. Early Illinois leadership recognized the need for a state agency committed to studying and understanding the living natural resources of Illinois. It is to the state's credit that the Illinois Natural History Survey has become during these past 125 years the largest and oldest organization of its kind in the nation.

A casual review might suggest that the Survey's early activities were largely surveys, that is, the careful cataloging and mapping of the flora and fauna of the state. Today's activities might easily be characterized as modern biology with emphases on the application of new technology and on studies addressing current environmental problems and the management of living natural resources. However, such casual inspection of the Survey's programs, past and present, would not identify and recognize the strengths which have enabled the organization to grow over the past twelve and a half decades.

Before the turn of the century, biologists from the State Laboratory of Natural History were indeed systematically sampling the state's terrestrial habitats as well as its rivers and streams. These early field investiga-

tions not only formed the basis for understanding these ecosystems and the natural histories of the organisms found therein, but also resulted in an informational record which is priceless in making comparisons with today's conditions. But further, Survey scientists developed biological-population sampling equipment and methodologies that have been adopted by biologists throughout the country. The resulting information was used to address such practical issues as increasing the production of fish populations in lakes; controlling agricultural pests, such as the chinch bug; and dealing with ticks and other wildlife problems. In addition, Survey scientists also began to develop a conceptual framework for these studies, a direction perhaps epitomized by the "lake-as-a-microcosm" concept of Stephen A. Forbes, the first Chief of the Survey.

The Illinois Natural History Survey retains these same basic ingredients. As described in the paper by L. M. Page in this volume, the Survey is conducting detailed life-history studies which provide information for understanding the evolutionary relationships among groups of species and, at the same time, result in recommendations about how to manage various species to ensure their perpetuation. The paper by D. F. Schoeneweiss, D. Neely, and E. B. Himelick clearly demonstrates a progression of approaches developed for controlling the diseases of urban and forest trees. These techniques depend upon a thorough knowledge of the life histories of the trees and their pests. The W. W. Cochran and C. G. Kjos paper discusses novel technology for investigating a fundamental biological phenomenon, migration of passerine birds. The paper by D. P. Philipp, C. Kaminski, and G.

Dr. Paul G. Risser is Chief of the Illinois Natural History Survey and is a plant ecologist.

S. Whitt recounts the use of enzymological methods to describe differences among fish populations which otherwise would not have been discerned. Just as importantly, this information can now be used as the basis for recommendations about fish stocking programs in Illinois.

A. S. Felsot's paper on environmental toxicology considers the fate and behavior of agricultural pesticides in the environment, and this paper clearly emphasizes some rather unique characteristics of the Survey. Agricultural entomology has been an important component of the Illinois Natural History Survey ever since the Illinois State Laboratory of Natural History merged with the State Entomologist's Office. Controlling insect pests with chemicals is a widespread practice but is an approach viewed with skepticism by some of those attempting to preserve the living natural resources of the state. However, the compatibility of these potentially opposing viewpoints lies in the Survey's broad understanding of biological principles. In making recommendations about the control of agricultural pests, the Survey employs the concepts of integrated pest management, which specifies the minimum use of chemicals and the maximum use of information about the life history of both the host organism and the pest organism. Thus, the Survey is in the unique position of being able to address very practical problems with natural history data and ecological information.

The three guest authors in this volume presented papers which served to place the Survey's program in a national context. D. H. Janzen discusses

current notions about the ways in which insects select and feed on plants. His point is that the customarily invoked mechanism based on the chemical constituents of the plant is focused too narrowly and that more natural situations will be explained by considering the natural history and evolutionary aspects of plant and insect interrelationships. In a more applied sense, R. L. Metcalf elaborates this thought with an elegant discussion of the evolutionary processes that led to the enormous array of secondary chemical compounds found in agricultural plants. C. R. Goldman reaffirms the holistic view of the lake ecosystem concept, using Lake Tahoe as the model. Here, again, his paper demonstrates the strength of understanding the natural history of the system and then managing the lake according to these biological principles.

As noted by L. I. Nevling, Jr., in his luncheon address, reflection on the past and future of the Illinois Natural History Survey indicates the unique attributes of the organization. The long-term purpose to understand the biology of the state and the dedication to do so are unusual commitments in this day when programs and objectives tend to be largely impulsive, ephemeral, and fragmented. The papers in this volume demonstrate the pervasive nature of the Survey's programs, which touch, directly or indirectly, every person in Illinois. The importance of the work, however, goes beyond the state's borders, since the state is a microcosm of the nation, and thus, the results of the program are applicable to all efforts to understand and manage biological resources in a changing world.

A Host Plant Is More Than Its Chemistry

Daniel H. Janzen

Field naturalists frequently observe that the intensity of insect herbivory in a natural defoliation event is not spread uniformly over individual conspecific plants and may even vary within one plant crown. Until the early 1960's, the general explanation would have been that heterogeneity in physical conditions, carnivory, and/or the arrival of the herbivores generate such lack of uniformity. During the past 20 years, much research on the chemical defenses of plants has paved the way for the now commonplace concept that such heterogeneity of herbivory in a defoliation event may also be caused by heterogeneity in the nutrient or defense properties of plants or plant parts (e.g., Kogan 1977). Indeed, a number of studies have found this to be the case. For example, squirrels browse much more heavily on terpene-poor ponderosa pines than on their more terpene-rich conspecifics a few meters away (Farantinos et al. 1981). Panamanian forest insects browse young leaves more intensely than they do conspecific old ones, presumably because of the greater nutrient value and lesser toughness of the former (Coley 1982, 1983a, b). Chrysomelid beetles and Finnish caterpillars vary their feeding patterns in response to seasonal changes in host leaf chemistry (Hare 1983; Haukioja & Niemela 1979).

What I would like to do in this essay is to give the pendulum a push back toward a middle ground, reminding all of us (including me) that when a herbivore moves onto a host plant it gets the outside of the plant as well as what is inside. Such integrative studies are now beginning to appear in the literature (e.g., Abrahamson et al.

1983; Coley 1982, 1983a, b; Connor et al. 1983; Haukioja 1980; Heinrich & Collins 1983; Kareiva 1982; Lawton 1983; McClure 1983; Niemela et al. 1982; Price et al. 1980; Rausher & Papaj 1983; Schultz 1983; Schultz et al. 1982; Stanton 1982; Thompson 1983; Washburn & Cornell 1981; Wint 1983). I feel that the philosophy that generates them deserves maximum encouragement.

I have two practical reasons for attempting this leavening, though I am sure that the reader will think of others. First, one has only so much time and resource to expend on a given study of the intensity of herbivory, and there is a very real question of whether efforts should be focused on determining the (potential) internal plant properties that drive the system or on designing observations and experiments to reveal the external factors crashing down on the lowly caterpillar. Second, in attempting to understand the ecological and evolutionary distribution of herbivores among their host plants, it is easy to forget that what might be termed the carnivory regime and climate regime of a host plant individual or population are as much traits of a plant as is its chemical profile. Both of these regimes should count for much in whether and to what degree a plant or plant part is a suitable host. When we ask why a caterpillar feeds on only one particular host species, it may be as much that it is highly adapted to the predator risks and desiccation regimes of that plant as that it is adapted to the plant's internal chemistry. By the same token, when we ask what does a herbivorous generalist have to do to be a generalist, it may be as much that it has to be able to withstand the predation risks of living on various kinds of backgrounds (e.g., Heinrich & Collins

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1983) as to have the gut chemistry to tolerate various kinds of food (e.g., Ahmad 1983). Which ability came first may be lost in the decomposed pages of time.

I also have an apologetic reason for attempting to meld two sequential fashions. I think we erred in not recognizing two blended questions in the seminal essay that argued that since the herbivores did not eat the green world to the ground, or even down very much, they must be regulated by the carnivores (Hairston et al. 1960). Question one is why don't all the herbivores eat up all the plants? The answer that lay undiscussed by Hairston et al. (1960) is that most of the green world is inedible to any given species of herbivore. Also lying dormant was the derivative evolutionary question of why doesn't any given herbivore species evolve the ability to eat many kinds of plants? Question two is the real question in Hairston et al. (1960); why don't the herbivores that can readily and with impunity consume a species of host plant eat their host to oblivion? Every plant species has at least one herbivore that can eat it. To some degree a plant's herbivores do consume it, thereby leaving resources for other plant species, but to a large degree they do not, with the consequence that competition and the physical environment determine much of the structure of vegetation arrays. The very same carnivory and climatic regimes that prevent herbivores from eating their hosts to oblivion are also the traits of the potential new host that must be overcome when a herbivore evolutionarily moves to, or incorporates, a new host.

Nothing I have said is new, but I feel that the emphasis is different from that of contemporary ecology and evolutionary biology; this emphasis may be witnessed in two recent books on coevolution (Futuyma & Slatkin 1983; Nitecki 1983). Virtually no attention is given to this subject, while the coevolution of herbivores and plant chemistry plays a prominent role in examples and in generation of theory.

I have chosen briefly to describe four systems as illustrative case histories rather than to dwell on hypothetical structure. I do this because of my opinion that theory in evolutionary ecology is intrinsically prone to outrun description of what is actually happening out there.

THE ARENA

The attitudes and examples in this essay derive from my experiences with the herbivore array of a lowland tropical forest, that of Santa Rosa National Park, in northwestern Guanacaste Province, Costa Rica (this site is described in detail in Janzen 1983a and in Boza & Mendoza 1981). This mosaic of deciduous forest, evergreen forest, semi-evergreen forest, and pastures regenerating to forests occupies about 11,000 ha from 0 to 350 m elevation between the Pan-American Highway and the Pacific Ocean. The area has a 5-6-month dry season (approximately December through April), and 1,000-2,000 mm of rain falls during the remainder of the year. Portions of the park were an operating cattle ranch from no later than 1710 to 1978. The vegetation contains at least 680 species broadleafed plants (at least 400 species of perennial woody plants) and supports at least 3,000 species of caterpillars plus several hundred species of other animals that eat living plant parts. There are checklists of plants (Janzen & Liesner 1980), birds (Stiles 1983), reptiles and amphibians (Scott et al. 1983), mammals (Wilson 1983), and butterflies (DeVries 1983) for the park. The plant distributions within this vegetation range from nearly monospecific stands of very large trees (e.g., 10-20-m-tall stands of *Quercus oleoides* Cham. and Schlecht., *Hymenaea courbaril* L., *Ateleia herbert-smithii* (Pittier) to highly mixed vegetation where as many as 200 species of woody plants may occur in 100 ha and adult conspecific crowns are usually sepa-

rated by one to many allospecific crowns. At Santa Rosa, herbivory by caterpillars, the focus of this essay, is characteristically highly heterogeneous among years and among individuals, species, and age classes of plants (e.g., Janzen 1981).

ANATOMY OF A DEFOLIATION EVENT

The event

During the 1983 rainy season, a representative defoliation event occurred at Santa Rosa. The impact of the herbivores was highly heterogeneous. I briefly describe the ecology of this impact as an example of a pattern that could have been generated either by the heterogeneity of internal plant chemistry or by mortality factors external to the plant (or both). In fact, the pattern seems to have been generated by external factors and therefore provides an example for the introductory comments of this essay. It is described in more detail elsewhere (Janzen unpublished manuscript). While the study was conducted in a patch of Santa Rosa forest of approximately 2 km² (Bosque San Emilio, approximately 2 km northeast of the park administration area), the 11,000-ha park contains tens of square kilometers of this type of forest. cursory examination of other forest patches showed that the events described here occurred at those sites as well.

The first generation

From 28 May to 4 June 1983, when 50–90-year-old secondary successional deciduous forest at Santa Rosa was just beginning budbreak following the first significant rains of the rainy season, the forest was sprinkled with ovipositing *Aellopos titan* (Cram.). One or more of these small diurnal sphingid moths (Haber & Frankie 1983) could be seen by simply standing and looking

through the forest for 5 minutes or less at any time during daylight hours. The moths darted among the shrubs and treelets at a height of about 1–3 m. They touched branchlets, twigs, and buds with legs and the tip of the abdomen. Upon encountering a plant of *Randia karstenii* Polak or *R. subcordata* (Stand.) Standley, the moth hesitated a moment longer and sometimes laid a single spherical pale green egg on the bud, newly expanding leaf, thorn, or twig it contacted (Fig. 1). It then flew to other branches of the same plant or, about equally frequently, off to neighboring plants. Both species of *Randia* were beginning budbreak; a few individuals were covered with a thin layer of newly expanding leaves, while others had only swelling buds. The outcome of this oviposition, by what must have been several thousand moths in the study area, was the deposition of tens of eggs to a thousand or more eggs on each *Randia* in the forest (of 214 plants briefly examined, all had some eggs).

For example, on 5 June, all or a major portion of the potential oviposition sites on 14, 1.5–5-m-tall *R. subcordata* were searched thoroughly for *A. titan* eggs. As many as 10 eggs had accumulated on some branch ends (Fig. 1C), but 1 or 2 per branch end or bud was more usual (Fig. 1A, B). The estimated or actual numbers of eggs on these plants ranged from 21 to 1,212, with an average of 197 (SD = 316). Smaller plants (0.7–1.4 m in height) had 1–19 eggs on them (\bar{x} = 6.0, SD = 5.1, n = 10). The small plants were not only shorter, but also had only one or a few stems and branchlets. While I did not count them, the numbers of *A. titan* eggs on the *R. karstenii* appeared to be about the same. Each hectare of this 2-km² patch of forest contains at least four individuals of these two *Randia* species that are 1.5 m or more in height, which allows a rough estimate of 800 oviposition plants carrying a minimum of about 160,000 *A. titan* eggs. If I assume that each female can lay 100 eggs, these eggs represent the oviposition by 1,600 moths.



Fig. 1. — (A) Egg of *Aellopos titan* laid on a spine of *Randia subcordata* at the time of budbreak. (B) Accumulated eggs of *A. titan* following multiple ovipositions over several days on *R. subcordata*. (C) Egg of *A. titan* laid on the underside of an expanding new leaf of *R. subcordata*. 30 May 1983. Santa Rosa National Park, Costa Rica.

From the outset, the number of eggs present on a given plant was the product of several processes. Even while females were ovipositing, eggs were being carried off by *Pseudomyrmex*, *Azteca*, *Crematogaster*, and other ants, picked off by warbler-sized and -shaped birds, and fed on by anthocorid bugs. The eggs hatched 5–6 days after oviposition; even as the first were hatching, more were still being laid. While minute parasitic Hymenoptera were observed ovipositing in the eggs in the field, no parasitoids were reared from a sample of 682 eggs collected from 24 different *R. subcordata* plants, and no parasitoids appeared when 100 of these eggs were reared to the adult stage.

The first-instar larvae are pale green, match well the color of the newly expanding *Randia* leaves, and wander widely through the foliage of the plant on which they hatch. They appear to be highly edible to the ants

and birds mentioned above, reduviid bugs, *Polistes* wasps, other wasps, small spiders, and carabid beetles; all of these animals were observed to capture and eat them or carry them off on numerous occasions. By 4–7 June, tens to hundreds of first- or second-instar *A. titan* larvae could be found on any *Randia* more than 1 m tall, and some larvae were present even on plants as small as 30 cm in height. On all plants the larvae appeared to be healthy and were feeding heavily.

I was absent from the site 8–13 June, and upon my return, it was evident that the outbreak had developed to the extent that three levels of defoliation could be recognized among both species of *Randia*. There were plants with only a few larvae (1–10 per plant by quick inspection), plants with moderate numbers of larvae (10–30 per plant), and plants with hundreds of larvae. On all plants, the larvae appeared

to be healthy and to have about the same size distribution. On 18–20 June, 49 *R. subcordata* plants were thoroughly searched at night for larvae. By searching at night with a strong flashlight, at least 99 percent of the larvae present on a plant were located. By these dates, virtually the entire population was in the ultimate (Fig. 2) or penultimate instar. A few larvae had already left their host plants to pupate

or, if the host was defoliated, to search for more food. No larvae were on 43 percent of the plants, and all of these plants showed minor defoliation; however, there was enough defoliation to make it clear that some *A. titan* caterpillars had developed to moderate size on these plants before leaving or being preyed upon. The plants (33 percent) with 1–10 larvae had either moderate defoliation (10–50 percent of their leaf



Fig. 2. — (A) Ultimate-instar caterpillar of *Aellopos titan*; this green morph has a white lateral posterior diagonal stripe and light lateral diagonal white and magenta side stripes; it is the most common morph (B) Ultimate-instar caterpillar of *A. titan*; this dark morph is dorsally lavender and ventrally black, with white lateral markings. It is the rare morph except during crowding, heavy shading, or total defoliation. The previous two instars of *A. titan* are extremely similar to these caterpillars. 20 June 1983, Santa Rosa National Park, Costa Rica.

surface area) or total leaf loss. In the latter case, the larvae present were wandering over the surface of the plant eating off petioles, leaf blade fragments, and buds. They were obviously a small remnant of much greater numbers of larvae on the tree. Finally, there were trees (25 percent) with 11 to several hundred larvae. For example, I counted, by removal sampling, 246 last-instar caterpillars from one *R. subcordata*, and there were at least another 200 on the tree (Fig. 3). At the time of the census, these densely populated trees still had 10–30 percent of their leaf surface remaining; however, within 5 days, when all larvae had been preyed upon or had left the tree to pupate, all of these leaves had been eaten. Such trees appeared to have had caterpillars that were slightly delayed in their development or initially to have had fewer caterpillars on them than those already stripped of their leaves had had. It was evident that complete defoliation (Fig. 3, 4) was a function of the

number of caterpillars on a plant and the size of the plant. Part of the heterogeneity of defoliation was generated purely by this interaction.

The large ultimate- and penultimate-instar larvae (Fig. 2), were eaten by small to medium-sized birds, reduviid bugs, scorpions, and unidentified mammals. One mammal scat, of a size that could have been produced by a gray fox, small cat, or procyonid, contained 26 head capsules of penultimate and ultimate instar *A. titan* larvae. While such an enormous population of moth larvae would seem to be an easy substrate for intense parasitization, of 617 ultimate and penultimate instar larvae collected and reared, only seven caterpillars were parasitized by tachinids, and none contained parasitic Hymenoptera (Table 1).

The prepupal wandering stage of *A. titan* walks or drops off a plant and burrows into the litter to pupate. Of those which pupated in captivity, all living individuals emerged from the pupal



Fig. 3. — *Randia subcordata* adult tree defoliated by *Aellopos titan*; 3 days before this photograph was taken, this tree had at least 446 ultimate-instar *A. titan* caterpillars on it. The top of the parachute background is 3.8 m above the ground at each end. 23 June 1983, Santa Rosa National Park, Costa Rica



Fig. 4 — *Randia karstenii* subadult treelet defoliated by *Aellopos titan*. 23 June 1983, Santa Rosa National Park, Costa Rica.

stage about 13–15 days after pupation (between 6 and 20 July). Pupal-stage duration was not influenced by wet or extremely dry conditions. The newly emerging adults simply left the site where they had developed; they were not observed at flowers that are standard nectar hosts for *Aellopos* (e.g., *Cedrela odorata* L., which were visited by hundreds of female moths at the time of oviposition in early June). Despite extensive and intensive noctur-

nal searches of *Randia* shrubs from mid-July to the end of August, only three *A. titan* larvae were located. There was no evidence of an attempted or realized second generation of the moth at this site or in other parts of the Santa Rosa forest.

The pupae in the litter were subject to moderate predation by vertebrates. Collared peccaries [*Tayassu tajacu* (L.)] and nine-banded armadillos (*Dasypus novemcinctus* L.) snuffled intensively through the litter below the *Randia* that had had large numbers of caterpillars, and I presume they were harvesting *A. titan* pupae. Spiny pocket mice [*Liomys salvini* (Thomas)] ate the pupae readily in the laboratory and foraged incessantly at night in the forest litter for seeds and insect pupae; on one occasion a mouse brought an *A. titan* pupa into a live trap and ate part of it there. However, living *A. titan* pupae could easily be found by sorting through litter until the time of adult eclosion in mid-July, and numerous newly eclosed adults were encountered on the foliage at that time. There is no doubt that despite the various sources of mortality mentioned above and later, a large number of adults eclosed in Bosque San Emilio and in other patches of deciduous forest in Santa Rosa.

Two weeks after the *A. titan* larvae had disappeared from the *Randia*, I walked a line transect through the Bosque San Emilio and estimated the intensity of defoliation of all *Randia* encountered (14 July 1983). Of 173 *R.*

Table 1. — Fate of 617 penultimate and ultimate instar *Aellopos titan* larvae collected from *Randia subcordata* and *R. karstenii* in Bosque San Emilio, Santa Rosa National Park, Costa Rica (1983).

Date and Host	(n)	Percent Eclosed	Killed by Disease			Parasitized Larvae
			As Larvae	As Pupae	Total	
18 June <i>R. s.</i>	(109)	60	15	26	41	0
18 June <i>R. k.</i>	(117)	60	17	21	38	1
19 June <i>R. s.</i>	(234)	42	28	28	56	3
20 June <i>R. s.</i>	(79)	82	4	14	18	3
23 June <i>R. s.</i>	(50)	90	0	10	10	0
24 June <i>R. k.</i>	(28)	93	0	7	7	0

subcordata, 41 percent were leafless (Fig. 3), 28 percent were moderately but conspicuously defoliated (often with one part of the crown more severely defoliated than another), and the remainder (31 percent) showed only traces of the feeding damage characteristic of *A. titan* larvae. Of 181 *R. karstenii* encountered, 63 percent were essentially leafless (Fig. 4), 30 percent were moderately defoliated, and the remainder appeared intact but had probably been fed on. Since *R. karstenii* leaves are very small and have a weak midrib, the larvae generally ate the entire leaf; small amounts of damage were therefore harder to recognize than they were on *R. cordata*. By the last half of August, all of the defoliated plants were putting out a new leaf crop and appeared approximately as they did during the first week of June. On 15 June 1983, a transect of forest along Quebrada Costa Rica (about 5 km SW of Bosque San Emilio and slightly drier) located 51 *R. karstenii*. All of these plants had lost all of their leaves to *A. titan*.

During the 1979–1982 growing seasons there was no defoliation of *Randia* by *A. titan* (or by any other insect). Frequent searches of numerous *Randia* plants during these 4 years yielded eight *Aellopos* larvae from Bosque San Emilio forest, six of which were parasitized by tachinids or Hymenoptera. The enormous number of adult female *A. titan* which appeared, as if by magic, in the Santa Rosa deciduous forest 25–28 May 1983 must have come from elsewhere, and when their offspring eclosed, they went elsewhere. Whether they arrived as a consequence of having concentrated in a large down-wind area in response to the odor of newly foliating *Randia*, or whether some more complex congregation event occurred, is beyond the scope of this essay.

My field notes from the 1978 rainy season suggest that there was a high density of *A. titan* on *Randia* in the Bosque San Emilio in late May and

early June. While I was not collecting caterpillars in the field at that time, other biologists brought me 23 casually encountered *A. titan* larvae from "*Randia*" in this forest.

This account suggests several questions pertinent to this essay. Why did the newly eclosed adults not attempt a second generation at Santa Rosa by ovipositing on the foliated *Randia*? Why were predation and parasitization rates not high enough to eliminate the first generation or at least depress it to the levels of the 1979–1982 rainy seasons? Why was the final result of this "outbreak" a very heterogeneously defoliated array of *Randia* trees?

No second generation

At the time of *A. titan* eclosion (early to mid-July), the undefoliated *Randia* had at least 5, perhaps 6, months of leafiness ahead of them. Since the egg-to-adult time for *A. titan* is about 35 days, there is ample time in the rainy season for at least three generations. Throughout the 1979–1982 rainy seasons, there were such generations at extremely low densities. In 1981, I recorded *A. titan* oviposition on *R. subcordata* as late in the rainy season as 10 January. In mid-August 1983, I encountered two last instar larva on *R. subcordata* and a single last instar larva on *R. karstenii*, but it was clear that no large pulse of eggs and larvae appeared on *Randia* foliage in July as it did in late May and early June.

Therefore it is clear that the newly eclosing *A. titan* females were confronted with a moderate number of leafy *Randia*, but either they rejected them as oviposition sites and went elsewhere or were programmed to leave the site irrespective of available food. Ironically, a leafy *Randia* that has escaped a defoliation event is probably an unsuitable oviposition site. If *Randia* are foliated because of leaf chemistry (unlikely; see below), then the female should not oviposit on leafy *Randia*. In contrast, until the second half of

August, defoliated individuals did not have enough leaves to support even a few caterpillars. They were leafless at the time of eclosion of the first generation. If, as I suspect, the foliated *Randia* is an indicator of high carnivory risk to eggs and caterpillars, then again, it is not a good oviposition site; the leafless *Randia* suggests a low risk site but offers no food. Selection should favor females that will ignore foliated *Randia* at the site of their birth and search in space or time for sites not subjected to recent defoliation.

It is appropriate to add here that I have observed *A. titan* females to oviposit on the new, partly expanded leaves of *R. subcordata* and *R. karstenii* during all months of the rainy season at Santa Rosa. Furthermore, I have reared their caterpillars on leaves of all ages in all months of the rainy season. While newly foliating *Randia* in late May and early June have more newly expanding leaves than at any other time, the plants also have some newly elongating branchlets at all times of the growing season. There are always some oviposition sites for *A. titan* during the rainy season in the Santa Rosa deciduous forests, even if they will only oviposit on very young foliage.

Relatively low carnivory rates

While eggs and larvae of *A. titan* suffered conspicuous and intense predation, it was not sufficient to eliminate a highly evident array of caterpillars. As a *Randia* was becoming fully defoliated, for the last 2–8 days virtually no search was necessary to see tens of *A. titan* caterpillars on its ever more naked branches and petioles. However, these plants were not being subjected to hordes of insectivorous birds, mammals, or carnivorous insects. During several hours of observing *Randia* heavily infested with ultimate and penultimate instar caterpillars, it was customary to encounter 5–10 reduviid bugs, each killing one caterpillar; several caterpillars being stung or carried off by ants; one or two being carried off

by small to medium-sized birds; and several apparently starving to death because they had fallen or wandered off their host plant. Some plants clearly had all of their caterpillars removed by carnivores, while others retained large numbers even after many had been removed; however, carnivore density was simply not high enough nor their searching thorough enough to depress the *A. titan* caterpillar density on all trees to a level even approximating the low level "normally" observed.

Either the Santa Rosa carnivore density was exceptionally low in 1983 or exceptionally large numbers of *A. titan* eggs were laid there in early 1983. I have no formal census data on carnivore density at Santa Rosa in 1979–1982, but certainly the 1983 density of birds and other predators did not seem to be any lower than were the 1979–1982 levels.

I should add, incidentally, that these levels are much lower than those readily visible in, for example, a Minnesota or Michigan woodlot in late May. However, I can state that there was no massive input of *A. titan* eggs and larvae in the 1979–1982 rainy seasons.¹

The startlingly low numbers of parasitized *A. titan* larvae (Table 1) are consistent with records for other species of caterpillars at Santa Rosa that have suddenly increased greatly in density (unpublished field records). A hypothesis consistent with this low rate of parasitization is that the enormous number of larvae satiated the ovipositional capacity of the parasitoids present. It was striking that four of the seven parasitized larvae had different species of parasitoids in them and that none of the parasitoids were species that I had reared from *A. titan* in the past.

While I could not monitor disease levels in the field, the results of rearing

¹Note added in press: Likewise, in the 1984 and 1985 rainy seasons at Santa Rosa there was no massive input of *A. titan*.

penultimate and ultimate instar wild-caught caterpillars show clearly that disease was taking a severe toll of the caterpillars. The 617 caterpillars collected on 18–24 June (Table 1) were placed in individual plastic bags and were fed with foliage from plants lightly to moderately defoliated by *A. titan* (no plants were available with no *A. titan* damage). The bags were new or had been used (less than 1 percent) to house pupae of undiseased Saturniidae. Overall 39 percent of the caterpillars died of an unknown disease as larvae and as pupae of all ages. By way of contrast, *Aellopos* penultimate or ultimate instar larvae collected during 1979–1982 at Santa Rosa (three species on four host plant species, $n = 53$) invariably produced either adults or parasitoids, even though they were reared in exactly the same manner. The data in Table 1 suggest that the larger the collection of caterpillars, the fewer are killed by disease. However, the relationship actually lies with the age of the caterpillars at the time of collection. The 19 June sample contained the largest number of penultimate instars and the 23 and 24 June samples contained only ultimate instars with 1–3 days remaining before pupation. In the earliest samples, there were infected caterpillars that were fated to die in nature as larvae and that then died in my rearing bags. In the latest samples, those caterpillars that were fated to die in nature as caterpillars had already done so.

It is unlikely that the *A. titan* "outbreak" escaped annihilation because the predators and parasitoids were occupied elsewhere with some other species of prey. The overall caterpillar density in Bosque San Emilia in 1983 was conspicuously lower than in 1979–1982. Furthermore, 5 weeks, one *A. titan* generation, is insufficient time for a functional response by the predator and parasite array. A numerical response depends on both the distance over which the carnivores must move and the areal extent of the high density

of prey. Little can be said about either in this tropical habitat, but it was clear that the high density of *A. titan* larvae covered hundreds of hectares. Also, this part of Costa Rica is not replete with large numbers of, for example, small insectivorous birds that could or would move to an "outbreak" of this sort.

In short, it appears that the local carnivores did not eliminate the *A. titan* outbreak because there were not enough of them to do so. I suspect that this was the case because (1) the outbreak occurred during the first weeks of the rainy season before whatever seasonal increase in carnivores that might occur had occurred, and (2) the habitat is not rich enough in prey to maintain a sufficiently high level of carnivores that they could consume a prey pulse with the properties of the *A. titan* caterpillars. Such an answer contains the implicit assumption that *A. titan* caterpillars are not suitable or available prey to a moderately large portion of the diverse carnivore array at Santa Rosa. The reasons range from physiological incompatibility to size and behavior. For example, the *Enicospilus* (Ichneumonidae) parasitoids that were heavily parasitizing large *Rothschildia lebeau* (Guer-Meneville) (Saturniidae) larvae at the same time in the same forest, have never been encountered in over a thousand rearings of *Aellopos* and other Sphingidae caterpillars in Santa Rosa. The *Pseudomyrmex* and *Azteca* ants that so eagerly kill and carry off first and second instar *A. titan* larvae show no attack response to penultimate and ultimate instar *A. titan* larvae. Coatis [*Nasua nasua* (L.)] readily eat the larvae but do not readily climb the very thin and spiny branches of *Randia*. White-faced monkeys [*Cebus capucinus* (L.)] generally do not forage as low as 1–3 m above the ground in the forest interior during the rainy season and might well have never noticed the outbreak going on below them. The few species of North American migrant birds that visit Guanacaste during the northern winters had long since departed (see Janzen 1980).

Heterogeneous defoliation

The array of predators in a tropical forest possesses sufficient patterned variation in its foraging to generate heterogeneous defoliation from an initial high level and thoroughly spread layer of eggs and caterpillars. One *Randia* may be close to and foraged extensively on by a colony of *Azteca* or *Camponotus* ants, and another only a few meters away may only be passed through by an occasional far-wandering *Pseudomyrmex* ant. A *Campylorhynchus* wren family may have only a single *Randia* in its foraging territory and may therefore thoroughly glean it of its caterpillars; another wren family may have 20 *Randia* in its territory and therefore only moderately glean several and ignore the remainder (F. Joyce, Division of Ecology and Systematics, Cornell University, personal communication). A reduviid bug that settles on a small *Randia* with 10 half-grown caterpillars may well kill all of them before they have done serious defoliation; the same bug on a neighboring tree with 30 caterpillars will at best only slow the time to total defoliation by a few days, since the surviving 20 caterpillars will be quite enough to eat all the leaves off the tree. Had only a few *A. titan* eggs been laid in the forest (as in 1979–1982), heterogeneity of predation would still have occurred, but the consequence would have been invisible against the background of the initial heterogeneity of oviposition. Had there been no carnivory in 1983, all the leaves would have been eaten off all the *Randia* trees, and there would have been major *A. titan* death by starvation. It can be argued that the failure of females to avoid previously laid eggs when ovipositing may well be due to the absence of selection for such behavior if it is usual for the number of surviving offspring to be unrelated to the number of offspring initially present on the plant. Her best chance is to distribute her eggs thinly over the *Randia* population, thereby maximiz-

ing the chance of placing some eggs on those *Randia* where there is low risk from predators.

The strong heterogeneity of defoliation could, at least in theory, also have been generated by heterogeneity in the suitability of the *Randia* foliage in terms of nutrients and secondary chemical defenses. Numerous natural history facts and suppositions argue against this possibility:

1. When second- to fifth-instar larvae were removed from *Randia* that they had defoliated and then were placed on *Randia* that had lost their initial caterpillars, they fed, developed, and pupated normally whether this was done in the field (under a protective net) or in plastic bags in the laboratory. In the laboratory, all larvae produced adults that were smaller than wild adults. However, they were equally dwarfed if they were fed leaves from their partly defoliated tree or leaves from trees quite free from damage (i.e., living in a plastic bag is suboptimal).

2. Defoliation was a function of tree size as well as of caterpillar numbers. A representative 2-m tall tree with 30 developing middle-sized larvae on it was defoliated by the time they left the tree to pupate; a 4-m tall tree with the same number of larvae suffered only minor damage, since it had many more leaves than did the smaller tree.

3. At least 40 different and foliated *Randia subcordata* trees were defoliated by harvesting their leaves to feed larvae in the laboratory. These larvae all developed normally with virtually no death except by disease, parasitoids, and laboratory accidents; their development time was not longer than that of their siblings left on *Randia* in the forest.

4. All foliated trees were fed on to some degree, and a careful search of many trees with no conspicuous damage revealed that one to five large and healthy caterpillars were feeding on them. When the foliage from these

trees was offered to second-instar larvae in the laboratory, these larvae fed readily and developed into normal adults.

It is tempting to wish that one could a priori know which trees were to be defoliated and therefore could obtain a leaf sample whose chemistry could be compared with those of leaves from trees not defoliated. However, this procedure was, and is, impossible when the moth has only one defoliating generation at a site in a season. Furthermore, all *Randia* individuals were fed on by at least one or more caterpillars; defoliation was a matter of degree. Finally, there is the problem of knowing what chemicals to search for in such a comparison. It might well turn out that the eventually defoliated trees would be found to differ chemically from those that were not defoliated. However, there would be no reason to believe that these particular chemical differences, rather than some other covarying plant traits, were responsible for the final levels of defoliation.

HETEROGENEITY AMONG LIFE FORMS AND HABITATS

The risk of carnivory is important to caterpillars (e.g., Heinrich & Collins 1983; Holmes et al. 1979). This risk is not uniformly distributed among plant life forms (e.g., Thompson 1983; Royama 1970; Niemela et al. 1982) nor among the habitat types associated with different life forms. For example, a single large caterpillar in the crown of a large tree that projects above the vegetation should have a quite different probability of being located by a bird than if it were in the crown of a small sapling of the same species of tree projecting from young secondary succession. Likewise, a caterpillar in prey-rich, forest-edge herbaceous vegetation is more likely to be encountered by a *Polistes* wasp than if it were in the prey-poor canopy of a patch of ever-

green forest. At Santa Rosa, the distribution of saturniid and sphingid caterpillars among their host plants provides an example.

At Santa Rosa, there are 30 breeding populations of Saturniidae (Janzen 1982) and at least 63 breeding populations of Sphingidae (Janzen 1984b). In an ongoing study, I have located at least one native host plant for 80 percent of the saturniids and 77 percent of the sphingids known or strongly suspected to breed at Santa Rosa (Tables 2 and 3). After examining only the host Latin binomials and caterpillar family names in Tables 2 and 3, it is evident that the huge caterpillars of sphingids and saturniids have little in common in their use of food plants (Janzen 1984b). Furthermore, at least half of the overlap in the two lists is a more apparent than a real similarity of food choice.

In keeping with current emphases on the causes of host specificity, several years ago a slightly reduced subset of the plants in Tables 2 and 3 was analyzed for phenolics and alkaloids (Janzen & Waterman 1983). The foliage of the saturniid hosts was found to contain significantly more phenolics and less water than did that of the sphingid hosts, while the sphingid hosts much more frequently contained alkaloids than did the saturniid hosts. These results are in strong agreement with two general impressions held by lepidopterists: (1) Most saturniids feed on tree foliage (traditionally viewed as rich in tannins), and (2) most sphingids feed on plants in families famous for toxic small molecules, resins, and copious latex flow. While not meaning to denigrate the reality of these patterns, there is obviously a quite different way to view the same set of host records.

It is evident that, as found in nature, the saturniid caterpillars are generally in the crowns of adult trees, while the sphingid caterpillars are found in plants ranging from small herbs to vines to saplings to crowns of large trees (Tables 2 and 3). The most

Table 2. — Larval hosts of Saturniidae in nature in Santa Rosa National Park, Costa Rica (as of December 1983).

Larva	Host	Microhabitat
Arsenurinae		
<i>Arsenura armida</i> (Cram.)	<i>Bombacopsis quinatum</i> (Jacq.) Dugand (Bombacaceae)	large tree crown
<i>Caio championi</i> (Drc.)	<i>Bombacopsis quinatum</i> (Jacq.) Dugand (Bombacaceae)	large tree crown
<i>Copiopteryx semiramis</i> (Cram.)	<i>Manilkara chicle</i> (Pittier) Gilly (Sapotaceae)	large tree crown
<i>Dysdaemonia boreas</i> (Cram.)	<i>Ceiba pentandra</i> (L.) Gaerth. (Bombacaceae) ^a	large tree crown
<i>Titaea tamerlan</i> (Maassen)	<i>Bombacopsis quinatum</i> (Jacq.) Dugand (Bombacaceae)	large tree crown
Ceratocampinae		
<i>Adeloneivaia isara</i> (Dognin)	<i>Lysiloma divariciata</i> (Jacq.) Macbride (Leguminosae) <i>Lysiloma auritum</i> (Schl.) Benth. (Leguminosae)	large tree crown large tree crown
<i>Citheronia bellavista</i> (Draudt)	<i>Phoradendron quadrangulare</i> (HBK) Krug & Urb. (Loranthaceae) ^b	parasite in crown of large tree
<i>Citheronia lobesis</i> (W. Rothschild)	<i>Cochlospermum vitifolium</i> (Willd.) Spreng. (Cochlospermaceae) <i>Bursera simaruba</i> (L.) Sarg. (Burseraceae) <i>Spondias mombin</i> L. (Anacardiaceae) <i>Psidium guajava</i> L. (Myrtaceae) ^c <i>Calycophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae) <i>Phoradendron quadrangulare</i> (HBK.) Krug & Urb. (Loranthaceae)	large saplings large tree crown large saplings shrubby treelet large tree crown parasite in crown of large tree
<i>Eacles imperialis</i> (Dry.)	<i>Cochlospermum vitifolium</i> (Willd.) Spreng. (Cochlospermaceae) <i>Bursera tomentosa</i> (Jacq.) Triana & Planch. (Burseraceae) <i>Astronium graveolens</i> Jacq. (Anacardiaceae) <i>Cedrela odorata</i> L. (Meliaceae)	large saplings and large tree crown large tree crown large tree crown large tree crown
<i>Othorene purpurascens</i> (Schaus)	<i>Manilkara chicle</i> Pittier (Gilly) Sapotaceae	large tree crown
<i>Othorene verana</i> (Schaus)	<i>Quercus oleoides</i> Cham. & Schlecht. (Fagaceae)	large tree crown
<i>Ptiloscota dargei</i> Lemaire	<i>Acacia tenuifolia</i> (L.) Willd. (Leguminosae)	saplings and large vine crown
<i>Schausiella santarosensis</i> Lemaire	<i>Hymenaea courbaril</i> L. (Leguminosae)	large tree crown
<i>Syssphinx colla</i> (Dyar)	<i>Pithecellobium saman</i> (Jacq.) Benth. (Leguminosae)	large tree crown
<i>Syssphinx mexicana</i> (Bdv.)	<i>Acacia collinsii</i> Safford (Leguminosae) <i>Acacia cornigera</i> L. (Leguminosae)	sapling to adult treelet crown sapling to adult treelet crown

Table 2. — Continued

Larva	Host	Microhabitat	
<i>Syssphinx molina</i> (Cram.)	<i>Pithecellobium saman</i> (Jacq.) Benth. (Leguminosae)	large tree crown	
	<i>Cassia grandis</i> L. (Leguminosae) ^c <i>Albizzia adinocephala</i> (Donn. Sm.) Britt. & Rose (Leguminosae)	large tree crown	
<i>Syssphinx quadrilineata</i> (G. & R.)	<i>Pithecellobium saman</i> (Jacq.) Benth. (Leguminosae)	large tree crown	
Hemileucinae			
<i>Automeris io</i> (F.)	<i>Crescentia alata</i> HBK. (Bignoniaceae) ^c	large tree crown	
	<i>Mimosa pigra</i> L. (Leguminosae)	shrub	
	<i>Cassia biflora</i> L. (Leguminosae)	shrub	
	<i>Rhynchosia reticulata</i> (Swartz) DC. (Leguminosae)	herbaceous vine	
	<i>Gliricidia sepium</i> (Jacq.) Walp. (Leguminosae)	sapling	
	<i>Automeris rubrescens</i> (Wlk.)	<i>Inga vera</i> Willd. (Leguminosae)	sapling
		<i>Rourea glabra</i> HBK. (Connaraceae)	scandent shrub
		<i>Guazuma ulmifolia</i> Lam. (Sterculiaceae)	large tree crown
		<i>Cassia biflora</i> L. (Leguminosae)	shrub
		<i>Quercus oleoides</i> Cham. & Schlecht. (Fagaceae)	sapling
		<i>Cordia alliodora</i> (R. & P.) Oken (Boraginaceae)	sapling
		<i>Lonchocarpus minimiflorus</i> Donn. Smith (Leguminosae)	sapling
		<i>Calycophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae)	large tree crown
DHJ 12175 (Bignoniaceae)		sapling vine	
<i>Zuelania guidonia</i> (SW.) Britt. & Millsp. (Flacourtiaceae)		large tree crown	
<i>Crescentia alata</i> HBK. (Bignoniaceae) ^c		large tree crown	
<i>Cassia grandis</i> L. (Leguminosae)		large tree crown	
<i>Automeris zugana</i> Drc.	<i>Annona purpurea</i> Moc. & Sesse (Annonaceae)	large tree crown	
	<i>Lonchocarpus costaricensis</i> Pittier (Leguminosae)	large tree crown	
	<i>Quercus oleoides</i> Cham. & Schlecht. (Fagaceae)	large tree crown	
	<i>Cydista heterophylla</i> Seib. (Bignoniaceae)	large woody vine	
	<i>Calycophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae)	sapling to large tree crown	
	<i>Hymenaea courbaril</i> L. (Leguminosae)	sapling	
	<i>Solanum hazenii</i> Britt. (Solanaceae)	large herb	
	<i>Lantana camara</i> L. (Verbenaceae) ^c	large herb/shrub	
	<i>Lonchocarpus eriocarinalis</i> Micheli (Leguminosae)	large tree crown	
	<i>Centrosema pubescens</i> Benth. (Leguminosae)	herb vine	

Table 2. — Continued

Larva	Host	Microhabitat
	<i>Cassia hayesiana</i> (B. & R.) Standl. (Leguminosae)	shrub/treelet
	<i>Inga vera</i> Willd. (Leguminosae)	sapling
	<i>Serjania atroliniata</i> Sauv. & Wr. (Sapindaceae)	large vine
<i>Dirphia avia</i> (Stoll)	<i>Hymenaea courbaril</i> L. (Leguminosae)	large tree crown
	<i>Cedrela odorata</i> L. (Meliaceae)	large tree crown
<i>Hylesia dalina</i> Schaus	<i>Casearia arguta</i> HBK. (Flacourtiaceae)	treelet
	<i>Malvaviscus arboreus</i> Cav. (Malvaceae)	shrub
<i>Hylesia lineata</i> Drc.	<i>Tabebuia rosea</i> (Vertol.) DC. (Bignoniaceae)	sapling
	<i>Bombacopsis quinatum</i> (Jacq.) Dugand (Bombacaceae)	large tree crown
	<i>Cordia alliodora</i> (R. & P.) Oken (Boraginaceae)	treelet
	<i>Hirtella racemosa</i> Lam. (Chrysobalanaceae)	treelet
	<i>Muntingia calabura</i> (Swartz) DC. (Elaeocarpaceae)	treelet
	<i>Casearia arguta</i> HBK. (Flacourtiaceae)	treelet
	<i>Casearia sylvestris</i> SW. (Flacourtiaceae)	treelet
	<i>Casearia corymbosa</i> HBK. (Flacourtiaceae)	treelet
	<i>Zuelania guidonia</i> (SW.) Britt. & Millsp. (Flacourtiaceae)	large tree crown
	<i>Acacia tenuifolia</i> (L.) Willd. (Leguminosae)	large vine crown
	<i>Cassia biflora</i> L. (Leguminosae)	shrub
	<i>Diphysa robinoides</i> Benth. (Leguminosae)	sapling
	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb. (Leguminosae)	large tree crown
	<i>Hymenaea courbaril</i> L. (Leguminosae)	sapling
	<i>Inga vera</i> Willd. (Leguminosae)	treelet
	<i>Lonchocarpus minimiflorus</i> Donn. Smith. (Leguminosae)	treelet
	<i>Lonchocarpus costaricensis</i> Pittier (Leguminosae)	sapling
	<i>Lysiloma auritum</i> (Schl.) Benth. (Leguminosae)	large tree crown
	<i>Machaerium kegelii</i> (Meisner) (Leguminosae)	sapling large vine
	<i>Mimosa pigra</i> L. (Leguminosae)	shrub
	<i>Myrospermum frutescens</i> Jacq. (Leguminosae)	treelet
	<i>Pithecellobium lanceolatum</i> (H. & B.) Benth. (Leguminosae)	treelet
	<i>Hyptis pectinata</i> Poit. (Labiatae)	large herb
	<i>Malvaviscus arboreus</i> Cav. (Malvaceae)	shrub
	<i>Banisteriopsis muricata</i> (Cav.) Cuatr. (Malpighiaceae)	low vine

Table 2. — Continued

Larva	Host	Microhabitat
	<i>Byrsonima crassifolia</i> (L.) HBK. (Malpighiaceae)	treelet
	<i>Stigmaphyllon ellipticum</i> (HBK.) Adr. Juss. (Malpighiaceae)	low vine
	<i>Psidium guineense</i> SW. (Myrtaceae)	shrub
	<i>Ouratea lucens</i> (HBK.) Engler (Ochnaceae)	shrub
	<i>Gouania polygama</i> (Jacq.) Urban (Rhamnaceae)	low vine
	<i>Calycophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae)	sapling
	<i>Chomelia spinosa</i> Jacq. D. (Rubiaceae)	treelet
	<i>Guettarda macrosperma</i> D. Sm. (Rubiaceae)	treelet
	<i>Xanthoxylum setulosum</i> P. Wilson (Rutaceae)	sapling
	<i>Allophylus occidentalis</i> (SW.) Radlk. (Sapindaceae)	treelet
	<i>Cupania guatemalensis</i> (Turcz.) Radlk. (Sapindaceae)	treelet
	<i>Paullinia cururu</i> L. (Sapindaceae)	low vine
	<i>Serjania schiedeana</i> Schlecht. (Sapindaceae)	low vine
	<i>Urvillea ulmacea</i> HBK. (Sapindaceae)	low vine
	<i>Byttneria aculeata</i> Jacq. (Sterculiaceae)	shrub
	<i>Byttneria catalpaefolia</i> Jacq. (Sterculiaceae)	low vine
	<i>Guazuma ulmifolia</i> Lam. (Sterculiaceae)	medium tree
	<i>Luehea speciosa</i> Willd. (Tilliaceae)	sapling
	<i>Lantana camara</i> L. (Verbenaceae) ^c	shrub
	<i>Erythroxylum havanense</i> Jacq. (Erythroxylaceae)	shrub
	<i>Calliandra emarginata</i> Benth. (Leguminosae)	shrub
<i>Periphoba arcaei</i> (Drc.)	<i>Eugenia salamensis</i> Donn. Sm. (Myrtaceae)	medium tree crown
	<i>Cassia biflora</i> L. (Leguminosae)	shrub
	<i>Guazuma ulmifolia</i> Lam. (Sterculiaceae)	large tree crown
	<i>Lysiloma auritum</i> (Schl.) Benth. (Leguminosae)	large tree crown
	<i>Spondias mombin</i> L. (Anacardiaceae)	large tree crown
	<i>Rourea glabra</i> HBK. (Connaraceae)	scandent shrub
	<i>Annona purpurea</i> Moc. & Sesse (Annonaceae)	treelet crown
	<i>Calycophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae)	large tree crown
	<i>Bombacopsis quinatum</i> (Jacq.) Dugand (Bombacaceae)	large tree crown

Table 2. — Continued

Larva	Host	Microhabitat
	<i>Cassia alata</i> L. (Leguminosae) ^c	large tree crown
	<i>Inga vera</i> Willd. (Leguminosae)	medium tree crown
	<i>Ardisia revoluta</i> HBK. (Myrsinaceae)	treelet
	<i>Astronium graveolens</i> Jacq. (Anacardiaceae)	sapling
	<i>Hymenaea courbaril</i> L. (Leguminosae)	sapling
	<i>Quercus oleoides</i> Schlecht. & Cham. (Fagaceae)	large tree crown
	<i>Miconia argentea</i> (Swartz) DC. (Melastomataceae)	sapling
Saturniinae		
<i>Copaxa moinieri</i> Lemaire	<i>Ocotea veraguensis</i> (Meisn.) Vlez (Lauraceae)	saplings and lower branches of treelet
<i>Rothschildia erycina</i> (Shaw)	<i>Exostema mexicanum</i> (Jacq.) Roem. & Schult. <i>Coutarea hexandra</i> (Jacq.) Schum. (Rubiaceae)	large tree crown treelet crown
<i>Rothschildia lebeau</i> (Guer.-Ménéville)	<i>Exostema mexicanum</i> Jacq. Roem. & Schult. (Rubiaceae) <i>Spondias mombin</i> L. (Anacardiaceae) <i>Spondias purpurea</i> L. (Anacardiaceae) <i>Casearia corymbosa</i> HBK. (Flacourtiaceae) <i>Zuelania guidonia</i> (Sw.) Britt. & Rose (Flacourtiaceae) <i>Xanthoxylum setulosum</i> P. Wilson (Rutaceae)	large tree crown large tree crown treelet treelet large tree crown large tree crown

^a Not yet found in nature but accepts readily and dies on other Santa Rosa Bombacaceae.

^b Not yet found in nature but accepts readily and has the appropriate color and behavior to use this host.

^c Plant introduced to Santa Rosa within past several hundred years.



Table 3 — Larval hosts of Sphingidae in nature in Santa Rosa National Park, Costa Rica (as of December 1983).

Larva	Host	Microhabitat
<i>Aellopos clavipes</i> (R. & J.)	<i>Randia karstenii</i> Polak (Rubiaceae)	sapling to treelet
<i>Aellopos fadus</i> (Cram.)	<i>Genipa americana</i> L. (Rubiaceae)	sapling to large tree
	<i>Alibertia edulis</i> A. Rich. (Rubiaceae)	shrub
<i>Aellopos titan</i> (Cram.)	<i>Randia karstenii</i> Polak (Rubiaceae) <i>Randia subcordata</i> (Stand.) Standley (Rubiaceae)	sapling to treelet sapling to treelet
<i>Agrius cingulatus</i> (F.)	<i>Merremia umbellata</i> (L.) Hall (Convolvulaceae)	herb vine

Table 3. — Continued

Larva	Host	Microhabitat
<i>Aleuron carinata</i> Wlk.	DHJ 12071 (Convolvulaceae) <i>Dolioscarpus dentatus</i> (Aubl.) Stand. (Dilleniaceae)	herb vine low perennial vine
<i>Aleuron iphis</i> Wlk.	<i>Tetracera volubilis</i> L. (Dilleniaceae)	low perennial vine
<i>Amplypterus gannascus</i> (Stoll)	<i>Ocotea veraguensis</i> (Meisn.) Vlez (Lauraceae)	sapling to treelet
<i>Amplypterus ypsilon</i> R. & J.	<i>Ocotea veraguensis</i> (Meisn.) Vlez (Lauraceae)	sapling to treelet
<i>Callionima falcifera</i> (Gehlen)	<i>Stemmadenia obovata</i> (Hook & Arn.) K. Schum. (Apocynaceae)	sapling to treelet
<i>Cautethia spuria</i> (Bdv.)	<i>Exostema mexicanum</i> A. Gray (Rubiaceae)	sapling to large tree
	<i>Coutarea hexandra</i> (Jacq.) Schum. (Rubiaceae)	treelet
<i>Cautethia yucatanana</i> B. P. Clark	<i>Exostema mexicanum</i> A. Gray (Rubiaceae)	treelet
<i>Cocytius duponchel</i> (Poey)	<i>Annona purpurea</i> Moc. & Sesse (Annonaceae)	sapling to treelet
	<i>Annona reticulata</i> L. (Annonaceae)	sapling to treelet
<i>Enyo ocypete</i> (L.)	<i>Tetracera volubilis</i> L. (Dilleniaceae)	low perennial vine
	<i>Cissus rhombifolia</i> Vahl. (Vitaceae)	herb vine
<i>Erinnyis ello</i> (L.)	<i>Sebastiania confusa</i> Lundell (Euphorbiaceae)	sapling to treelet
	<i>Sapium thelocarpum</i> Schm. & Pitt. (Euphorbiaceae)	sapling
	<i>Manilkara chicle</i> (Pittier) Gilly (Sapotaceae)	large tree
<i>Erinnyis lasauxii</i> (Bdv.)	<i>Sarcostemma glauca</i> HBK. (Asclepiadaceae)	low vine
<i>Erinnyis oenotrus</i> (Cram.)	<i>Fosteronia spicata</i> (Jacq.) G. Mey (Apocynaceae)	low perennial vine
<i>Eumorpha anchemola</i> (Gram.)	<i>Cissus rhombifolia</i> Vahl. (Vitaceae)	low perennial vine
	<i>Cissus sicyoides</i> L. (Vitaceae)	low perennial vine
<i>Eumorpha satellitia</i> (L.)	<i>Cissus rhombifolia</i> Vahl. (Vitaceae)	low perennial vine
	<i>Cissus sicyoides</i> L. (Vitaceae)	low perennial vine
<i>Eupyrroglossum sagra</i> (Poey)	<i>Chomelia spinosa</i> Jacq. (Rubiaceae)	sapling to treelet
	<i>Guettarda macrocarpa</i> D. Sm. (Rubiaceae)	sapling to treelet
<i>Isognathus rimosus</i> (Grt.)	<i>Plumeria rubra</i> L. (Apocynaceae)	large tree
<i>Manduca barnesi</i> (Clark)	<i>Godmania aesculifolia</i> (HBK.) Standl. (Bignoniaceae)	sapling
<i>Manduca corallina</i> (Drc.)	<i>Cordia alliodora</i> (R. & P.) Oken (Boraginaceae)	sapling to large tree
<i>Manduca dilucida</i> (Hy. Edw.)	<i>Sapranthus palanga</i> Fries (Annonaceae)	sapling to treelet
	<i>Annona reticulata</i> L. (Annonaceae)	sapling to treelet
<i>Manduca florestana</i> (Cram.)	<i>Pithecoctinium crucigerum</i> (L.) A. Gentry (Bignoniaceae)	low perennial vine
	<i>Cydista heterophylla</i> Seib. (Bignoniaceae)	low perennial vine
	<i>Tabebuia ochracea</i> (Cham.) Standl. (Bignoniaceae)	sapling
	<i>Callichlamys latifolia</i> (L. Rich) K. Schum. (Bignoniaceae)	low perennial vine
	<i>Arrabidaea chica</i> (H. & B.) Verl. (Bignoniaceae)	low perennial vine
	<i>Cornutia grandifolia</i> (Schlecht. & Cham.) Schau. (Verbenaceae)	shrub
	<i>Ceratophytum tetragonolobum</i> (Jacq.) Sprague & Sandw.	low perennial vine

Table 3. — Continued

Larva	Host	Microhabitat
<i>Manduca lefeburei</i> (Guer.)	<i>Plenontoma variabilis</i> (Jacq.) Miers (Bignoniaceae)	low perennial vine
	<i>Stachytarpheta frantzii</i> Polak (Verbenaceae)	shrub
	<i>Casearia sylvestris</i> SW. (Flacourtiaceae)	sapling to treelet
	<i>Casearia corymbosa</i> HBK. (Flacourtiaceae)	sapling to treelet
<i>Manduca muscosa</i> (R. & J.)	<i>Verbesina gigantea</i> Jacq. (Compositae)	giant herb
	<i>Lantana camara</i> L. (Verbenaceae)	shrub
	<i>Lasianthaea fruticosa</i> (L.) K. Becker (Compositae)	shrub
	<i>Baltimora recta</i> L. (Compositae)	herb
<i>Manduca occulta</i> (R. & J.)	<i>Melanthera aspera</i> (Jacq.) Small (Compositae)	herb
	<i>Wedelia calycina</i> L. C. Rich (Compositae)	herb
	<i>Solanum ochraceo-ferrugineum</i> (Dun.) Fern (Solanaceae)	herb
	<i>Solanum hazenii</i> Britt. (Solanaceae)	herb
<i>Manduca rustica</i> (F.)	<i>Solanum accrescens</i> Standl. & Mort. (Solanaceae)	herb
	<i>Cestrum</i> DHJ 12029 (Solanaceae)	shrub
	<i>Lantana camara</i> L. (Verbenaceae) ^a	shrub
	<i>Stachytarpheta frantzii</i> Polak (Verbenaceae)	shrub
<i>Manduca sexta</i> (L.)	<i>Cordia panamensis</i> Riley (Boraginaceae)	sapling
	<i>Pithecoctenium crucigerum</i> (L.) A. Gentry (Bignoniaceae)	low perennial vine
	<i>Amphilophium paniculatum</i> (L.) HBK. (Bignoniaceae)	low perennial vine
	<i>Merremia umbellata</i> (L.) Hall (Convolvulaceae)	herb vine
<i>Neococytius cluentius</i> (Cram.)	DHJ 12071 (Convolvulaceae)	herb vine
	<i>Hyptis verticillata</i> Jacq. (Labiatae)	herb
	<i>Capsicum annum</i> L. (Solanaceae)	herb
	<i>Lycopersicon esculentum</i> Mill. (Solanaceae) ^a	herb
<i>Nyceryx coffeae</i> (Wlk.)	<i>Piper marginatum</i> Jacq. (Piperaceae)	shrub
<i>Pachygonia drucei</i> R. & J.	<i>Calycophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae)	sapling to large tree
	<i>Doliocarpus dentatus</i> (Aubl.) Stand. (Dilleniaceae)	low perennial vine
<i>Pachylia ficus</i> (L.)	<i>Ficus insipida</i> Willd. (Moraceae)	sapling to large tree
	<i>Ficus continifolia</i> HBK. (Moraceae)	sapling to large tree
	<i>Ficus obtusifolia</i> HBK. (Moraceae)	sapling to large tree
	<i>Ficus ovalis</i> (Liebm.) Miq. (Moraceae)	sapling to large tree
	<i>Brosimum alicastrum</i> Swartz. (Moraceae)	sapling

Table 3. — Continued

Larva	Host	Microhabitat
	<i>Chlorophora tinctoria</i> (L.) Gaud. (Moraceae)	sapling to large tree
<i>Pachylia syces</i> (Hbn.)	<i>Castilla elastica</i> Cerv. (Moraceae) <i>Ficus ovalis</i> (Liebm.) Miq. (Moraceae)	sapling large tree
<i>Pachyloides resumens</i> (Wlk.)	<i>Forsteronia spicata</i> (Jacq.) Mull (Apocynaceae)	low perennial vine
<i>Perigonia lusca</i> (F.)	<i>Calcophyllum candidissimum</i> (Vahl.) DC. (Rubiaceae)	sapling to large tree
<i>Protambulyx strigilis</i> (L.)	<i>Guettarda macrosperma</i> D. Sm. (Rubiaceae) <i>Astronium graveolens</i> Jacq. (Anacardiaceae)	sapling to treelet sapling to large tree
<i>Pseudosphinx tetrio</i> (L.) <i>Sphinx merops</i> Bdv.	<i>Spondias mombin</i> L. (Anacardiaceae) <i>Plumeria rubra</i> L. (Apocynaceae) <i>Lantana camara</i> L. (Verbenaceae) ^a	sapling to large tree large tree shrub herb
<i>Unzela pronoe</i> (Drc.)	<i>Hyptis pectinata</i> Poit. (Labiatae) <i>Tetracera volubilis</i> L. (Dilleniaceae)	low perennial vine
<i>Xylophanes anubus</i> (Cram.)	<i>Psychotria nervosa</i> Sw. (Rubiaceae) <i>Psychotria horizontalis</i> Sw. (Rubiaceae)	shrub shrub/herb
<i>Xylophanes ceratomioides</i> (G. & R.) <i>Xylophanes chiron</i> Dry.	<i>Hamelia patens</i> Jacq. (Rubiaceae) <i>Psychotria pubescens</i> Sw. (Rubiaceae) <i>Psychotria horizontalis</i> Sw. (Rubiaceae)	shrub shrub shrub
<i>Xylophanes juanita</i> R.	<i>Faramea occidentalis</i> (L.) A. Rich. (Rubiaceae) <i>Psychotria pubescens</i> Sw. (Rubiaceae) <i>Psychotria horizontalis</i> Sw. (Rubiaceae) <i>Psychotria nervosa</i> Sw. (Rubiaceae)	sapling shrub shrub/herb shrub
<i>Xylophanes maculator</i> (Bdv.)	<i>Psychotria horizontalis</i> Sw. (Rubiaceae)	shrub/herb
<i>Xylophanes pluto</i> (F.) <i>Xylophanes porcus</i> (Hbn.) <i>Xylophanes turbata</i> (Hy. Edw.)	<i>Hamelia patens</i> Jacq. (Rubiaceae) <i>Hamelia patens</i> Jacq. (Rubiaceae) <i>Hamelia patens</i> Jacq. (Rubiaceae) <i>Psychotria microdon</i> (DC.) Urban (Rubiaceae)	shrub shrub shrub to treelet shrub/herb
<i>Xylophanes tyndarus</i> (Bdv.)	<i>Faramea occidentalis</i> (L.) A. Rich. (Rubiaceae)	treelet

^a Host plant introduced to Santa Rosa National Park.

revealing addendum to this pattern is that if those same saturniid caterpillars are placed on small saplings inside screen nets, they develop into quite normal adults. This is true whether they are transferred as first-instar or any later-instar caterpillars. I have done this with *Rothschildia lebeau* on *Spondias mombin* L. and *Xanthoxylum setulosum* P. Wilson; *R. erycina* (Shaw) on *Exostema mexicanum* A. Gray and *Coutarea hexandra* (Jacq.) Schum.; *Eacles imperialis* (Dry.) on *Cochlospermum vitifolium* (Willd.) Spreng.; *Citheronia lobesis* W. Rothschild on *Calycophyllum candidissimum* (Vahl.) DC., *Spondias mombin*, and *Cochlospermum vitifolium*; *Arsenura armida* (Cram.), *Caio championi* (Drc.), and *Titaea tamerlan* (Maassen) on *Bombacopsis quinatum* (Jacq.) Dugand; *Othorene purpurascens* (Schaus) on *Manilkara chicle* (Pittier) Gilly; *Othorene verana* (Schaus) on *Quercus oleoides*; *Syssphinx molina* (Cram.) on *Pithecellobium saman* (Jacq.) Benth., *Cassia grandis* L., and *Albizia adinocephala* (Donn. Sm.) Britt. & Rose; *Syssphinx colla* (Dyar) on *Pithecellobium saman*; *Adeloneivaia isara* (Dognin) on *Lysiloma divaricata* (Jacq.) Macbride and *L. auritum* (Schl.) Benth.; and *Dirphia avia* (Stoll) and *Schausiella santarosensis* Lemaire on *Hymenaea courbaril*. The net protects the caterpillars from carnivores but does not, I assume, seriously modify the microclimate of the plant's physiology.

The opposite experiment, putting these species of saturniid larvae on a host plant sapling in nature without a protective net, results in rapid removal of the caterpillars by ants, wasps, birds, scorpions, mammals, and spiders. The few survivors are very often parasitized. I am in the process of conducting large-scale experiments which will yield an understanding of the variation and how it compares with the mean and variance of the same experiments in adult host plant crowns. However, a few preliminary results are instructive.

On 18 July 1983, I placed 340 first-instar, newly hatched *Rothschildia*

lebeau caterpillars on a 4-m tall bushy *Spondias mombin* sapling growing in a tangle of secondary succession. The lower trunk was ringed with Tanglefoot, and the surrounding vegetation was trimmed so that the host plant did not contact any other plant. By 8 August, 21 days later, only 13 caterpillars remained, all late penultimate instar. On 15 August, 3-5 days before they were due to wander off the plant to pupate, I removed the 12 remaining survivors, all of which spun cocoons. Of these caterpillars, 5 contained a large ichneumonid wasp larva (*Enicospilus*), 3 contained larvae of tachinid flies, 3 died of disease inside their cocoons before they could pupate, and 1 produced a healthy pupa.

On 30 June, I placed 120 third- and early fourth-instar larvae of *Syssphinx molina* on 60 sapling *Pithecellobium saman* growing in roadside secondary succession within 100 m of adult *P saman*. Shortly before these larvae (Fig. 5A) were due to leave the plant to pupate in the litter and only 11 days after they had been placed out, I collected the 14 survivors. Three of these contained larvae of a species of *Thyreodon*, an ichneumonid wasp apparently specific to this caterpillar and its close relatives, and six produced healthy pupae; the remainder died of disease. As yet I have no extensive data on the survivorship of *Rothschildia lebeau* or *Syssphinx molina* caterpillars in the crowns of their large tree host plants, but numerous anecdotal observations suggest that it will be greater than the low levels of survival mentioned above.

There is a very conspicuous exception to the generality that saturniids are concentrated in the crowns of adult trees. Hemileucine saturniids, the 10 moth to extratropical New World readers, are found both on juveniles of their hosts and on species of plants that are normally small as adults and are therefore imbedded in low secondary succession (these caterpillars are found as well in the crowns of large trees; see Table 2). Hemileucine caterpillars (Fig. 5B, C) are the most severe urticators of

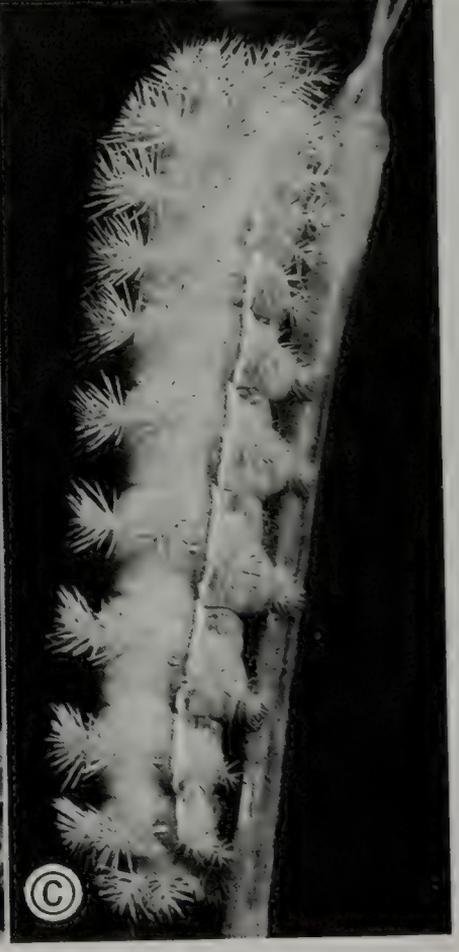


Fig. 5. — (A) Ultimate-instar larva of *Syssphinx molian*; this green morph has a greenish-white lateral stripe, yellow thoracic horns (scoli), and posterior dorsal gold toothlike spines. (B) Ultimate-instar urticating larva of *Periphoba arcaei*; this green caterpillar has a pale whitish-green lateral line with a lavender line just above it. (C) Ultimate-instar urticating larva of *Automeris io*; this green caterpillar has a white lateral line with a dark red lateral line just above it and lower lateral dark red patches with white dots. July-August 1983, Santa Rosa National Park, Costa Rica.

the saturniid world. As such they are largely invulnerable to a major subset of the vertebrate carnivores that probably find it more profitable to search for food in secondary succession than in the huge monospecific expanses of leaves in the forest canopy.

It is too early in this investigation to be able to offer a clean hypothesis about what allows sphingid caterpillars to feed on such a diversity of plant life forms (Table 3), especially on the small ones. However, some possibilities come to mind (cf. Janzen 1984b).

1. Sphingid adults live for weeks to months (as compared with 3–10 days for saturniid females) and therefore have more time to seek out widely scattered small individual hosts on which to lay only one or very few eggs at a time; with only a few nights to search for a host, a saturniid female may find it more profitable to search for a few large crowns and lay many eggs on each than to have to locate many saplings.

2. By being initially widely scattered, sphingid caterpillars avoid density-dependent effects, such as are likely to occur when, for example, a *Polistes* wasp finds one of many saturniid caterpillars on a plant and repeatedly returns to harvest them.

3. Because they are extremely host-specific, sphingid caterpillars are on average more cryptic than are saturniid caterpillars and therefore have a greater chance of surviving the visually oriented component of the more intense carnivory that, I suspect, occurs in the low vegetation of secondary succession.

4. Sphingid caterpillars grow more rapidly to a given size than do saturniids of the same body weight; they are therefore exposed to agents of larval mortality for a shorter period than are saturniid caterpillars.

5. Sphingid caterpillars may have chemical or physical defenses against invertebrate carnivores, defenses that saturniids lack. I have seen the same *Polistes* that aggressively harvests

young *Caio championi* caterpillars from sapling *Bombacopsis* land on *Manduca sexta* (L.) caterpillars and simply walk on in search of food, apparently treating the caterpillars as though they were part of the plant.

Three species of "primitive" sphingids (Smerinthinae) at Santa Rosa offer instructive exceptions to the generality that sphingids and saturniids have different hosts at Santa Rosa. *Protambulyx strigilis* (L.) caterpillars are commonplace on *Spondias mombin* and *Astronium graveolens* Jacq., ranging from 1.5-m saplings to the crowns of 20-m, full-grown trees; they are found on all sizes of their hosts from forest understory to tree falls to large expanses of recent secondary succession along roads and in old fields. They are heavily parasitized by tachinids on all of these plant life forms and in all habitats. In forests, and on forest edges, *Rothschildia lebeau* (Saturniidae) caterpillars are found only in the crowns of medium-sized to large *Spondias mombin*; it is extremely difficult to imagine what besides predator pressure could have been responsible for the evolution or ecology of this restriction to adult *S. mombin*. However, since female *R. lebeau* do occasionally oviposit on sapling *S. mombin*, and I have on seven occasions found well-developed *R. lebeau* larvae on *S. mombin* saplings in secondary succession, it may be that there is little evolution involved. Rather, the *R. lebeau* females may be ovipositing throughout the *S. mombin* population, but carnivores may be eliminating those on the saplings. If this is the case, were *S. mombin* the only *R. lebeau* host plant in the park and were *S. mombin* a small treelet only found in early secondary succession, *R. lebeau* might well be absent from the park. It is also evident that *P. strigilis* is substantially more cryptic than is *R. lebeau* when on *S. mombin*.

Ampliterus gannascus (Stoll) and *A. ypsilon* R. & J., the other two smerinthine sphingids at Santa Rosa, feed exclusively on *Ocotea veraguensis*

(Meisn.) Vlez. *O. veraguensis* is a shrub-by subcanopy treelet found throughout the understory of several forest types at Santa Rosa. It is the only lauraceous plant in the habitat. *A. gannascus* and *A. ypsilon* are encountered feeding on the foliage of *O. veraguensis* at all heights, from 1-m saplings to the tops of the crowns of 8-m tall large adult plants. The saturniid *Copaxa moinieri* Lemaire has *O. veraguensis* as its sole host at Santa Rosa. In contrast to other saturniids, *C. moinieri* is conspicuous in feeding entirely on the saplings and lower branches of its host and is virtually never found more than 3 m above the ground. *O. veraguensis* may range from forest edge to heavily shaded forest understory, but the vast majority are in the forest understory. However, if the caterpillars are placed on foliage in crowns of adult *O. veraguensis* under protective nets or on similar foliage in plastic bags in the laboratory, they develop quite normally. Here again, the sphingid feeds throughout the life forms of its host plant, while the saturniid is restricted to a particular subset of its host population. While as yet untested, one selective pressure for this behavior is easy to postulate. Since the host is a forest understory plant, feeding solely on the foliage within about 3 m of the ground places caterpillars in a zone quite free of foraging by white-faced monkeys. White-faced monkeys are eager to eat large caterpillars, and in the last instars, the caterpillars of *C. moinieri* are quite easy to find because of the characteristic damage that they do when feeding. This is so when there is a defoliation event, at which time the leafless shrubs are cleaned of caterpillars by the human collector, and presumably would be as well by insectivorous monkeys if they foraged close to the ground.

There are at least six other species of *Copaxa* in Costa Rica. A summary of *Copaxa* host records (Janzen unpublished manuscript) suggests that they are specialists on Lauraceae and may be able eat the foliage of any species of

Ocotea, *Nectandra*, or *Persea*. Why then don't they occur at Santa Rosa, where *O. veraguensis* is common? At least three species of *Copaxa* occur only 10–13 km to the east in a more evergreen forest that is continuous with the Santa Rosa forest. Could it be that these other species of *Copaxa* feed higher in the foliage of their host plant and therefore don't survive at Santa Rosa because this zone is lethal on *O. veraguensis* in the dry forest of lower stature, as found at Santa Rosa?

In short, when a sphingid hops to a new host plant, it gets more than the plant's chemistry. The plant's nutrient value may be high and its defenses may be easily bypassed by existing chemical pathways, but if a green caterpillar has to sit on a brown leaf all day, its fitness on that plant may well be zero. Likewise, if a species of saturniid caterpillar is essentially immune to most vertebrate carnivores because it has severely urticating spines, it has a major trait that predisposes it to the evolution of the biochemical ability to feed on a variety of host species. This appears to be the case with the hemileucine saturniids. They, severe urticators, are found on many kinds of leafy backgrounds, as indicated by their long host lists.

On the other hand, I do not wish to denigrate the importance of plant chemistry in all of this. If a caterpillar lineage comes up with a high quality general-purpose detoxifying system, as the ancestral species to the hemileucines must have done, then the mutant that subsequently invented urticating hairs had the companion trait necessary to allow the explosive radiation that produced and maintained the most species-rich and widespread of the four New World saturniid subfamilies. Over half the New World saturniids are hemileucines; the most species-rich genus, *Hylesia*, with over 200 species (C. Lemaire personal communication), has not only severely urticating caterpillars (see Janzen 1984a for a review), but aggregating caterpillars as well.

CAN A CATERPILLAR GET A FREE RIDE?

A major aspect of the evolutionary accumulation of a plant species' herbivore load is the intensity of fitness depression of the plant by an evolutionarily incoming caterpillar. Put most simply, the more severe is the caterpillar's impact, the more likely is the newcomer to depress the density or local distribution of the plant to a level at which it will not support the caterpillar population or will select for a defense trait that will evict a portion of the herbivore load, or both. In short, one expects that the smaller the bite the herbivore takes, the more likely it is to be able to persist on a new host plant. But bites are measured not in grams of seeds or area of leaves, but in units of population change or fitness depression.

There is, however, one rarely discussed way in which a herbivore can take large bites without depressing the fitness of the host plant. If the herbivore feeds on a subset of the host population that is fated to die prior to reproduction irrespective of the herbivore's impact, it will have no fitness-depressive effect whatsoever. Additionally, if it feeds on a plant that will live to reproduce, then the fitness-depressing effect of its herbivory should be directly proportional to the fitness of that plant relative to its conspecifics. In other words, the worst way to move evolutionarily among host species or increase your host list is to take big bites out of the individuals of the population with the highest potential fitness. At the opposite extreme are the herbivores that feed on plants that are clearly genetically dead though physiologically living – the green aborted leaf or fruit on the forest floor, the branch newly broken out of the tree crown, the seed defecated on the floor of a dry bat cave, the annual herb that has matured and shed its seeds, and so on. A detritivore is defined as an organism that feeds on a dead plant (or

animal), and from the viewpoint of evolutionary ecology, *dead* is defined as having zero potential fitness. While no living wild plant has zero probability of surviving to first reproduction, it is certain that the probability of attaining any given fitness value is neither distributed evenly among the members of the population nor at random with respect to a multitude of environmental variables. The questions become whether sufficient cues exist by which herbivory can be evolutionarily or ecologically directed so that its impact is reduced, and whether individual selection can generate the necessary traits. To ask the question in a different way, are there caterpillars with little or no impact on their host populations simply because they feed (for whatever reason) on that subset of the plant population that has severely reduced potential fitness?

Such a set of questions calls attention to a major difference between plants and animals as hosts or prey. Since animals move around, it is harder to identify individuals, cohorts, or arrays that have a high likelihood of not attaining full adult status than is the case with plants. Despite the fact that we all know about this difference, ecologists have not developed either a terminology or conceptual base with which to discuss easily its potential significance to competition, herbivory, edaphic responses, etc.

Before examining some examples at Santa Rosa, a hypothetical example is in order. First, consider the case of a monophagous caterpillar species that is distributed over its host plants in a manner unrelated to the probability of any particular plant's attaining its potential fitness. Assume the caterpillar to be on 20 percent of the host individuals and that each caterpillar set (on each plant) eats half the leaves off its plant before pupating. The 10 percent of the plant population with a moderate chance of becoming adult (e.g., individuals growing in tree falls) will have 20 percent of its individuals

damaged to this degree. The remaining 90 percent of the plant population will be damaged likewise, but assume that only 1 percent of these plants have a chance of surviving (i.e., those growing where a tree *will* fall). With respect to natural selection, the selective pressure for a defense trait that will repel the caterpillar is generated by 50 percent herbivory of 20 percent of 10.9 percent of the individuals, while the amount of leaf eaten by the caterpillar population is 50 percent of 20 percent of 100 percent of the individuals. In short, enough leaf material to sustain a species of caterpillar may be harvested with only the amount of impact that would have been generated by a much less voracious species of caterpillar feeding on a plant population with a high proportion of individuals with a high chance of attaining their potential fitness. Alternatively, if the incoming caterpillar fed only on individuals with a high chance of surviving, it would have the same impact with much less herbivory that it would have if it also included ill-fated conspecifics in its diet. This scenario may also be stated as, "The more the caterpillar population is focused on ill-fated plants, the more likely it is to persist." At the limit, the caterpillar feeding on shed leaves is totally free of evolutionary responses by the plant to its feeding. Likewise, as the percentage of the plant population made up of ill-fated plants rises, there is a rise in the amount of herbivore load that will be sustained free of selective charge if the herbivores are distributed at random or focused on the ill-fated plants.

Two kinds of ecological complexity should be added to this hypothesized process. First, if the herbivory raises the probability that a plant will die before reproduction or that it will be a less prolific reproducer, there is the complication that the same amount of herbivory is likely to lower the realized fitness of a weakened plant more than that of a healthy one. This differential response may alleviate some of the ill-

fated plant effect (eliminate some of the free ride) by rendering the herbivore less of a detritivore and more of a predator or parasite.

Second, while the herbivore subsisting largely or totally on ill-fated plants may not be selecting for traits to repel itself even if this leads to earlier plant death than would otherwise have occurred, it will still be ecologically thinning out its host plants. Furthermore, it will have to survive despite the defenses selected for by other more fitness-reducing species of herbivores, just as must the more conventional detritivores consuming litter.

It is critical to recognize that the selective process that may result in a larger herbivore load on ill-fated individuals or in larger herbivore loads on species that normally have a high proportion of ill-fated individuals does not favor local mutant herbivores for this trait per se. The individual herbivore that feeds on an ill-fated plant in preference to a plant with high potential fitness does not raise its own fitness. Rather, the selective process is that of the plant suffering or repelling herbivores that are serendipitously arriving through the evolution of other traits or by immigration.

What fraction of the leaf-eating herbivores in Santa Rosa habitats are largely supported by ill-fated plants with little or no potential fitness? Furthermore, what proportion of the herbivores subsists on ill-fated plants because those plants were actively sought by ovipositing females or because their habitats are so sought? In both cases, I assume that the selection for this choice was not driven by a selective value to the individual female ovipositing on the plant with a low potential fitness. It is easy to imagine that many of the Santa Rosa seed predators subsist on seeds that have zero fitness because of their site of deposition following dispersal (or lack thereof). It is much more difficult to divine the potential fitness of the young growing plants whose leaves are

important food for so many caterpillars at Santa Rosa. There certainly are many species of caterpillars at Santa Rosa that wholly or largely feed on saplings of forest canopy trees in the deeply shaded understory where the host has virtually no chance of survival to reproduction unless a tree fall occurs at that site. I cannot yet offer data on the influence of this herbivory on how long a plant can wait before finally dying of starvation, distorted stems, disease, etc.

CLIMATE IS A HOST-PLANT TRAIT

The physical environment undoubtedly influences caterpillar fitness. We tend to forget that each local population of plants, and even distinctive subsets of the population, is associated with a distinctive microclimate. The caterpillar has to contend with this as much as with the directly genetically programmed traits of the plant and the plant's distinctive carnivory regime. Variation in this climatic regime over a plant's distribution may as well as responsible for the absence of a caterpillar in parts of the plant's range as is geographic variation in host plant chemistry. That the saturniid moth *Schausiella santarosensis* is apparently found only in northwestern Guanacaste Province, Costa Rica, while its host tree, *Hymenaea courbaril*, ranges from southern Mexico to central South America, could have many causes besides local uniqueness of *H. courbaril* chemistry. Among these causes may be the Santa Rosa climate.

At Santa Rosa, there are many examples of climatic components of what might be termed the suitability profile of caterpillar host plants. One that is annoyingly omnipresent is the failure of many species of saturniids to have at least the minimum of three generations per year that could occur if host foliage properties were the only

challenge to the caterpillar. While in theory such failures may be equally attributable to seasonal change in carnivory risk or leaf chemistry, there are times when climate seems to be the likely primary cause.

The four saturniids that feed on the foliage of *H. courbaril* offer an example. This tree bears resin-rich leaves (e.g., Langenheim et al. 1982) throughout the year, except for approximately 2 weeks in December or January (early dry season) when the old leaf crop is dropped and a new one is put out immediately thereafter. All four species of saturniids that eat *H. courbaril* leaves can be reared readily under nets in the field or in plastic bags in the laboratory on foliage collected at any time of year (unpublished field notes).

H. courbaril foliage of all ages is eaten by all four species in nature and in the laboratory. Throughout the dry season, from at least January until shortly before the first rains in late April or early May, three of the four saturniids are dormant in cocoons or as pupae in the litter below the fully leafed adult *H. courbaril*, and *Hylesia lineata* Drc. is dormant as eggs in an arboreal felt nest constructed by the female (Janzen 1984a). *Dirphia avia* anticipates the rains and times its emergence so that ovipositing females are in the forest as much as a week before the rains. The eggs require 2–3 weeks to hatch, with the consequence that the caterpillars begin feeding during the rains. *Schausiella santarosensis*, *Periphoba arcae* (Drc.), and *Automeris zugana* Drc. adults emerge within 3 weeks after the first heavy rains, and their first-generation caterpillars are present for the first 2–3 months after the rains begin. *H. lineata* eggs hatch shortly after the rains begin as well, with the same consequence. Most of the pupae of the first generation of *S. santarosensis* remain dormant in the variably wet and dry litter below the *H. courbaril* for 9–10 months before eclosing to repeat the process the next year; however, a small fraction of these

pupae eclose about 3 weeks after pupation and constitute a second generation during the second half of the rainy season. This latter generation again demonstrates that the leaves of *H. courbaril* are chemically quite suitable as food for *S. santarosensis* at this time of year. The pupae of this second generation then join those of the first generation in remaining dormant below the leafy trees throughout the dry season. The other three saturniids regularly have two generations on the rainy season *H. courbaril* leaf crop (as well as on other species of hosts) and then become dormant at the end of the rainy season. It is hard to avoid the working hypothesis that the reason that these moths ignore a food source on which they could pass at least two more generations is because the dry season heat and wind, and attendant desiccation, are inimical to their development in the crown of a large tree. The first-instar larvae are probably the most susceptible, but desiccation during molting and even during pupal formation may also be a problem.

Larval mortality from desiccation will probably turn out to be a major reason for delaying oviposition until the rains start, even when the host plant is in full leaf. For example, at the beginning of the 1983 rainy season (late May), there was sufficient rain to cause some *Cochlospermum vitifolium* to leaf out. This plant is a natural host of *Eacles imperialis* (Table 2). I placed hundreds of 1-day-old first-instar *E. imperialis* larvae on these leafy *C. vitifolium*. The plants were then naturally subject to winds, high temperatures, direct insolation, and dry air as severe as was characteristic of midday a few weeks earlier during the dry season. It was dry enough to stop further *Cochlospermum* branch elongation. While the caterpillars did feed, few obtained enough water to replace that lost by desiccation, and I watched them quite literally dry up and blow off during the following 2 days. Two weeks

later, after rainy season humidity, cloudiness, and still air had set in, similar inoculations of the same plants resulted in nearly 100-percent larval survival (the larvae were protected from carnivores with netting in these experiments). The same change occurred with *Rothschildia lebeau* first-instar larvae put on insolated sapling *Spondias mombin* during the same days. For both species, the foliage of their host plants during the dry weather was excellent fodder when given to siblings of the dead caterpillars in plastic bags in the laboratory.

In short, at the beginning of the rather erratic 1983 rainy season, the leaves of major host plants of *E. imperialis* and *R. lebeau* were present and edible but, in effect, unavailable. In addition, there was spatial heterogeneity to their availability. Inoculation experiments, using siblings of the victims at the beginning of the rainy season, were quite successful when the young caterpillars were placed on host plants that happened to be growing in the shade and wind-buffered air of a patch of evergreen trees. Had these shaded plants been of a different species, one of the other host species of these two moths, it would be easy to conclude that these ecologically available species of host plants had different weather regimes from those of *C. vitifolium* and *S. mombin*, thereby giving them a longer period of susceptibility to the caterpillars during the year. It is likewise easy to imagine that this different regime might well make them an acceptable host for a species of caterpillar that has no other species of host in the habitat.

The weather becomes a trait of the host plant in more ways than just its direct effect on the caterpillar. By determining the duration of leafiness, the weather determines such things as the number of caterpillar generations possible. This may in turn determine the length of a generation, because the

number of generations per rainy season must be an integral number. The length of a generation may in turn determine which hosts are too good and which are inadequate. An inadequate host may be one that the caterpillar can eat with impunity, yet lacks sufficient nutrients for the caterpillar to attain a reasonable size by the time it must pupate if it is to remain in synchrony with the remainder of its population. A too-good host might be one that makes the caterpillar grow too fast; however, in this case, I would expect quick selection for a fixed larval period coupled with heavier caterpillars on better host species or individuals. Viewed the other way around, a given nutrient and defensive chemistry may generate a moth egg-to-adult cycle that is incompatible with the seasonality of the site even if the resultant adult moths are quite normal in weight and other physiological parameters.

DISCUSSION

A host plant is not the focus of the ecological and selective regime of a moth and its caterpillars. Rather, the focus is a space bounded by parameters involving carnivores, climate, host chemistry, host fitness depression through herbivory, and a variety of other traits. In a certain sense I am defining a Hutchinsonian niche for a caterpillar and arguing that this niche is not centered on any one of these traits. This notion is emphasized by recognizing that in any particular point in season, space, or ontogeny there are many individuals of the caterpillar's host plant population that are not being fed on by that species of caterpillar; this distribution is not necessarily generated by randomly placed misses, but because of predictable caterpillar failure or disinterest under this or that circumstance. A par-

ticular host is necessary, but not sufficient, for caterpillar presence.

But is it even necessary? Why not eat just any plant? The current answer, and I am sure the largely correct one, is that in any given snapshot in evolutionary time, a caterpillar species is genetically (and subsequently, ecologically as well) programmed so that it feeds on only a few species of plants in the habitat; female oviposition behavior is here viewed as merely an extension of caterpillar behavior. However, there are at least two ways in which this answer is probably incomplete. First, and I think this is generally accepted by students of animal-plant interactions, there are probably more species of plants in the habitat that can be physiologically processed by the caterpillar species than the caterpillar species actually eats in nature. I have discussed here some of the reasons why these plants may not be used as hosts; the physical climate, predators, etc., may stop the evolution of the choice of that plant, and current ecological processes may prevent its use even if it is chosen by the ovipositing female. Second, given the right collection of ecological circumstances, perhaps just about any plant would be a suitable host in ecological time and certainly in evolutionary time.

In other words, is it unthinkable that, if a species of moth were confronted with a habitat rich in plant species but quite lacking in carnivores (including diseases), inclement weather, competitors, and the ability of plants to evolve further, it might well evolve a digestive physiology such that any individual caterpillar could feed on many or even all plant species? We can imagine that the genetic programming might be too complex and that the biochemical machinery somewhat incompatible for a caterpillar to contain all the collective food-processing abilities of the several thousand species of caterpillars now feeding on the plants of Santa Rosa. But what if,

instead, the caterpillar simply developed a series of biochemical filters that, albeit slowly and incompletely, simply extracted the easily removed nutrients from the food and passed the rest on out? At Santa Rosa, *Hypercompe icasia* Cram. (Arctiidae) has over 60 species of broadleaved host plants recorded for it to date (in half as many plant families) and is one of the most slow-growing caterpillars I have ever reared. The sympatric *H. suffusa* Schaus has more than 50 recorded hosts, and there is almost no overlap of its host list with that of *H. icasia*; it not only grows very slowly, but if the food dries up, it spins a flimsy silk nest and waits until more green leaves appear. It can wait as long as 3 months at ambient temperatures. Why do most other Santa Rosa caterpillars appear to lack such digestive abilities? I doubt that it is because *Hypercompe* has invented some miraculous digestive system never hit upon by other Lepidoptera. I view *Hypercompe* not as the epitome of anything, but simply one of many ways to cope with the wide variety of selective and ecological pressures that confront a caterpillar.

I have mentioned quite enough complications in this essay that it seems truly a miracle for there to be any patterns at all. However, patterns do exist. The large moths at Santa Rosa – saturniids and sphingids – can be partitioned with respect to many of the traits mentioned here. I have already mentioned that sphingids are generally found in carnivore-rich mixes of small plants in low vegetation as well as in the crowns of large trees, while saturniids are much more caterpillars of the crowns of large trees. Sphingids rely heavily on crypsis specific to the host plant (or even leave the host plant during the day), while saturniids have both ostentatious real defenses and mimicry in addition to a more generalized crypsis. Closely linked to this contrast, sphingid caterpillars are more host-specific than are

saturniids and grow faster than do saturniids.

On the one hand, it is nothing new to stress that a host plant is more than just its chemistry. But the topic needs stress now for two reasons. First, most analyses of nonchemical traits (e.g., plant apparency, size of the plant, or plant population as an island) have examined them as large-scale attributes, with the stress being on how these traits correlate with some caricature of host plant chemistry or numbers of insect species (e.g., Southwood et al. 1982). Such analyses are an essential part of the story but bypass the fine-scale interactions between species and individuals (e.g., Karban and Ricklefs 1983; Lawton 1982; Rausher and Papaj 1983; Connor et al. 1983) and the small-scale nonchemical traits. The nonchemical traits deserve the same detailed attention as specificity determinants that secondary compound chemistry is now receiving. Second, the topic needs stress because of the inherent difficulty in the technology of the subject. One cannot determine a caterpillar's risk of being eaten, for example, from any intrinsic trait of the plant (or the caterpillar) that can be obtained from laboratory analyses of collected materials. Equally, the depression of host plant fitness by a caterpillar population cannot be determined from any compilation of facts about plant species, including vegetation analyses, percentage of herbivory, percentage of cover, and all those other things traditionally measured. These traits are situation dependent. They have meaning only in context.

Here it is appropriate to digress on the subject of the concept of average or baseline herbivory. Plants live a long time. Grant proposals are for 3 or fewer years, and field studies are rarely more than one to two times this duration. A commonplace herbivory regime is small amounts for a run of years, with severe defoliation occurring at long and

irregular intervals. Since severe defoliation events are sufficiently far apart that any one study usually sees none or only one of them, there is a strong temptation to view them as "unusual" and therefore not to be considered in determining the intensity of herbivory. While it does not make biological sense to *average* the years of peak herbivory with the many more years of much lower herbivory, somehow the impact of the plant's lifelong herbivory regime needs to be taken to be the same norm.

In characterizing the entire herbivory regime with its causes for variation, one finds that many of the nonchemical traits of the plant take on great importance. Leaving aside herbivore-induced changes in chemistry (e.g., Edwards & Wratten 1983), the defense chemistry and nutrients in a particular set of leaves are relatively invariant as causes of herbivory fluctuation when compared with other traits. Most of the individual caterpillars that actually attempt to feed on a given species of plant either can or cannot do it. And if they can, they can do it over much or all of a plant's lifespan. It is easy to forget that much of a plant's herbivore defenses are against those animals that, because of these defenses, are virtually never responsible for any leaf loss. We are in the silly situation that much of the study of secondary compound chemical ecology occurs in the vacuum of having no idea what herbivores selected for the defenses, and the intensity of much of the herbivory we measure is determined and patterned by events generally not measured by ecologists that study herbivory. The ultimate irony is that just as in the defense budgets of nations, the largest cost levied by herbivores is probably the cost of the defenses rather than the amount of material removed during herbivory (Janzen 1983b).

I have argued that a multispecies mix of small plants has a very different

carnivory regime than does an equal-sized large tree crown, which is essentially a monospecific stand. For almost all biologists, the closest approximation of the multispecies mix of small plants is roadside and old field secondary succession. Such habitats are often analogized with natural disturbance sites such as tree falls, river banks, landslides, etc. I would only emphasize that the analogy is not a close one and likely to be particularly deceptive with respect to the case at hand. For example, the old field does not have nearby intact forest as an herbivore reservoir, refuge, and barrier between small portions of the old field. Likewise, tropical roadsides are, for example, generally continually bathed in dust, which is one of the best contact pesticides known (especially for small insects like parasitoids). For example, the only reason that the *Syssphinx molina* experiments mentioned earlier could be conducted was that they were conducted along a rarely traveled paved road with no shoulders.

It is clear that any herbivore entering a new habitat is stepping into a battlefield rich in plant defenses selected for by other herbivores and by the constraints of defense economics. This situation applies even more to the nonchemical traits of a host plant, the traits I have been discussing; many of the traits of importance were not even selected for by biotic agents, to say nothing of herbivores. The opportunities for coevolution have been minimal. The traits that render a *Hymenaea courbaril* crown a low-yield area for a carnivore were certainly not selected for by the four saturniid caterpillars that feed with relative impunity on the leaves in large *H. courbaril* crowns. It is unlikely that host leaf colors, shapes, and sizes, are selected for through their rendering caterpillars of a particular species easily found by carnivores.

Unfortunately for evolutionary ecology, it is at least theoretically pos-

sible for natural processes to produce a habitat full of interacting caterpillars and their hosts with no coevolution and even very little (if any) evolution. This is particularly true for the nonchemical traits of plants. One can imagine an arriving caterpillar finding a number of edible species of plants but ending up using only a small fraction of the species and biomass because of the negative effects of processes like those mentioned in this essay. Whether the caterpillar persists until it is evolutionarily modified by the many new selective pressures put upon it should depend largely upon nonchemical factors, if there is even one species of plant present that the caterpillar can eat.

The immigration placement of a caterpillar in a new habitat, and its ecological adjustment to the plants there, has much in common with the process of the introduction of new pollinators, new dispersal agents, animal-dispersed plants, etc. At first, the persistence of the invader (or a resident newly deprived of its interactant) depends on other organisms with traits similar to those of the organisms it left behind, even if the invader cannot achieve the same level of fitness that it had originally. At least theoretically, the interactions could then continue indefinitely with no evolution — though the population structure of the incoming species might be quite different than it was where it came from (as might also be those of its new associates). In fact, it is easy to imagine a species being passed from interactant to interactant over long evolutionary time, with a truly new phenotype appearing only rarely but with largely the same phenotypes of organisms continuing to interact in this or that habitat (e.g., Janzen 1983c). Perhaps evolutionary rates proceed most rapidly where species richness is lowest, since in such a situation the probability that alternate or substitute interactants are present is lowest. Yet, there has to be enough diversity of substrate

for the immigrant at least to get established. At the other extreme, if there are many similar species in a habitat, the addition of one more may result in virtually no discernible evolutionary change, because each of the ecologically similar species adjusts just a small amount.

SUMMARY

To the herbivore evolutionarily moving onto a host, or surviving there, a host plant has, in addition to its chemistry and other personal traits, a carnivore regime, weather regime, and fitness regime that must be overcome by the herbivore. The interplant heterogeneity of a Costa Rican defoliation of *Randia treelets* by *Aellopos titan* sphingid caterpillars is described as due to heterogeneity in the carnivory regime rather than in the interplant chemistry. That Costa Rican saturniid caterpillars feed primarily in the crowns of large trees while in the same habitat sphingid caterpillars are distributed over many more plant life forms and sizes is attributed to saturniids (except the severely urticating species) being comparatively incompetent at contending with the more intense carnivory regime of dense, low, and plant-species-rich vegetation rather than to saplings having different foliar chemistry than have their large parents. The saturniid phenology of there not being caterpillars on evergreen trees during the dry season in the same forest is ascribed to desiccation during this time of year rather than to different leaf chemistry in the dry season. Finally, I argue that the impact of herbivory, and hence the likelihood that it will select for defense traits against a herbivore, is related to the potential fitness of the actual plants fed upon. A plant that is slated

to die for other reasons is evolutionarily dead even if physiologically living; the accumulation, over evolutionary time, of an herbivore load by ecologically distinctive conspecifics of different potential fitness should differ with that potential fitness. Furthermore, the accumulation of an herbivore load by a species of plant may well be influenced by the proportion of the population of growing juveniles that are in the category of "evolutionarily dead."

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Plant Kairomones and Insect Pest Control

Robert L. Metcalf

"There can be hardly an entomologist today who does not know that host selection is the very heart of agricultural entomology and that secondary plant substances are the clues to the problem." — G. Fraenkel (1969)

"The extraordinary variety of insect plant relationships is likely to be based on more diverse mechanisms than can be foreseen at present. The promise of rewards is rich for investigators who approach the problem free of deeply rooted bias." — A. J. Thorsteinson (1960)

Estimates suggest that there are at least 100,000 chemical compounds produced during the growth and development of the more than 200,000 species of flowering (vascular) plants (Harborne 1982). The vast majority of these chemicals are the so-called "secondary plant compounds," not essential for the normal physiology of the plants, but rather the seemingly capricious outpourings of nature's chemical factories, the alcohols, esters, ketones, terpenoids, steroids, alkaloids, flavonoids, phenylpropanoids. It is only when we examine carefully the evolutionary processes that have brought about the diversification and speciation of plants that this enormous array of organic chemicals takes on purposeful and orderly significance.

The external plant environment is pervaded by these compounds of secondary metabolism that ooze from leaves, blossoms, and fruits. While humans are well aware of many of them because they define the colors, odors, and tastes that characterize our interactions with plants, there are countless others, less conspicuous in either quality or quantity, that dominate the lives of the 500,000 or so species of insects that have coevolved with the flowering plants. Many of these allelochemicals generate olfactory or gustatory stimuli that convey behavioral messages to species involved in the coevolutionary

and ecological interrelations of food webs. From an arthropogenic point of view these allelochemicals are perceived by insect sensory receptors as attractants, repellents, or arrestants, and in a more complex way, as antibiotics that disrupt normal growth, development, fecundity, and longevity or as anti-xenotics that disrupt normal host selection processes. From the viewpoint of the processes of coevolution between plants and insects, these allelochemicals are classified as *allomones* if they convey adaptive advantage to the plant producer and as *kairomones* if they convey adaptive advantage to the insect receiver (Kogan 1983).

Fraenkel (1959) reviewed much of the early history of our understanding of the reasons for the existence of plant allelochemicals and suggested the criteria for their positive identification as isolation and identification of the chemical, initiation of the kairomone or allomone response when applied to a neutral surface, and demonstration of a quantitative relationship between the concentration of the allelochemical and the insect response. The same chemical compound may act as an allomone, protecting the plant against some herbivores, and as a kairomone, stimulating the feeding of other herbivores, depending upon the vagaries of mutations and coevolution. Specific kairomones may be formed by a wide variety of plant families, and thus, these kairomones may be attractive to particular insect pests that exhibit a wide host range.

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tary in conformation to the structures of the kairomones. The specific kairomone receptor is the product of millions of years of coevolution between host plant and insect pest and has been gradually modified by successive mutations that have provided the insect with adaptive advantages in terms of previously inaccessible ecological niches. As plant allelochemicals have become more and more diversified, insect kairomone receptors have become shaped to accommodate them.

PHENYLPROPANOIDS IN COEVOLUTION OF THE DACINI

The fruitflies of the tribe Dacini (order Diptera, family Tephritidae) constitute a closely related and rapidly evolving group of more than 1,000 species found in the Old-World tropics (D. E. Hardy, University of Hawaii, personal communication). The female flies have sharp piercing ovipositors and typically insert their eggs into a wide variety of fruits and vegetables in which the larvae develop. Many of the Dacinae are remarkable for their wide host range: *Dacus dorsalis* Hendel, the oriental fruitfly, has been reared from more than 150 plants, and *D. tyroni* (Froggatt), the Queensland fruitfly, from more than 106 hosts (May 1953). *D. cucurbitae* (Coquillett) the melon fly, has been recorded as attacking more than 40 different kinds of plants in 12 families, including melons, cucumbers, squash, gourds, tomatoes, and peppers (Hardy 1949). Many other species of this subfamily are much more restricted in host range (Allwood & Angeles 1979), and the host plant preferences for the majority of species seem not to be recorded.

Howlett (1912, 1915) first reported that citronella oil was attractive to the male fruitflies, *Dacus diversus* Coquillett and *D. zonatus* (Saunders), in India and subsequently demonstrated that 3,4-dimethoxyallylbenzene, or methyl eugenol, a constituent of citronella oil, was highly attractive to males of these

flies and of *D. dorsalis* (= *D. ferrugineus* (Fabricius)).

D. cucurbitae males were shown to be highly attracted to 4-(*p*-methoxyphenyl)-2-butanone, or anisyl acetone (Barthel et al. 1957), and 4-(*p*-acetoxyphenyl)-2-butanone, or cue-lure, was developed subsequently as a more effective lure (Beroza et al. 1960). Cue-lure is intrinsically less attractive than its hydrolysis product, 4-(*p*-hydroxyphenyl)-2-butanone, raspberry ketone or Willison's lure (Kaiser et al. 1973; Drew 1974), a natural product first isolated from the raspberry (Schinz & Seidel 1961).

Drew and his coworkers, in a monumental series of trapping experiments in Australia and New Guinea, have surveyed the response of more than 150 species of the tribe Dacini to methyl eugenol and to cue-lure or raspberry ketone (Drew 1974; Drew et al. 1981; Drew & Hooper 1981). From their data and those of others (see *Review of Applied Entomology*), it appears that approximately 90 species of Dacini have been shown to respond to cue-lure or raspberry ketone and 40 species to methyl eugenol. No species has been shown to respond to both types of lure, and all species within each complex of closely related species responded to the same lure, indicating that the olfactory response has profound evolutionary implications. Hardy (1979) estimates that 90 percent of all Dacini respond to one or the other of these lures.

Both methyl eugenol and raspberry ketone are phenylpropanoid secondary plant compounds derived during plant evolution from phenylalanine through a common precursor, *p*-hydroxycinnamic acid or *p*-coumaric acid (Geissman & Crout 1969; Friederich 1976), as suggested in Figure 2. It appears that an ancestral Dacini in Southeast Asia must have developed an association with rotting fruits containing coumaric acid and that this compound became a kairomone regulating early Dacini behavior. The Tephritidae are believed to have arisen in the Paleocene era about 65 million years ago (Fig. 1).

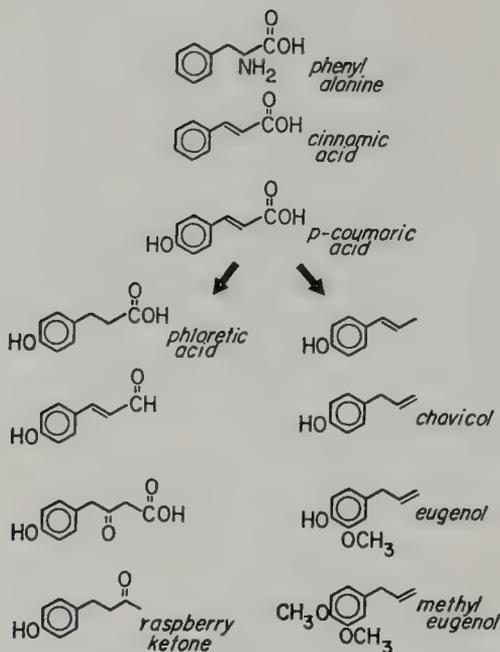


Fig. 2. — Plant evolution of phenylpropanoids from phenyl alanine. Arrows indicate divergence leading to the development of kairomones for two distinct groups of Dacini.

Both methyl eugenol for *D. dorsalis* and raspberry ketone for *D. cucurbitae* are attractive in nanogram quantities on filter paper, and *D. dorsalis* has been shown to respond by attraction, orientation, and feeding to as little as 100 pg of ^3H methyl eugenol present on the antennae where the olfactory receptors are located (Metcalf et al. 1981). Thus, the sensitivity of the responses of these fruitflies to these two kairomones approaches that of various male lepidoptera to the female sex pheromones. However, in contrast to the very precise stereochemical conformity between sex pheromone and receptor (Blum et al. 1971; Priesner et al. 1975), the kairomone receptors of both *D. dorsalis* and *D. cucurbitae* are responsive over a range of about 10^8 in concentration and to a wide variety of organic chemicals with structural resemblances to methyl eugenol or to raspberry ketone (Metcalf et al. 1975, 1979, 1981, 1983b) (Table 1). The male Dacini respond to odorant compounds by a characteristic behavioral sequence of a)

orientation, b) searching, c) arrest, and d) compulsive feeding (Metcalf et al. 1979) that is highly reproducible. The degree of complementarity or "fit" of individual odorants to the kairomone receptors on the male Dacini antennae can be judged by determining the least amount of odorant, applied to filter paper under standardized conditions and exposed to fruitfly populations of uniform age, that produces the behavioral sequence. This value is termed the limit of response (LR) (Metcalf et al. 1979, 1983).

Methyl eugenol is widely distributed in plants, and there are numerous recorded observations of male Dacini aggregating and feeding on plant sources, as shown in Table 1. Phloretic acid has recently been found in the blossoms of *Cucurbita pepo* Linnaeus (Itokawa et al. 1983), and its presence may account for the association of at least 10 species of Dacini, including the melon fly *Dacus cucurbitae*, with various Cucurbitaceae.

KAIROMONE RECEPTOR INTERACTIONS IN THE DACINI

The sensory receptor organs that trigger the responses of male Dacini to the phenylpropanoids are located on the scape of the antenna, and bilateral antennectomy abolishes the response (Metcalf et al. 1975). The antennal receptors, as revealed by scanning electron microscopy, are typical *sensilla basiconica*. The most notable feature of the Dacini response to phenylpropanoid kairomones is the sharp demarcation of the tribe Dacini into species responding to 4-(p-hydroxyphenyl)-2-butanone, or raspberry ketone, and its close analogues, e.g., *Dacus cucurbitae*, the melon fly, and species responding to 3,4-dimethoxyallylbenzene, or methyl eugenol, and its close analogues, e.g., *Dacus dorsalis* (Drew 1974; Drew & Hooper 1981).

The data in Table 2 show the sensitivity of response (LR) of these two key

Table 1. — Plants containing methyl eugenol to which male Dacini are attracted.^a

Family	Plant Species	<i>Dacus</i> Species
Anacardiaceae	<i>Mangifera indica</i> Linnaeus (mango flower)	<i>D. diversus</i> Coquillett, <i>D. correctus</i> (Bezzi)
Araceae	<i>Colocasia antiquorum</i> Schott	<i>D. dorsalis</i> Hendel, <i>D. zonatus</i> (Saunders)
Bromeliaceae	<i>Vriesea heliconioides</i> (Humboldt, Bonpland & Kunth) Hooker ex Walpers (blossom)	<i>D. dorsalis</i>
Caricaceae	<i>Carica papaya</i> Linnaeus (papaya flower)	<i>D. dorsalis</i> , <i>D. diversus</i>
Labiatae	<i>Ocimum basilicum</i> Linnaeus <i>O. sanctum</i> Linnaeus (tulsi)	<i>D. dorsalis</i> <i>D. correctus</i>
Lecythidaceae	<i>Couroupita guianensis</i> Aublet (cannon-ball tree, blossom)	<i>D. dorsalis</i>
Leguminosae	<i>Cassia fistula</i> Linnaeus (golden shower tree, blossom)	<i>D. dorsalis</i>
Myrtaceae	<i>Pimenta racemosa</i> (Miller) J. W. Moore <i>Syzygium cumini</i> (Linnaeus) Skeels (= <i>Eugenia jambolana</i>) (jamun tree)	<i>D. diversus</i> , <i>D. dorsalis</i> , <i>D. zonatus</i> <i>D. caudatus</i> , <i>D. diversus</i> , <i>D. dorsalis</i> , <i>D. zonatus</i>
	<i>S. aromaticum</i> (Linnaeus) Merrill & L. M. Perry (= <i>Eugenia aromaticum</i>) (clove)	<i>D. zonatus</i>
Piutaceae	<i>Pelea anisata</i> Mann (leaf, twig)	<i>D. dorsalis</i>
Saxifragaceae	<i>Zieria smithii</i> Andrews (leaf) <i>Brexia madagascariensis</i> (Lamarck) Noronha (blossom)	<i>D. cacuminatus</i> (Hering) <i>D. dorsalis</i>

^a Howlett (1915), Kawano et al. (1968), Metcalf et al. (1975), Fletcher et al. (1975), Shah & Patel (1976).

species to a variety of phenylpropanoids and related compounds (Metcalf et al. 1983b). It is evident that *D. cucurbitae* shows maximum response to phenylpropanoids with a *p*-OH group on the phenyl ring and a C=O group about 2 atomic diameters removed from the phenyl ring, as typified by raspberry ketone and methyl phloretate (see Fig. 2). *D. dorsalis* shows maximum response to phenylpropanoids with *m*- and *p*-CH₃O groups on the phenyl ring and a side chain with an unsaturated double bond, as typified by methyl eugenol and methyl isoeugenol. Neither species responded appreciably to the most effective odorants for the other species. The antennal receptors of *D. cucurbitae* and *D. dorsalis* must provide

maximum structural complementarity to the kairomones which promote maximum attraction and feeding stimulation, raspberry ketone for *D. cucurbitae* and methyl eugenol with *D. dorsalis*. The degree of structural overlap between the two types of receptors is minimal, as shown in Table 2.

Present-day understanding of the evolution of phenylpropanoid synthesis in the plant kingdom indicates phenylalanine as a precursor and *p*-hydroxycinnamic acid (*p*-coumaric acid) as the common ancestral substance from which there was divergence to the eugenol-methyl eugenol and to the raspberry ketone-phloretic acid phenylpropanoids pathways (see Fig. 2) (Friedrich 1976; Metcalf et al. 1979, 1983b).

Table 2. — Limit of response (LR) of *Dacus cucurbitae* and *D. dorsalis* to kairomone analogues. ^a

	LR in Micrograms	
	<i>D. cucurbitae</i>	<i>D. dorsalis</i>
4-HOC ₆ H ₄ CH ₂ CH ₂ C(O)CH ₃ ^b	0.03	> 1,000
4-HOC ₆ H ₄ CH ₂ CH ₂ C(O)OCH ₃ ^d	0.01	> 1,000
4-HOC ₆ H ₄ CH ₂ OC(O)CH ₃	0.1	1,000
4-HOC ₆ H ₄ CH ₂ C(O)OCH ₃	0.1	1,000
4-HOC ₆ H ₄ CH=CHC(O)OH ^f	1,000	> 10,000
4-HOC ₆ H ₄ CH=CHC(O)OCH ₃ ^c	3	> 10,000
4-HOC ₆ H ₄ CH ₂ CH ₂ C(O)OH ^e	10	> 10,000
4-CH ₃ OC ₆ H ₄ CH ₂ OC(O)CH ₃	1.0	3,000
3-CH ₃ OC ₆ H ₄ CH ₂ OC(O)CH ₃	3,000	> 10,000
2-CH ₃ OC ₆ H ₄ CH ₂ OC(O)CH ₃	10,000	3,000
4-CH ₃ OC ₆ H ₄ CH=CHCH ₃	10,000	10
3,4-(CH ₃ O) ₂ C ₆ H ₃ CH ₂ OC(O)CH ₃	10,000	10
3,4-(CH ₃ O) ₂ C ₆ H ₃ CH ₂ CH ₂ C(O)OH	> 10,000	1,000
3,4-(CH ₃ O) ₂ C ₆ H ₃ CH ₂ CH ₂ C(O)OCH ₃	10,000	3.0
3,4-(CH ₃ O) ₂ C ₆ H ₃ CH ₂ CH=CH ₂ ^g	1,000	0.01
3,4-CH ₃ O) ₂ C ₆ H ₃ CH ₂ CH ₂ C(O)OH	> 10,000	1,000
3,4-CH ₃ O) ₂ C ₆ H ₃ CH ₂ CH ₂ C(O)OCH ₃	10,000	3.0
3,4-CH ₃ O) ₂ C ₆ H ₃ CH=CHC(O)OH	> 10,000	1,000
3,4-CH ₃ O) ₂ C ₆ H ₃ CH=CHC(O)OCH ₃	3,000	3.0

^a Metcalf et al. 1983.^b raspberry ketone^e phloretic acid^c methyl coumarate^f *p*-coumaric acid^d methyl phloretate^g methyl eugenol

The positive response of *D. cucurbitae* to *p*-hydroxycinnamic acid and the lack of response by *D. dorsalis* suggest that the kairomone receptor in *D. cucurbitae* is the more primitive type and that this species and the others in the large group of more than 90 species known to respond to raspberry ketone are more closely related to the ancestral forms of Dacini that coevolved with plants containing cinnamic acid. With the evolutionary development of oxygenase enzymes in plants, *para*-hydroxylation of cinnamic acid to *p*-coumaric

acid was a likely first step in kairomone transformation. Subsequently, the *p*-hydroxyphenylpropanoids were methoxylated to *p*-methoxy and still further oxygenated to form 3,4-dihydroxy, 3-methoxy-4-hydroxy and eventually 3,4-dimethoxyphenylpropanoids (Friedrich 1976; Hanson & Havir 1979). Then, as secondary plant compounds became more lipophilic through methylation and acetylation and were sequestered as essential oils, the antennal receptor site was modified to accept more lipophilic molecules, such as raspberry ketone and methyl phloretate (Metcalf et al. 1983b). *D. dorsalis* and the smaller group of related species responding to methyl eugenol apparently represent descen-

dents of a mutant form whose antennal receptors developed complementarity to the 3,4-dimethoxyphenylpropanoids, thus opening up new ecological niches.

There is good evidence that the primary attractive site on the male *D. dorsalis* antennal receptor is complementary to the *p*-CH₃O group of methyl eugenol (Metcalf et al. 1983). For this series of compounds there is a high degree of negative correlation between LR values for *D. dorsalis* and the π value for octanol/water partition of the substituent side chain, demonstrating the lipophilic nature of the receptor (Metcalf et al. 1981).

Chemical Ecology of Host Selection in the Dacini

The role of phenylpropanoid kairomones in the regulation of the behavioral ecology of the Dacini is complex. The lack of responsiveness of the females to these substances is puzzling. However, it appears that in the presence of male Dacini the kairomones can act as short-range ovipositional stimulants. The sex pheromones of the Dacini are produced in rectal glands of the males and attract virgin females. Thus, the plant kairomones may promote host selection by producing male aggregation and consequent sex pheromone release to bring females to suitable sites, where short-range ovipositional stimulation occurs (Metcalf et al. 1983b).

CUCURBITACINS IN COEVOLUTION OF THE LUPERINI

The more than 300,000 described species of beetles of the order Coleoptera comprise nearly one-third of all insects and form the largest order of living organisms. The preponderance of species of Coleoptera feed on plants, and representatives first appeared about 260 million years ago in the Permian era (Fig. 1; Riek 1970).

The Chrysomelidae, or leaf beetles, (over 20,000 described species) feed almost exclusively on plants, and the coevolutionary association between plants of the family Cucurbitaceae and beetles of the tribe Luperini provides the most comprehensive example of the role of allelochemicals acting as kairomones to promote host selection and feeding by phytophagous insects. The family Cucurbitaceae contains some 900 species of plants in about 100 genera, many familiar as the gourds, squash, cucumbers, and melons of *Cucurbita*, *Cucumis*, *Citrullus*, *Lagenaria*, *Marah*, *Sicyos*, *Echinocystis*, *Ecbalium*, and *Bryonia*. At least 100 species in 30 genera of Cucurbitaceae have been shown to contain a group of more than 20 oxygenated tetracyclic triterpenoids, the cucurbitacins (Cucs) (Fig. 3). The Cucs are responsible for the characteristic bitter taste of most wild Cucurbitaceae (Rehm 1960; Lavie & Glotter 1971). Current thinking holds that the Cucs were selected by coevolutionary processes to protect the Cucurbitaceae against attack by a wide variety of both invertebrate and vertebrate herbivores. The Cucs are the most intensely bitter substances yet characterized and can be detected in aqueous solution at concentrations as low as 1 ppb (Metcalf et al. 1980). They are also extremely toxic, with intraperitoneal LD₅₀ values of Cuc A mouse 1.2, rat 2.0, Cuc B mouse 1.0 mg per kg (David & Vallance 1955). There have been instances of severe poisoning and death in sheep and cattle that consumed bitter *Cucumis* and *Cucurbita* fruits during drought conditions (Watt & Breyer-Brandwijk 1962). Very recently an epidemic of human illness in Australia resulted from the eating of zucchini-type *Cucurbita pepo* fruit that contained about 1 mg per g of Cucs (fresh weight), apparently as the result of a genetic reversion (Ferguson et al. 1983a). A number of insect pests, including the leaf beetles *Phyllotreta nemorum* (Linnaeus), *P. undulata* (Kutschera), *P. tetrastigma* (Comolli),

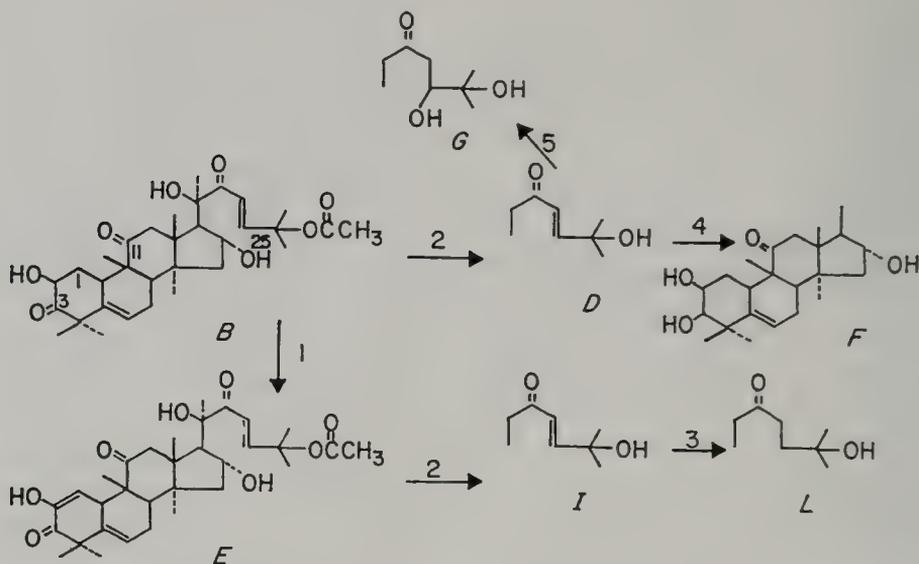


Fig. 3. — Suggested plant evolution of cucurbitacins B, E, D, I, F, G, and L. Numbers refer to specific enzymes involved: 1) cucurbitacin Δ^{23} dehydrogenase, 2) cucurbitacin acetyltransferase, 3) cucurbitacin Δ^{23} reductase, 4) cucurbitacin C3-hydroxylase, and 5) cucurbitacin C24-hydroxylase (Lavie & Glotter 1971).

Phaedon cochleariae (Fabricius), *P. cruciferae* (Goeze), and *Cerotoma trifurcata* (Forester), are strongly deterred from feeding by the presence of Cucs (Nielson et al. 1977; Metcalf et al. 1980).

In contrast, the most important insect pests of Cucurbitaceae worldwide are found in a large group of beetles of the tribe Luperini, comprising 1,528 species of Old-World Aulacophorina (535 species) and the New-World Diabroticina (993 species) (Wilcox 1972). Luperini contains such destructive pests of cultivated crops as *Diabrotica undecimpunctata howardi* Barber, the spotted cucumber beetle or southern corn rootworm; *D. undecimpunctata undecimpunctata* Mannerheim, the western spotted cucumber beetle; *D. balteata* LeConte, the belted or banded cucumber beetle; *Acalymma vittatum* (Fabricius) and *A. trivittatum* (Mannerheim), the striped cucumber beetles; *D. barberi* (Smith and Lawrence), the northern corn rootworm; *D. virgifera virgifera* LeConte, the western corn rootworm; *D. virgifera zea* Kryson and Smith; *D. speciosa* Germar of

South America; *Aulacophora foveicollis* of Asia, Africa, and Europe; and *A. femoralis* of Siberia, China, and South-east Asia. The larvae of these beetles are rootworms, and the adults are found feeding on cucurbits, corn, beans, peppers, and a variety of other plants.

Host plant records are sorely lacking, and Wilcox (1972) in the authoritative *Coleopterorum Catalogus* lists only 29 for 1,528 species of Luperini; 72 percent of the records are for Cucurbitaceae. A literature search has disclosed 49 species, listed in Table 3, as feeding on Cucurbitaceae (e.g., Taki-zawa 1978). These 49 species represent more than 80 percent of the published host records for the Luperini and portray a relationship between these beetles and the Cucurbitaceae that is widely distributed between the Old-World Aulacophorina and the New-World Diabroticina. Compulsive feeding of the Luperini beetles on the leaves and fruits of wild, bitter Cucurbitaceae has been described for many of these species, and *Diabrotica balteata*, *D. barberi* (as *D. longicornis*),

Table 3. — Chrysomelidae: Galerucinae: Luperini Associated with Cucurbitaceae^a

Species	Plant Hosts	Locations
Aulacorphorina		
Aulacophora		
<i>A. abdominalis</i> (Fabricius)	cucumber, melons, pumpkin	Indonesia, Australia
<i>A. atripennis</i> (Fabricius)	gourds, pumpkin, muskmelon	Indonesia
<i>A. bicolor</i> (Weber)	wild, cultivated Cucurbitaceae	Taiwan, Indonesia, China, India, Japan, Phillipines
<i>A. cincta</i> (Fabricius)	snake gourd, bitter gourd, bottle gourd	India, Ceylon
<i>A. coffeae</i> (Hornstedt)	melons, pumpkin	Indonesia, Fiji
<i>A. excavata</i> Baly	<i>Citrullus</i> , <i>Cucumis</i> , <i>Cucurbita</i> , <i>Lufta</i>	India
<i>A. femoralis</i> (Motschulsky)	wild, cultivated Cucurbitaceae	Siberia, Japan, Phillipines, Viet Nam
<i>A. foveicollis</i> (Lucas)	pumpkin, squash, muskmelon	Asia, Africa, S. Europe
<i>A. hilaris</i> (Boisduval)	pumpkin, marrow	Australia, Micronesia
<i>A. lewisii</i> Baly	wild, cultivated Cucurbitaceae	S.E. Asia, Pacific Islands
<i>A. loochooensis</i> Chujo	Cucurbitaceae	Ryukyu Islands
<i>A. nigripennis</i> <i>nigrippennis</i> Motschulsky	squash, cucumber	Siberia, China, Japan, Korea, Taiwan
<i>A. n. nitidipennis</i> Chujo	Cucurbitaceae	Ryukyu Islands
<i>A. olivieri</i> Baly	melons, cucumber, pumpkins, squash	Australia
<i>A. quadrimaculata</i> (Fabricius)	<i>Citrullus lanatus</i> (Thunberg) Matsumura & Naki, <i>Cucurbita pepo</i> Linnaeus	Pacific Islands, Australia
<i>A. similis</i> (Olivier)	<i>Citrullus lanatus</i> , <i>Cucumis</i> <i>melo</i> Linnaeus, <i>C. sativus</i> Linnaeus, <i>Cucurbita pepo</i>	S.E. Asia, Samoa, Fiji
Paridea		
<i>P. angulicollis</i> (Motschulsky)	<i>Gymnostemma pentaphyllum</i> (Thunberg) Makino, <i>Trichosanthes cucumeroides</i> Maximowitz ex Franchet & Savatier	China, Japan, Taiwan
<i>P. costata</i> (Chujo)	wild Cucurbitaceae	China, Taiwan
<i>P. sauteri</i> (Chujo)	wild Cucurbitaceae	Taiwan
<i>P. sexmaculata</i> (Laboissiere)	wild Cucurbitaceae	Taiwan
<i>P. testacea</i> Gressitt & Kimoto	wild Cucurbitaceae	China, Taiwan
Agetocera		
<i>A. discedens</i> Weise	wild Cucurbitaceae	Taiwan
<i>A. taiwana</i> Chujo	wild Cucurbitaceae	Taiwan
Lamprocopa		
<i>L. delata</i> (Erichson)	Cucurbitaceae	Ethiopia, Angola, Zambesi, Madagascar
Paragetocera		
<i>P. involuta</i> Laboissiere	wild Cucurbitaceae	China, Tibet, Taiwan
Diabrotica		
<i>D. balteata</i> Leconte	Cucurbitaceae cultivars	USA, Columbia, Venezuela, Cuba

Table 3. — Continued

Species	Plant Hosts	Locations
<i>D. cristata</i> (Harris)	Cucurbitaceae	Central USA
<i>D. longicornis</i> (Say)	<i>Cucurbita foetidissima</i> Humboldt, Bonpland & Kunth	Central USA Costa Rica, West Indies, Cuba, Puerto Rico
<i>D. graminea</i> Baly		
<i>D. speciosa</i> (Germar)	<i>Cucurbita andreana</i> Naudin	Mexico to Argentina
<i>D. tibialis</i> Jacoby	Cucurbitaceae	S. Texas, Mexico
<i>D. virgifera</i> Leconte	<i>Cucurbita foetidissima</i>	Central USA
<i>D. undecimpunctata</i> <i>howardi</i> Barber	Cucurbitaceae cultivars	Central & S. USA
<i>D. undecimpunctata</i> <i>undecimpunctata</i> Mannerheim	Cucurbitaceae cultivars	W. USA
Acalymma		
<i>A. bivittatum</i> (Fabricius)	Cucurbitaceae	Cuba, French Guiana, Brazil
<i>A. bivittatum amazonum</i> Bechyne	<i>Cucurbita maxima</i> Duchesne	Guiana, French Guiana, Brazil
<i>A. b. bivittatum</i> (Kirsch)	<i>C. maxima</i>	Argentina, Brazil, Bolivia, Peru
<i>A. b. exiguum</i> Bechyne & Bechyne	<i>C. maxima</i>	Ecuador, Peru
<i>A. blandulum</i> (Leconte)	<i>C. foetidissima</i>	Central & SW. USA
<i>A. coruscum</i> (Harold)	<i>C. pepa</i> , <i>C. maxima</i>	Columbia, Venezuela
<i>A. gouldi</i> Barber	<i>Echinocystis lobata</i> (Michaux) Torrey & Gray, <i>Sicyos</i> <i>angulatus</i> Linnaeus	Central USA
<i>A. isogenum</i> Bechyne & Bechyne	<i>Cucurbita maxima</i>	Venezuela
<i>A. peregrinum</i> (Jacoby)	<i>Cucumis melo</i> , <i>Marah</i>	S. Texas, Mexico
<i>A. punctatum punctatum</i> Bechyne	<i>Cucurbita maxima</i>	Brazil
<i>A. p. coreum</i> Bechyne	<i>C. maxima</i>	Venezuela
<i>A. trivittatum</i> (Mannerheim)	Cucurbitaceae cultivars	W. USA, Costa Rica
<i>A. vinctum</i> (Leconte)	<i>Cucurbita okeechobeensis</i> (Small) Bailey	Florida, Georgia
<i>A. vittatum</i> (Fabricius)	Cucurbitaceae cultivars	Central & E. USA
Paranapiacaba		
<i>P. connexa</i> (Leconte)	Cucurbitaceae	S. Texas, Mexico
<i>P. tricineta</i> Say	Cucurbitaceae	SW. USA

^a Bogawat & Pandey (1967), Maulik (1936), Metcalf (1979), Smith (1966), Takizawa (1978), and Wilcox (1972).

D. cristata (Harris), *D. u. undecimpunctata*, *D. u. howardi*, *D. u. virgifera*, *Acalymma trivittatum*, *A. vittatum*, and *Aulacophora foveicollis* have been shown to feed compulsively upon pure crystalline cucurbitacins on inert surfaces, such as filter paper or silica gel (Chambliss & Jones 1966a; Sinha & Krishna 1969, 1970; Sharma & Hall 1971; Metcalf et al. 1980). Adults of *Diabrotica u. howardi* and *D. u. virgifera* have been shown to consume >2,000 mg/kg of Cuc B without any perceptible ill effects (Metcalf et al. 1980). Studies with ¹⁴C-labeled Cuc B fed to *D. balteata*, *D. barberi*, *D. cristata*, *D. u. howardi*, and *D. u. virgifera* demonstrated that these beetles possess well

developed detoxication and excretory systems for Cucs (Ferguson & Fischer 1985).

These species of *Diabroticina* are able to detect nanogram quantities of Cucs by means of well-developed chemosensory organs located on the maxillary palpi (Metcalf et al. 1980), and the limit of response to pure cucurbitacins on silica gel thin layer plates

varies with the individual species and the chemical nature of the Cuc (Table 4). The high degree of sensitivity and specificity of response of the beetles are demonstrated by the "beetle prints" resulting from the feeding of *Diabroticina* on Cucs extracted from Cucurbitaceae and separated by thin-layer chromatography (TLC) (Fig. 4). Using this technique, we have studied the

Table 4. — Limit of response (LR) of *Diabroticina* beetles to pure cucurbitacins.

Species	LR in Micrograms of Cucurbitacin							
	B	D	E	F	G	I	L	Egly.
<i>Diabrotica balteata</i>	0.01			10	3	5		0.1
<i>Diabrotica cristata</i>	0.1		0.3					
<i>Diabrotica barberi</i>	0.1		0.3					
<i>Diabrotica undecimpunctata howardi</i>	0.001	0.03	0.01	1.0	3.0	0.1	0.01	0.05
<i>Diabrotica undecimpunctata undecimpunctata</i>	0.003		0.03					
<i>Diabrotica virgifera</i>	0.01	0.1	0.3	0.1	3.0	0.3	1.0	0.03
<i>Acalymma vittatum</i>	0.3		10					50

CUCURBITA

AND LUN OKE PAR TEX PEP PEP PEP PEP
CV18 CV25 CV29 CV19

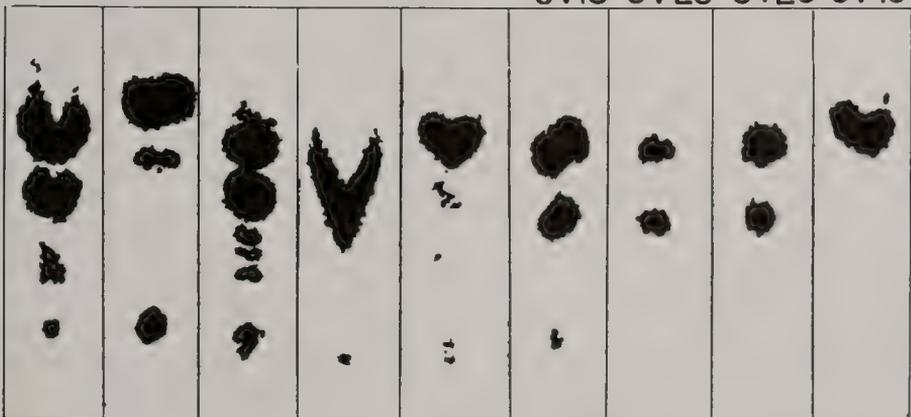


Fig. 4. — Beetle prints from feeding of *Diabrotica u. howardi* on thin-layer chromatograms of chloroform extracts of *Cucurbita* cotyledons. The dark areas eaten from the plates are the various cucurbitacins present. AND = *andreana*, LUN = *lundelliana*, OKE = *okechobeensis*, PAR = *palmeri*, TEX = *texana*, and PEP = *pepo* cultivars. (Ferguson et al. 1983c. Reprinted with permission of the Journal Economic Entomology).

quantitative distribution of the Cucs in 18 species of *Cucurbita*, as shown in Table 5 (Metcalf et al. 1982). No Cucs were detectable in leaves, fruits, or roots of the domesticated species *C. ficifolia*, *C. maxima*, *C. mixta*, *C. moschata*, and *C. pepo* (zucchini) down to a limit of 0.02 mg per g of fresh weight. Indeed, fruits of these species would be inedible if Cucs were present. The Cucs content of the fruits of wild species ranged from 0.53 mg per g in *C. pedatifolia* to 3.2 mg per g in *C. andreana*. The nature of the Cucs present and the beetle feeding responses observed agree reasonably well with evolutionary groupings based on numerical taxonomy (Rhodes et al. 1968), cross compatibilities (Bemis et al. 1970), and isozyme analysis (Puchalski & Robinson 1978). Group (1) included the Cuc B- and Cuc D- forming species found in subgroup (a) *C. andreana* and *C. ecuadorensis* and subgroup (b) *C. gracilior*, *C. palmeri*, and *C. sororia*. Group (2) included the Cuc E- and I- forming species found in subgroup (a) *C. martinezii* and *C. okeechobeensis* and subgroup (b) *C. cylindrata*, *C.*

palmata, *C. foetidissima*, and *C. texana* formed a preponderance of Cuc E glycoside (Metcalf et al. 1980, 1982).

The role of the Cucs as feeding stimulants was demonstrated conclusively by painting microgram quantities of Cuc B on soybean leaves, not eaten normally by *Diabrotica barberi*, *D. u. howardi*, and *D. u. virgifera*. All three species fed heavily upon leaf areas treated with Cuc B. In field experiments, these beetles ate a variety of weeds treated with Cuc extracts and homogenates of bitter *Cucurbita*. The plant *Iberis umbellata* Linnaeus, or candy tuft, (Cruciferae) is one of the few species outside the Cucurbitaceae known to produce Cucs. Plants of this species interspersed with bitter *Cucurbita* were massively attacked by *D. u. howardi* and *D. u. virgifera* and were completely defoliated and killed within 2 weeks. Thin-layer chromatography of *Iberis* extracts isolated Cucs E and I, which were readily fed upon by *Diabrotica* beetles (Metcalf et al. 1980).

Evaluation of Diabroticina feeding patterns on TLC chromatograms from extracts of *Cucurbita andreana* contain-

Table 5. — Cucurbitacin content of fruits of *Cucurbita* spp. ^a

<i>Cucurbita</i> spp.	Cucurbitacin (mg per g of fresh weight)					
	B	D	E	I	Unknown	Glycoside
<i>andreana</i> Naudin	2.78	0.42				
<i>cylindrata</i> Bailey			0.10	0.18	trace	0.30
<i>ecuadorensis</i> Cutler & Whitaker	0.43	0.18				
<i>ficifolia</i> Bouché			- <0.02 -			
<i>foetidissima</i> Humboldt, Bonpland & Kunth			0.36	1.59	0.49	0.91
<i>gracilior</i> Bailey	1.13	0.03				
<i>lundelliana</i> Bailey	0.63	0.15			trace	
<i>martinezii</i> Bailey			0.36	0.45	0.03	
<i>maxima</i> Duchesne			- <0.02 -			
<i>mixta</i> Pangalo			- <0.02 -			
<i>moschata</i> (Duchesne) Poiret			- <0.02 -			
<i>okeechobeensis</i> (Small) Bailey			0.26	0.37	0.09	
<i>palmata</i> S. Watson						0.83
<i>palmeri</i> Bailey	0.81	0.11			0.27	
<i>pedatifolia</i> Bailey	0.29	0.27				
<i>pepo</i> Linnaeus			- <0.02 -			
<i>sororia</i> Bailey	0.54	0.27				
<i>texana</i> Gray			0.07	0.37		0.75

^a Metcalf et al. (1982).

ing CuCucs B and D, *C. okeechobeensis* containing Cucs E and I, and *C. texana* containing Cuc E glycoside showed an almost identical qualitative response for *Diabrotica balteata*, *D. cristata*, *D. barberi*, *D. u. howardi*, *D. v. virgifera*, and *Acalymma vittatum* (Metcalf et al. 1980).

There is substantial evidence of the lengthy coevolutionary association of Cucurbitaceae plants and Luperini beetles. The genus *Cucurbita* is indigenous to the Americas, where it has existed since pre-Columbian times. It is considered to have its center of origin in the tropical or semitropical region of southern Mexico, from which the 27 species (22 wild, 5 cultivated) have radiated to North and South America (Whitaker & Bemis 1964, 1975). The present distribution of species of *Cucurbita* is (Whitaker & Bemis 1964): Southern Mexico and Central America, 14 species; Northern Mexico, 6 species; Northern South America, 4 species; Southern North America, 8 species.

The *Diabrotica* beetles have remarkably similar geographic distribution, as shown in Fig. 5. The putative area of origin of this genus is in northern South America or Central America, from which a few species have radiated into both southern South America and North America (data from Wilcox 1972).

Fig. 5 also shows the species distribution of the *Aulacophora* (Maulik 1936), the Old-World counterparts of the *Diabrotica*, which also must have coevolved with Cucurbitaceae. This genus appears to have evolved in Indonesia and to have radiated into southeast Asia, extending north to China and Siberia and south to Australia. The very close systematic relationships of the Aulacophorina and Diabroticina, the intimate association of both subtribes with Cucurbitaceae, and their common response to cucurbitacins strongly suggest a common ancestral co-evolution with an early cucurbitaceous species during a geologic per-



Fig. 5. — Distribution and numbers of described species of Diabroticina in the New World and Aulacophorina in the Old World. (Data from Wilcox 1972).

iod when continental land bridges were present (Metcalf 1979).

KAIROMONE RECEPTOR INTERACTIONS IN THE DIABROTICINA

Among the Diabroticina beetles the primary sensory receptor organs that trigger the compulsive feeding response to the cucurbitacins are located on the maxillary palpi of both sexes. Surgical amputation of the maxillary palpi abolishes the compulsive feeding response, but this response is not altered by antennectomy (Metcalf et al. 1980). Scanning electronmicroscopy of these organs in *Diabrotica balteata*, *D. cristata*, *D. barberi*, *D. u. howardi*, *D. v. virgifera*, and *Acalymma vittatum* has demonstrated similar morphology of the sensory receptors in all species, and their ultra structure is under study (J. R. Larsen, University of Illinois, unpublished research). These species of Diabroticina respond qualitatively to the spectrum of Cucs found in chloroform extracts of *Cucurbita andreana*, *C. okeechobeensis*, and *C. texana*, as separated by TLC on silica gel thin layer plates, in an almost identical pattern (see Fig. 4). Thus, there is no evidence of any significant change in the spectrum of response to the Cucs by the various species of Diabroticina over an evolutionary period of more than 40 million years, as estimated from isozyme studies (Harvey et al. 1983). This evolutionary stability of receptor response is remarkable in view of the substantial differences in the present host preferences of these species of Diabroticina. The adults of a number of North American species have a proclivity for feeding on cucurbits and have been given trivial names suggesting this: *Diabrotica balteata*, the belted or banded cucumber beetle; *D. u. howardi*, the spotted cucumber beetle; *D. u. undecimpunctata* Mannerheim, the western spotted cucumber beetle; *D. picticornis* Horn, the painted

cucumber beetle; *D. (Paranapiacaba) connexa* (LeConte), the saddled cucumber beetle; *Acalymma trivittatum*, the western striped cucumber beetle, and *Acalymma vittatum*, the striped cucumber beetle (Chittenden 1910). The most generalized feeders are probably *D. balteata*, whose adults also feed on cucumber, squash, melons, beans, soybeans, eggplant, and vetch, and *D. u. howardi* and *D. u. undecimpunctata*, whose adults feed on cucumbers, melons, squash, beans, soybeans, peas, cabbage, peppers, and corn (Chittenden 1910). *Acalymma trivittatum* and *A. vittatum* are more specialized, and the adults generally restrict their attacks to cucumber, squash, and melons. The northern corn rootworms, *Diabrotica barberi* Smith and Lawrence, and the western corn rootworm, *D. v. virgifera*, were originally described from adults collected on blossoms of *Cucurbita foetidissima* (Smith & Lawrence 1967) and *D. v. virgifera* adults readily attack cucumber, squash, and melons (Howe et al. 1976). The larvae of both species apparently develop only in the roots of grasses, especially corn, and the adults feed avidly on corn silks and pollen. Branson & Krysan (1981) suggest that both the northern and western corn rootworms have become pests of corn only relatively recently through convergent evolution. *D. cristata* is found almost exclusively in relict prairies and may develop only on the roots of prairie grasses, such as *Andropogon*, but the adults have been collected from squash blossoms (personal observation). The demonstration that functional Cuc receptors are present in these species suggests not only that they originally coevolved with the Cucurbitaceae, but also that the development of other host preferences may have been relatively recent (Branson & Krysan 1981).

The data in Table 4 indicating the limits of response (LR) for the various species of Diabroticina exposed to a variety of pure Cucs indicate that Cuc B was consistently detected at lower levels than was any of the other Cucs.

Therefore, it appears that Cuc B has maximum complementarity to the Cuc receptors on the maxillary palps and is likely to be the primitive Cuc to which the sensory receptor of an ancestral Luperini must have become evolutionarily tuned (Metcalf et al. 1980, 1982). This possibility is supported by the chemical resemblance of Cuc B to bryogenin, considered the parent tetracyclic triterpenoid formed from mevalonic acid (Geissman & Crout 1969). Bryogenin and Cuc B both have the cyclohexane moiety in ring A, differing from Cuc E, which has a partially aromatized ring with a C=C bond (Fig. 3). Cuc B is the dominant form found in the Cucurbitaceae and was detected in 91 percent of 46 species examined by Rehm et al. (1957); Cuc E was detected in 42 percent of the species. Furthermore, Cuc B was the dominant form found in the cotyledons of 19 species of wild *Cucurbita*, *Cucumis*, and *Citrullus* and in 46 commercial cultivars of these genera, even when the mature leaves and fruits contained Cuc E (Ferguson et al. 1983c). Cuc E is formed from Cuc B by an enzyme, cucurbitacin Δ^1 dehydrogenase; Cuc D is formed from Cuc B and Cuc I from Cuc E by cucurbitacin acetyl esterase. The chemical relationships between these and other Cucs having alterations in the degree of oxygenation of ring A or in the unsaturation of the C23=C24 side chain are shown in Fig. 3. It appears that all of the common Cucs can be formed from Cuc B.

The sensitivity of response of the *Diabroticina* examined to the various pure Cucs (Table 4) was *D. u. howardi* = *D. u. undecimpunctata* > *D. balteata* > *D. virgifera* > *D. barberi* > *D. cristata*. *Acalymma vittatum* is considerably less responsive. Cuc B was consistently detected at levels 0.1 – 0.3 of that of Cuc E, and the deacetoxy Cucs D and I were substantially less effective in triggering the compulsive feeding response than were Cucs B and E.

The changes in maxillary receptor sensitivity to the various Cucs demonstrated by all the species of *Diabro-*

ticina examined impel speculation about the nature of the Cuc receptor. It seems likely that receptor depolarization follows allosteric changes in the receptor protein resulting from interactions of the free paired electrons associated with the several oxygen atoms in the Cuc molecules (Metcalf et al. 1980). The structural change in Cuc B by introduction of a single double bond at ring A to form Cuc E seems trivial (Fig. 3), yet this change produces a tenfold decrease in receptor affinity (Table 4). The introduction of the C=C into ring A substantially changes the orientation of the three contiguous O atoms (C3=O, C2-OH, and C11=O) from a staggered configuration in the cyclohexyl moiety of Cuc B to a planar configuration in Cuc E. This change seems ample, from my observations of molecular models, to decrease receptor affinity and depolarization (Metcalf et al. 1980). Cucs D and I exhibit about a tenfold decrease in receptor affinity compared with their C25 acetoxy derivatives, Cucs B and E (Fig. 3). This fact suggests that the acetoxy-C=O must also be involved in complete binding to the receptor.

PLANT KAIROMONES AS ATTRACTANTS AND ARRESTANTS FOR INSECT PEST CONTROL

The intrinsic nature of the coevolutionary process that produced the specific interactions between plant kairomones and insect sensory organs that lead to profound behavioral changes suggests that kairomones can be employed for insect control in a variety of baits and traps. This use of the instinctual behavior of the insect pest in the presence of the kairomone chemical is analogous to the use of insect sex pheromones for population monitoring, removal trapping, and mating confusion (Shorey & McKelvey 1977; Mitchell 1981; Nordlund et al. 1981).

There has been surprisingly little application of this use of kairomones for insect control, and several of the most successful examples were developed without appreciation of the role of the kairomones in the chemical ecology of the pests (Mitchell 1981).

Kairomone Baits for Monitoring and Controlling Dacini Fruitflies

Howlett (1915) first demonstrated that methyl eugenol was a specific attractant to males of several species of Dacini, including the oriental fruitfly *Dacus dorsalis*. During the outbreak of *D. dorsalis* in Hawaii following its discovery there in May 1946, oil of citronella was evaluated by the USDA as an attractant and was so effective that it was used as the standard substance for monitoring oriental fruitfly populations (Steiner 1952). Oil of citronella contains about 8 percent methyl eugenol, and it was soon demonstrated that the purified chemical was far superior in attracting male *D. dorsalis*, for which it is also an arrestant and compulsive feeding stimulant (Steiner 1952). Methyl eugenol was shown to attract male *D. dorsalis* upwind from as far as 0.5 mile away and to stimulate male fruitflies to compulsive feeding that can kill them from overindulgence. The use of methyl eugenol for population monitoring of *D. dorsalis* was rapidly adapted to a variety of invaginated glass and plastic traps containing water to drown the flies. Traps containing about 1 g of methyl eugenol trapped as many as 2,600 – 7,300 male *D. dorsalis* in a single day. The simple 8-oz (230-ml) bottle trap baited with methyl eugenol on a cotton wick has become a standard monitoring device to detect incipient oriental fruitfly invasions (Steiner 1957).

A simple box trap for area-wide control of *D. dorsalis* was developed by treating the inside of 3- × 12- × 16-inch (75- × 300- × 400-mm) wick boxes with 0.5 g of parathion insecti-

cide as a wettable powder and overspraying with 2 ml of methyl eugenol (Steiner 1952). Such traps, open on one side, attracted and killed 13,000 – 15,000 fruitflies per trap. These traps were used to control *D. dorsalis* through male annihilation in pineapple fields in Hawaii, and it was shown that marked flies were attracted from as far as 1 – 1.5 miles (1.6 – 2.4 km) away. In a 125-acre (50-ha) pineapple field, 45 box traps killed thousands of male flies and substantially reduced the male fly population over an area of at least 4 square miles (10.4 km²).

The male annihilation method has been refined by employing cane fiber blocks 2.5 inches (62.5 mm) square and 0.37 inch (9.25 mm) thick saturated with a bait mixture of 97 percent methyl eugenol and 3 percent naled insecticide (dimethyl 1,2-dibromo-2,2-dichloroethyl phosphate), so that each block contained about 23.3 g of methyl eugenol and 0.7 g of insecticide. These were dropped from aircraft at the rate of 125 per square mile (2.6 km²) over the island of Rota in the Mariannas at about 2-week intervals for 8 months. The wild *D. dorsalis* population was monitored by methyl eugenol trapping and declined from a pretreatment count of 262 male *D. dorsalis* per trap to 18.4 males per trap after the first treatment and to 0.028 male per trap after the fourth treatment. No flies were caught after the 7th month, and the oriental fruitfly population was reduced by at least 99.6 percent (Steiner et al. 1965). This extremely efficient control effort used only 3.5 g of insecticide per acre (0.4 ha) per application and remains a classic demonstration of the efficiency and effectiveness of kairomone lures for insect pest control.

Raspberry ketone (Willison's lure) and its *p*-acetoxy-derivative, cue-lure, have been widely used for monitoring populations of male Dacini, such as the Queensland fruitfly, *Dacus tyroni*, and the melon fly, *D. cucurbitae*, that respond to this kairomone (Drew 1974; Drew & Hooper 1981). Fiberboard

blocks 2.5 inches (62.5 mm) square and 0.5 inch (12.5 mm) thick were treated with a bait mixture of 95 percent cue-lure and 5 percent naled insecticide so that each block contained about 23.75 g of cue-lure and 1.25 g of insecticide. These blocks were tied 2–5 feet (0.6–1.5 m) above the ground on trees or stakes at the rate of about 585 blocks per square mile (2.6 km²) over an isolated area of the island of Hawaii and were replaced with freshly treated blocks each month for 4 months (Cunningham & Steiner 1972). The wild *D. cucurbitae* population was monitored by cue-lure trapping and declined from a pretreatment count of 169 male *D. cucurbitae* per trap to 62 males per trap after the first treatment (96.3 percent decline) to 0.22 per trap after the fourth treatment (99.9 percent decline). This level of population reduction was maintained for over 60 days. This extremely efficient control effort used only 1.2 g of insecticide per acre (0.4 ha) per treatment and illustrates again the very high efficiency of kairomone baiting and the safety and specificity of this method of insect pest control.

The male annihilation technique using poisoned kairomone baits has produced high levels of control of several species of Dacini and, when applied to island populations, has resulted in the eradication of the Queensland fruitfly, *D. tyroni*, from Easter Island (Bateman et al. 1973). This method should be used with great caution against indigenous infestations because, as Hardy (1979) has emphasized, only a fraction of the 1,000 species of *Dacus* and related genera of Tephritidae are of commercial importance as pests of agricultural crops. Overenthusiastic efforts to eradicate pest species by the use of kairomone lures can lead to the devastation and even extinction of the endemic fauna in the Oriental, Australian, and Ethiopian zoogeographic regions. Thus no eradication program should be undertaken until the probable environmental impacts have been fully assessed.

Kairomone Baits for Monitoring and Controlling Diabroticina Beetles

The tetracyclic triterpenoid cucurbitacins B and E are of high molecular weights and of very low volatility in contrast to methyl eugenol or raspberry ketone (the estimated v.p. of methyl eugenol is 0.01 mm Hg at 25 °C) and do not have any long-range vapor attractancy for Diabroticina beetles. The Cucs, however, resemble methyl eugenol and raspberry ketone in that they are powerful arrestants and compulsive feeding stimulants, detectable by Diabroticina beetles on inert surfaces at concentrations as low as 1 ng (Metcalf et al. 1980). In contrast to the phenylpropanoid kairomones for the Dacini, Cucs kairomones appear to be effective with both male and female Diabroticina.

Despite their lack of vapor attractancy, the Cucs can be used successfully to monitor Diabroticina beetle populations for integrated pest management (IPM) programs, and their kairomonal activity can be exploited for use in poison baits in a way that is analogous to the successful use of methyl eugenol and raspberry ketone for control of the Dacini. Whereas methyl eugenol and raspberry ketone and its analogue cue-lure are relatively simple organic chemicals that can be made synthetically, the Cucs are very complex chemicals that have not been synthesized. Nevertheless, the relatively high Cuc content of wild bitter *Cucurbita* provides a useful source of kairomones for study. Early experiment with Diabroticina beetles exposed equally to sliced bitter and sweet *Cucurbita* fruit demonstrated conclusively that the great preponderance of the Diabroticina beetles (95–98 percent) remained feeding on bitter fruits, such as *C. andreana* (Contardi 1939), *C. foetidissima* (Sharma & Hall 1973), and *C. pepo* (Howe et al. 1976). In a comparison of the arrestant powers of fresh, sliced fruits of 11 species of *Cucurbita* with total Cuc contents ranging from <0.02 mg per g (*C. max-*

ima, *C. mixta*, *C. moschata*, and *C. pepo*) to 3.20 mg per g (*C. andreana*), the correlation coefficient between average numbers of beetles feeding and Cuc content was 0.70 for *Diabrotica u. howardi* and 0.58 for *D. v. virgifera* (Metcalf et al. 1982). These bitter *Cucurbita* baits are rapidly consumed by *Diabroticina* beetle feeding, and the arrestant effect is lost within a day or two. The effectiveness can be prolonged for several weeks by sprinkling sliced bitter *Cucurbita* fruit with about 0.1 g of rapidly acting contact insecticide, such as trichlorfon or methomyl. Such treated bitter *Cucurbita* fruits remained effective in killing *Diabroticina* beetles for 3 weeks, even after heavy rains, and single fruit halves killed in excess of 2,000 beetles (Fig. 6) (Rhodes et al. 1980).

The prolonged arrestant power of dried bitter *Cucurbita* fruit for *Diabroticina* beetles is remarkable and illustrates the profound effect of the Cuc kairomones on beetle behavior. Ground or pelleted bitter Cuc fruits from *C. andreana* and *C. texana* or roots of *C. foetidissima* retain arrestant power for more than 3 years of storage indoors, and when impregnated with 0.1 percent w/w of a variety of carbamate and organophosphorus insecticides, are effective in arresting and killing *Diabroticina* beetles for 3 weeks or more under summer field conditions (Metcalf et al. 1983). These dry poisoned kairomone baits are being used to monitor *Diabroticina* populations to determine economic thresholds for IPM programs. Shaw et al. (1984) developed a 4-oz (120-ml) plastic vial, with holes to admit *Diabroticina*, baited with about 0.1 g of dried bitter *Cucurbita* bait containing carbaryl insecticide that is efficient and effective.

To use the Cuc kairomones for control of *Diabroticina* beetles, it is necessary to have an abundant source of bitter *Cucurbita* fruit, and wild *Cucurbita* spp. do not provide dependable sources of Cucs. They are more difficult to grow in temperate regions and yield less than domesticated species,

and in some cases fruiting is dependent upon the photo-period. Genes controlling the formation of Cucs were transferred to domesticated cultivars by crossing *C. andreana* × *C. maxima* to produce long-vined plants with large fruits, averaging 3.90 kg and containing a total of 1.26 mg of Cuc B and D per gram of fresh weight. The dried bait contained 5.0 mg of Cucs per gram. A hybrid of *C. texana* × *C. pepo* produced bushy plants with fruits averaging 0.73 kg and containing a total of 0.48 mg of Cucs E, I, and E-glycoside per gram of fresh weight. The dried bait contained 6.1 mg of Cucs (F₁ fruit) and 3.0 mg of Cucs (F₂ fruit) per gram (Rhodes et al. 1980; Metcalf et al. 1983). Another source of Cuc kairomones is in the roots of *C. foetidissima*, which contain about 3.1 mg of Cucs E, I, and E-glycoside per gram of fresh weight (Metcalf et al. 1982). Dried *C. foetidissima* roots, grown as a semi-commercial crop for starch production in Arizona, contained 4.0 mg of Cucs per gram (Berry et al. 1978).

These air-dried and ground *Cucurbit* baits were impregnated with a variety of insecticides, including the carbamates, carbaryl, carbofuran, bendicarb, and methomyl; the organophosphates, malathion, dimethoate, terbufos, and isofenphos; and the pyrethroids, fenvalerate, permethrin, and decamethrin. It was determined that the most effective concentrations of insecticides were 0.1 percent w/w for carbamates and organophosphates and 0.01 percent w/w for pyrethroids. Such baits have been evaluated for *Diabroticina* beetle control in cucurbits, sweet corn, and dent corn by broadcasting them at rates of 10–100 lb (4.5–45 kg) of bait per acre (0.4 ha). Applications of these baits at 10–30 lb (4.5–13.5 kg) per acre produced reductions of adult *Diabrotica u. howardi*, *D. virgifera*, and *Acalymma vittatum* ranging from 75 to 99+ percent within 1 to 3 days. Baits poisoned with methomyl and isofenphos were effective at application rates of 4.5–13.5 g of insecticide per acre (0.4 ha), and the decamethrin bait at rates as low as 0.45 g per acre



Fig. 6.—*Diabrotica* beetles killed after 5 days of feeding on cut fruit of *C. pepo* × *C. texana* hybrid dusted with 0.1 g of methomyl insecticide (Rhodes et al. 1980).

(0.4 ha). (Metcalf et al. 1982, 1983a). In experiments in sweet and dent corn such applications killed from 160,000 to 230,000 *Diabroticina* beetles per acre (0.4 ha) and remained effective for at least 2 weeks. A notable feature of the Cuc-kairomone insecticide baits is that the quantity of insecticide required per unit of area is only about 1 percent of that required for conventional spray applications for *Diabroticina* beetle control. The applications are highly selective because of the kairomonal effect on the *Diabroticina*, and other insects, including beneficial insects, are not appreciably affected.

HOST-PLANT RESISTANCE BY ANTIXENOSIS (NONPREFERENCE)

Antixenosis is a major type of host-plant resistance to insect attack in which the plant lacks the characteristics desired by insect pests and is an unsuitable host. Antixenosis, therefore, is the major resistance factor limiting most phytophagous insects to a monophagous or oligophagous host range. Increasing appreciation of the role of plant allelochemicals acting as kairomones, suggests that genetic manipu-

lations to remove them from cultivars is a logical approach to host-plant resistance. Indeed, this removal has occurred inadvertently in the Cucurbitaceae from primitive man's efforts to find palatable squash, melons, and cucumbers free of the bitter cucurbitacins. However, antixenosis has had only limited exploitation in the development of pest-resistant cultivars compared with the development of antibiosis, involving genetic manipulation to produce or increase allelochemicals or other factors adverse to host selection and pest development and reproduction (Kogan 1983).

The importance of antixenosis as a mechanism for host-plant resistance in the Cucurbitaceae to cucumber beetles (*Diabroticina*) has been demonstrated for the squash *Cucurbita pepo* (Nath & Hall 1965), the watermelon *Citrullus lanatus* (Chambliss & Jones 1966b), and the cucumber *Cucumis sativus* (DaCosta & Jones 1971b). In the Cucurbitaceae, cucurbitacin synthesis is initiated by a single dominant "bitter gene," *Bi*, and antixenotic resistance is associated with the recessive phenotype, *bi bi* (DaCosta & Jones 1971a; Robinson et al. 1976). Nonbitter fruit may develop from bitter seedlings in the presence of a modifier suppressing synthesis in the fruit. Quantitative

estimations of the total Cuc content in *Cucurbita* have shown a partial dominance for low Cuc content with a multi-genic additive type of inheritance (Nath & Hall 1965). The Cuc content of the cotyledon leaves appears to be substantially independent of that in mature leaves and fruits (Ferguson et al. 1983b).

Protection of the early growth stages of Cucurbitaceae cultivars from attack by *Diabroticina* beetles is a major necessity for the successful survival of these plants. Study of 46 cultivars of *Cucurbita*, *Cucumis*, and *Citrullus* showed that substantial amounts of Cucs were present in the seedling stages of 29 of these cultivars at a limit of detection of about 0.1 ppm of fresh weight. These Cucs were demonstrated by extraction and thin-layer chromatography, followed by the feeding of the spotted cucumber beetle, *Diabrotica u. howardi*, and the banded cucumber beetle, *D. balteata* (Ferguson et al. 1983b).

Field experiments showed that there was almost complete correlation between Cuc content of the cotyledon leaves of 25 *Cucurbita* cultivars and the extent of the destruction of seedling plants by early spring and summer feeding of *Diabrotica u. howardi* and *Acalymma vittatum* beetles (Ferguson et al. 1983b). This demonstration of the value of antixenosis provides a useful example of means for the selection of *Cucurbita* cultivars with substantial antixenotic host-plant resistance to *Diabroticina* pests. Such antixenotic host-plant resistant varieties can play an important role in IPM programs. It should be emphasized that the cucurbitacins also function as allomonones to confer host-plant protection against a variety of herbivores apart from the *Diabroticina*. Therefore, the ultimate effect of antixenosis in crop protection is one of balance. For the Cucurbitaceae, the depredations of the *Diabroticina* and the wilt diseases that they inoculate are so severe that the balance appears to be tilted strongly in favor of antixenotic protection.

KAIROMONES IN TRAP CROPS

From evolutionary considerations, it appears that the use of kairomones *in situ* in plants attractive to insects should provide an optimum way to control insects (Martin 1940:317). The principle of insect control by "trap cropping" has its origin in folklore but can be developed on a rational basis through knowledge of the qualitative and quantitative nature of the kairomone contents responsible for insect attraction, arrest, compulsive feeding, and oviposition. Curtis (1860) recommended controlling the parsnip webworms, *Depressaria depressella* (Hübner) and *D. daucella* (Denis & Schiffermüller), (Oecophoridae) by setting parsnip plants (*Heracleum sphondylium* Linnaeus) 6–10 feet (1.8–3.0 m) apart among carrots (*Daucus carota* Linnaeus) (Umbelliferae). The webworm moths prefer to lay their eggs upon the parsnips, and the larvae develop in the parsnip heads and can be destroyed by cutting and burning or by drowning.

A modern example of successful trap cropping is Newsom's (1978) suggestion that lima beans (*Phaseolus lunatus* Linnaeus) planted contiguously with soybeans (*Glycine max* (L.) Merrill) will trap the Mexican bean beetle, *Epilachna varivestis* Mulsant. The principle of trap cropping is stated to be an important component of IPM for soybean pests, reflecting economy, minimum adverse effects on beneficial insects, reduction of environmental pollution by pesticides, and minimal selective pressure to delay insecticide resistance.

Detailed knowledge of the kairomones present in plant species and varieties now affords a firm scientific basis for the application of the trap-crop principle. Contardi (1939) speculated about the use of bitter *Cucurbita andreana* as a trap crop to protect cucurbit cultivars from attack by *Diabrotica speciosa*. A single vine of *Cucurbita ecuadorensis*, whose leaves

contain a total of 0.41 mg of Cuc B per gram of fresh weight, planted at the periphery of a 0.1-acre (0.04-ha) melon patch of *Cucumis melo* cultivar was observed to have arrested hundreds of spotted cucumber beetles, while only a single beetle was found in the muskmelon. Experiments using a design of hybrid *Cucurbita andrena* × *C. maxima* plants, one on each side of plots of 20 muskmelon plants, *Cucumis melo*, showed that 82 percent of *Diabrotica u. howardi*, *D. v. virgifera*, and *Acalymma vittatum* were found on the trap crop (average 18 per plant) compared with those found on the melons (average 4.2 per plant) (unpublished data). Such trap crops can be used in conjunction with occasional applications of contact insecticides to destroy the pests on the trap crop, or the trap crop can be planted over an application of granular systemic insecticide. Scientifically designed trap cropping, employing species or cultivars with high kairomone levels that do not hybridize with cultivars, offers a technological challenge to the organic farmer and an economical method for substantially decreasing the use of insecticides.

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Early Contributions of Insect Toxicology To the Evolution of Environmental Toxicology

Allan S. Felsot

The celebration of an anniversary connotes the remembrance of the past from the perspective of the present with anticipation for the future. Science, like law, is built upon precedent. The continued advancement of any scientific endeavor must entail a periodic assessment of where that discipline has been. Historical observations inevitably lead to a better understanding of the present state of the art and of future needs. It is appropriate on the occasion of the 125th anniversary of the Illinois Natural History Survey to examine the historical roots of one of its disciplines. The study of environmental toxicology is relatively new, but it has a long tradition of support within both the Survey's Section of Economic Entomology and the University of Illinois' Department of Entomology.

Environmental toxicology is a broadly based discipline that involves the integrated efforts of scientists from many other disciplines. It is currently enjoying unprecedented public attention in the media. Not since the publication of *Silent Spring* (Carson 1962) has more public attention been focused on environmental contamination from chemicals and the potential biological effects. Amidst all the controversy surrounding the manufacture, use, and disposal of synthetic organic chemicals, it is easy to forget how this environmental awareness came about. More importantly, the evolution of the science that provided the fundamental basis for this awareness has become obscured.

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It is hypothesized that the field of environmental toxicology began as a subdiscipline of applied entomology. Early environmental toxicological research was mainly conducted by economic entomologists who needed to know the effective dose required to kill pest insects and the environmental factors that would affect the efficacy of the pest control operation. Today, the Entomological Society of America recognizes pesticide chemistry and toxicology as research areas within the scope of two of its disciplinary sections. The objective of this paper is to document the early contributions of economic entomologists (especially insect toxicologists) to the development of environmental toxicology by examining the entomological literature prior to 1962 (the year of publication of Carson's *Silent Spring*). This objective was accomplished by scanning the *Journal of Economic Entomology* (JEE), volume 1 (1908) through volume 55 (1962), for papers that dealt with environmental toxicology. In addition, papers from other journals were cited if they seemed to have had a significant influence on the content and direction of the insect toxicological research reported in JEE.

Seven areas of research that form the essence of modern environmental toxicology could be seen in the applied entomological literature. These included the measurement of toxicity; symptomatology, mode of action, and metabolism; insecticide resistance; pesticide selectivity and comparative toxicology; insecticide residues and analytical methods development; hazard evaluation; and environmental chemodynamics. The contributions of entomologists to each of these areas were reviewed.

MEASUREMENT OF TOXICITY

Chemicals have long been used to help control insect pests. Early accounts of insect toxicology were anecdotal with little quantitative data from which to determine effective dosages even though the number of chemicals available was very limited by today's standards. Economic entomologists recognized the need to develop a standardized system for comparing the toxicity of different chemicals and for determining the efficacy of control.

Early studies were devoted to finding appropriate bioassays for the determination of toxicity of cyanide fumigants. Coleman (1911) developed a bioassay to determine the most effective concentration of cyanide gas against scale insects. He observed mortality of insects in the laboratory at one-sixteenth the dosage that had been prevalent in fumigation work. Hartzell (1924) was the first to use correlation analysis to study the relation of control efficiency to dosage, temperature, and percentage of open space. Dosage was found to exert the greatest influence on control. Abbott (1925) presented a technique that is still used routinely for correcting the observed mortality that may occur in the untreated population of a bioassay.

A technique for comparing the relative toxicities of several chemicals to a variety of invertebrate and vertebrate species was first reported by Marcovitch (1928). He adapted a mathematical formula, using time and concentration as variables, to determine the numerical toxicities of arsenical and fluorine compounds. He suggested that the mosquito be used as a standard test organism in insect toxicology as the white rat was for pharmacological studies. Comparative toxicity tests of different compounds were also studied by Campbell (1930). Campbell used the concept of median lethal dose, the dose which kills 50 percent of a large group of animals, to express the toxicity of different compounds to the silkworm and

mosquito. The concept of median lethal dose had been proposed earlier by Trevan (1927) to replace the prevalent expression of minimal lethal dose, which was regarded as highly variable. Campbell further showed the importance of the route of exposure to the toxicity of a compound. Shepard & Richardson (1931) also used Trevan's (1927) ideas to draw "toxicity curves," described as being characteristic of a specific insecticide regardless of how the dosage was measured.

After Trevan's concept of median lethal dose was published, many toxicologists observed that the response of animal populations to increasing dosages of a toxicant followed a sigmoidal pattern. Bliss (1934) used this characteristic phenomenon to develop a standardized technique for determining mortality at a specified dosage. He transformed dosage to logarithmic units and percent mortality to probability units that he termed probits. The dosage-mortality curve became linear and thus amenable to regression analysis. In later work, Bliss (1935a) developed statistical procedures for calculating dosage-mortality curves. In a related paper Bliss (1935b) introduced the term "LD50" to replace median lethal dose in comparisons of dosage-mortality data. Later, Bliss developed techniques for expressing mortality relative to time of exposure and the relationship between exposure time and concentration (Bliss 1937, 1940). Although researchers have studied the intricacies of the dosage-mortality curve and have suggested improvements (e.g., Sun & Shepard 1947; Wadley & Sullivan 1943; Beard 1949; Lanchester 1951), Bliss' techniques have remained standard practice in all fields of toxicology.

SYMPTOMOLOGY, MODE OF ACTION AND METABOLISM

Observations on pesticide symptomology, mode of action, and metabo-

lism are classified today as pharmacokinetic or toxicodynamic studies. Early observations of symptoms exhibited by poisoned insects gave clues to the mode of insecticide action (Shafer 1911a,b; Tischler 1935). Mode of action studies gradually became more sophisticated with the evolution and advancements in biochemistry. For example, Fink (1927) compared glutathione levels in normal insects and in insects treated with arsenicals. His observations were in agreement with the published findings on arsenic toxicity in vertebrates (Voegtlin et al. 1925), that arsenic interfered with the normal functioning of glutathione. Metcalf & March (1949) produced a highly cited study on the mode of action of parathion in insects that influenced the course of insect toxicology research. These authors conducted pioneer studies on the relation of the chemical structure of a series of organophosphorus insecticides to toxicity and cholinesterase inhibition. They were the first to show that there was a direct relationship between *in vitro* cholinesterase inhibition and *in vivo* toxicity.

The importance of metabolism in explaining differential toxicity among insect species was recognized early in the entomological literature (Fernald 1908). Prior to World War II few metabolism studies were reported because analytical methods were too insensitive for the determination of toxicants and metabolites in small tissue samples. However, the value of radiotracer methodology as a sensitive detection technique was shown in studies on arsenic disposition in the silkworm (Campbell & Lukens 1931; Norton & Hansberry 1941). After the introduction of DDT, the metabolism of chlorinated hydrocarbons in insects was studied by using only wet chemical methods of analysis (Ferguson & Kearns 1949; Sternburg et al. 1950; Sternburg & Kearns 1956). Most studies on insect metabolism after 1950 employed radioisotopes of the chlorinated hydrocarbon and organophosphorus insecticides (e.g., Roan et

al. 1950; Lindquist et al. 1951a,b). In the 1950's and thereafter radioisotopes were increasingly used to study the metabolism and distribution of insecticides in nontarget vertebrates (e.g., Pankaskie et al. 1952; Robbins et al. 1956; March et al. 1956a,b; Lindquist et al. 1958; Kaplanis et al. 1959).

Another area of early toxicodynamic research in the entomological literature is the study of the effect of chemical interactions on toxicity and metabolism. Specifically, synergistic interactions between insecticides and nontoxic compounds, such as sesamin, were found to be important in increasing the toxicity of the unstable pyrethrums (Haller et al. 1942; Kerr 1951). Robbins et al. (1959) first reported the synergism of organophosphates by piperonyl butoxide in mammals. The interactions between synthetic organic insecticides and botanical insecticides were also studied (Sun 1948).

INSECTICIDE RESISTANCE

The study of insecticide resistance has received a great deal of attention by insect toxicologists. Although many reviews of this subject have appeared since the 1940's (e.g., Quayle 1943; Babers 1953; Brown 1968; Georghiou & Taylor 1976), several points pertinent to the development of environmental toxicology should be noted. First, insect resistance was originally reported in 1914 by Melander and involved the decreased effectiveness of lime-sulphur against the San Jose scale. Prior to 1940 most reports involved resistance of scale insects or the codling moth to various fumigants (Quayle 1943). After the introduction and widespread use of DDT in the mid-1940's, reports of resistance grew exponentially. March & Metcalf (1949a,b) were probably the first in the United States to report both DDT resistance and possible cross resistance to other chlorinated hydrocarbon insecticides in houseflies. Until that time most resistance studies involved anecdotal re-

ports of decreased control of pests in the field or the comparison of insecticide toxicity against laboratory strains and field-collected populations. A breakthrough in understanding the biochemical basis of resistance came with the reports of differences in DDT metabolism between susceptible and resistant houseflies (Sternburg et al. 1950; Perry & Hoskins 1951). When Sternburg et al. (1953) reported that DDT was enzymatically dehydrochlorinated by resistant houseflies, the stage was set for sophisticated studies on detoxication mechanisms and the biochemical genetics of resistance.

PESTICIDE SELECTIVITY AND COMPARATIVE TOXICOLOGY

Pesticide selectivity refers to the determination of the relationship between chemical structure and toxicity in various target and nontarget species. Comparative toxicology includes studies of differences among invertebrates and vertebrates in detoxication mechanisms and pesticide interactions with biochemical targets.

Kearns and his coworkers (e.g., Kearns & Flint 1937; Metcalf & Kearns 1941; Dahm & Kearns 1941) pioneered the concept of testing a large number of compounds in a homologous series against different insects to determine the effect of chemical structure on toxicity. Early studies focused on nitrogen-containing synthetic organics, such as cyclohexylamine, picramic acid, toluenesulfonyl chloride, and alkyl secondary amines. Other structure-activity studies followed with investigations of phosphorous esters (Ludvik & Decker 1947, 1951), N-heterocyclics (King & Frear 1943), DDT analogs (Metcalf 1948), and N-methyl carbamates (Metcalf et al. 1960, 1962). Some studies were qualitative in the sense that long lists of compounds and percentages of mortality were presented. Other studies became more quantitative by graphing the relationship be-

tween mortality and specific chemical properties (e.g., Dahm & Kearns 1941; Fukuto et al. 1961; Metcalf et al. 1962).

Pesticide selectivity studies were important in reconciling the role of biological control of insect pests with that of chemical control. For example, Ripper et al. (1951) published a comprehensive study on the comparative toxicity of insecticides between pests and their natural enemies. Today, quantitative structure-activity correlations play an important role in the discovery of new pest control agents and in the development of compounds that are selective for target organisms.

Although research had been conducted on the toxic effects of pesticides on nontarget vertebrates, few studies directly compared responses of insects and vertebrates before the advent of the synthetic organic insecticides. Marcovitch (1928) was perhaps the first entomologist to compare the toxicity of inorganic insecticides between mosquitoes, earthworms, and rabbits. Goldfish and cockroaches were compared in an investigation of the toxic effects of nicotine (Ellisor 1936). The first comprehensive comparative toxicological study was reported by Metcalf & March (1950). These workers compared the properties of acetylcholinesterase from the bee, the housefly, and the mouse to study the relationship between parathion derivatives and insecticidal action. The motivation behind studies of this nature is clear from the authors' conclusion, "A detailed knowledge of the properties of various cholinesterases and correlation of the structure of various organic phosphate anticholinesterases with their specific action may result in the development of insecticides with a greater margin of safety to warm-blooded animals than those currently in use, and may enable the entomologist to select compounds toxic to certain insect pests, but relatively harmless to beneficial parasites and predators." Metcalf & March (1950) greatly influenced the course of toxicology as evidenced by the volume of

research devoted to comparative toxicological studies in the 1950's and 1960's (e.g., Johnson et al. 1952; Casida & Stahmann 1953; March et al. 1955, 1956a; O'Brien 1956, 1957a,b; O'Brien et al. 1958; Krueger & Casida 1957; Krueger & O'Brien 1959; Krueger et al. 1960; Casida et al. 1960; Afshar-pour & O'Brien 1962).

INSECTICIDE RESIDUES AND DEVELOPMENT OF ANALYTICAL METHODS

The problem of pesticide residues on food and in the environment has concerned entomologists since the early 1900's. JEE has long served as a forum for the reporting of residues. This function was especially important when there was essentially no other outlet for this kind of investigation. Prior to World War II and the introduction of DDT, most investigations centered on the occurrence of arsenic and lead residues owing to the heavy spraying of lead arsenate for the control of orchard pests. Early studies were concerned with arsenic residues in soils because of the potential for phytotoxicity to trees in alkaline soils (Ball et al. 1910; Headden 1910). Later studies measured the arsenic and lead content of sprayed apples (O'Kane 1913; MacLeod et al. 1927; Hartzell & Wilcoxon 1927, 1928; McLean & Weber 1928). Attention was also given to residues of the organic insecticides, nicotine, and derris (Norton & Billings 1941; Cassil 1941).

The introduction of DDT into general use in agriculture greatly increased the amount of insecticides used. Consequently, the attention devoted to pesticide residues greatly increased. The prolonged persistence of DDT was quickly recognized. Almost every crop that had been sprayed with DDT was studied for residues (e.g., Wilson et al. 1946b; Borden 1947; Smith et al. 1948a; Eden & Arant 1948). Residues of other synthetic

organic insecticides, especially the organophosphates, were investigated almost as soon as they were introduced (e.g., Ginsburg et al. 1949, 1950; Hoskins 1949; Smith et al. 1952; Gunther & Jeppson 1954; Gunther et al. 1954; Brett & Bowery 1958).

The tremendous interest in pesticide residues after the introduction of the synthetic organics was more than mere concern about the possibility of exceeding established tolerances. Shortly after the general introduction of DDT it was discovered that this chemical could be bioconcentrated in milk and passed through the food chain (Telford & Guthrie 1945; Woodward et al. 1945; Wilson et al. 1946a). Many reports on the occurrence of DDT and other chlorinated hydrocarbon insecticides in milk and meat products appeared in JEE after 1946 (e.g., Smith et al. 1948b; Carter et al. 1949a,b; Claborn et al. 1950a,b; Frear et al. 1950; Bushland et al. 1950; Fahey et al. 1955; Ely et al. 1957). These studies generally showed that DDT could bioconcentrate in milk regardless of whether the insecticide was applied directly to cows, barns, or feed. Studies of organophosphate and carbamate insecticide residues in milk soon followed the DDT studies, but these indicated no significant bioconcentration (Goulding & Terriere 1959; Eheart et al. 1962).

Pesticide residues were also studied in poultry and eggs. Lindane, a chlorinated hydrocarbon, was found at high levels in fat and eggs several months after poultry houses had been sprayed, and recommendations for its use were cancelled (Ivey et al. 1961). Residues of Co-Ral, an organophosphate, were extensively studied by Dorough et al. (1961a,b). These authors emphasized the need also to study metabolite residues. Bioconcentration of carbamate insecticides was shown to be insignificant in a study of carbaryl residues in poultry products (McCay & Arthur 1962).

It should be noted that residue studies of organophosphate and carba-

mate insecticides during the 1950's and 1960's were using detection limits of approximately 0.1 ppm. Today, detection limits easily reach the 0.01 or 0.001 ppm level, and the probability of finding "biodegradable" pesticide residues in food has increased accordingly.

Food processing, such as the milling of wheat, was found to aid in residue reduction (Schesser et al. 1958). Siakotos (1956b) observed that vaporized lindane could enter stored packaged foods regardless of the container. Since it was observed that pesticide residues on food were generally inevitable, some attention was devoted to techniques for residue removal. A number of studies were conducted on the removal of lead arsenate residues from fruit (Robinson 1929; Fisher 1931; Weber & McLean 1933); later, the effect of washing on organophosphates was studied (Smith et al. 1955).

Concomitant with the need for accurate pesticide residue determinations was the development of sensitive analytical methods. Although other journals published analytical methods for pesticide residues (e.g., *Journal of the Association of Agricultural Chemists*, published prior to World War II, and the *Journal of Agricultural and Food Chemistry*, initiated in 1953), JEE had been a reliable forum for this kind of information since its inception. Early reports included methods for the analysis of nicotine (Safro 1917), lead arsenate (Hamilton & Smith 1925; Ginsburg 1928), oil (Ebeling 1940; McCall & Kagy 1940), and rotenone (Gunther 1942).

The widespread use of the synthetic organic pesticides stimulated investigation of more sophisticated and diverse techniques that were required for the analysis of the growing number of sampling matrices (Carter 1955). Originally the chlorinated hydrocarbons were determined by total chlorine analysis (Ginsburg 1946). Eventually, chromatographic separation methods and, later, colorimetric analysis were adopted for the analysis of many organochlorine insecticides (e.g., DDT,

Schechter & Haller 1945; aldrin and dieldrin, O'Donnell et al. 1954, 1955; heptachlor and chlordane, Polen & Silverman 1952; lindane, Schechter & Hornstein, 1952; EDB, Sinclair & Crandall 1952). Radiolabelled pesticides were useful for testing the extraction of residues from complex matrices, such as milk (Timmerman et al. 1961). A cholinesterase-inhibition technique, useful for detecting organophosphate insecticides (Giang & Hall 1951), was modified for analyzing weak inhibitors, such as the organophosphorodithioates (Miskus et al. 1959; Miskus & Hassan 1959). The bioassay of extracts, using mosquito larvae, was employed as a sensitive technique for the detection of toxic compounds and metabolites (Bushland 1951; Hartzell 1952). Sampling techniques to ensure reliable residue data were also studied (Cassil et al. 1943; Anderson & Gunther 1951; Van Middeltem et al. 1956; Huddleston et al. 1960b; Lichtenstein et al. 1960).

In sum, the literature on insecticide residues shows a long-standing and deep concern among entomologists about health hazards in food supplies. Perhaps the prevailing philosophy was expressed best by White (1934), who stated at a meeting of the American Association of Economic Entomologists, "Let us not again go along for years putting on other poisons in total ignorance of the amounts going to the consumer and of the effects upon his health." This theme was acted upon in 1951 when the chairmen of most midwestern departments of entomology met in Chicago and prepared the outline of a research project entitled, "Hazards Resulting from the Use and Misuse of Pesticides and Means for their Elimination" (E.P. Lichtenstein personal communication). This project was activated in 1954 and represented one of the first regional projects (NC-19) established in entomology. The objective of this cooperative venture was to isolate, define, minimize, or eliminate hazards connected with the use of pesticides.

HAZARD EVALUATION

Hazard evaluation involves the determination of acute and chronic effects on nontarget organisms and on the environment from direct or indirect exposure to pesticides or their metabolites. Four main areas of hazard evaluation research that have appeared in the entomological literature are hazards to livestock and other mammals; hazards to nontarget insects, fish, and birds; effects on soil biota and plants; and effects on human health.

The use of insecticides to protect livestock from insect infestations that might reduce production efficiency had been investigated since the late 1920's (Melvin 1932). Naturally, the safety of the animals was a major concern. Early studies focused on the physiological and toxic effects of oil sprays on cattle (Melvin 1932; Freeborn et al. 1934; Atkeson et al. 1944). No acute effects owing to the treatment of forage with pyrethrum (De Ong 1937) or cryolite (Wilford & Mott 1944) were observed in pastured livestock. In other tests it was observed that the injection of pyrethrum extract into rats produced severe adverse reactions (Leonard 1942), but a similar mode of exposure to cryolite failed to produce acute toxic symptoms (Sweetman & Bourne 1944). Feeding studies with chickens showed no adverse effects with low doses of arsenic bait, but it reduced egg laying at high doses (Wilson & Holmes 1936).

The first widespread use of DDT after World War II was for the control of livestock pests. Immediately after the introduction of DDT there was a proliferation of reports on its effects on a wide variety of animals. Much of this research attempted to establish safe levels of insecticide exposure resulting from single or repeated administrations by direct spraying or by feeding (e.g., Orr & Mott 1945; Telford & Guthrie 1946; Wilson et al. 1946a; Bushland et al. 1948; Batte & Turk 1948; Welch 1948; Radeleff 1950). Both acute toxic symptoms and histopathological changes

were recorded in response to extremely high dosages and dosages likely to be received under normal use conditions. In general, low dosages of many of the chlorinated hydrocarbons had little effect, but moderate to severe histopathological effects were noted at the highest dosages.

Ingle (1947) used white rats to compare the acute and chronic toxicities of chlordane and DDT. From 1950 to 1955 there were a number of studies on the toxicity of the new chlorinated cyclo-diene insecticides to poultry (Eden 1951; Turner & Eden 1952; Arant 1952; Sherman & Rosenberg 1953, 1954). Moore (1952) studied the toxic effect of lindane vapors on canaries and pigeons.

After the early 1950's, research was directed to the acute effects of exposure to the organophosphate insecticides. Studies were conducted on the toxicity of direct application (Furman & Weinmann 1956), exposure through treated forage (Dobson et al. 1960), and exposure to vapors (Tracy et al. 1960). Research was also directed toward the toxicity of systemic organophosphate insecticides intentionally added to feeds (Radeleff & Woodard 1956, 1957). Methods for measuring cholinesterase activity in erythrocytes were developed to determine the degree of exposure of livestock to organophosphate residues (Robbins et al. 1958; Hermenze & Goodwin 1959). Effects of organochlorine and organophosphate insecticides on the metabolism and motility of mammalian spermatozoa were studied by Beck (1953).

The use of DDT and organophosphates as mosquito larvicides stimulated research on the acute toxicity of these pesticides to fish and aquatic invertebrates (Ginsburg 1945, 1947; Eide et al. 1945; Darsie & Corriden 1959; Mulla & Isaak 1961). Some studies determined the acute toxicity to fish of insecticides that could reach water through indirect routes (Schulze et al. 1952; Haynes et al. 1958). Other studies investigated the ecological ef-

fects of insecticides on aquatic communities (Tiller & Cory 1947; Hitchcock 1960; Webb 1960).

Arsenic baits used in grasshopper control were found nontoxic to pheasants (Lilly 1940). DDT-treated insects were fed to nestling birds in one study, and toxicity was only manifested when the birds' food supply was limited (George & Mitchell 1947).

Although the effects of insecticides on bees had received much attention before 1900 (Shaw 1941), little research had been conducted on the hazards of insecticides to other beneficial insects, including predators and parasites, before the introduction of DDT (Haug & Peterson 1938). Both arsenicals and DDT were the focus of much of the research on pollinators before 1950 (Doane 1923; Webster & Crews 1934; Linsley & MacSwain 1947). Observations by many workers of the resurgence of pest populations and the emergence of secondary pests after crops were sprayed with DDT (DeBach 1947; Newson & Smith 1949; Griffiths 1951) stimulated further research on the acute toxicity of various insecticides to beneficial insects (Ripper et al. 1951).

Concern for the potential hazards associated with pesticide accumulation in soil was manifested long before the introduction of the persistent chlorinated hydrocarbons. Hyslop (1914) expressed concern about the effect of cyanide on beneficial soil microbiota. Others studied the effect of the accumulation of lead and calcium arsenate on their phytotoxicity (Scott & Karr 1942; Fleming et al. 1943). The concern with adverse effects on microbiota and with phytotoxicity continued after the introduction of DDT (Wilson & Choudhri 1946; Morrison et al. 1948; Cullinan 1949; Stitt & Evanson 1949; Gould & Hamstead 1951; Simkover & Shenefelt 1951) even though the accumulation of DDT residues from earlier applications had not been recognized until the 1950's (Chisholm et al. 1950; Ginsburg & Reed 1954; Lichtenstein 1957). Most studies did show some phytotoxic effects from chlorinated hydrocarbons,

such as lindane (Morrison et al. 1948). In general, few effects on soil microorganisms or microarthropods were observed after insecticide treatments (Bollen et al. 1954a,b; Hartenstein 1960).

Since the early 1970's great emphasis has been placed on the assessment of human exposure to pesticides. Recently a research conference and workshop on minimizing occupational exposure to pesticides were conducted (Gunter 1980). Entomologists have always been interested in this topic because of their own potential exposure. The first study on human hazard assessment published in JEE concerned the effects of fumigation with hydrocyanic gas (Yothers 1910). A number of studies before World War II commented on the hazards to human health from various pesticides, including arsenic (O'Kane 1916; Hockett 1934;), derris (Wells et al. 1922), and cryolite (Marcovitch & Stanley 1938). Wilson & Holmes (1936) assessed the hazards of eating arsenic-tainted poultry by comparing the residue values obtained from arsenic-fed chickens with levels known to be toxic to humans. Marcovitch & Stanley (1938) also used cryolite residue values on food and the median lethal dose to humans to determine the "factor of safety" for this pesticide.

Chlorinated hydrocarbon insecticides (especially DDT) were initially thought to be safe for humans because large differences in acute toxicities of these compounds were observed between insects and mammals. Human hazard assessments of these compounds were absent from the early entomological literature. On the other hand, several entomologists conducted detailed hazard evaluations of the organophosphate insecticide, parathion (Griffiths et al. 1951; Ashdown et al. 1952; Braid & Dustan 1955; Quinby et al. 1958). Due to the extremely high acute toxicity of parathion and its lack of selectivity, it was deemed responsible for a number of severe injuries and deaths resulting from occupational ex-

posures. Studies showed that absorption of parathion through the skin over several exposure periods created the greatest hazard to applicators and field hands. Metcalf (1951) developed a technique for estimating blood cholinesterase that was useful in the detection of possible exposure to organophosphorus insecticides. Fulton et al. (1955) evaluated the efficiency of respiratory protective devices for agricultural use. Protective clothing, gloves, and respirators had long been known to afford protection against overexposure to pesticides (Metcalf 1951). Entomologists have consistently recommended using pesticides only when necessary and taking proper safety precautions.

ENVIRONMENTAL CHEMODYNAMICS

The study of the fate and behavior of pesticides in the environment has emerged as a relatively new discipline called environmental chemodynamics (Haque & Freed 1974). Pesticide chemodynamics essentially involves four areas of research:

1. Physicochemical properties of pesticides that influence their behavior in the environment;
2. Mechanisms of the partitioning of pesticides among environmental components (air, water, soil, biota);
3. Attenuation processes affecting pesticide fate (e.g., photodecomposition, chemical and microbial degradation, etc.);
4. Understanding and modeling of environmental transport processes.

The ultimate objective of environmental chemodynamic research is to assess accurately the exposure of target or nontarget organisms to a pesticide or any contaminant. Since exposure to a chemical is largely dependent on its environmental distribution, the ecological impact of pesticides in any ecosystem is directly related to the sum of the chemodynamic processes.

Pesticide chemodynamic research appearing in *JEE* between 1908 and

1962 included: residue dynamics on plants; translocation into plants and systemic dynamics; metabolism in plants and transformation products; persistence and translocation in soil; volatilization; formulation chemistry; and bioconcentration. The determination of pesticide residues on crops had received a great deal of attention owing to the establishment of tolerances by the Food and Drug Administration and the concern about hazards to human health. In contrast, the interest in residue dynamics seemed to be motivated by rapid decreases in insecticidal activity after application. Early studies investigated the effect of fruit growth and climatic conditions on residue losses (Hamilton 1929; Fahey & Rusk 1940). The effect of sunlight and oxygen on residues was also studied (Jones et al. 1933; Gunther 1943), and methods were explored for the inhibition of insecticide decomposition (Gunther et al. 1948). Some studies were concerned only with the dispersion of residues on foliage and their subsequent rates of loss (MacLeod & Sherwood 1937; Gunther et al. 1946; Dawsey & Markwood 1940).

In the 1950's the focus of pesticide research shifted to the study of residue dynamics with respect to the evaluation and elimination of hazards. Translocation of foliar-applied materials into other parts of the plant, such as the fruit, and the actual location of the residues therein were studied (Smith & Clifford 1950; Blinn et al. 1959; Matsumura 1960). Other studies concentrated on the effects of application rate, number of applications, weathering, and crop dehydration in reducing residues (Stansbury & Dahm 1951; Sloan et al. 1951a,b; Dahm 1952; Hopkins et al. 1952a,b; Westlake & Butler 1953; Waites & Van Middlelem 1958). Many researchers graphically displayed residue persistence data with the concentration recovered as a dependent variable and the time after application as an independent variable. The resulting curves were biphasic; an initial rapid loss of pesticide was followed by a much

slower degradation rate (e.g., Decker et al. 1950; Hopkins et al. 1952a,b; Fahey et al. 1952). Gunther & Blinn (1955) discussed these curves as representing a two-step process in which the rapid initial loss of residue is related to weathering, and the slower loss is related to metabolically induced alterations.

The application of systemic insecticides to soil has been viewed as a relatively efficient and selective method for controlling pests. Questel & Connin (1947) were first to show that the treatment of soil with parathion produced plant tissues lethal to the European corn borer. Terriere & Ingalsbe (1953) showed that potato tubers absorbed chlorinated hydrocarbon insecticides from soil as long as 3 years after the initial treatment. Getzin & Chapman (1959) proved that soil type greatly influenced the amount of insecticide translocated from the soil. Reynolds & Metcalf (1962) showed that there was a direct relationship between the water solubility of a chemical and the amount taken up by a plant.

The metabolism and systemic dynamics of organophosphate insecticides were extensively studied by Metcalf, March, Casida, and their coworkers. Casida et al. (1952, 1954) showed that plants could metabolize octamethylpyrophosphoramidate to a toxic, anticholinesterase product. Metcalf et al. (1955, 1957a) and Fukuto et al. (1956) showed that phorate and the isomers of Systox were oxidized in plants to toxic metabolites. Gannon & Decker (1958) demonstrated that aldrin, a chlorinated cyclo-diene, was oxidized in plants to the equally toxic epoxide, dieldrin. Metcalf & March (1952) and Metcalf et al. (1954, 1956, 1957b) conducted detailed, comprehensive studies on the systemic dynamics of radiolabeled organophosphates. Radioautographs of whole leaves were used to visualize distribution of the insecticide.

Throughout the 1950's studies proliferated on the persistence of the chlorinated hydrocarbon and cyclo-diene insecticides in soil (Fleming &

Maines 1953, 1954; Kiigemagi et al. 1958; Young & Rawlins 1958; Lichtenstein & Polivka 1959; Lichtenstein et al. 1960). Little work had been published on the persistence of the organophosphates at that time (Menn et al. 1960). The major concern seemed to be with the accumulation of residues in soil and their possible phytotoxic effects. There was also a need to understand residue dynamics so that control of soil pests could be optimized. Lichtenstein and his coworkers conducted extensive research on the effects of soil type, temperature, moisture, mode of application, and cover crop on pesticide persistence and translocation (Lichtenstein 1958; Lichtenstein & Schulz 1959b, 1961; Lichtenstein et al. 1962). Some work was reported on the adsorption of insecticides by soils (Chisholm & Koblitsky 1943; Getzin & Chapman 1959; Weidhaas et al. 1961) and on volatilization (Harris & Lichtenstein 1961). In most of the insecticide-soil interaction studies, soil organic matter content appeared to be the most significant property affecting pesticide translocation and persistence. Edwards et al. (1957) showed an inverse relationship between soil organic matter content and toxicity.

Several studies proved that insecticides could be oxidized in soil to biologically active metabolites. Gannon & Bigger (1958) and Lichtenstein & Schulz (1959a) were the first to show that aldrin and heptachlor were transformed into the toxic epoxides, dieldrin and heptachlor epoxide. Lichtenstein & Schulz (1960) showed that the transformation was biological and did not take place in autoclaved soils. The organophosphate insecticide, phorate, was also shown to be oxidized in soil or by soil microorganisms to products similar to those found in plants by Metcalf and his coworkers (Ahmed & Casida 1958; Getzin & Chapman 1960).

Several early experiments measured the volatility of insecticide formulations containing nicotine, DDT, and some fumigants in relation to effects on insect control (DeOng 1923; Roark &

Nelson 1929; Fleck 1944). One study reported the contamination of food and air by lindane applied as a surface spray (Siakotos 1956a). Other studies of formulations measured the efficiency of various materials as carriers for different insecticides (Headlee & Rudolfs 1922; Eddy 1926; Weidhaas 1957) and the stability of various spray mixtures (Gunther 1947; Cutkomp 1947).

No studies were found in JEE prior to 1962 that measured bioconcentration factors, but the accumulation of insecticides in nontarget organisms after they had fed on treated forage or after area-wide sprays was studied (Wilson et al. 1946a). Early studies reported the absorption of arsenic by vegetables grown in soils treated with lead arsenate (McLean et al. 1944). Dairy cows pastured in fields sprayed with chlorinated hydrocarbon and cyclodiene insecticides secreted the pesticides in their milk (Entomology Research Division 1959; Gannon & Decker 1960). DDT residues were found in dairy and poultry products from New York farms following widespread aerial spraying for gypsy moth control (Huddleston et al. 1960a). One study showed that leaves from elm trees injected with the organophosphate, Tetram, were toxic to earthworms and rats (Al-Azawi et al. 1961).

CONCLUSIONS

The publication of *Silent Spring* (Carson 1962) has been credited with informing the general public of the hazards of pesticide use and creating an attitude of environmental awareness. The purpose of this historical review of environmental toxicology was to trace the evolution of this environmental awareness from the perspective of the entomological literature. It became clear after reviewing over 200 papers published primarily in the *Journal of Economic Entomology* between 1908 (volume 1) and 1962 (volume 55) that the interest in environmental toxicology evolved from the research efforts

of insect toxicologists before and immediately after World War II. JEE, originally published as the proceedings of the *American Association of Economic Entomologists*, served as a continuous forum for a multitude of insecticide toxicology studies. The *Journal of Agricultural and Food Chemistry*, published by the American Chemical Society, also served as a forum after 1953.

Today more than 10 journals regularly publish research on environmental toxicology. Many of these journals have existed for less than 15 years. Toxicological research encompasses a great number of environmental contaminants, and researchers are trained in a wide variety of fields. It is pertinent to note that the current and past scientific advisory panels to the U. S. Environmental Protection Agency have had entomologists trained in insect toxicology as members. The combination of strong training in biology and chemistry has enabled insect toxicologists to adapt their research to a wide range of environmental problems that go well beyond the bounds of traditional economic entomology. With considerable foresight Moore (1923) observed, "The economic entomologist should be well grounded in chemistry, especially organic and physical chemistry for the purpose of enabling him to see and solve the problems in connection with the use of insecticides."

In retrospect, it appears that economic entomologists have traditionally been concerned with both the benefits and the risks of pesticide use. The dilemma of the entomologist in balancing crop protection with environmental protection was perhaps best expressed by Dr. George Decker of the Illinois Natural History Survey. In a presentation about DDT residues before the Insect Control Committee of the National Research Council, Decker (1946) said, "The entomologist frequently finds himself in difficult positions. He is expected to assist the farmers by supplying information on the latest and best possible recommendations for the control of insect pests. At the same time,

he is obligated to guard against recommending any procedure or treatment that might endanger the life or health of man or beast. In the absence of reliable data, he must proceed with reasonable caution and must at all times avoid being carried away by current waves of public opinion. Today, he must balance the merits of DDT against the

hazards that might accompany its use and weigh carefully the evidence on both sides of the equation."

It is incumbent upon insect toxicologists to understand and explain the diverse aspects of the fate and behavior of insecticides in the environment so that they may be used in the most efficient and safest manner possible.

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Biotic and Abiotic Stresses as Primary and Predisposing Factors Affecting Illinois Trees

D. F. Schoeneweiss, Dan Neely, and E. B. Himelick

Illinois, the Prairie State, is in the heart of the nation's breadbasket. Deep, flat, prairie soils and equitable climate are ideal for the modern, highly mechanized production of row crops. With nearly 12 million acres of corn and 10 million acres of soybeans annually, Illinois is a major agricultural state and is known around the world for high yields. In the face of this intensive agriculture, it is small wonder that the forests and woodlots of Illinois have received only limited attention as valued natural resources. With less than 11 percent of its total acreage forested, Illinois ranks last among states east of the Mississippi in proportion of wooded area (Stewart 1980).

Before 1800, over 40 percent of the state was covered by forest, particularly in southern, western, and northern Illinois and along major rivers (Herendeen & Rolfe 1983). By 1858, the date from which the Illinois Natural History Survey marks its beginning, much of the wooded land had been cleared for farming. As long ago as 1886, members of the State Laboratory of Natural History, a forerunner of the Survey, were voicing concern over the rapid loss of Illinois' trees (Carter 1958). The acreage of forest has continued to decline to the present day due to logging, disease, clearing for cropping, and the development of urban and industrial complexes. Because of the relative scarcity of trees, their protection and preservation in Illinois are of vital concern to its citizens.

FOREST RESOURCES OF ILLINOIS

The forest resource base in Illinois can be divided into two categories,

rural and urban (Stewart 1980). The rural base consists of national, state, county, and private forests; tree plantations; farm woodlots; and windbreaks. The urban base is made up of trees on parkways and private property and trees in municipal and industrial plantings. In rural areas, windbreak trees, which were widely planted after the dust bowl years of the 1930's, have all but disappeared, as have many farm woodlots, due to the increased conversion of acreage to row crops. The resulting loss of fertile topsoil by wind and water erosion on deforested land has become a vital issue facing the state. Of the 3.5 million acres of Illinois forest remaining in 1967, 96 percent was designated as commercial forest, with 93 percent of this commercial portion in private ownership (Stewart 1980). The Shawnee National Forest in southern Illinois totals 277,000 acres, with county forests making up 126,000 acres and state forests only 11,500 acres. Nearly all of the rural forest is hardwoods, predominantly oak (42 percent) and hickory (11 percent).

The extent and value of the urban forest resources of Illinois have not been adequately defined. Community-owned forests in the 55 largest urban areas total over 50,000 acres (Stewart 1980). It has been estimated (Himelick 1976) that there are over 25 million trees along streets and on private property in urban areas of the state. Some idea of the dollar value of urban shade trees can be gained by looking at the cost of the removal and replacement of

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diseased or damaged trees. The mean in-house costs nationwide for municipal tree and stump removal are \$140 per tree, with an additional \$45 for replacement planting (Anonymous 1982). If the job is contracted, as is commonly done in cities, the mean costs are \$208 for removal and \$86 for replanting. Removal and replacement take up 43 percent of municipal tree care budgets. It is estimated that in 1980, 57 communities in Illinois with over 25,000 population spent a total of \$11,280,000 for municipal tree care (Stewart 1980). If the costs for privately owned trees were added to this figure, the estimate would likely be doubled.

Tree care in Illinois supports several major horticultural industries. Illinois ranks among the top 12 states in the production of nursery stock, including trees, with an estimated wholesale value of over \$100 million annually. Many growers import planting stock from other states and export high-quality specimen landscape trees throughout the eastern United States and Canada. Other sizable industries dealing with trees in the state are represented by the Illinois Landscape Contractors and Illinois Commercial Arborists associations. Also directly involved in tree planting and care are the Illinois Department of Transportation, the Division of Forestry in the Department of Conservation, and the many county and municipal governments in the state (Stewart 1980). Thus, trees are an important economic as well as aesthetic natural resource.

BIOTIC AND ABIOTIC STRESSES

Trees, like all living things, can become weak and sick and eventually can die. Even forest trees growing in a natural habitat are damaged by insects, diseases, and climatic stresses. During the rapid agricultural and industrial expansion of the last century, the nation's forests were viewed by many as inexhaustible supplies of lum-

ber and as natural barriers to agriculture to be cleared so that the land could be put to better use as farmland. This concept was challenged when the chestnut blight fungus appeared in New York State in 1904 and within 30 years virtually eliminated one of the most valued tree species in North America. Since then, several droughts and such pests as the gypsy moth and the oak wilt and Dutch elm disease fungi, have destroyed vast numbers of trees, emphasizing the vulnerability of our forest resources.

Biotic Stresses

Stresses caused by insects and diseases are classed as biotic (Fig. 1). Nearly all tree species are under constant attack by pests, most of which are endemic and may be present wherever trees are growing. Disease stresses of trees are caused by fungi, bacteria, viruses, mycoplasma-like organisms (MLO), and nematodes (Hepting 1971). Except for crown gall and fire blight (bacteria), elm phloem necrosis (MLO), and pine wilt (nematode plus fungus), the major known biotic diseases of trees are caused by fungi (Carter 1975; Hepting 1971; Himelick 1976). Fungus species that require living plant tissue as a growth substrate are obligate parasites, those that grow on nonliving organic media as well as plant tissue are facultative parasites (Baker & Cook 1973; Wheeler 1975). Parasitic fungi vary considerably in their ability to attack higher plants. Obligate parasites and virulent or aggressive facultative parasites may attack otherwise healthy plants and act as primary stress factors causing disease damage. Weak or nonaggressive parasites cause damage only if plants are predisposed by other stresses (Schoeneweiss 1975b).

Fungal pathogens enter susceptible and resistant host plants with equal frequency (Baker & Cook 1973; Wheeler 1975). Even wound pathogens that cannot penetrate host plant surfaces directly find avenues of entrance through small wounds, cracks, and lenticels that are present on all plants.

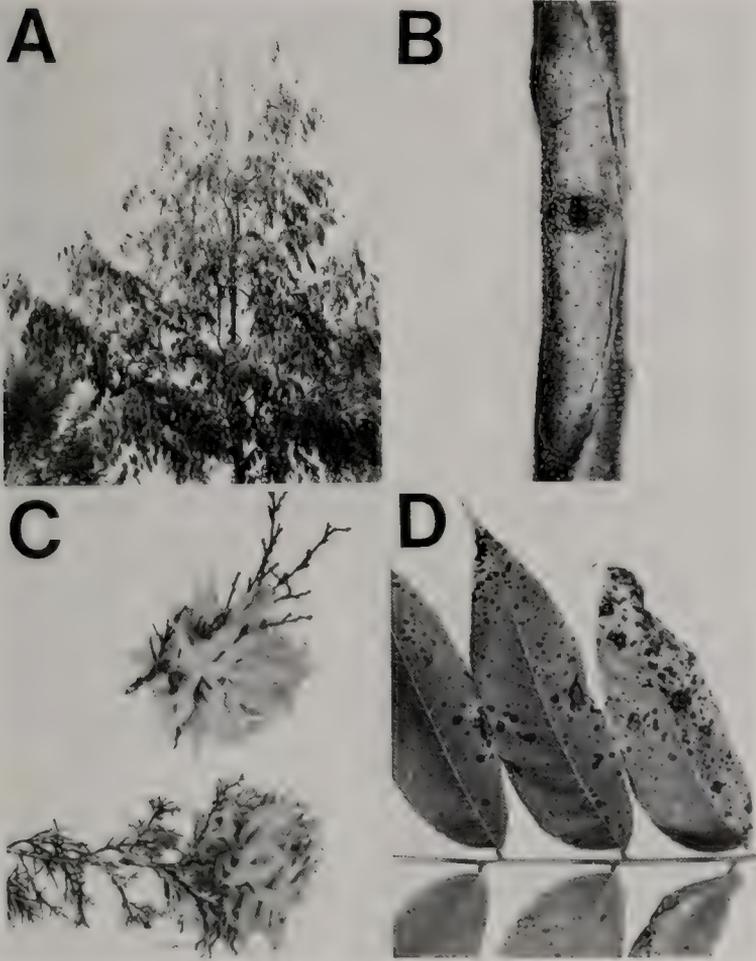


Fig. 1. — Biotic stresses as primary factors affecting Illinois trees. (A) *Verticillium* wilt on green ash. (B) *Nectria* canker on thornless honey locust. (C) Sporulating cedar-apple rust galls on red cedar. (D) Anthracnose lesions on black walnut.

Consequently, disease outbreaks and epidemics are influenced by environmental conditions of light, temperature, and humidity (Colhoun 1973). If a susceptible host and a virulent pathogen are present and environmental conditions favor infection, disease damage will appear. Disease outbreaks reach epidemic proportions when pathogen inoculum is abundant and large numbers of susceptible hosts are available, as is the case with street and parkway plantings in which species diversity is lacking. Some spore-bearing fungi and certain bacteria are spread from tree to tree by wind and rain, and others are transmitted by animals, primarily insects.

Where pathogens and host trees have coexisted for many years, trees

have usually developed resistance to disease through mutation and natural selection. Pathogens introduced into a population of trees that have not developed resistance can cause devastating disease epidemics. In 1934, the Dutch elm disease fungus came into this country from Europe. The American elm, which was widely planted as a parkway tree throughout North America and was also a common woodland species, had virtually no resistance to the fungus. As populations of the European elm bark beetle vector built up, an epidemic of Dutch elm disease began in the east and is still spreading toward the west coast. As already mentioned, the chestnut blight fungus, which spread rapidly by wind- and rain-carried spores, killed

nearly all of the American chestnuts within three decades, because the species was uniformly susceptible. This remains the only case on record of a plant pathogen virtually eliminating its host species (Hepting 1971).

Abiotic Stresses

Physical, chemical, and environmental factors that adversely affect tree health are called abiotic stresses, or physiological diseases (Parker 1965). The most common environmental stress factors are drought, flooding, and freezing temperatures. Man-induced stresses include wounds, toxic chemicals, pollutants, nutrient deficiencies, changes in soil grade and drainage, soil compaction, and loss of roots during transplanting. Trees suffering from abiotic stress may exhibit a wide variety of symptoms (Fig. 2), from the dropping of older leaves to severe wilting, dieback, and eventual death. When damage occurs as a result of these factors without the involvement of a pathogen, the stress exerted is a primary abiotic stress.

Nearly all trees suffer at one time or another from abiotic stress, but there are several critical periods when they are most susceptible to injury. A young seedling or a transplant struggling to establish a root system may be killed by even a short drought. After a tree becomes established, it is usually able to survive all but unusually severe abiotic stresses for many years. Once the tree approaches maturity, however, the root system has ramified throughout the upper layers of soil and attained an increasingly delicate balance with the soil environment or rhizosphere. Abiotic factors, such as drought, flooding, soil compaction, or toxic chemicals, can stress mature and overmature trees and initiate a state of decline (Himelick 1976). Trees transplanted into a landscape setting and those in natural stands that are thinned by building contractors are frequently subjected to conditions that are likely to cause stress. In addition, landscape and parkway trees all too often are

planted in disturbed soils where compaction, alkalinity, and poor nutrient status are unfavorable for tree growth. The increased use of herbicides with lawn fertilizers has also damaged many trees in urban areas (Neely & Crowley 1974).

The most critical period in the life of most urban trees is associated with transplanting, when abiotic stresses may become limiting factors in tree survival and performance. All tree planting stock, whether moved bare rooted or with a root ball, loses a major portion of its absorptive root system (Watson & Himelick 1982b). As a consequence, the uptake of water is reduced, and transplants may suffer drought stress even though soil moisture content is adequate for established trees. To decrease weight and save shipping costs, more trees are being moved with tree spades or with small root balls; therefore, the amount of stress they are subjected to is increasing.

Predisposing Stresses

Although biotic and abiotic factors can, and often do, act as primary stresses affecting trees, it is common for several factors to interact in causing tree damage. When a tree is weakened by one stress so that it becomes more susceptible to another stress, the tree is said to be predisposed (Schoeneweiss 1975b). Trees stressed by drought, flooding, freezing, or other factors often become predisposed to diseases caused by weak or nonaggressive pathogens that are not able to damage nonstressed trees (Schoeneweiss 1981). Most stem cankers, diebacks, and root rots occur on trees that have been predisposed by other stresses, especially recently transplanted trees, which are often in a weakened condition and are predisposed to biotic diseases (Himelick 1976).

The interactions between abiotic and biotic stresses make the diagnosis of tree damage difficult, often requiring an examination of the tree by an expert to determine the cause of the problem

and to recommend the most effective prevention or treatment. Plant pathologists at the Illinois Natural History Survey have provided such expertise as a service to Illinois citizens and institutions for over 50 years

HISTORY OF TREE DISEASE RESEARCH IN ILLINOIS

The involvement of the Illinois Natural History Survey with trees and their diseases is nearly as old as the Survey itself. In 1881, Thomas J. Burrill, who was on the staff of the Illinois State Laboratory of Natural History as well as that of the state university, demonstrated for the first time that a plant disease, fire blight of pear, was caused by a bacterium. He later published articles on fungal and bacterial diseases of several forest, roadside, and street trees (Carter 1958). Stephen A. Forbes, director of the State Laboratory and guiding force in the evolution of the Natural History Survey, reported on a widespread dying of elms in Illinois in 1883 and again in 1912.

Broad interest in the vegetational resources of Illinois led to the creation in 1921 of the Section of Botany, headed by Leo H. Tehon. Shortly thereafter, when elms began to die in many areas of the state, J. C. Carter joined the staff as a full-time plant pathologist to conduct research on the causes and control of tree diseases. In 1935, the name of the section was changed to Applied Botany and Plant Pathology (Carter 1958) and was later shortened to Botany and Plant Pathology.

In the 1930's research in plant pathology focused on disease problems of street and parkway elms. The rapid dying of elms was due to a disease called phloem necrosis, originally thought to be caused by a virus but recently shown to be caused by a mycoplasma-like organism (Carter 1958). Several other elm diseases were studied by Carter, including bacterial wetwood (Carter 1964). The effort devoted to tree disease research in Illinois was in-

creased after the fungal disease known as oak wilt was found here in 1942. By 1950, when Dutch elm disease appeared in Illinois, Survey plant pathologists were actively conducting research on tree diseases, and additional staff was added to meet this new threat to the rural and urban tree resources of the state.

In 1955, plant pathologists scattered through several departments of the University of Illinois were brought together into a new Department of Plant Pathology. Since Survey pathologists were well established in tree disease research at the time and the university pathologists were primarily interested in diseases of agronomic crops, the Survey accepted the responsibility for research on tree diseases, a commitment that continues today.

Over the years, Survey plant pathologists have cooperated in solving tree problems with many other state agencies, including the Departments of Transportation and Conservation and the Bureau of Plant and Apiary Protection in the Department of Agriculture. As a state-supported institution, the Natural History Survey has provided diagnostic and counselling services to all Illinois residents. During the peak years of the Dutch elm disease epidemic in the 1950's and 1960's, several thousand plant specimens were processed annually in the pathology laboratories. With the opening of the university's plant clinic in 1975, much of the specimen load has been reduced or diverted elsewhere; however, Survey pathologists continue to provide the public with diagnostic and counselling services. Nurserymen, landscapers, arborists, city foresters, pest control operators, Christmas tree growers, and private citizens receive willing cooperation in solving their tree disease problems.

In contrast to agronomic crops, involving only a relatively few species of hosts and pathogens, many abiotic and biotic factors affect dozens of species and cultivars of trees. Keeping up to date on tree disease problems requires

a continually evolving program of basic and applied research. As one problem is solved, new ones arise and become issues needing attention.

RESEARCH ON BIOTIC STRESSES AS PRIMARY STRESS FACTORS

Both the initiation and expansion of research projects on tree diseases at the Illinois Natural History Survey from the 1930's through the 1950's were motivated by the sudden appearance and rapid spread of vascular wilt diseases: phloem necrosis of elm in 1930, oak wilt in 1942, and Dutch elm disease in 1950 (Carter 1958).

Elm Phloem Necrosis

Little was known about phloem necrosis when it was identified in Illinois in the 1930's except that it was thought to be caused by a virus transmitted by the elm leafhopper. Since virus diseases could not be controlled with chemicals and the application of foliar sprays to control leafhoppers on large trees is seldom practical, research efforts were mostly centered on disease diagnosis and the recording of disease spread and development. Accurate Survey records of the urban epiphytotic of phloem necrosis and Dutch elm disease in the Champaign-Urbana communities (Carter & Carter 1974) are of value in predicting potential tree losses in other similar communities if control programs are not initiated early enough.

Oak Wilt

The American oaks are the most important group of hardwoods in Illinois and furnish more native timber than any other group of broad-leaved trees. Oak species have also been used extensively as shade and ornamental trees. By 1950, the fungus disease, oak wilt, first identified in Illinois in Winnebago County in 1942, was destroying large areas of oak timber in northern Illinois. Intensive studies on the distribution of the fungus in Illinois, potential vectors, and procedures to control its spread were begun in 1951 with a

grant from the Cook County Forest Preserve District, later supplemented and eventually replaced with state and federal funds (Carter 1968; Himelick 1958).

Oak wilt disease was found to be present in almost every Illinois county with large areas of native oaks (Himelick 1958). The sexual and asexual spore stages of the fungus and their role in the life cycle of the fungus were described (Himelick & Fox 1961). Squirrels and various sap-feeding insects were shown to be potential vectors of the fungus (Himelick & Curl 1955; Himelick & Curl 1958) although none proved to be efficient enough to pose a threat of epidemic disease. Survey pathologists found that the most significant spread occurred through root grafts from diseased to adjacent healthy trees, and methods were tested for interrupting these root grafts. Both mechanical trenching and the use of the soil sterilant Vapam to form chemical barriers (see Dutch elm disease) prevented the spread of the fungus through root grafts (Himelick & Fox 1961). Poisoning trees with sodium arsenite or potassium iodide prevented the formation of fungus pads (Curl 1955) from which spores of the fungus could be carried by insect and animal vectors to healthy trees (Himelick & Fox 1961). The disease is now limited to small pockets of timber in which control measures have not been used.

Oak wilt was, and still remains, a potential threat to the predominantly oak forest and woodlots of the state. If an efficient vector appears, Illinois forests would become highly vulnerable to oak wilt epidemics. Therefore, Survey pathologists are keeping a close watch for any sudden increase in the incidence of oak wilt.

Dutch Elm Disease

In contrast to the oak wilt fungus, the fungus that causes Dutch elm disease, and its bark beetle vector, found conditions in Illinois ideally programmed for disease epidemics. The streets and boulevards of most cities in

the Midwest were planted almost exclusively to American elms, which are highly susceptible to the disease. The European elm bark beetle, an introduced species, breeds in dying elms. When the beetle arrived in advance of the fungus, beetle populations built up rapidly on elms dying from phloem necrosis. In 1950, the Dutch elm disease fungus appeared in Coles County and rapidly spread throughout the lower half of the state, where phloem necrosis was prevalent. By 1959, Dutch elm disease was found in all 102 counties of the state (Carter & Carter 1974). This phenomenal spread was much more rapid and extensive than that which had occurred earlier in the eastern states. Consequently, a program was initiated in the 1950's to attempt to find means of controlling the disease or at least slowing down its rapid spread so that communities could replace dying elms over an extended period.

The beautiful colonnades of parkway elms in Illinois cities began dying rapidly in the 1950's from Dutch elm disease. Since the disease appeared to spread from infected trees to adjacent trees along parkways, Survey pathologists made extensive studies of disease progression and found that the fungus also moved from tree to tree through root grafts. Root grafts were so common among parkway trees that up to 100 percent of the trees within 20 feet and 90 percent of the trees within 35 feet of infected trees also became infected (Himelick & Neely 1962). To halt this type of spread, several methods were devised and evaluated for breaking or interrupting elm root grafts. Mechanical trenching proved to be effective but costly. Several soil fumigants were applied by different methods to kill roots and form a barrier between adjacent trees (Neely & Himelick 1965). The most effective treatment found was the injecting of the soil sterilant Vapam, diluted 1:3 with water, into 3/4-inch diameter holes 15 inches deep and 6 inches apart in a line between adjacent elms. Vapam treatments reduced adja-

cent tree infections by 60 percent in all Illinois cities where it was tested (Neely & Himelick 1965). This method became a standard recommendation for the control of Dutch elm disease in Illinois cities and was subsequently adopted as a control procedure in other states.

Control strategies were also devised and tested to prevent or reduce the overland spread of the fungus by bark beetles emerging from brood galleries in diseased elms. Over 1 million beetles had been estimated emerging from a single dying elm; therefore, strict sanitation in the form of the prompt removal and destruction of dying trees and branches became an essential component of any effective control program. Unfortunately, few communities were able to organize and fund community-wide control programs until many trees had already been lost to the disease. The biggest problem for communities where elms were dying was that the prompt removal of dying trees was essential to contain the disease epidemic, but sufficient funds and manpower for tree removal were simply not available. To help alleviate this situation, Survey pathologists developed a technique based on previous oak wilt research in which either sodium arsenite at the rate of 100 g/l of water or potassium iodide at the rate of 500 g/l was placed in axe frills at the base of a tree (Himelick & Neely 1961). This treatment caused such rapid tree death that the tree did not become suitable for beetle breeding. The treatment gave almost complete prevention of beetle colonization and allowed communities to remove dead elms at convenient times while maintaining an effective control program.

With the advice and recommendations of Survey pathologists, 55 Illinois cities had begun control programs for Dutch elm disease by 1957 (Neely 1967). The basic program included strict sanitation and the application of DDT sprays. When DDT was banned in 1968, more than half of the cities dropped their control programs, while the remainder substituted the less

effective insecticide methoxychlor for DDT. In cities with no control programs, over 90 percent of the elm populations were lost to disease by 1966 (Neely 1967), and those that dropped their programs soon lost most of their remaining elms. The 21 cities that have continued control programs through 1982 have retained from 30 to 50 percent of their original elm population, allowing the gradual replacement of dying elms with other tree species over a 25-year period (Neely 1984). Control strategies developed at the Survey have served as models for community-wide Dutch elm disease control programs in many parts of the country.

Another phase of research which found practical application was a comprehensive study on the spread of the Dutch elm disease pathogen within infected elms. When inoculations were made at the base of the trunk, the fungus was recovered at a height of 6 feet in 3 days, and at 6 days was present in the tops of trees 4 to 5 meters high. In contrast, twig inoculations, simulating beetle feeding transmission, resulted in downward movement of only 2 cm per day, and it was weeks or months before the fungus reached the main stem (Neely 1968). Unless a main stem was reached in the first year of inoculation, the fungus became localized. Using this information, Survey pathologists found that if infected branches were surgically removed before trees showed more than 5 percent wilt (flagging) symptoms, up to 65 percent of the infected trees could be saved (Himelick & Cephlecha 1976). Therefore, early detection and prompt pruning were included in control recommendations.

Many additional studies on Dutch elm disease were conducted, including a survey of resistant species and cultivars of elm. Of 13 species and subspecies of *ulmus* on the University of Illinois campus, only *U. americana* L., *U. rubra* Muhl., and *U. thomasi* Sarg. were lost to the disease (Neely & Carter 1965). Unfortunately, nearly all parkway trees on the campus and in

the twin cities of Champaign-Urbana were *U. americana*. Of the original population of 14,103 American elms, only 47 trees remained in 1972 (some of these have since succumbed to disease); the rest were killed by either phloem necrosis or Dutch elm disease (Carter & Carter 1974). This loss resulted from the lack of any control program in the twin cities. Fortunately, other communities in the state that followed Survey recommendations were able to retain many of their elm trees.

Verticillium Wilt

Verticillium wilt is a vascular disease caused by a soil-borne fungus, *Verticillium dahliae* Kleb., and is the only vascular tree disease that affects a wide range of unrelated annual and perennial plant species (Himelick 1969). In Illinois, the disease is rare among forest trees, but it has become increasingly prevalent in ornamental plantings (Fig. 1A). Presently, 60 species of trees and shrubs are known to be susceptible (Himelick 1969). There is evidence that the fungus varies in virulence, and the indiscriminate movement of nursery stock from one state to another has resulted in distribution of the more virulent strains to areas of Illinois where they were not previously present.

Survey pathologists have researched the biology, control, and host range of *Verticillium* over many years. Diagnosis is difficult because trees weakened by root infection usually decline and become more susceptible to the effects of other stresses. Attempts at chemotherapy with fungicides have been unsuccessful. Feeding and watering infected trees are the only treatments that have proved helpful in extending the longevity of trees having Verticillium wilt.

OTHER BIOTIC DISEASES AS PRIMARY STRESS FACTORS

Sycamore Anthracnose

American sycamore, a common river-bottom species in the eastern half

of the United States, has been widely planted as a shade tree on parkways and private property. It is a hardy, fast-growing species, but its value as an urban shade tree is limited by a fungal disease known as sycamore anthracnose (Himelick 1962; Neely 1976). Occasionally, sycamores appear quite healthy throughout the summer, but in most years anthracnose damage ranges from moderate to severe defoliation early in the growing season. In response to numerous requests from nurserymen, arborists, and homeowners for disease control recommendations, pathologists at the Natural History Survey conducted research on the biology and control of this disease.

A taxonomic study of the pathogen revealed that it was distinct from the oak anthracnose fungus (Neely & Himelick 1967), and it was established as a separate species (Matteoni & Neely 1979). The disease cycle on sycamore was found to be composed of several stages (Himelick 1962). The fungus overwinters in current-season twigs and causes bud, twig, and shoot blight symptoms following bud break in the spring. It also forms stem cankers in which spores are produced that serve as a source of new infections. During late spring and summer, spores infect leaves, causing the leaf-blight stage. The fungus invades leaf petioles and grows downward into the stem, where it remains over the winter. Since the fungus spends most of its cycle within petiole and stem tissues, the disease is difficult to control with surface-active fungicides. Mercury fungicides, which penetrate plant tissues and act as localized systemics, gave good control of anthracnose, but mercuries have been banned from use because of their high mammalian toxicity. No other foliar fungicides tested have been effective; however, pressure injection of trees with the fungicide Arbotech has given good control for as long as 3 years (Himelick & Duncan 1982).

Research on the anthracnose cycle led to the development of a predictive

model for disease outbreaks. Pathologists found that temperature controls the severity of shoot blight, the most damaging stage of the disease (Neely & Himelick 1963a). If mean daily temperatures during the 2 weeks following first leaf emergence average less than 13°C (55°F), severe damage occurs. When temperatures from 13° to 16°C (55° to 60°F) occur, damage is moderate, and at temperatures over 16°C (60°F) no shoot blight appears. Cool temperatures in both fall and spring favor fungal growth in twigs. After several years of testing and refinement, this model has proved to be quite accurate in predicting anthracnose severity and is useful in decision making as to if and when fungicides should be applied for disease control.

Walnut Anthracnose

Black walnut (*Juglans nigra* L.) has long been a highly valued native tree in Illinois, both as a source of cabinet-grade and veneer lumber, and as a producer of edible nutmeats. Walnut plantations have sprung up throughout the southern part of the state as farmers and other landowners have rushed to take advantage of the increasing demand and rising prices for walnut products. Because of nationwide interest in walnut, the U.S. Forest Service made funds available for research on walnut culture and pest control. A Survey plant pathologist received a grant to study control measures for walnut anthracnose (Fig. 1D), the most serious disease of walnut (Neely 1979).

Since effective control measures for a plant disease depend upon a thorough knowledge of the growth habits and life cycle of the pathogen, studies were conducted on the anthracnose fungus, using artificial media in the laboratory and host plants in the field and greenhouse. Detailed information was obtained on pathogen growth and sporulation (Matteoni & Neely 1979) and on host susceptibility at different growth stages (Black & Neely 1978a).

Wide variation was recorded in resistance to anthracnose among various species and hybrids within the genus *Juglans*, with a tendency toward greater resistance when trees are producing rapid growth (Black & Neely 1978b).

Results of fungicide trials showed that several compounds gave good control of walnut anthracnose, the best being benomyl (Benlate) applied as a foliar spray. Two applications are required, the first in late May to control ascospore infection and the second in early July for conidial infection (Neely 1979). Since rapidly growing trees appeared to be more pathogen resistant, various fertilizer combinations were applied to plantation walnuts. The application of nitrogen, at the rate of 3 kg N/ha of soil surface, resulted in a 60-percent decrease in defoliation by the end of the season (Neely 1981). Consequently, Survey plant pathologists now recommend a combination of fungicide sprays and fertilization for maximum control of walnut anthracnose.

TREE SELECTION FOR DISEASE RESISTANCE

Control of biotic tree diseases may involve several methods or approaches. These include chemotherapy, surface and soil applications of fungicides, sanitation, fertilization to promote tree vigor, and selection and breeding (Carter 1975). Since the breeding of trees requires many years, selection among available types is far more common than breeding in the development of disease-resistant trees (Carter 1966). In most cases, species and varieties within a genus vary in resistance to biotic pathogens (Bingham et al. 1971); however, accurate information on genetic resistance in trees is often lacking due to the considerable time and effort needed to obtain this information. Survey pathologists working with tree diseases over the years have made surveys and kept records of host resistance

to several of the common tree diseases. Most of these studies have been conducted in cooperation with the Morton Arboretum at Lisle, Illinois, where a wide range of tree species and varieties is located. Lists have been published of junipers resistant to twig blight (Schoeneweiss 1969) and cedar rusts (Himelick & Neely 1960) and of varieties of horse chestnut and buckeye resistant to leaf blotch (Neely & Himelick 1963b). Results of surveys and inoculation experiments have been combined into a list of woody hosts susceptible to the *Verticillium* wilt fungus (Himelick 1969). This information is valuable to growers and propagators in selecting and selling trees that are resistant to diseases.

DISEASE CONTROL WITH FUNGICIDES

With the development of organic pesticides after World War II, the most common method of disease control was the application of fungicides. However, the overuse and abuse of such pesticides, combined with increased environmental awareness, has led in recent years to the banning or restriction of pesticide usage. The amount of scientific data now required before a fungicide can be labeled for a specific use imposes a particularly severe constraint on the control of tree and shrub diseases, which are considered minor uses. With funds provided by the federal program for minor-use pesticides, Survey pathologists have tested many fungicides on ornamental plants and have submitted data on phytotoxicity to aid in obtaining label clearance so that these compounds can be legally used for disease control on nursery and landscape plants.

Fungicide Bioassay Procedures

To select a suitable fungicide to control a plant disease and to determine the proper timing and number of

applications needed, it is necessary to know at what rate of application the fungicide is effective, whether it will remain active on or in the host, and whether the activity will persist or be lost through weathering. These data are usually obtained through the use of bioassays in fungicide screening tests. Because most bioassays gave inconsistent results, Survey plant pathologists developed a cellophane disc technique, which can detect small amounts of fungicide (as low as 0.01 ppm) and may be used in the field as well as in the laboratory (Himelick & Neely 1965). This technique is simple, fast, and economical, and it is now used to determine whether a fungicide kills or merely inhibits disease organisms and whether it will persist on or in plant tissues long enough to give good disease control.

Chemotherapy

The term chemotherapy refers to the internal treatment of infected plants with chemicals to cure disease or arrest further infection. The field of chemotherapy for tree diseases is in its infancy. Injection into the soil and direct injection of systemic fungicides into the vascular system of trees have been used in attempts to control vascular wilt diseases, but results have often been either negative or inconclusive. Survey pathologists developed a pressure-injection apparatus with which they have injected as much as 110-150 l of dilute systemic fungicides into several tree species (Himelick 1972). American elms in the early stages of Dutch elm disease have been saved by pressure injections of the fungicides Benlate and Arbotect (Himelick 1972), and good control of sycamore anthracnose for up to 3 years has been achieved with the injection of Arbotect (Himelick & Duncan 1982). We expect that other serious diseases of shade and ornamental trees will be controlled by pressure injection in the future with new systemic fungicides.

RESEARCH ON ABIOTIC STRESSES AS PRIMARY STRESS FACTORS

Although damage symptoms on trees are often attributed to infectious diseases, the fact is that much damage to trees and other plants is caused by abiotic stresses (Levitt 1980a, 1980b; Parker 1965). Since Survey tree pathologists are concerned with the protection and preservation of trees in general, many research projects have been conducted on abiotic stresses.

Herbicide Damage

The increased use of herbicides for weed control in both rural and urban areas of Illinois is reflected by a higher incidence of damage on sensitive tree species. Rural windbreaks and woodlot trees are being injured by herbicides used on crops, while urban trees are showing the effects of weed-and-feed lawn fertilizers which have become quite popular for the control of weeds in turf grasses (Fig. 2B). A recent study at the Survey revealed that the herbicide dicamba, commonly incorporated with lawn fertilizers, consistently caused significant damage to trees (Neely & Crowley 1974). Tree species differed in sensitivity to this compound, and the extent of damage varied with soil type and the amount of spring rainfall. Pathologists at the Survey have cautioned against the use of dicamba in the vicinity of trees and other woody plants.

Iron Chlorosis

Yellow foliage and slow growth are typical of many tree species planted along streets and around homes where the original topsoil has been removed or mixed with subsoil. The average urban soil has relatively poor physical, chemical, and biological characteristics. In Illinois, chlorosis (yellow foliage) is a common physiological stress on pin oak (Fig. 2D) and to a lesser



Fig. 2. — Abiotic stresses as primary factors affecting Illinois trees. (A) Oak decline in northern Illinois. (B) Injury from lawn herbicide on yew. (C) Loss of roots during transplanting. (D) Iron chlorosis symptoms on pin oak leaves.

extent on sweet gum, white oak, bald cypress, river birch, red maple, and hackberry. Several Survey pathologists have investigated the cause and control of the chlorosis problem.

Soil tests from areas of chlorotic trees have consistently shown that chlorosis is generally associated with pockets of alkaline clay soils, quite common in urban areas in the northern part of the state (Schoeneweiss 1973). The yellowing of leaves, with veins remaining green, is a typical symptom of iron deficiency and can be corrected by treating plants with certain iron-containing compounds if the iron is in the proper form (Wallace 1971). Field research has centered around both soil injection and direct trunk implantation of iron compounds. Trunk implantations with ferric citrate

and ferric ammonium citrate were found to be effective on pin oak, red oak, and swamp white oak; cypress; and sweet gum (Neely 1973; Himelick & Himelick 1980). These compounds are now commercially available in Medicaps® and are being used nationally to correct chlorosis by commercial arborists, nurserymen, and operators of fruit orchards. Applications of inorganic iron compounds to the soil, prior to the 1960's a standard recommendation, was totally ineffective in the alkaline clay soils of Illinois. However, pressure injection of liquid organic compounds, known as iron chelates, corrected even advanced stages of chlorosis in highly alkaline soils for 3 or more years (Schoeneweiss 1973). Either treatment may be used for iron chlorosis in Illinois.

Nutrient Deficiencies

Many urban trees planted in disturbed soils have poor growth characteristics due to deficiencies of nutrients. Although the fertilizing of parkway, street, and private-property trees in cities is a common practice, most fertilization recommendations are based on studies of crop plants or turf grasses and have not been evaluated on trees. To find out what nutrient materials and methods of application are best for promoting tree growth, Survey pathologists applied several different fertilizer combinations by several methods to experimental blocks of shade tree species at five locations throughout Illinois. They found that trees responded to soil applications of nitrogen fertilizers and that the response was directly related to nitrogen content regardless of how the fertilizer was applied or other nutrients present (Neely & Himelick 1966). Ammonia, ammonium sulphate, urea, and ureaform were equally effective, based on equal nitrogen content. Optimum growth response was obtained with young, newly established trees when fertilized in April at the rate of 3 Kg N/ha of soil surface (Neely & Himelick 1966; Neely et al. 1970). Growth response varied with tree species, but all treated trees were healthier than untreated controls. Proper fertilizing of urban trees enhances tree vigor and helps trees resist attack by many stress-related disease and insect pests.

Transplanting Stress

The bulk of the root systems of trees are lost when they are dug and moved from the nursery to a planting site (Watson & Himelick 1982a). Because of high labor costs for hand balling nursery stock, more trees are now being moved with large mechanical tree spades, which cut off a larger portion of the root system than does hand balling (Fig. 2C). Consequently, losses of transplanted trees from damage caused by abiotic stresses (Himelick 1976) and predisposition to biotic

stresses (Schoeneweiss 1965, 1966) have increased.

Survey plant pathologists recently conducted a 4-year study on the patterns of root distribution and regeneration of seven species of trees transplanted with a commercial tree spade (Watson & Himelick 1983). The study was conducted in the Survey arboretum at Urbana, where core samples from root balls and the soil could be taken to the laboratory for detailed examination. Data were collected on root carbohydrate content, vertical and horizontal distribution of the original root system at the time of digging, and regeneration of fibrous feeder roots after transplanting.

They found that as much as 98 percent of the original root system was lost during digging, yet the survival rate after 1 year was 97 percent, due to careful maintenance of the trees after transplanting (Watson & Himelick 1982b). Because the tremendous loss of roots caused many trees to become severely water stressed in mid-summer, frequent irrigation was essential for survival. New fibrous roots formed at the severed ends of the roots at the edge of the root ball and were most numerous in the upper 10 cm of soil. Root regeneration was proportional to carbohydrate content, which was lowest during the period of bud break and new shoot growth in early spring, indicating that trees should not be moved until new growth has matured or, preferably, after the onset of dormancy in the fall.

Results of this study were compiled in a transplanting manual, published by the International Society of Arboriculture (Himelick 1981), for the purpose of developing uniform transplanting procedures. Use of this information should help to reduce losses of urban shade and ornamental trees after transplanting.

Oak Decline

Several thousand large, established oaks have died or are in various stages of decline on private and public prop-

erty in cities adjoining Lake Michigan (Fig. 2A). Aerial reconnaissance, using high-resolution photography, has shown extensive loss of valuable trees in many of the urban areas north of Chicago, where oak is the predominant shade tree (Himelick 1976). Although declining trees have been attacked by disease and insect pests, the death of high proportions of the root systems, caused by alternating periods of excess soil moisture and drought, is responsible for the decline.

Through field research it was demonstrated that a 5- to 10-cm layer of wood chips placed over the root area and the addition of surface-applied fertilizer were highly beneficial in restoring the vigor of declining trees. Fine root development more than doubled in the top 15 cm of soil among trees that were mulched in this manner. Large, 75- to 100-year-old oaks also showed measurable response in greener foliage compared with that of untreated trees.

STRESS PREDISPOSITION

Many of the biotic diseases of trees that cause significant damage, such as the stem cankers, diebacks, and root rots, only appear on trees that have been predisposed to disease by abiotic

stresses (Fig. 3) (Schoeneweiss 1981). Others, such as Hypoxylon canker on aspen and Armillaria root rot of maple and oak, that cause minor injury to vigorous trees may become much more damaging to trees under stress (Schoeneweiss 1978). Interactions between abiotic and biotic stresses have long been recognized, yet few studies had been conducted until recently on stress predisposition in woody species. Environmental stresses that occur under field conditions are both highly variable and unpredictable, making it difficult to obtain reliable data on stress-disease interactions from field studies. Most of the useful information has come from studies on controlled stress research at the greenhouse and growth chamber facilities of the Illinois Natural History Survey. Although many different stresses may act or interact in predisposing trees to diseases, research thus far has been concentrated on drought, freezing, and defoliation stresses.

Drought Stress

The influence of drought, or water stress, as a predisposing factor in stem canker diseases of trees was investigated by placing potted tree seedlings in various stages of wilt into a specially designed humidity cabinet under equi-

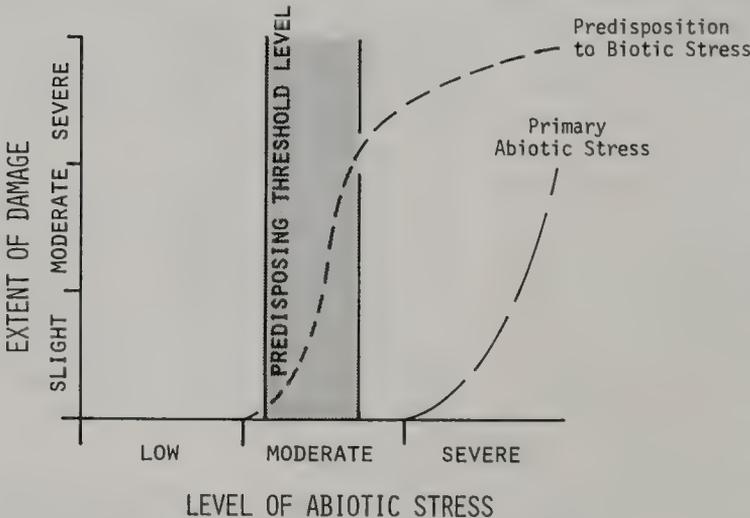


Fig. 3. - The extent of primary damage caused by abiotic stress compared with the extent of biotic disease damage resulting from stress predisposition at increasing levels of abiotic stress severity. Trees may become predisposed to infectious disease organisms at moderate levels of stress, while direct or primary stress damage usually appears only on severely stressed trees.

librium conditions of high humidity, constant temperature, and reduced light (Schoeneweiss 1975a). Under these conditions, plant water potentials became stable, and the level of water stress was correlated with the development of stem cankers caused by weak or nonaggressive pathogens (Crist & Schoeneweiss 1975; Schoeneweiss 1975b, 1978, 1983). These studies revealed that woody stems became predisposed to disease when plant water potentials fell below a threshold level of -12 to -13 bars (1 bar = 0.97 atmosphere) and that disease development increased with increasing stress severity (Crist & Schoeneweiss 1975). The predisposing level would be considered moderate stress, as most tree species do not show signs of wilting at this level. In the field, water potentials of trees may fall well below the threshold level on a hot, windy day yet recover at night without causing predisposition. For predisposition to occur, plant water potentials must remain below the threshold level for several days before trees appreciably lose disease resistance (Wene 1979). Trees regain resistance several days after the stress is relieved. Most trees are under prolonged water stress during droughts and after transplanting and should be irrigated regularly at these times to prevent predisposition to biotic disease.

Freezing Stress

The predisposing effect of freezing stress was studied by placing dormant potted tree seedlings in a programmable walk-in freezer and lowering the chamber temperature to below freezing (Schoeneweiss 1974, 1977). Stems inoculated with canker fungi became predisposed to disease when stem temperatures exceeded a threshold degree, usually around -20°C (-13°F). Predisposed plants regained resistance within 1 to 2 weeks after stems were thawed (Wene 1979). Again, the level of stress resulting in predisposition was considered moderate, since no direct injury was apparent, and frozen plants that were not inoculated were indistin-

guishable from unfrozen controls after growth resumed (Schoeneweiss 1981).

Defoliation Stress

Loss of foliage during the growing season reduces the photosynthetic capacity of trees and may weaken them sufficiently to predispose them to biotic diseases (Schoeneweiss 1981). Defoliating insects, like the gypsy moth and cankerworms, have been followed by the decline and death of trees due to canker, dieback, and root rot fungi. Controlled studies at the Survey, where tree seedlings were manually defoliated, resulted in predisposition to canker fungi when plants were defoliated beyond a threshold period of several weeks (Crist & Schoeneweiss 1975; Schoeneweiss 1967). If allowed to refoliate, seedlings recovered without ill effects in the absence of biotic pathogens.

Plant Tissues Affected by Different Stresses

Although many environmental stresses predispose trees to weak biotic pathogens and all seem to require some threshold level that must be exceeded, the effects of stress on plants may be quite different. Drought, defoliation, and most other stresses weaken the entire plant and may predispose any portion of the plant to attack (Schoeneweiss 1981). In contrast, freezing stress predisposes only that portion exposed to temperatures below the threshold degree (Wene & Schoeneweiss 1980). Freezing stress has a greater effect on older wood tissues, while other stresses predispose bark and sapwood (Schoeneweiss 1981). Pathogens also colonize the xylem of stems stressed by freezing to a much greater distance beyond canker margins than they do with other stresses. In pruning diseased stems to help stressed trees recover, it is helpful to know what environmental stress was involved.

Stress-Related Pathogens

The appearance of stem cankers, diebacks, and root rots is usually an in-

direct effect of predisposing abiotic stress. Some of the organisms that cause the diseases are present on planting stock imported from other states, but most are common saprophytes of woody tissues and are widely distributed. These pathogens are often referred to as "secondary" organisms, and their role in causing damage has been disregarded; however, trees recover from stress without ill effects in the absence of these pathogens. Therefore, they should be thought of as essential components of the damage resulting from stress (Schoeneweiss 1981). As different environmental stresses may differentially predispose tree species to disease, information derived from controlled studies with specific hosts and pathogens in combination is useful in formulating recommendations for disease prevention or treatment. Outbreaks of diseases resulting from stress predisposition may not be noticed for days, months, or even years after the stress has been relieved. Climatic data and the cultural history of a tree may provide clues to the factors contributing to disease damage.

CURRENT RESEARCH ON BIOTIC AND ABIOTIC STRESSES

Given the number and complexity of biotic and abiotic stresses and the wide range of species and cultivars of trees grown in Illinois, tree disease research is a continually changing and evolving process. Even in a paper of this size, many of the research projects conducted by Natural History Survey plant pathologists over the years must of necessity be omitted. In this section we briefly look at some of the major problems under investigation at the present time.

Histology and Biochemistry of Predisposition

When a tree is predisposed to disease by stress it becomes more susceptible to another stress, in most cases a

biotic pathogen (Schoeneweiss 1975b). Since nonstressed trees are able to resist attack by most pathogens, a histological or biochemical change most likely occurs in the predisposed host before infection (Bell 1981). Which mechanisms change or break down during predisposition is a controversial subject about which little is known. Research is currently under way at the Survey to help answer these questions.

Weak or nonaggressive stem-canker fungi are examples of biotic agents that only attack trees that have been predisposed to disease. When stems of nonstressed and stress-predisposed tree seedlings, inoculated with canker fungi, were examined with the light and scanning electron microscopes, no morphological barriers or deposits were found that could account for resistance to fungal growth in vascular tissues (Wene 1979). In resistant stems, the canker fungi appear to be inhibited biochemically or degraded by host enzymes (McPartland & Schoeneweiss 1984). More research is needed to understand which mechanisms operate and how trees become predisposed. Once the resistance mechanisms are identified and characterized, it may be possible to select or breed trees less sensitive to predisposing stress or to apply treatments to enhance the expression or genetic resistance to stress.

Wound Healing

Tree wounds serve as avenues of entrance for disease and decay organisms. Although much has been written about wound healing and wound treatment, few recommendations have been based on sound research data. In studies being conducted on the healing of various sizes and shapes of wounds on different tree species, pathologists at the Natural History Survey have found that wound closure is directly related to radial stem growth. Large wounds close more per unit of radial growth than do small ones, but wounds on fast-growing trees within a species close less per unit of growth than those of slow-growing

trees (Neely 1983). Some tree species are more efficient in wound closure than others. If trees are maintained properly, wounds of less than 1.2 cm in diameter, such as those resulting from trunk injections, close within a year. Tests are under way on the closure and healing of branch pruning wounds, common on nursery and landscape trees. Data from this study will provide a sound basis for recommendations on wound treatment.

Modeling of Cedar Rust Infections

Cedar rusts are common and troublesome diseases of crabapple and hawthorn. Using pathogen and environment as the variable functions, we have developed models to predict the likelihood of infection by the cedar-apple and cedar-hawthorn rust fungi. These models will be tested against natural field infection to evaluate their accuracy in forecasting disease epidemics. If accurate, they would be of considerable value as a basis for effective fungicide recommendations.

Tree-Grass Competition

In most urban parkway and landscape settings trees are surrounded by turf grasses. As a result, these trees are often stressed due to competition between tree and grass roots for available water and nutrients. Pathologists at the Survey are collecting data on growth rates of trees in experimental plots with and without living turf cover and with and without supplemental fertilization. The aim is to determine whether killing the turf with herbicides will improve tree vigor. Hopefully, effective means of preventing or reducing stresses in landscape trees will be derived from this study.

Honey Locust Decline

Of the many declines that occur on shade and ornamental trees, one of the most serious is the decline of the thornless honey locust. Because honey locust has been the preferred species used to replace elms lost to Dutch elm disease, it has been widely planted in urban

areas of Illinois, and decline has become a prominent problem. Isolation and inoculation studies with fungi from declining trees indicate that *Thyronectria astro-americana* (Speg.) Seeler is a major cause of decline of older, established locust (Stim & Himelick 1981). Symptoms include cankers that girdle twigs and branches and, in advanced stages of decline, large, elongated cankers that develop on the trunk. An insect borer is associated with the canker and may be a vector of the fungus responsible for the damage. Symptoms appear particularly during periods of drought. Studies are in progress to determine if various cultivars of honey locust show resistance to the fungus.

Pine Wilt

For the past 5 years, a rapid decline of pines has been observed in both urban areas and pine plantations in Illinois and neighboring states. The incidence of this disease increased dramatically during 1980 and 1981, particularly among Scotch and Austrian pines in Illinois, and in some areas reached epidemic proportions. Many nurserymen and growers of Christmas trees have become concerned about the potential economic loss that could occur if the disease continues to spread. The pine wilt nematode, *Bursephalenchus xylophilus* Mamiya & Kiyohara, and a blue-stain fungus, *Ceratocystis ips* (Rumb.) C. Moreau, appear to be closely associated with the disease (Himelick 1982). An international conference on pine wilt was held recently in Illinois, and a cooperative research effort involving entomologists, nematologists, and plant pathologists from the Natural History Survey and the University of Illinois has been initiated to investigate various aspects of the pine wilt syndrome.

OUTLOOK FOR ILLINOIS TREES

In spite of research efforts by Natural History Survey plant pathologists, damage caused by biotic and abiotic

stresses to Illinois trees is likely to increase through the foreseeable future. Urban trees, in particular, are being neglected because of high maintenance costs. Frequently, more nursery stock is moved with tree spades or grown in containers; in both cases, root systems are often inadequate to assure tree health after transplanting until new roots are established.

Modern farming practices in Illinois, particularly the application of large quantities of herbicides and the plowing of every available square foot of land for row crops, are highly unfavorable to tree health. As a result, rural windbreak and woodlot trees are in poor condition, and many are showing signs of decline.

While stresses are becoming more prevalent as factors affecting Illinois trees, the demand for trees in the state is increasing. Continuing urbanization is creating a greater demand for more shade and ornamental trees for beautification and as noise and pollution filters. The tremendous loss of topsoil to erosion on farm fields may stimulate

new interest in windbreak plantings. Tree plantations for the production of biomass as an energy source and for windbreaks are becoming popular. Reforestation of mine spoils and marginal land is being funded at the state and federal levels. All of these factors are contributing to a greater demand for tree planting stock.

The chances for the introduction of a disease organism that could result in a tree disease epidemic has increased in recent years. Many of the new cultivars grown in Illinois nurseries are propagated in other regions of the country and are imported as planting stock along with the pathogens that occur in those regions. Under Illinois conditions, some of these pathogens will undoubtedly become serious threats.

For these and many other reasons, biotic and abiotic stresses affecting Illinois trees will continue to be issues requiring attention from Natural History Survey plant pathologists. Information from both basic and applied research will be needed to meet these issues.

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Morning Session Summary

Catherine E. Eastman and Marcos Kogan

The Illinois Natural History Survey, as envisioned by its first chief, Dr. Stephen A. Forbes, was to concern itself not merely with the cataloging of organisms and their distribution in Illinois, but also with the study of the relationships of organisms with their environment (Mills et al. 1958; Hays 1980). The presentations in this symposium today indicate that such studies are still a primary focus of Survey research in keeping with the finest work of our sister biological research institutions and universities.

The environment within which organisms must exist has changed considerably since the early days of the Survey. For example, one has only to look at the landscape of central Illinois to understand the impact that the needs of an increasing human population have had on our own environment and that of other organisms. With the change from marshy prairie and forested hills to drained, plowed farmland well under way in the 1850's, the diverse vegetation well adapted to a prairie environment was replaced by an overwhelming dominance of two plant species – corn and wheat. Such is the case today, although soybeans have replaced wheat in acreage. Monoculture techniques and plant breeding programs have changed the chemical and physical defenses of plants, and soil, air, and water pollutants have made plants more vulnerable to attack by herbivores and disease agents. Pesticides applied to supplement natural plant defenses are yet another environmental element affecting target and nontarget organisms alike. The growth

of cities and industry has affected the environment as well by displacing the original plant cover and by releasing enormous amounts of industrial and urban wastes. Thus, we as biological researchers must concern ourselves with problems associated with inherently unstable agroecosystems, with the reduction of suitable habitats and the consequent decline of wildlife populations, and with the difficulties in determining basic biological relationships among organisms in an environment increasingly subject to human manipulation.

The presentations in this symposium are examples of the challenges presented to researchers investigating complex biological systems. In a broad sense most of the talks this morning have been concerned with stresses affecting plants and plant defense biology. Such stresses include herbivore injury, infections by disease agents, competition with other plant species, and a range of abiotic factors, among them temperature and moisture extremes. Stress from one source, such as frost damage or insect feeding, may make the plant more vulnerable to other stresses, such as invasion by pathogenic organisms.

It is in response to the net selective influences that are exerted by these stresses that plant defenses are evolved. In the last 25 years the defensive properties of plant production of secondary metabolites have received increasing attention. The roles that these compounds may play in the producer plant's environment may be quite complex (Rosenthal & Janzen 1979). For example, flavonoids may serve both to screen plants from ultraviolet radiation and to attract pollinators. Phytoalexins presumed to be produced by plants in response to invasion by bac-

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teria or fungi have also been shown in recent work by Survey researchers to deter feeding by the Mexican bean beetle. And some metabolites, such as the cucurbitacins, which are repellent or outright toxic to many herbivores, may also serve as feeding excitants for other phytophagous species. Yet despite the importance of this line of research, a plant's particular chemical profile alone cannot explain plant-herbivore interactions. The microclimate and the types of carnivores present in the plant's environment also contribute to the degree of suitability of a plant or plant part as a host for a particular herbivore.

Pesticides are superimposed on plant defenses when such defenses are deemed inadequate for crop production goals. Their effect in the environment ripples out from the immediate target pest on the host plant to include non-target organisms and for varying distances in the host plant's abiotic environment. Yet the stability of these pesticides often is dependent on that same environment, which determines whether the pesticide will be subject to microbial or ultraviolet degradation or whether it will persist for months or years in a biologically active form.

That astute observer of scientific endeavor and human nature, Mark Twain, is reported to have said that "Researchers have already cast much darkness on the subject, and if they continue their investigations, we shall soon know nothing at all about it." The pursuit of the principles underlying biological relationships often seems to uncover more questions than answers. But those who are both charged and blessed with the task of conducting such investigations can seek comfort in the knowledge that each attempt sheds a little more light on the nature of these relationships and of life itself.

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Long-term Biological Research In a Rapidly Changing Environment

Lorin I. Nevling, Jr.

This is a great weekend in Illinois for those interested in plants and animals. This morning the Field Museum opened *Plants of the World*, the largest permanent exhibition of plant models ever presented. At this time, just a few miles from here, the Board of Trustees of the Pacific Tropical Botanical Garden sits in session. Tomorrow, the Chicago Botanic Garden in Glencoe will dedicate a magnificent bronze statue of Linnaeus, perhaps the single most influential person in the history of systematic biology. The most significant event, however, is that in which we have the honor to participate – recognition of 125 years of service by the Illinois Natural History Survey to the people of Illinois.

As with many great institutions, the Survey had no precise beginning but evolved through time. Clearly, its genesis began with the proposal that a Natural History Society of Illinois be organized at the Illinois State Normal University. In June of 1858, the society was formed, its constitution providing that specimens be collected and be deposited in the museum of the university. In due course, a state charter was issued, and in 1871, as a *quid pro quo* for financial assistance, the society relinquished ownership of the museum to the state. Subsequently, the Illinois Museum of Natural History at Normal was rechristened the Illinois State Laboratory of Natural History. The Direc-

tor of the State Laboratory, Stephen A. Forbes, who also served as State Entomologist, received a professional appointment to the Illinois Industrial University (subsequently the University of Illinois), where we are today. The Laboratory moved with him, as did the Office of the State Entomologist. The two offices remained separate until 1917, when the General Assembly wisely combined them into the Illinois Natural History Survey. The word “survey” clearly implies census, but Forbes, as first Chief of the Survey, interpreted it as the relationship between living organisms and the environment, a forward-looking ecological concept that has directed the Survey to the present day and continues to set the course for the future.

Clearly, during its long history innumerable persons have made outstanding efforts on behalf of the citizens of Illinois through the medium of the Illinois Natural History Survey. Some have devoted entire professional lives to the Survey. Much of their effort has been obscured by time although a legacy remains in the form of publications, collections, and accumulated data. As a unit of state government subject to the whims of political change, the Survey has drifted through an array of reporting structures, most of which were not especially helpful in furthering its activities. Some of these arrangements were, in fact, hostile.

A major organizational breakthrough was made when the Illinois Department of Energy and Natural Resources was formed. Several governmental units, including the Illinois Natural History Survey, with interrelated interests and goals were assembled under this department.

Dr. Lorin I. Nevling, Jr., is Director of the Field Museum of Natural History, Chicago, Illinois, and serves as a member of the Board of Natural Resources and Conservation, the governing board of the Illinois Natural History Survey. Dr. Nevling presented this address at the 125th anniversary celebration luncheon.

Perhaps for the first time in its long history, the Survey received positive support from the Director to whom it reported. Former Director Beal and current Director Witte must know that we appreciate their support, financial to the extent possible, but equally important, their active interest in the programs of the Survey. Neither has been passive, and both have insisted on programs based on efficiency and effectiveness. This insistence has caused internal examination and, in some instances, the development of new and exciting directions.

The responsibilities of the Survey are founded in law and include:

- to maintain a biological survey;
- to study the biological processes of ecological systems;
- to acquire, organize, and utilize information about the entire fields of entomology, zoology, and botany;
- to recognize needs for, and provide recommendations about, the protection, development, and use of biological resources, including agriculture;
- to publish and furnish information about biological resources and their enjoyment, use, and management according to scientific principles.

Clearly, to respond to such a complex set of activities a diverse, dedicated, *thoroughly* professional staff is required. Today, the staff numbers about 200. The Survey is organized administratively into five scientific research sections so as to respond efficiently to the various demands. These sections are Aquatic Biology, Botany and Plant Pathology, Economic Entomology, Faunistic Surveys and Insect Identification, and Wildlife Research. Laboratory and field facilities are scattered appropriately throughout the state. Each section relies heavily on the collections and accumulated data of the Survey. The collections, *in toto*, number about 6,000,000 items and are the largest and most comprehensive for the state. The larger segments of the collections are:

1. Insects	4,875,000
2. Fish	500,000
3. Plants	210,000
4. A specialized library of bound volumes.	34,000

Specimens do not of themselves constitute a collection — they must be *organized* in some fashion, preserved, and maintained. The Survey's responsibility extends to the use of collections through research.

The term, *research*, can mean a multiplicity of kinds of effort which, for the sake of simplicity, can be thought of in the case of the Survey as being of two nonmutually exclusive types: basic research and applied research. The Survey is actively engaged in both.

When the term, *research*, is used in the scientific community, basic research is almost always implied. Basic research stresses original scholarship, i.e., it adds to the base of human knowledge. Typically, the questions that are to be answered are posed by the individual researcher, and it is this ability which makes the Survey scientist most akin to a university research professor. The Survey makes a heavy investment in basic research because our future problem-solving capability will depend significantly on the bedrock of knowledge provided by basic research.

For example, is it important to maintain a large insect collection and research program? Up to 3,000 animal species, mostly insects, are occasionally or potentially harmful. About once every 3 years, a new insect pest of major importance enters Illinois. Without comprehensive collections and trained personnel, prompt identification would not be possible, and prompt identification is one of the keys to effective control. Some of the recent pests which have found Illinois to be a land of opportunity are the western corn rootworm, gypsy moth, crucifer weevil, and a Mexican bean beetle that feeds on soybeans.

Some other basic research programs of the Survey are the floristic and faunistic surveys which have made Illinois one of the biologically best

known areas in the world. The Survey's data base is unquestionably the finest of any state. One of the benefits of the Survey's long existence is the opportunity to repeat surveys at intervals and, thus, to monitor changes that have occurred in populations and natural habitats within the state.

Eventually and irreversibly, we will find it necessary to undertake a biological survey of the United States. When that day comes, Illinois will provide the keystone leadership for the nation.

Two examples of the importance of resurveys, both from ornithology, show the value of such activities. Beginning with classical work in 1885, *The Ornithology of Illinois*, published in two volumes in 1889 and 1895, the Survey has produced a series of bird studies unequalled in any other state. In 1906, the Survey began a series of statewide censuses of birds in Illinois. These surveys were repeated 1956–1958 and found about the same number of breeding birds in Illinois. But in 1909, 18 species constituted 70 percent of the breeding birds, whereas in 1957 only 9 species constituted 70 percent. These changes were brought about by habitat changes, and these changes are still occurring rapidly.

Canada geese were first studied by the Survey in 1941, and these studies continue today. As a result, we now understand the condition factors of the birds and their relation to seasonal stress, management techniques, and various diseases and parasites. In 1962, a Survey scientist rediscovered the then-presumed-extinct giant Canada goose and provided the rationale necessary to reestablish this subspecies over much of its former range.

Research on the soil insecticides aldrin and heptachlor conclusively demonstrated that the epoxides of these insecticides are translocated from the soil and are stored in the oil of soybeans and in the oils and waxes of pumpkins. Aldrin and heptachlor were widely used as soil insecticides in the 1950's and 1960's, and the Survey's

research has had a tremendous impact nationally and internationally in controlling the unwarranted use of these chemicals.

Other ecological research includes the study of ponds, streams, rivers, and more specialized bodies of water, such as reservoirs and cooling lakes. In specialty areas, there are, for example, studies of fish larvae, genetics, and behavior; insect behavior, including overwintering, migration, and dispersal; as well as insect-host interactions.

Applied research is the application of basic research findings to a problem to develop a resulting product or answer. The questions are usually thrust on, or assigned to, a researcher, and it is the kind of research most often carried on in the corporate world under the title, research and development. As the needs of the people of Illinois drive many research questions, much of the Survey's work is of this nature and encompasses many diverse elements, including:

Studies carried out under a grant or contract for governmental agencies or business firms when their needs fit Survey interests and expertise. Usually, these studies are designed to answer specific management questions.

Major plant-related activities, including the identification of plants and plant diseases for the public and industry. Two examples are the discovery of the causal agent in brittleroot disease of horseradish and its transmission by the beet leafhopper, and the concept – now well accepted in corn-producing states – that black cutworm larvae that damage young corn plants in the spring come from eggs oviposited on the weeds in a field before the corn is planted.

Effects of soil and air pollutants on plant growth and development and crop yield and quality.

Studies on the prevention and control of diseases of greenhouse plants, woody ornamentals, and

shade trees. Specific problems, such as oak wilt and walnut and sycamore anthracnose, are being addressed.

In zoology some projects are:

Identification services for the public and industry, management plans for fish, aquaculture, or the best use of wildlife resources for the preservation of the prairie chicken.

Development of insect pest management programs by integrating cultural, biological, and chemical controls into crop production systems. A marvelous achievement was the publication of the manual, *Soybean Insect Identification and Management in Illinois*.

Studies of the transmission of diseases and parasites between wild and domestic animals and between wild animals and man.

For years, Survey scientists have carried on interdisciplinary research. This is the end of the rainbow for most research institutions. At the Survey, the rainbow is just down the hall or up the stairs.

A particularly impressive piece of interdisciplinary long-term research is being continued on the Illinois River system. From the first years of its formation, the Survey has worked on this river, relating changes in water quality and river use to changes in the plankton, benthos, and fishes. Diversion of Lake Michigan waters through the system, channelizations with locks and dams for navigation, enrichment by sanitary wastes from Chicago, and draining of the floodplain lakes for agriculture have caused dramatic changes in the aquatic communities. The Survey's investigations of these changes have attracted an impressive array of scientists, have made the Illinois one of the world's best-studied rivers, and recently have gained national support to intensify the investigations for another two decades under the National Science Foundation's Long-term Ecological Research program.

No matter what the nature of the research carried out by the Survey, the

results must be made available to the appropriate publics. This publication of results is accomplished in a variety of scholarly journals, books, monographs, brochures, and special reports.

In the last year alone, staff activities have resulted in five books, 17 book chapters, 98 scientific journal articles, 85 project reports, and 94 papers presented at professional meetings.

Newsletters and press releases are sent weekly to newspapers and radio and television stations throughout the crop season to keep the public abreast of developing problems. There are programs and workshops for school children and specialized groups, such as the professional pest consulting industry. *Every* person in the state is touched directly or indirectly by Survey research results, such as recommendations concerning the protection of crops from crop pests, on reducing disease in ornamental plants, and for the management of fish and wildlife populations.

Survey scientists also attend the meetings of, and are active in the affairs of, national and international scientific organizations. In short, the Survey is everywhere and has developed substantial local, national, and international reputations.

Previously, I mentioned the positive step of placing the Survey under the Department of Energy and Natural Resources. We were placed there along with our sister organizations, the Illinois State Water Survey and the Illinois State Geological Survey. A history of cooperative efforts among the three Surveys existed, but cooperative efforts usually were on a scientist-to-scientist rather than Survey-to-Survey basis.

Within recent years, a series of changes in the leadership of the Department and the three Surveys has occurred. The principals were Michael B. Witte, Director; Robert E. Bergstrom, Acting Chief of the Geological Survey; Stanley A. Changnon, Chief of the Water Survey; and Paul G. Risser, Chief of the Natural History Survey.

The chorus was comprised of the members of the Illinois Board of Natural Resources and Conservation. In my opinion, a synergistic reaction has taken place among the parties in such a way that the Surveys are changing more than at any time in their combined histories. Change is a frightening thing to all of us, but we are convinced that the opportunities are unlimited.

Stimulated by Director Witte and the Board, the Surveys presented proposals for interdisciplinary research that were inter-Survey in nature. These proposals were innovative and had far-reaching consequences. Only a few could be funded, but the effort has produced a new spirit of cooperative research among the Surveys.

What are the demands on the Survey likely to be in the future? A few can be predicted. We will:

Monitor the health of species populations and ecosystems. We will recognize significant changes, separating long-term trends from short-term fluctuations, especially for species population numbers and distribution as well as for ecosystem characteristics, such as primary production and nutrient cycling and retention.

Respond to specific problems as these issues arise, but also maintain a steady basic research program driven by scientific questions.

Draw together diverse disciplines to address, in a coherent fashion, complex topical problems, such as hazardous waste management and wildlife populations in landscapes continually managed by man, and organize information for decision-

making that combines ecological with economic considerations.

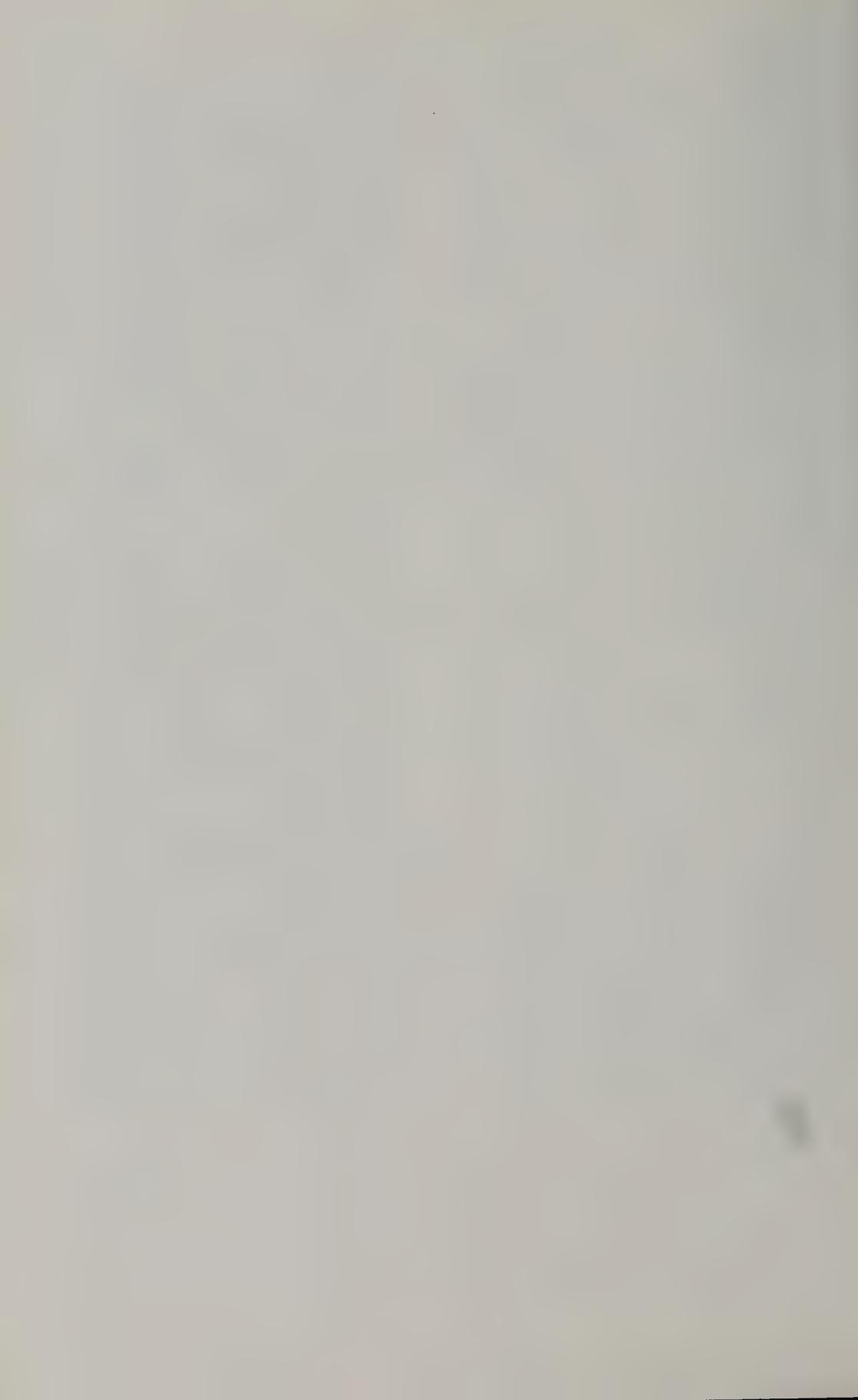
Develop the ability not only to describe the natural resources of the state, but to predict the consequences of alternate management schemes and possible demographic and energy scenarios.

Provide a central location where one can obtain information about natural resources or receive guidance as to the location of natural-resource data and information.

Maintain a competitive edge in the quality of natural-resource research, not only to solve our problems effectively and manage our resources wisely, but to continue to attract and retain the very best scientific staff.

Finally, we will need to move fully into the computer age so that the incredible data locked into collections can be fully utilized. It seems to me that this will be the only way to maintain open-end excellence with closed-end funding. Our immense data base, if united with those of our sister Surveys of Water and Geology, will form the most potent environmental data base available *anywhere*.

I am certain that Stephen Forbes would be proud of all those, past and present, who have contributed their talents to bring the Illinois Natural History Survey closer to the idea of understanding the relationships among living organisms and the environment. No one can tell what the most important problems of society will eventually turn out to be, but we can be sure that many of them will be tied to a deeper understanding of ourselves and our environment.



Lake Tahoe: A Microcosm for the Study of Change

Charles R. Goldman

The concept of "The Lake as a Microcosm" was first proposed by Dr. Stephen Alfred Forbes, first Chief of the Illinois Natural History Survey. This work (Forbes 1925), presented before the Peoria, Illinois Scientific Association in 1887, has become a classic among ecologists and is often cited as an example of the interdependence of organisms within a lake. In developing this theme to its maximum, Forbes suggested that the organisms of Illinois lakes were largely independent of their terrestrial surroundings. It can be convincingly argued that in 1887 the plants and animals inhabiting Illinois lakes were in fact a lot more independent of their surroundings than they now are. It is clear, however, from reading his monumental work, *The Fishes of Illinois* (Forbes & Richardson 1908), that he was aware of the sewage pollution from Chicago entering the Illinois River system. Today, man is having a dramatic effect on most of the world's watersheds, which in turn play an increasingly dominant role in establishing the physical characteristics of lakes. These characteristics include color and transparency as well as such biologically mediated factors as fertility and trophic status.

Eighteen years before Forbes' article appeared in the United States, S. A. Forel (1869) was founding the science of limnology at Lausanne, Switzerland, on the shores of beautiful Lake Geneva. His brilliant treatise, *Monographie Limnologique*, provided a bench mark for the study of the drastic changes that were to alter this lake as well as the Lake of Zurich during the century

to follow (Forel 1892, 1895). Immediately following the 1983 International Congress of Limnology in Lyon, France, an entire week was devoted to assessing the status of Lake Geneva and attempting to develop a strategy to bring nutrient loading from both Swiss and French sources under control (Fig. 1). Perhaps by coincidence or as a result of scientific information exchange, John Le Conte (1883a, b, 1884) measured the transparency of Lake Tahoe near the crest of the Sierra Nevada in 1873. Le Conte's observations of Lake Tahoe appeared in a regional stagecoach journal, *The Overland Monthly*. Lake Tahoe, bordered by two states rather than two countries, has been successful in achieving total sewage diversion from its basin, yet continues to decline in water quality from an array of nonpoint nutrient sources (Fig. 2).

Disturbance of the Tahoe basin has been very recent in the geologic sense of time. The first major perturbation occurred about 1846 when most of the mountainsides surrounding the lake were cleared of virgin timber to be used for shoring up the mines of the Comstock in Nevada. The second disturbance came during the years immediately following World War II after new growth had reestablished the forest. This period was marked by rapid human population growth (Fig. 3) and a great deal of road and housing construction. Despite the efforts of conservation groups and state and federal agencies to regulate development, growth continues to this day. As the tourist and resident population of the basin increased, from about 10,000 in 1955 to nearly 80,000 in 1979, real estate prices rose rapidly, and the year-round use of the basin has continued to increase. With this growth, the

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Fig. 1. - Lake Geneva, nestled in the Alps, is bordered by both Switzerland and France. It has suffered from heavy nutrient loading from both countries for more than a century. Photo by the author.



Fig. 2. - Looking southeast across Lake Tahoe from 19,000 feet (5,800 m). The enormous volume of the lake has served to buffer the nutrient input from its disturbed watershed. Still, the primary productivity has increased at the rate of 6.3 percent per year. Photo by Robert C. Richards.

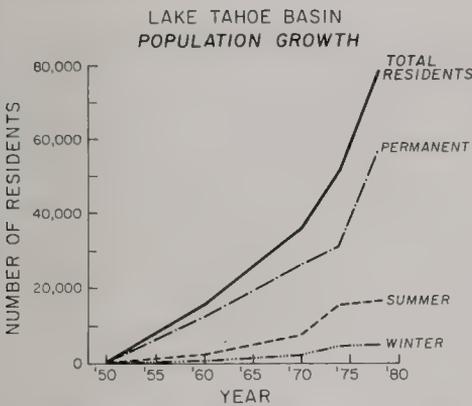


Fig. 3. — Population growth in the Lake Tahoe basin from about 1950 through 1977. The population has been divided into winter, summer, and permanent residents. The sum of both seasonal and year-round residents is presented as total residents.

deterioration of Lake Tahoe, like that of many of the world's lakes, has accelerated. This paper continues the documentation of the changing lake and attempts to isolate some of the major factors involved. Through a better understanding of whole-system response, it should be possible to make more intelligent management decisions and eventually stabilize the fertility of lakes at some acceptable level.

EUTROPHICATION OF LAKES

Naumann (1919) used the concept of trophic status to distinguish between the oligotrophic mountain lakes and the more productive eutrophic lakes of the lowlands. Many of the world's lakes, like Tahoe, have experienced a steady increase in fertility as their watersheds have been developed for agriculture, silviculture, or urban communities. Documentation of the change has often included a variety of chemical measures of fertility, such as nitrogen and phosphorus concentrations, changes in the species composition and abundance of algae, and decreases in hypolimnetic oxygen concentration during stratification. Observations of oxygen depletion under winter ice cover or following

algal blooms were first made possible by the well-known Winkler technique for measuring dissolved oxygen. The measurement of primary productivity has provided a highly sensitive integration of chemical, physical, and biological conditions in lakes (Goldman 1963; Goldman & Wetzel 1963). Comparison of the contrasting vertical profiles of *in situ* measures of primary productivity from lakes of different trophic status has previously been presented (Goldman 1968). These profiles show how the euphotic zone is compressed as algal growth shades out the deeper water.

Perhaps the most publicized example of eutrophication in North America has been Lake Erie, which, during the last several decades, has undergone a dramatic increase in fertility and general deterioration in water quality. This eutrophication resulted from a combination of urban and agricultural discharge and caused serious seasonal oxygen depletion in much of the lake. Efforts to reduce nutrient loading appear to be meeting with success, and improved conditions have been reported in recent years. Because water levels have also been higher than average in the Great Lakes in recent years, simple flushing of the system may also be a factor in their improvement. It will be important to follow their trophic status through different hydrologic conditions in the years ahead.

In addition to Erie, others of the Great Lakes have also increased in fertility, with a concomitant change in the fisheries (Beeton 1969). The invasion of the sea lamprey and alewife had dramatic effects on Great Lakes fisheries, but industrial and domestic pollution also have caused great concern. Despite continuing public and governmental agency concern about heavy metals and industrial organics accumulating in fisheries products, there is a general impression that control measures are currently returning high dividends for the investments in pollution control

and fisheries management. There remains, however, the need for cautious concern. Although increased fertility doubtlessly provides the potential for an increase in the standing crop of fishes, large populations of exotic predatory salmon may begin to exert a negative impact on their food resources. The alewife population, in particular, has undergone dramatic reductions, and other fishes may be subject to similar predation. Further, the large reduction in alewives may be expected to have influenced zooplankton populations.

Perhaps the first example of eutrophication (Ruttner 1963) was the Zurichsee in Switzerland, which became eutrophic in 1896 and showed a difference in fertility between its upper and the lower basins. In what was probably the first attempt at lake restoration, sewage treatment was initiated and has been credited with greatly improving the condition of this lake.

Another large Swiss lake, the Bielersee, became eutrophic following

the diversion of the river Aare into the lake and the concomitant increase in nutrient loadings after 1930 (Tschumi et al. 1982). Despite phosphorus reductions of more than 50 percent, Bielersee has shown little improvement. Nitrogen loading remains high from a drainage area that has been increased by 2.6 times. It is apparent that the phosphorus levels are still sufficient to sustain eutrophic conditions at the current level of nitrogen input.

Even Siberia's Lake Baikal, the world's oldest and deepest freshwater body, has not been immune to the impact of man's activities (Fig. 4). The harvest of the slowly growing, mixed deciduous and coniferous forests along its shores and the discharge from a large cellulose plant and other industries along the Selenga River were responsible for catalyzing what was certainly the most publicized, if not the first, environmental movement in the Soviet Union. Fortunately, the lake's enormous volume (23,000 km³) provides



Fig. 4. - Lake Baikal, USSR, is the oldest and deepest lake in the world. Despite its enormous volume, it has been subject to pollution from forest cutting and industrial development. The 500-ton limnological research vessel *Vereschagin* lies at anchor. Photo by the author.

tremendous dilution of pollutants (Goldman 1973). The largest lake in Europe, Ladoga, near Leningrad, is also subject to pulp mill pollution as well as other industrial contamination, and progressive eutrophication has been reported.

Although many of the world's major lakes have experienced varying degrees of eutrophication, detailed studies of change at various levels of the food chain have usually been lacking. One long-term data set developed by Lund (1964), which featured the annual silicon depletion cycle of diatoms in Lake Windermere, England, is noteworthy although the lake does not appear to have changed much during the 16-year record.

The public is usually first alerted to pollution by the appearance of dead fish along the shore or by the development of large blooms of blue-green algae, which can give a once-blue lake the green appearance of a lawn. An unusually warm summer, drought, or the application of commercial fertilizers to the watershed may trigger a severe algal bloom and sudden public awareness that a problem exists. It is likely, however, that the problem of excessive nutrients has been developing over a considerable time. When the change occurs over many years, only the keenest observers notice it, and without long-term collection of good data, change is difficult or impossible to prove.

In the western United States the most detailed studies of the progress of eutrophication have been done for Lake Washington by Professor W. T. Edmondson and for the earliest stages of change in Lake Tahoe, by the author. The Lake Washington studies used measures of chlorophyll *a* concentration as evidence for the increasing fertility of the system, while the Tahoe studies measure the change in the rate of photosynthesis over time.

Concentrations of chlorophyll *a* in Lake Washington increased steadily with the algal concentration as sewage loading increased between 1950 and

1963. The blue-green alga, *Oscillatoria rubescens* de Candolle, became the dominant form in Lake Washington, as it had in Lake Zurich a century earlier. With the collection of sewage from around the lake perimeter and its diversion to Puget Sound, beginning in 1963, transparency returned as chlorophyll values gradually declined during the next decade (Edmondson 1972a, b). With the exception of these last two studies and a long series of fisheries records and chemical measurements from the Great Lakes, there is, in general, a lack of long-term data sets on the limnological changes that have occurred in North American lakes experiencing eutrophication. The value of long-term studies in better understanding how aquatic ecosystems function is now becoming generally recognized (Goldman & Horne 1983; Likens 1983; Goldman & de Amezaga in press). The Lake Tahoe data set is the basis for the following analysis of the first stages of eutrophication in an ultraoligotrophic lake.

LAKE TAHOE

Lake Tahoe was known only to the Paiute Indians until its discovery by General Fremont in 1844. Mark Twain in *Roughing It* described Lake Tahoe as "surely the fairest sight the whole world affords" and marveled at its clarity. In addition to Mark Twain's observations and the historical records on the Tahoe fishery, probably the most important single data point was that of transparency obtained by John Le Conte in September 1873. Without this simple measure of water clarity, taken with an ordinary white dinner plate serving as a Secchi disc, there would have been endless dispute as to the transparency of Lake Tahoe before development began in earnest.

The lake is the tenth deepest in the world (505 m) and is uniquely situated for study of the early stages of eutrophication. This ultraoligotrophic lake

has a small (800 km²) watershed for a lake with 500 km² of surface area. Its enormous volume of 156 km³, with a retention time of about 700 years, provides a large buffering effect for nutrients entering the lake from tributary streams draining the forests, roads, parking lots, golf courses, and building sites of its highly disturbed watershed. Due to the long residence time of the water most of the nutrients entering the lake remain there with little flushing action and only slow sedimentation to reduce them. In addition to stream-borne nutrients and sediment, air pollution is now visible, and storms bring acid rain to the basin as well as an important, but as yet inadequately measured, dry fallout (Fig. 5).

Located at the crest of the Sierra Nevada, Lake Tahoe was first recognized as a graben fault basin by Le Conte (1875). It was probably formed during the upthrust of the mountain range between 3 and 9 million years ago and has a morphometry similar to

that of a giant bathtub. The 450-m contour line of depth is very close to shore around most of its perimeter. Important to the lake's trophic status is its relatively infertile watershed consisting largely of decomposed granite derived from the great Sierra Nevada batholith as well as some Precretaceous metamorphic rocks, Pliocene volcanics, and a few cinder cones from the Holocene (Hyne et al. 1972). Ice damming of the Truckee River outlet of the lake occurred during the last period of Pleistocene alpine glaciation. At that time the water in the lake reached levels as much as 150 m higher than it is today.

Because of Lake Tahoe's extremely low productivity, which, since 1959, has ranged from 0.12 to 0.26 g C m⁻² day⁻¹, the more conventional measures of fertility, such as oxygen depletion, chlorophyll *a*, and change in chemical composition, have had little meaning. Oxygen levels have remained at or near saturation all the way to the bottom of the deepest part of the lake



Fig. 5. — Air pollution is now frequently visible in the Tahoe basin during inversions. The smog layer is visible from Rubicon Point on the west side to Tahoe Keys at the south end. Photo by Robert C. Richards, February 1976.

(505 m), and there has been no detectable trend in the nutrient content of the surface waters from year to year. The increased nutrient loading has been so diluted and so quickly incorporated into algal growth that annual increases in such important inorganic nutrients as nitrogen and phosphorus have not been detectable. However, a depletion of nitrate has been found in the surface waters during the main growing season, resulting in a distinct "nitra cline" (Paerl et al. 1975). Following the pattern of vertical stratification of nitrate through the following fall and winter gave the first proof that waters in Tahoe actually mixed all the way to the bottom. However, for practical purposes this mixing occurs only during particularly stormy, cold winters. Deep mixing can provide a greatly elevated nitrogen concentration for the spring growing season and is an important factor in determining year-to-year variations in productivity. When mixing occurs, internal nutrient loading from this deep nutrient storage is likely to be reinforced by runoff from the very storms that cause the mixing. The deep waters of the lake provide a large reserve of nitrate during years when winter mixing is incomplete (Goldman 1981).

My data collection for Lake Tahoe began in 1958 and 1959 with the first measurements of primary productivity, using the sensitive carbon-14 method (Steeemann-Nielsen 1952) with the modification of Goldman (1963). Transparency and an array of other limnological measures were also included as well as extensive bioassays of nutrient-limiting factors (Goldman 1964, 1981; Goldman & Armstrong 1969; Arneson 1979). Intensive sampling began in 1967 and has continued to this time. The measurement of primary productivity provides a sensitive integration of the physical, chemical, and biological factors controlling photosynthesis by the free-floating phytoplankton component of this low-fertility environment. In addition, the data have enabled us to show significant change long before

conventional methods would have detected it. The primary productivity of the lake has more than doubled in a 20-year period at an average rate of increase of over 6 percent per year (Fig. 6).

Peak years of productivity in this progression took place in 1975 and 1980. After those years of particularly high primary productivity, there followed 2 consecutive years of lowered productivity. If only a single lake had been studied, one might easily and erroneously have concluded that weather or changing meteorological conditions, such as were caused by El Niño (Strub et al. in press) in the western United States, were responsible. But data collection using exactly the same technol-

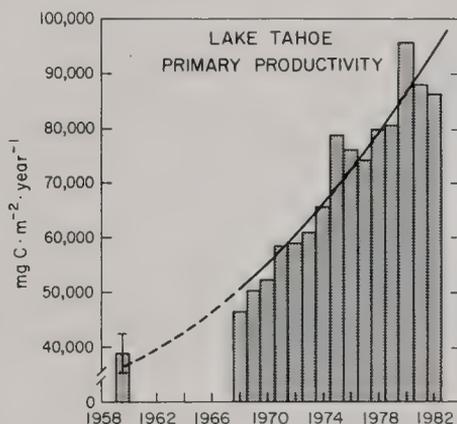


Fig. 6. — Annual primary productivity in Lake Tahoe, California-Nevada, between 1958 and 1982. Each year represents the integration of weekly or biweekly measurements made using the Carbon-14 method at a series of depths extending from the lake surface to 105 m. Approximately 35 sampling dates for each year are represented in this figure. The curve represents a least-squares fit over this time span.

ogy had been started at another subalpine lake, Castle Lake, in 1959 and has continued without interruption for 25 years. This small (50 ha) lake, like Tahoe, has a very small watershed relative to its surface area and shows nitrogen limitation. No upward trend in productivity is evident in this lake (Goldman & de Amezaga in press). In attempting to correlate the precipita-

tion at Lake Tahoe with the annual primary productivity, we discovered that there was no correlation if a direct regression was run. However, if we plotted the percentage of change from the previous year's productivity, a positive relationship emerged (Fig. 7). This finding suggests that the lake's "memory" of the previous year's productivity is more important in establishing the positive relationship with rainfall than is the irregular but upward trend in fertility evidenced by the productivity curve (Fig. 6).

The relationship between rainfall and primary productivity in Lake Tahoe, however, is somewhat more complicated than this explanation implies. Not only does rainfall influence the annual nutrient input to the system, but it is also related to storms which cause internal nutrient loading of the euphotic zone and deep mixing of the nitrogen-enriched hypolimnion of the lake. Further, a rainy year, because of increased cloud cover, causes a reduction in solar radiation and in temperature. In 1982, for example, high rainfall as a result of El Nino was accompanied by one of the darkest years on record at Lake Tahoe (Fig. 8). This darkness may have decreased the ex-

pected productivity from nutrient runoff and contributed to the reduction of the average depth of the euphotic zone from the previous year by almost 2 m (Fig. 9). Therefore, 1982 did not fit the regression of more typical years. The high nutrient levels from the heavy runoff in 1982 coupled with deep mixing enabled the phytoplankton to use the decreased available light more efficiently in both Castle Lake and Lake Tahoe than they had in the previous year (Goldman & de Amezaga in press).

Another evidence of the value of long-term data collection was apparent when it was discovered that the two cladoceran members of the endemic zooplankton population, *Daphnia* and *Bosmina*, had disappeared from the lake. The opossum shrimp, *Mysis relicta* lovén, introduced as a food for the resident lake and rainbow trout populations as well as for the Kokanee salmon, emerged as the major suspect in the ensuing investigation (Richards et al. 1975; Goldman et al. 1979). Following a crash in the *Mysis* population, first *Bosmina* and then *Daphnia* have made weak but promising returns to the plankton of the lake (Fig. 10). Observations of other western lake systems indicate that *Mysis* will coexist

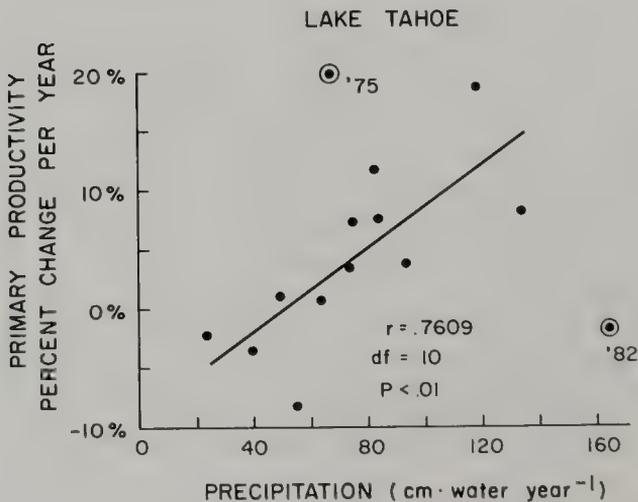


Fig. 7. — Percentage change in annual (1 January–31 December) primary productivity in Lake Tahoe is regressed on total precipitation for the corresponding "water year" (1 October–30 September) for the period 1969–1982. Two unusual years, 1975 and 1982, have been excluded from the regression. (From Goldman & de Amezaga in press).

with cladocerans if the fertility level is appreciably higher than Tahoe's and if warm water provides thermal refuges for the cladocerans.

One way to extend the information time series for any lake study is to ex-

amine lake sediments. Lakes are, after all, reservoirs of history in the sense that they usually store in their sedimentary records evidence of the events that have occurred on their watersheds. Erosional deposition from the building

Annual Solar Radiation

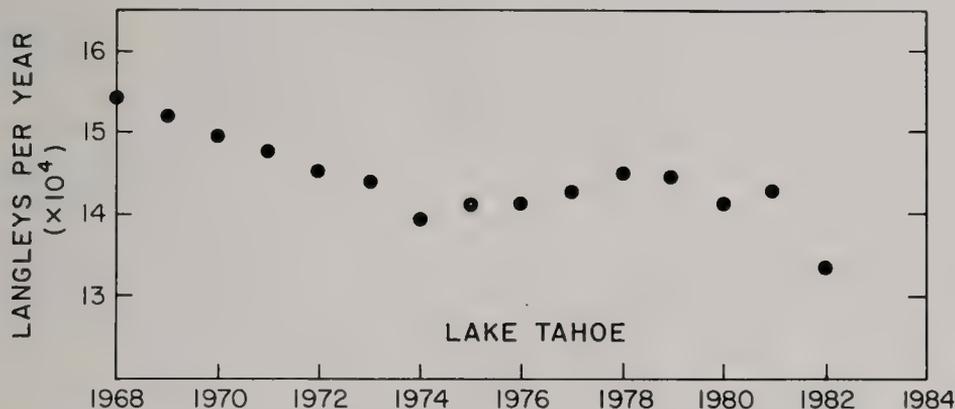


Fig. 8. — Annual solar radiation measured at Lake Tahoe, California-Nevada, between 1968 and 1982. Daily light curves made with a continuously recording pyrheliometer were digitized and summed to obtain the total solar radiation for the year in langley's.

LAKE TAHOE 1981 (.....) - 1982 (—) P.P.R. (MG C·M⁻³·HR⁻¹)

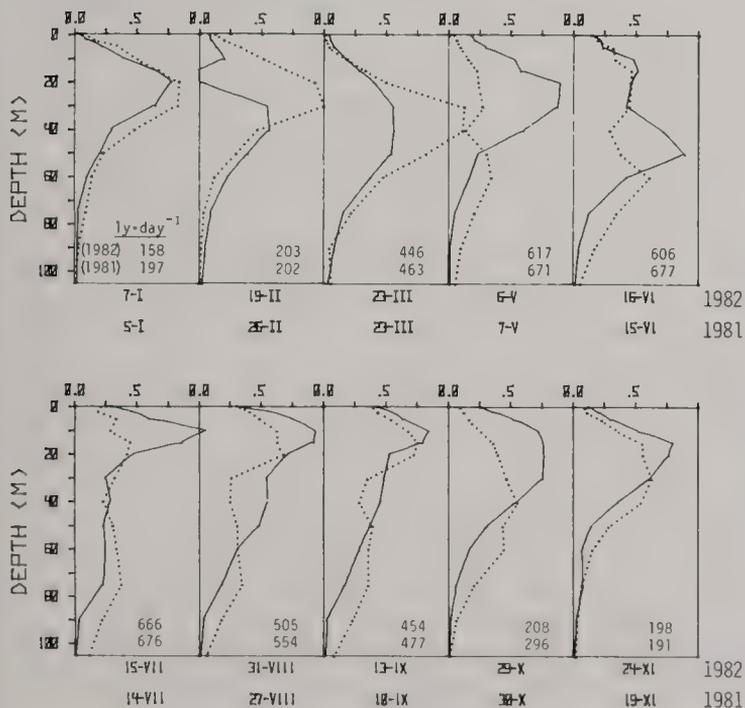


Fig. 9. — Vertical profiles of primary productivity taken *in situ* in Lake Tahoe in 1981 and 1982. The peak of production was higher in the water column during the cloudy, high-precipitation year 1982 as compared with 1981, which was clearer and drier. The solar radiation available on each day is shown at the bottom of each vertical profile. The rather consistently higher solar radiation in 1981 is evident.

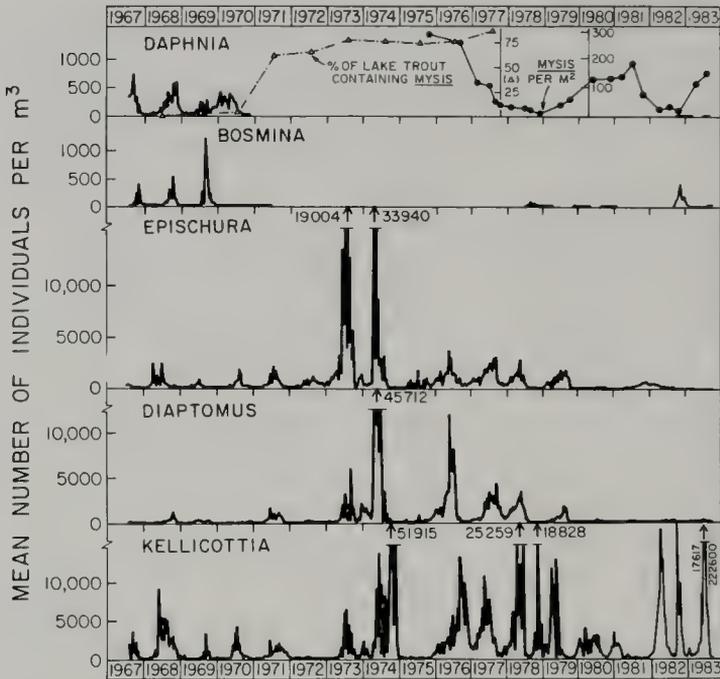


Fig. 10 – Variations in populations of *Daphnia*, *Mysis*, *Bosmina*, *Epischura*, *Diaptomus*, and *Kellicottia* in Lake Tahoe between 1967 and 1983. *Mysis* values from the years 1968 to 1977 are based on the percentages of lake trout containing *Mysis* during creel censuses by the California Department of Fish and Game. Beginning in 1975, *Mysis* values were determined on the basis of a lakewide average (data through 1980 from Goldman [1981]).

of the Roman road, Via Cassia, about 2,000 years ago is evident from a sediment core (Cowgill & Hutchinson 1970). Sediment from erosion, ash from volcanic eruptions, as well as that portion of the biota which is resistant to decay may lie undisturbed in sediments for thousands of years. Further, pigments (Valentyne 1960) and evidence of water chemistry may also be retained in the paleolimnological record.

One of the arguments presented for the continued development of the Tahoe basin was that the lumbering activities of the 1860's did not appear to have done serious damage to the water quality of Lake Tahoe. By examining sediments, we were able to demonstrate that damage done during the initial removal of timber from the basin was small in comparison to the disturbance that has accompanied modern developments. Samples taken in midlake with a large box-coring device clearly show that much more nitrogen is now entering the lake relative to carbon (Fig. 11A). Fig. 11B shows the carbon content of nearshore sediments in the vicinity of extensive lumbering activity

during the 1860's. Although there are insufficient lead dates to confirm the 1860 level, it is indicated by estimated sedimentation rates. Similarly, the input of another important algal nutrient, iron, has greatly increased with erosion from the steep slopes of the basin (Fig. 12). In addition, the diatom composition has shifted from centric forms to increasing numbers of pennates (Fig. 13). Finally, Pb-210 dating of the sediments indicates a more rapid rate of accumulation during the last several decades than occurred during the period of forest cutting in the 1860's (Byron & Goldman 1984).

As we look back in time, so must we look forward. The future of Lake Tahoe can be predicted with increasing certainty as the years of data are added, one to another. What seemed to some to be speculation or doomsmanship in the 1960's has been transformed into highly significant regressions. Further, visible periphyton growth now covers the once clean littoral zone so that, in spring, any observer can see a green margin around Tahoe (Fig. 14). Primary productivity correlates significantly

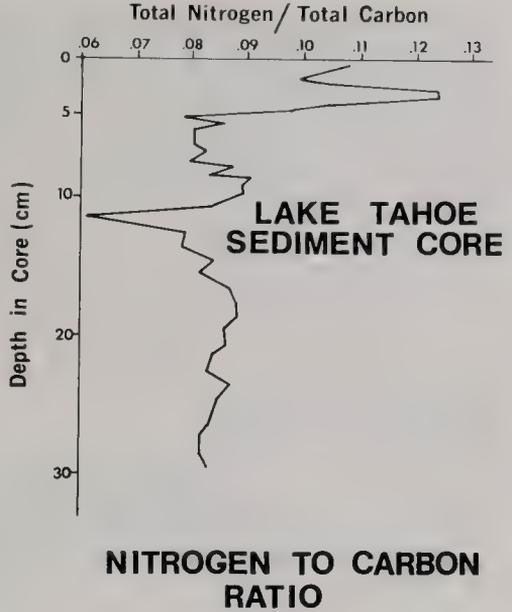
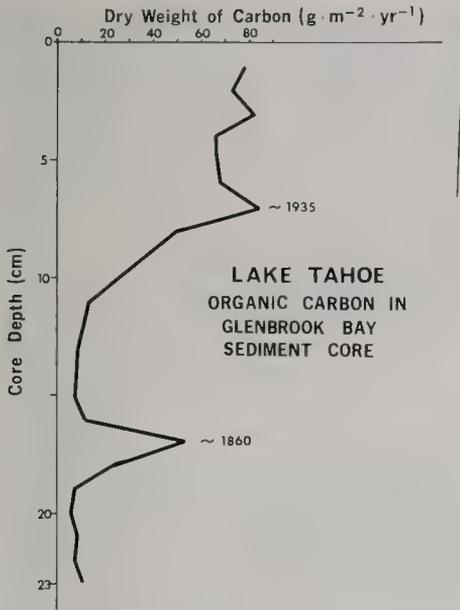


Fig. 11. - (A) The dramatic increase in nitrogen deposited as sediment in Lake Tahoe is evident from a midlake core sample. The higher nitrogen-to-carbon ratio in recent years is obvious (Byron & Goldman unpublished). (B) High organic carbon input is evident from this nearshore sediment core collected in Glenbrook Bay. This area was subjected to extensive timber clearing during the 1860's. Both charcoal and sawdust are to be found in the sediments here.

at the 1-percent level with the decline in transparency and, if projected into the future, predicts a lake of very ordinary transparency within about 40

years (Fig. 15). With each year that the productivity continues its rise, the

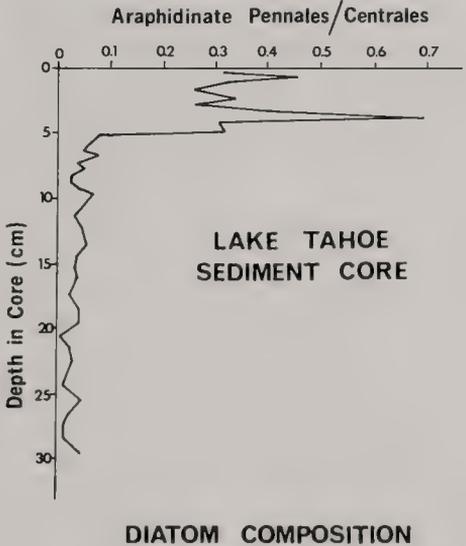
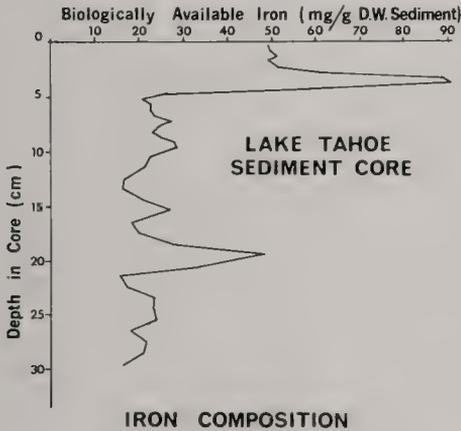


Fig. 12. - Distribution of biologically available iron in a midlake core sample from Lake Tahoe. The rise at 20 cm probably represents the 1860 lumber removal, and the increase above 5 cm is probably due to recent development in the basin (Byron & Goldman unpublished).

Fig. 13. - The ratio of araphidinate pennate to centric diatoms versus depth within a Lake Tahoe sediment core (Byron & Eloranta in press).



Fig. 14. – Periphyton covers the littoral zone of Lake Tahoe during the spring months. This underwater photograph was taken near Sunnyside (northwest Tahoe) on 8 May 1982 at a depth of 4 m. When this growth breaks loose, it coats the beaches with a brown slime. Photo by Stanford Loeb.

regression line steepens and the number of future years with clear waters in “the lake in the sky” is reduced. The damaged watersheds must be repaired now through the application of innovative biological engineering and further development must be more strictly regulated. Otherwise, future generations will look back and wonder why,

with so much knowledge and technology available, we failed to preserve the quality of this remarkable lake microcosm whose exceptional transparency became a legend.

ACKNOWLEDGMENTS

This work, done over a period of 25 years, would not have been possible

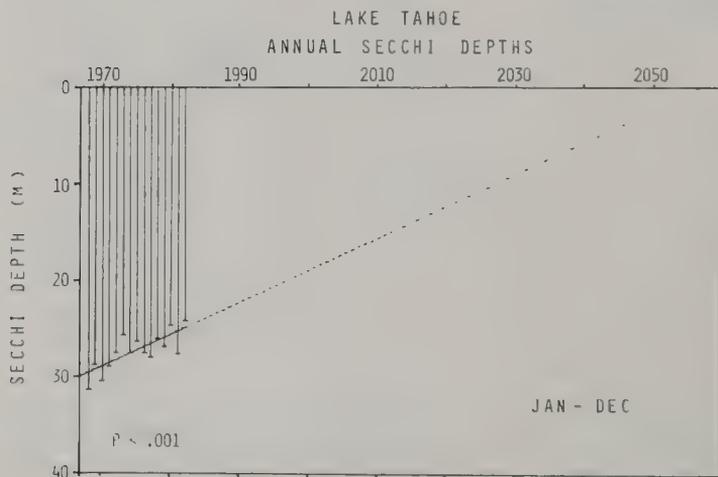


Fig. 15. – The regression constructed from the average annual Secchi depth in Lake Tahoe from 1968 through 1982. The regression line as extended is admittedly futuristic as it extends to a theoretical zero point, which occurs sometime after the middle of the next century. With each additional data point, the regression line steepens and the degree of steepness provides some insight into alternative futures.

without the tireless efforts of the Tahoe Research Group. Robert C. Richards has been particularly invaluable in the collection of data during the last 17 years of this effort and has provided valuable photographic documentation. Data reduction and figure preparation were largely accomplished by Patricia Arneson and Evelyne de Amezaga. Word processing of the manuscript was kindly provided by Carol Barnes, Anne C. Forcella, and Meryllene Smith. George Malyj provided important assistance with various aspects of coordination.

This paper is dedicated to the memory of my father, Marcus Selden Goldman (1894-1984), who first interested me in the streams and lakes of Illinois and, for more than 50 years, enthusiastically endorsed the varied activities of the Illinois Natural History Survey. He was a close friend of many of its staff, an enthusiastic amateur ichthyologist (Goldman 1977), a life member of the Izaak Walton League of America, and a staunch supporter of conservation activities everywhere.

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A Comparison of the Embryonic Development of Northern, Florida, and Reciprocal F₁ Hybrid Largemouth Bass in Different Thermal Environments

David P. Philipp, Christine Kaminski, and G. S. Whitt

The two subspecies of largemouth bass, *Micropterus salmoides salmoides* and *M. s. floridanus*, naturally occur in different geographic and climatic regions of the United States, with hybrids occurring in a zone of intergradation between these regions. Genetic differences between these stocks are reflected by differing physiological responses to the thermal environment. To determine the extent to which these differences contribute to natural geographic separation of the subspecies, we produced the embryos of the four genetic stocks of largemouth bass (*M. s. salmoides*, *M. s. floridanus*, *M. s. salmoides* ♀ × *M. s. floridanus* ♂, and *M. s. floridanus* ♀ × *M. s. salmoides* ♂) in vitro, using artificial fertilization techniques. The developmental success of the embryos and the schedule of embryogenesis for each stock were compared at each of a series of temperatures. The developmental success of each stock at each incubation temperature was determined by total hatching percentage. In addition, the thermal requirements for embryonic development of each of these four stocks were compared by determining the α -threshold temperatures of development as well as the number of thermal developmental units re-

quired to reach each of 22 key embryonic stages. Significant differences in the thermal requirements for embryogenesis exist among these different stocks of largemouth bass. The implications of these findings on current and future largemouth bass management programs are discussed.

The morphological differences between the northern largemouth bass, *Micropterus salmoides salmoides* (Lacepede), and the Florida largemouth bass, *M. s. floridanus* (Le Sueur), were discussed by Bailey & Hubbs in 1949. Since that time a number of studies designed to further assess the differences between the subspecies have been conducted (Hart 1952; Clugston 1964; Addison & Spencer 1972; Zolczynski & Davies 1976; Inman et al. 1977; Cichra et al. 1981; Smith & Wilson 1981; and Wright & Wigtil 1981). These studies have shown that a variety of biological differences exist between these two subspecies.

Our recent electrophoretic survey of the genetic structure of largemouth bass populations in the United States (Philipp et al. 1981, 1982, 1983) has quantified the degree of genetic divergence between these two subspecies. We have described a fast and reliable means of identifying pure northern, pure Florida, or intergrade populations of largemouth bass, that of the electrophoretic determination of the allele frequencies at the Idh-B and Aat-B loci. Meristic and morphometric counts routinely used in the past by fisheries biologists to distinguish these types of populations (Bryan 1969; Addison & Spencer 1972; Buchanan 1973; Inman

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et al. 1977; Moyle & Holzhauser 1978; and Bottroff & Lembeck 1978) are ambiguous and, hence, unreliable. In at least one study (Pelzman 1980) electrophoretic techniques also proved unreliable, since analyses were inappropriate and data were misinterpreted.

Our biochemical genetic analyses of largemouth bass populations (Philipp et al. 1981, 1982, 1983) also demonstrate that the intergrade zone between the ranges of the two pure subspecies, as it exists today (northern Florida, Mississippi, Alabama, Georgia, South Carolina, North Carolina, Virginia, and Maryland), is much more extensive than that described by Bailey & Hubbs (1949). As a result, the previously assigned genetic status of the stocks of largemouth bass used as representatives of the two pure subspecies in many previous studies appears questionable. In the absence of genetic confirmation of the stocks used, the data generated by these earlier studies and their resulting conclusions must be considered very cautiously.

In 1959, Florida largemouth bass, or at least largemouth bass containing some portion of the genome of *M. s. floridanus*, were introduced into certain waters in California (Sasaki 1961). The subsequent establishment of largemouth bass populations with a substantial proportion of the gene pool contributed by the Florida subspecies has been well documented (Smith 1971; von Geldern & Mitchell 1975; Bottroff & Lembeck 1978; Moyle & Holzhauser 1978). The populations of largemouth bass which existed in California prior to 1959 were the result of introductions of northern largemouth bass imported from Illinois in 1891 (Shebley 1917) and were not the result of immigration and natural selection, since the state of California is well outside the native range of largemouth bass (MacCrimmon & Robbins 1975). It is not surprising that the introductions of largemouth bass from Florida were successful in southern California, since the climatic conditions more closely resemble those of Florida than of Illinois.

The apparent success of the recent introductions of *M. s. floridanus* in southern California waters and the demand from fishermen for more and larger largemouth bass have apparently provided the impetus for a number of states to initiate Florida largemouth bass programs. These programs range from controlled research with limited introductions to large-scale propagation and widespread stockings. Unlike California, many of these states already contained populations of naturally established largemouth bass. Due to the lack of reliable, quantitative data concerning the genetic differences of the native and introduced stocks and the relative fitnesses of these stocks in different environments, the long-term effects of these introductions upon the existing largemouth bass fisheries cannot be accurately predicted at this time. However, the impact of these stocking programs on the genetic integrity of the native largemouth bass populations in these states could be catastrophic. We have postulated (Philipp et al. 1981, 1982, 1983) that when alleles present in the Florida subspecies are introduced into a population of the northern subspecies, the unique genic combinations initially present may become irreversibly altered. In addition, some of the Florida alleles are likely to be less fit for these new environments. Although the resulting populations may be genetically sufficient in terms of short-term survival, the long-term effect of this genetic mixture would be a lowering of fitness in the recipient population. For these reasons, we have recommended that programs designed to introduce the Florida subspecies into states outside of peninsular Florida but within the native range of the largemouth bass be halted until appropriate research has determined the effects on the recipient populations.

Factors which affect year-class strength among largemouth bass populations are complex. It has been suggested that spawns hatched early in a given year may suffer substantially

less mortality than those hatched later in the season (Aggus & Elliot 1975). Therefore, in mixed populations, differential thermal effects upon the reproductive behavior and the rate and success of development between northern and Florida largemouth bass embryos may play a crucial role in determining the relative contribution of each stock to the total year-class production. The current study was designed to assess thermal effects upon the rate and success of the development of embryos of genetically defined stocks of both pure subspecies, *M. s. salmoides* and *M. s. floridanus*, and of both reciprocal F_1 hybrids.

MATERIALS AND METHODS

Parental Stocks

Northern largemouth bass were collected from Clinton Lake, Illinois. Electrophoretic analyses of individuals from this population showed the frequency of the northern Idh-B allele (Idh-B¹) and the sum of the northern Aat-B alleles (Aat-B¹ and Aat-B²) both to be 1.000, confirming that this population consisted of pure *M. s. salmoides* (Philipp et al. 1981, 1982, 1983). Florida largemouth bass were collected from Lake Dora, Florida. Electrophoretic analyses of individuals from this population showed the frequency of the Florida Idh-B allele (Idh-B³) and the sum of the Florida Aat-B alleles (Aat-B³ and Aat-B⁴) both to be 1.000, confirming that this population consisted of pure *M. s. floridanus* (Philipp et al. 1981, 1982, 1983). Adult males and females from only these two genetically confirmed populations were used as brood stock throughout this study.

Production of Embryos

Florida largemouth bass (FLMB) and Florida ♀ × northern ♂ F_1 hybrid largemouth bass ($F \times N$) embryos were produced at the Florida Game and Freshwater Fish Commission, Eustis Fisheries Research Laboratory. North-

ern largemouth bass (NLMB) males were collected in December 1980 from Clinton Lake, Illinois, and were held indoors at 10°C at the Illinois Natural History Survey (INHS). On 2 February 1981, these fish were marked with a right pectoral clip, transported to Florida, and allowed to reach reproductive readiness in outdoor earthen ponds at the Richloam State Fish Hatchery. During February 1981 ripe male NLMB, retrieved from the hatchery, and ripe male FLMB, collected from Lake Dora by electrofishing, were brought to the Eustis laboratory, where they were held in indoor flow-through raceways. On 21 and 26 February 1981, mature, ripe female FLMB were collected from Lake Dora, Florida, by electrofishing and were brought to the Eustis laboratory. The eggs from individual FLMB females were manually stripped into a bowl, mixed, and split into two aliquots in separate petri dishes. One aliquot was fertilized with sperm from a single FLMB male and the other with sperm from a single NLMB male, using methods described in Childers (1967) and Philipp et al. (1979).

Northern largemouth bass (NLMB) and northern ♀ × Florida ♂ F_1 hybrid largemouth bass ($N \times F$) embryos were produced in essentially the same manner, with the following exceptions. FLMB males, collected from Lake Dora in February 1981, were marked with a left pectoral clip and were air shipped to the Illinois Natural History Survey to be held indoors at 10°C until they were stocked outdoors in INHS earthen ponds on 10 March 1982 and were allowed to reach reproductive readiness. During May 1981, FLMB males retrieved from INHS ponds and NLMB males collected from Clinton Lake by electrofishing were brought to the INHS laboratory and held indoors. On 13, 22, and 28 May, mature, ripe NLMB females were collected from Clinton Lake by electrofishing and were brought to the INHS laboratory. NLMB and $N \times F$ embryos were produced in the laboratory, using the pro-

cedures described previously for producing FLMB and $F \times N$ embryos.

Rearing of Embryos

Procedures and equipment used for rearing the FLMB and $F \times N$ embryos were identical to those used for rearing the NLMB and $N \times F$ embryos. The very dense egg-sperm mixtures, produced as has been described, were allowed to stand in minimal water for 5 minutes to allow for completion of the fertilization process. These newly fertilized eggs were transferred to plastic containers holding about 2–3 cm of water. The eggs were thinly spread within these containers and incubated for 1 hour at 24°C until initial cleavage. For each cross, samples of 100 normally cleaving eggs (2–4 cell stage) were then removed, transferred to each of a number of glass finger bowls containing 24°C water, and allowed to adhere to the glass. The embryos in each finger bowl were acclimated for 1 hour to a specified test temperature, the bowls were covered with nylon netting to allow water circulation but prevent loss of embryos, and the bowls were immersed in an aerated, filtered, 75-liter constant temperature bath at the test temperature. The temperature of each incubation bath was monitored continuously, using dual water temperature probes and a calibrated 12-channel recorder (Chino Works, Ltd., Tokyo, Japan, Model EW 1200).

Morphological development of each set of embryos reared at each temperature was visually monitored, using a dissecting microscope. Prior to retinal pigmentation, each set of embryos was monitored every 2–4 hours. After retinal pigmentatin had progressed, the frequency of visual observation was reduced to every 6–8 hours. The times required to reach each of 22 key morphological stages were recorded for the embryos at each test temperature. Dead eggs or embryos were counted, removed, and recorded at each visual inspection. A photographic record of the morphological development of

these embryos was made, using an Olympus JM dissecting microscope with an Olympus photographic attachment and an Olympus OM-2 camera.

Data Analysis

The success of development was determined by calculating for each set of embryos the percentage of eggs which hatched and of these the proportion which appeared normal.

The α -threshold temperature of development, a theoretical thermal value below which embryonic development ceases (Childers 1967), was determined. For each set of embryos raised at each temperature, the time required to reach each of 11 readily identifiable morphological stages was determined, and the cumulative average temperature of development was calculated from the thermal record for each of these stages. For each of the four genetic stocks (NLMB, $N \times F$, $F \times N$, and FLMB) at each developmental stage, average cumulative temperature was plotted versus the inverse of developmental time in hours. The regression equation describing the linear relationship for each of the four stocks was determined from these values (10–12 data points per stage for the FLMB and $F \times N$ embryos and 16–18 data points per stage for the NLMB and $N \times F$ embryos). The \times -intercept determined from each equation is the α -threshold temperature determined for that stock, using the values for that developmental stage. The final α -threshold temperature for each genetic stock was determined as the average of the values for these 11 stages.

The number of thermal developmental units (TDU) required for an embryo to reach a given stage of development is defined as the number of degree-hours above the α -threshold temperature which must be accumulated. TDU values were calculated, using the final value for the α -threshold temperature together with the times of development and average cumulative temperatures for each set of

embryos of each genetic stock at each of 22 morphological stages of development.

RESULTS

Patterns of Development

No qualitative differences in morphogenetic events could be detected among the four genetic stocks of largemouth bass studied (NLMB, $N \times F$, $F \times N$, and FLMB). Therefore, the following morphological features and their developmental sequence hold for the embryogenesis of all four stocks.

The cortical reaction occurs immediately upon fertilization, with the cortical layer becoming raised by 1 minute after fertilization. There follows a confluence of cytoplasm around the zygote nucleus and the resultant formation of the germinal disc. Cleavage is telolecithal, the initial formation of the two-cell stage occurring within 1 hour at 24°C. Rates of development during the rest of this study depended upon temperature and will be discussed in detail later. Fig. 1A through 1P illustrate the periods of morphogenesis of one set of embryos, FLMB embryos raised at $24.2 \pm 0.4^\circ\text{C}$. These pictures illustrate the patterns of development for each of the four stocks of largemouth bass embryos studied (NLMB, $N \times F$, $F \times N$, and FLMB). The developmental progression paralleled that described for other centrarchid species (Morgan 1951; Balon 1959; Champion & Whitt 1976; Taubert 1977).

Early cleavage (Fig. 1A) continues, eventually resulting in blastula formation (Fig. 1B). Epiboly commences (Fig. 1C) and progresses through the yolk plug stage (Fig. 1D) prior to the formation of a body axis (Fig. 1E). Embryonic development continues with the formation of increasing numbers of somite pairs (Fig. 1F). The optic cup and pericardial cavity continue to develop. The embryonic heart begins beating, and true circulation with colorless blood starts shortly afterward (Fig. 1G). The tail increases in length, and body contractions increase in number and severity. Red blood cells containing hemo-

globin appear just prior to hatching (Fig. 1H). Hatching occurs fairly synchronously for most eggs at normal temperatures (90 percent of the eggs hatched in a 3–4 hour period at 24°C). The newly hatched embryo is still quite underdeveloped (Fig. 1I), having only limited and unguided movement. After hatching, the heartbeat becomes more vigorous, and the first pigment granules become visible in the retina (Fig. 1J). Pectoral and pelvic fins form as the retina becomes quite darkly pigmented (Fig. 1K). The tapetum lucidum develops, to give the eye at first a silvery and later a golden appearance (Fig. 1L). During this period the rudiments of many of the internal organs, such as the liver, urinary bladder, intestine, and swim bladder, are developing. Following this stage the jaw begins to form (Fig. 1M) and eventually starts to open and close regularly (Fig. 1N), as body pigmentation commences. At this point, the embryos begin to swim off the substrate with increasing regularity (Fig. 1O), eventually reaching a free-swimming stage and active feeding as yolk sac absorption is completed (Fig. 1P). Our monitoring of the development of largemouth bass ceased at this point and did not include an investigation of the subsequent fry and fingerling stages.

Effect of Temperature on Developmental Success

The percentage of eggs from which embryos (normal and abnormal) hatched was calculated for each set of embryos reared. These results are given in Table 1. The results for the NLMB and FLMB embryos are also compared graphically in Fig. 2. Comparing the two pure subspecies, the FLMB embryos exhibited optimal hatching rates at temperatures (20°–28°C) substantially higher than those exhibited by the NLMB embryos (17°–24°C) (Table 1, Fig. 2). These temperature ranges are somewhat lower than the values reported by McCormick & Wegner (1981). In addition, the lower thermal limits for successful hatching were higher for FLMB embryos than for

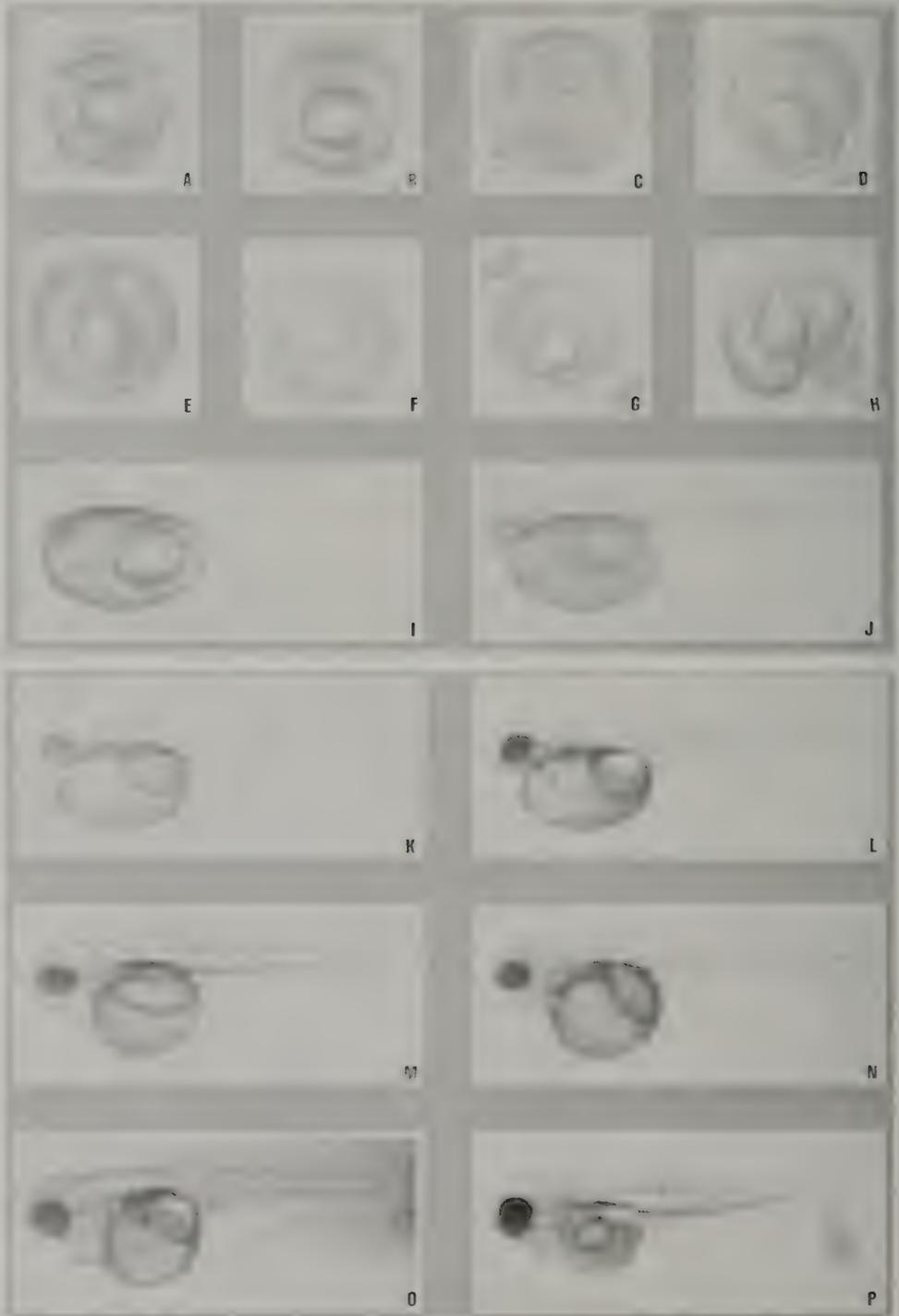


Fig. 1. - The morphogenesis of largemouth bass embryos. (A) Early cleavage. (B) Blastula. (C) Epiboly-50 percent. (D) Yolk plug. (E) Body axis. (F) Somite development. (G) Heartbeat. (H) Prehatch. (I) Posthatch. (J) Onset of retinal pigmentation. (K) Dark retinal pigmentation. (L) Golden eyes. (M) Jaw formation. (N) Jaw movement. (O) Swim-up. (P) Freely swimming and actively feeding.

NLMB embryos. Conversely, the upper thermal limits for successful hatching were lower for NLMB embryos than for FLMB embryos. Less than 15 percent of hatched embryos appeared morphologically abnormal at each test temperature except for the NLMB and $N \times F$ at 30.5°C (100 percent abnormal in each case), the NLMB and $N \times F$ at 30.3°C (68.6 percent and 75.0 percent abnormal, respectively), and the FLMB and $F \times N$ at 18.5°C (16.3 percent and 18.5 percent abnormal, respectively).

The tendency for both hybrids to exhibit developmental patterns more similar to that of the maternal than that of the paternal subspecies was notable (Table 1). Although the relationship between temperature and hatching percentage for $N \times F$ embryos paralleled that for NLMB embryos, the absolute hatching percentage for the $N \times F$ embryos was lower than that for the NLMB embryos at most temperatures. The relationship between temperature and hatching percentage for the $F \times N$ embryos paralleled that for the FLMB embryos as well. However, the absolute hatching percentage for the $F \times N$ embryos was greater than that for the FLMB embryos at most temperature.

Thermal Limits of Embryogenesis

The α -threshold temperature of development were calculated for each of the four stocks of largemouth bass (NLMB, $N \times F$, $F \times N$, and FLMB) using data from each of 11 distinct developmental stages (body axis; 10, 15, 20, and 25 somites; heartbeat; 50-percent hatching; onset of, light, and even retinal pigmentation; and jaw movement). We chose to monitor these 11 stages because they were easily identifiable visually. Because the rates of development for the NLMB and $N \times F$ embryos were similar at all of the temperatures studied, the data for these two stocks were combined for α -threshold temperature calculations. Data for the FLMB and $F \times N$ embryos were similarly combined (Table 2).

The overall α -threshold value for each stock was calculated as the aver-

age of the values calculated individually from the data for each of the 11 individual developmental stages used (Table 2). The overall α -threshold temperature determined for the NLMB and $N \times F$ embryos, 12.62 ± 0.27 , was significantly higher ($P < 0.01$, Wilcoxon's signed-ranks test, Sokal & Rohlf 1973) than that determined for the FLMB and $F \times N$ embryos, 11.52 ± 0.77 . In addition, the stage-specific α -threshold temperatures calculated for the NLMB and $N \times F$ embryos were higher than those calculated for the FLMB and $F \times N$ embryos at each of the developmental stages used (Table 2).

The upper thermal limits of development can be estimated by extrapolating from the decrease in hatching percentage for a few of the trials at elevated temperatures, $>30^\circ\text{C}$ (Table 1). NLMB and $N \times F$ embryos did not hatch at temperatures above 30.5°C, and even at temperatures between 30° and 30.5°C there was an extremely high percentage of morphological deformities. These results agree closely with those reported by McCormick & Wegner (1981) for northern largemouth bass embryos. FLMB and $F \times N$ embryos, however, successfully hatched at 30.8°C, although at 31.7°C no success-

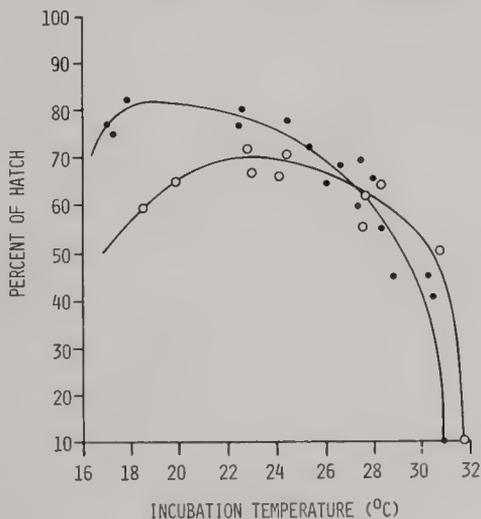


Fig. 2. — The effect of temperature on the hatching success of northern largemouth bass (—●—) and Florida largemouth bass (—○—).

Table 1. — Hatching percentages of largemouth bass eggs incubated at various temperatures.

Largemouth Bass Stocks							
NLMB		N × F		F × N		FLMB	
Temp (°C)	Per-cent Hatch	Temp (°C)	Per-cent Hatch	Temp (°C)	Per-cent Hatch	Temp (°C)	Per-cent Hatch
34.0	0	34.0	0	36.0	0	36.0	0
30.9	0	30.9	0	31.7	0	31.7	0
30.5	31	30.5	30	30.8	47	30.8	41
30.3	35	30.3	24				
28.8	35	28.8	28				
28.4	45	28.4	37	28.4	52	28.4	54
28.0	56	28.0	53				
27.5	59	27.5	57	27.7	63	27.7	52
27.4	49	27.4	55	27.6	54	27.6	46
26.6	58	26.6	53				
26.1	54	26.1	49				
25.3	62	25.3	55	24.5	66	24.5	61
24.5	68	24.5	61	24.2	65	24.2	56
22.6	70	22.6	66	23.0	61	23.0	57
22.5	67	22.5	64	22.8	71	22.8	62
17.8	72	17.8	60	19.8	54	19.8	55
17.2	65	17.2	61	18.5	54	19.8	55
17.0	67	17.0	62				

Table 2. — Alpha-threshold temperatures (°C) of development for the four stocks

Developmental Stages	Embryos of NLMB and N × F F ₁ Hybrid	Regression Equation (Correlation Coefficient)	Embryos of FLMB and F × N F ₁ Hybrid	Regression Equation (Correlation Coefficient)
Body axis formation	12.17	$y = 0.00492x - 0.0599$ (0.944)	12.07	$y = 0.00550x - 0.0664$ (0.980)
10 somites	12.49	$y = 0.00400x - 0.0499$ (0.891)	10.67	$y = 0.00394x - 0.0420$ (0.975)
15 somites	12.58	$y = 0.00358x - 0.0451$ (0.905)	11.10	$y = 0.00354x - 0.0393$ (0.984)
20 somites	12.79	$y = 0.00334x - 0.0427$ (0.928)	11.41	$y = 0.00322x - 0.0367$ (0.990)
25 somites	12.69	$y = 0.00300x - 0.0380$ (0.914)	12.23	$y = 0.00314x - 0.0385$ (0.990)
Initial heartbeat	12.72	$y = 0.00272x - 0.0346$ (0.926)	12.22	$y = 0.00277x - 0.0339$ (0.990)
50-percent hatch	12.76	$y = 0.00184x - 0.0235$ (0.972)	12.18	$y = 0.00184x - 0.0224$ (0.994)
Onset of retinal pigmentation	12.89	$y = 0.00162x - 0.0209$ (0.900)	12.52	$y = 0.00147x - 0.0184$ (0.974)
Light retinal pigmentation	12.60	$y = 0.00131x - 0.0164$ (0.983)	11.14	$y = 0.00113x - 0.0126$ (0.970)
Even retinal pigmentation	12.15	$y = 0.00110x - 0.0134$ (0.986)	10.14	$y = 0.000904x - 0.00917$ (0.957)
Initial jaw movement	13.03	$y = 0.000877x - 0.0115$ (0.987)	11.01	$y = 0.000670x - 0.00738$ (0.958)
Mean	12.62		11.52	
Standard deviation	0.27		0.77	

ful hatching was observed. It appears, therefore, that the upper thermal limit for successful embryonic development of FLMB and F × N embryos is 0.5°–1.0°C higher than that for the NLMB and N × F embryos.

Thermal Requirements of Embryogenesis

Using the overall α -threshold temperatures calculated for the NLMB and N × F embryos and for the FLMB and F × N embryos, 12.62 ± 0.27 and 11.52 ± 0.77 , respectively, the numbers of thermal developmental units (TDU) required to reach each of 22 development stages were calculated and are shown in Table 3. For the first 12 stages (mid-blastula through end of hatching), embryos from all stocks required comparable thermal input (TDU). However, for the remainder of development, the FLMB and F × N embryos required substantially greater thermal input (TDU) than did the NLMB and N × F embryos, ranging from 11.3 percent more for the onset of retinal pigmen-

tion to 29.0 percent more for the final yolk absorption stage.

DISCUSSION

The environmental thermal regimes which exist among the aquatic communities throughout the United States are extremely varied. Temperature plays a potentially major role in the processes of natural selection, genetically tailoring stocks of largemouth bass to specific environments (Childers 1975). Genetic differences between the two subspecies of largemouth bass, *M. s. salmoides* and *M. s. floridanus*, have been assessed and documented (Phillip et al. 1981, 1982, 1983). Indeed, a variety of physiological and behavioral differences most likely result from these genetic differences, each stock reacting somewhat differently to thermal conditions. Because these physiological and genetic differences among the two subspecies and their hybrids determine their relative fitness in a given environ-

Table 3. — Developmental unit requirements of the four stocks.

Developmental Stages	Embryos of the NLMB and N × F F ₁ Hybrid (SD)	Embryos of FLMB and F × N F ₁ Hybrid (SD)
Mid-blastula	69 (14)	53 (11)
Half epiboly	123 (29)	122 (24)
Yolk plug	166 (23)	158 (23)
Initial body axis	197 (23)	193 (22)
10 somites	249 (36)	240 (19)
15 somites	278 (33)	275 (20)
20 somites	312 (37)	310 (19)
25 somites	345 (30)	340 (18)
Heartbeat	379 (41)	385 (18)
Begin hatch	503 (48)	508 (17)
50-percent hatch	556 (48)	576 (17)
End hatch	619 (53)	660 (13)
Onset of retinal pigmentation	670 (44)	746 (53)
Light retinal pigmentation	769 (44)	851 (58)
Even retinal pigmentation	865 (54)	993 (75)
Initial jaw movement	1,199 (77)	1,452 (122)
Onset of body pigmentation	1,318 (89)	1,574 (136)
Red spleen formation	1,372 (110)	1,674 (135)
Begin swim-up	1,501 (132)	1,833 (111)
Begin free swimming	1,715 (185)	2,136 (159)
Active free swimming	1,873 (208)	2,417 (177)
Yolk absorbed	2,031 (229)	2,620 (203)

ment, a quantitative assessment of thermal response differences among these stocks is critically needed for effectively formulating present and future management programs for largemouth bass.

Although Swingle (1956) reported that most largemouth bass spawning occurs between 68° and 75°F (20°–24°C), Chew (1974) documented spawning of FLMB in Lake Weir, Florida, at 59°F (15°C). Fluctuations in water temperature during the spring spawning season are usually not as severe in lakes in peninsular Florida as they are in lakes in more northerly regions. Largemouth bass spawns in Florida lakes during the earliest portion of the seasonal spawning period may be less likely to result in the exposure of eggs or embryos to very cold temperatures (<12°C) than would correspondingly early spawns in northern regions. It has been suggested that, in mixed populations, the Florida subspecies tends to spawn earlier in the season, at lower temperatures, than does the northern subspecies of largemouth bass (Hunsacker & Crawford 1964; Bottroff & Lembeck 1978; Moyle & Holzhauser 1978). Observations of spawning in ponds at the Illinois Natural History Survey during 1981 agreed with this suggestion (unpublished results); further experimentation is currently under way to verify this finding.

Interestingly, the α -threshold temperature of development of the FLMB (11.52 ± 0.77) is significantly lower than that of the NLMB (12.62 ± 0.27). This relationship suggests a survival strategy of delayed spawning in the northern subspecies which presumably reflects a more variable, lower mean water temperature during spawning periods in the north. In addition, the northern subspecies apparently can use environmental incubation temperatures more efficiently. This use is evidenced by the significantly lower number of thermal developmental units required by NLMB embryos to reach the free swimming and actively feeding stage ($2,031 \pm 229$) than that

required by the FLMB ($2,620 \pm 203$). Only at temperatures below about 16.2°C would FLMB eggs require less incubation time than NLMB eggs to reach the free swimming and actively feeding stage. At "normal" incubation temperatures NLMB embryos reach this stage sooner than do FLMB embryos. For example, at 20°C NLMB embryos would reach the free swimming and actively feeding stage at 272 hours, whereas the FLMB would require 309 hours to reach this stage. This more rapid development gives NLMB embryos a clear advantage over FLMB embryos at temperatures normally encountered during incubation periods in the wild (17°–25°C).

Interestingly, in comparing the embryological development of the two subspecies, major differences in numbers of thermal developmental units required occur at retinal pigmentation and later. These periods of embryonic development are associated with organogenesis and are periods during embryogenesis in which many of the genes encoding metabolic enzymes become activated (Philipp et al. 1979). This observation is consistent with the hypothesis that many of the metabolic processes up to the retinal pigmentation period may be under the control of maternal enzymes or m-RNA molecules synthesized during oogenesis. This observation also suggests that the two subspecies may have diverged in certain of their gene regulatory processes and now respond differently to temperature. The differences in the initial timing and levels of enzyme expression in developing embryos of these four stocks (NLMB, N \times F, F \times N, and FLMB) strongly support this suggestion (Philipp et al. 1983; Parker, Philipp, & Whitt unpublished results).

The two subspecies also differ in hatching success at various incubation temperatures. The peak of successful hatching for the NLMB occurs at lower temperatures (17°–22°C) than that for the FLMB (21°–24°C). In addition, the FLMB embryos apparently survive higher incubation temperatures than

do the NLMB (Fig. 2). These relationships probably provide the NLMB and FLMB embryos an advantage in their respective environments.

It is interesting that the $N \times F$ embryos have consistently lower hatching percentages than their thermal counterpart NLMB embryos but that the opposite holds true for the $F \times N$ and FLMB embryos (Table 1). This set of relationships is an example of the inherent differences between reciprocal hybrids. We have postulated that these nonadditive asymmetrical responses by reciprocal hybrids result from differences in the interactions of the paternal genes with the maternal gene effector molecules (Whitt et al. 1977; Philipp et al. 1983).

Our analyses reveal that the developing embryos of NLMB and FLMB react differently to different temperatures. We feel that these differences have resulted from these two subspecific genomes having evolved independently in response to different thermal selective pressures. We postulate that to better survive colder climates, NLMB have evolved a reproductive strategy of delayed spawning until they encounter higher temperatures. This strategy helps to prevent premature spawns, which could be destroyed by severe cold. In addition, NLMB have evolved schedules of embryonic gene expression, and thus mechanisms of controlling embryonic metabolism and morphogenesis, that operate efficiently and rapidly at lower temperatures. These patterns of gene expression also allow NLMB embryos to reach maximal hatching rates at lower temperatures than those required by FLMB embryos. However, during the protracted spawning seasons in peninsular Florida, early spawns produce individuals as much as 3 months earlier than late spawns. FLMB appear to have evolved a reproductive strategy which allows them to spawn at lower temperatures than those at which NLMB spawn. These early fish have distinct competitive advantages over fish spawned later. FLMB embryos have

also evolved an increased tolerance to incubation temperatures higher than those of NLMB embryos. Thus, FLMB embryos are better able to tolerate the warm water temperatures found in peninsular Florida during the largemouth bass spawning season.

The divergence of developmental response to temperature in the two subspecies of largemouth bass has significant implications for management programs. Fitness probably varies greatly, depending upon the geographic location of the population, the physical characteristics of the body of water being considered, and the weather conditions during a given spawning season. However, it is not unreasonable to assume that, in the long run, stocks of largemouth bass introduced into inappropriate thermal environments will not perform as well as stocks which are introduced into thermal environments for which they have been genetically tailored. Our findings support the recommendation that management programs which result in mixing the two subspecies be discontinued. Precautions must be taken to protect the genetic integrity of the two subspecies. Specifically, we recommend that no largemouth bass containing any portion of the genome of the Florida subspecies be propagated for introduction into waters north of the intergrade zone as described by Philipp et al. (1981, 1982, 1983). We also recommend, of course, that the introduction of largemouth bass containing any portion of the genome of the northern subspecies into waters of peninsular Florida be prohibited.

For maximum effectiveness, it is imperative that sound genetic principles be incorporated into current and future fisheries management programs (Smith & Chesser 1981; Philipp et al. 1981, 1982, 1983). Individual genetic stocks which constitute a species must be identified, characterized, and recognized as distinct units requiring individual consideration in management efforts. The genetic integrity of discrete stocks must be preserved, because as

Ryman (1981) has so aptly stated, "Genetic variation in natural populations constitutes a biological resource that must be properly managed so as not to reduce future opportunities for use of the resource."

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Evolution of Reproductive Behaviors in Percid Fishes

Lawrence M. Page

Percid fishes are freshwater derivatives of a marine perciform, perhaps an anadromous serranid (McCully 1962; Collette & Banarescu 1977). They appear to be relatively recent (i.e., most evolved during the Pliocene or later) but have undergone a tremendous radiation in North America, where they now comprise about 151 species in five genera. Among North American freshwater fishes, only minnows (Cyprinidae), with about 225 species, are more diverse. Together, percids and minnows constitute almost half of the temperate North American freshwater fish fauna. In addition to being diverse groups, these fishes often occur in large populations and are important in determining the ecological characteristics of North American streams and lakes. Elsewhere, percids are present only in temperate Eurasia, where there are 14 species in six genera. Two genera, *Stizostedion* and *Perca*, occur in both North America and Eurasia (Table 1).

Several reasons exist for studying the reproductive habits of organisms. Among these are that (1) reproductive habits are inherently interesting; (2) reproduction is that activity toward which all life processes ultimately are directed and, therefore, understanding its variations is important if we wish to protect or manage species; and (3) reproductive characteristics provide information useful in estimating evolutionary (phylogenetic) history. Percids are especially interesting in this last regard because, as a recent and diverse group, transitions among their various types of reproductive behaviors remain evident today. Reconstructing the evolutionary history of reproductive behav-

iors of percids results in a better understanding of the relationships among species.

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TYPES OF REPRODUCTIVE BEHAVIORS

Accompanying the evolution of a large diversity of percids has been the evolution of a variety of reproductive

Table 1. — Percid taxa and their distributions

Taxa	Number of Species	Distribution
Etheostomatinae		
Luciopercini		
<i>Stizostedion</i>	5	Holarctic
Etheostomatini		
<i>Percina</i>	ca. 38	Nearctic
<i>Ammocrypta</i>	7	Nearctic
<i>Etheostoma</i>	ca. 103	Nearctic
Romanichthyini		
<i>Zingel</i>	3	Palaearctic
<i>Romanichthys</i>	1	Palaearctic
Percinae		
<i>Percarina</i>	1	Palaearctic
<i>Perca</i>	3	Holarctic
<i>Gymnocephalus</i>	4	Palaearctic

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strategies, and in the most advanced states, parental care of the eggs. Among the 76 species of percids for which spawning behaviors are known, six types of behavior are recognized, some of which can be subdivided further, as discussed below. These six types, named for the mode of egg-deposition, are termed (1) broadcasting, (2) stranding, (3) burying, (4) attaching, (5) clumping, and (6) clustering.

Broadcasting

Broadcasting is the primitive mode of reproductive behavior among fishes and is retained in primitive percids. Eggs and sperm are discharged in large numbers, often in a frenzy of activity involving several individuals. A coarse substrate, usually composed of rocks or plants, is chosen to provide crevices and other hiding places for the fertilized eggs. In its most primitive state, broadcasting makes no other behavioral provisions for the eggs, either before or after spawning.

Stizostedion vitreum (Mitchill) and *S. canadense* (Smith) broadcast their eggs between March and June in streams and in areas of lakes with sufficient water movement to ventilate the eggs (Eschmeyer 1950; Nelson 1968). Spawning usually occurs in the evening (Ellis & Giles 1965) or at night (Eschmeyer 1950), and territories are not established (Ellis & Giles 1965).

Courtship consists of an individual of either sex approaching another individual from behind or from the side and pushing against it. The approached fish either withdraws or, if sexually responsive, makes quick darts forward and upward. This increased activity often elicits the attention of other individuals, and soon a compact group forms, which periodically rushes forward and upward. Eggs and sperm are released during a forward rush of activity (Ellis & Giles 1965). Spawning groups vary from two individuals to several individuals of both sexes (Fig. 1). Eggs are adhesive for a few hours, and they may adhere to rocks or plants for a short time; ultimately they fall to the bottom and into interspaces among the components of the substrate (Fig. 2), where they presumably are less exposed to predation (Colby et al. 1979). *S. marinum* (Cuvier) and *Percarina demidoffi* Nordmann appear to exhibit similar, perhaps identical, behavior (Berg 1949) although descriptions of spawning are vague.

Stizostedion lucioperca (Linnaeus) exhibits a modification of this behavior in that eggs and sperm are broadcast over a circular pit previously constructed by the male. The pit is lined with gravel, shells, or plant material (often roots) and is guarded before and after spawning by the male, who also fans the fertilized eggs (Kryzhanovshy et al. 1953). Mating in this more special-



Fig. 1. — *Stizostedion vitreum* congregated on spawning grounds at Lake Gogebic, Michigan, 4 May 1948. From Eschmeyer (1950). (Photo provided by the Institute for Fisheries Research, Fisheries Division, Michigan Department of Natural Resources.)

Fig. 2. — Eggs of *Stizostedion vitreum* on spawning ground at Lake Gogebic, Michigan, 12 May 1948. From Eschmeyer (1950). (Photo provided by the Institute for Fisheries Research, Fisheries Division, Michigan Department of Natural Resources.)



ized, nesting broadcaster may be monogamous (Deedler & Willemsen 1964).

Broadcasters

Group A. Spawn over open substrate

Stizostedion vitreum (Eschmeyer 1950)

S. canadense (Nelson 1968)

S. marinum (Berg 1949)

Percarina demidoffi (Berg 1949)

Group B. Spawn over male-constructed pit

S. lucioperca (Kryzhanovshy et al. 1953)

rington 1947; Hergenrader 1969) and *P. fluviatilus* Linnaeus (Seeley 1886:27; Wheeler 1969:322; Treasurer 1981). It also may occur in *Gymnocephalus cernua* (Linnaeus), as described by Seeley (1886:36) and Wheeler (1969:321), although some authors (e.g., Nikol'skii 1961:369; Muss 1978:161) discuss spawning in *Gymnocephalus* without mentioning egg strands.

Stranders

Gymnocephalus cernua (Seeley 1886)

Perca flavescens (Worth 1892)

P. fluviatilus (Seeley 1886)

Stranding

Stranders have the unique habit of encasing their eggs in long gelatinous strands. A ripe female is followed by several males through beds of vegetation (sometimes tree roots or debris) in slowly flowing or standing water. The males release sperm as she extrudes a convoluted egg strand (Worth 1892; Treasurer 1981). The strand is gelatinous, transparent, hollow, and arranged in bellowslike transverse folds. When first laid, the shape of the egg mass is similar to that of the ovarian cavity (Fig. 3), but eventually it stretches (Fig. 4) and may reach a length of 2.4 m and a width of 10 cm (Hardy 1978). Egg stranding is known to occur in *Perca flavescens* (Mitchill) (Worth 1892; Har-

rington 1947; Hergenrader 1969) and *P. fluviatilus* Linnaeus (Seeley 1886:27; Wheeler 1969:322; Treasurer 1981). It also may occur in *Gymnocephalus cernua* (Linnaeus), as described by Seeley (1886:36) and Wheeler (1969:321), although some authors (e.g., Nikol'skii 1961:369; Muss 1978:161) discuss spawning in *Gymnocephalus* without mentioning egg strands.

Stranding is probably a direct derivative of broadcasting. The eggs become encased in gelatin in the ovaries and when emitted remain part of a cohesive mass rather than becoming independently scattered. The derivation of stranding from percid spawning behaviors other than broadcasting is less likely, because each is specialized in a way that seems to preclude the evolution of stranding.

For a female to put all of her eggs in one highly visible basket, which stranding certainly does, and then abandon them would seem to be a strategy quickly selected against unless the eggs somehow are protected intrin-

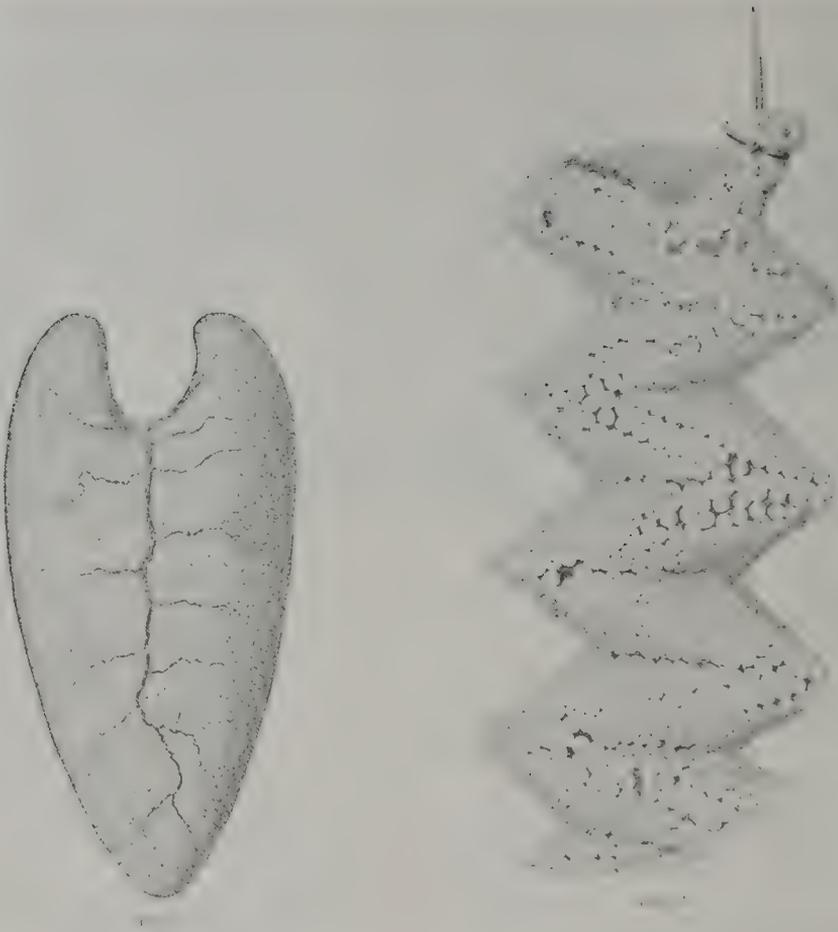


Fig. 3. — Eggs of *Perca flavescens* encased in ovaries (left) and in gelatinous strands after being spawned (right). From Worth (1892).

sically against predation and disease. Having toxic, or at least distasteful, eggs would be an obvious strategy, but observations by Seeley (1886:27) of predation by "birds and various fishes" on perch eggs put this method in doubt. Treasurer (1983) reported low mortality of perch eggs and attributed it to the improved ventilation and midwater position (thereby avoiding siltation) of the strand.

Burying

Egg-burying behavior is similar to broadcasting except for the important distinction that the release of eggs occurs just below, rather than above, the

surface of the substrate. In egg burying the female works her body partially below the surface of the substrate and, with her genital papilla buried and a male mounted on her back, expels eggs (Fig. 5). The substrates usually used are loose gravel, sand, or mixed gravel and sand. Egg burying is characteristic of many darters, including all species of *Percina* for which spawning observations have been published and many species of *Etheostoma*. Some egg buriers are thought to be territorial (Winn 1958), but other than the indirect protection associated with territoriality, eggs receive no parental care. Among darters, burying represents the primi-

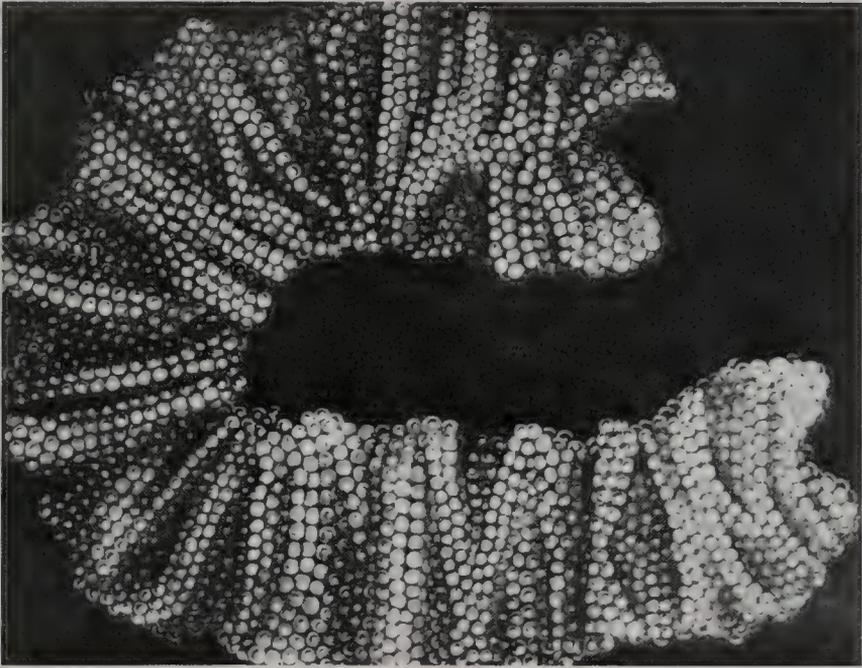


Fig. 4. — Egg strand of *Perca flavescens*. From Pearse & Achtenberg (1921).

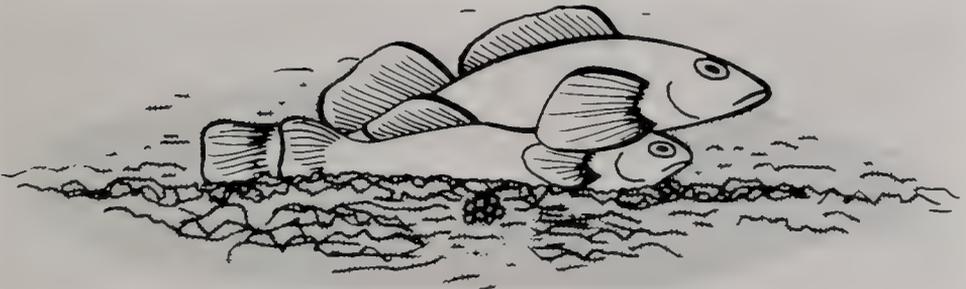


Fig. 5. — Egg-burying behavior. With a male mounted on her back, a partially buried female deposits eggs below the surface of the substrate. Eggs are fertilized as they are laid and then are abandoned by both parents.



Fig. 6. — Egg-attaching behavior. (A) The female selects the site of egg deposition. (B) The male mounts the female and releases sperm as eggs are attached to plants. The eggs subsequently are abandoned.

tive form of reproductive behavior; among percids, it represents an egg-hiding modification of broadcasting behavior.

Buriers

- Percina (Alvordius) maculata* (Petravicz 1938)
P. (A.) peltata (New 1966)
P. (A.) notogramma (Loos & Woolcott 1969)
P. (Ericosma) evides (Page et al. 1982)
P. (Hypohomus) aurantiaca (Howell 1971)
P. (Cottogaster) copelandi (Winn 1953)
P. (Percina) caprodes (Winn 1958)
Etheostoma (Litocara) nianguae (Pflieger 1978)
E. (Psychromaster) tuscumbia (Koch 1978)
E. (Etheostoma) tetrazonum (Pflieger 1978)
E. (E.) variatum (May 1969)
E. (Doration) stigmaeum (Winn 1958)
E. (Nothonotus) juliae (James 1983)
E. (N.) rufilineatum (Stiles 1972)
E. (N.) camurum (Mount 1959)
E. (N.) bellum (W. D. Voiers personal communication)
E. (N.) tippecanoe (Trautman 1981)
E. (Fuscatelum) parvipinne (B. M. Burr personal communication)
E. (Ozarka) cragini (Distler 1972)
E. (Oligocephalus) spectabile (Winn 1958)
E. (O.) caeruleum (Winn 1958)
E. (O.) radiosum (Scalet 1973)
E. (O.) swaini (Ruple et al. 1984)

Attaching

Attaching behavior is a derived behavior known among percids only in the genus *Etheostoma*. The female selects the site of egg deposition (presumably in some species within a male's territory), typically a plant or large rock, and with the male following her, elevates to the site. As she does so, the male follows and mounts, the two vibrate, and eggs and sperm are released (Fig. 6). Usually one to three adhesive eggs are released during each spawning act and are pushed by the female onto a plant, rock, or other object. At-

taching eggs to plants seems to involve behavior identical to that of attaching eggs to rocks; the substrate used is that which is readily available in the habitat. Eggs are abandoned and receive no direct parental care, although as in some burying species, territorial behavior may provide some protection.

Attachers

- Etheostoma (Etheostoma) blennioides* (Fahy 1954)
E. (Nanostoma) zonale (Winn 1958)
E. (N.) coosae (O'Neil 1981)
E. (N.) baileyi (Page personal observation)
E. (N.) simoterum (Page & Mayden 1981)
E. (N.) duryi (Page et al. 1982)
E. (N.) barrenense (Winn 1958)
E. (N.) rafinesquei (Winn 1958)
E. (N.) sp. (Red Snubnose) (B. M. Burr personal communication)
E. (N.) sp. (Lowland Snubnose) (B. M. Burr personal communication)
E. (Ioa) vitreum (Winn & Picciolo 1960)
E. (Vaillantia) chlorosomum (Page et al. 1982)
E. (Belophlox) okaloosae (Collette & Yerger 1962)
E. (Villora) edwini (Williams 1976)
E. (Ozarka) boschungii (Boschung 1979)
E. (O.) trisella (W. C. Starnes personal communication)
E. (Oligocephalus) lepidum (Strawn 1956)
E. (O.) asprigene (Page et al. 1982)
E. (O.) grahami (Strawn 1956)
E. (O.) ditrema (Seesock et al. 1978)
E. (Boleichthys) exile (Winn 1958)
E. (B.) fusiforme (Fletcher 1957)
E. (B.) gracile (Braasch & Smith 1967)
E. (B.) proeliare (Burr & Page 1978)
E. (B.) fonticola (Schenck & Whiteside 1977)
E. (B.) microperca (Burr & Page 1979)

The presence of both egg-burying and egg-attaching species within three subgenera of *Etheostoma* (*Etheostoma*, *Ozarka*, and *Oligocephalus*) suggests that egg attaching is derived directly from egg burying and has arisen independently in several unrelated groups

of darters. In fact, at least two species which usually attach their eggs have been observed to bury eggs under certain conditions (Petravicz 1936; Page & Mayden 1981). Egg attaching apparently also has arisen independently among species within subgenera; its distribution among species of *Ozarka* is inconsistent with the distribution of morphological synapomorphies (Fig. 7).

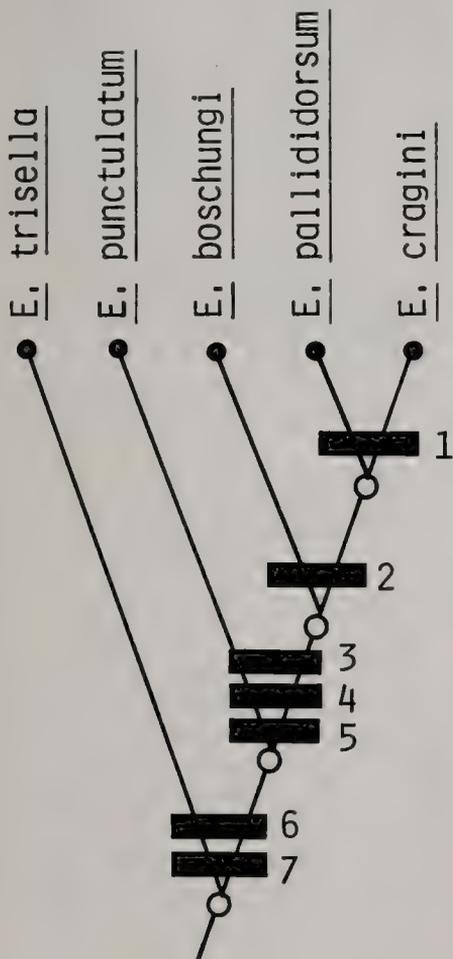


Fig. 7. — Hypothesized phylogenetic relationships among species of *Ozarka*. Synapomorphies (black rectangles) are (1) 25 or fewer pored lateral-line scales, (2) seven infraorbital pores, (3) interrupted supratemporal canal, (4) incomplete lateral line, (5) bright orange margin on the first dorsal fin, (6) bright orange venter on the breeding male, (7) heavily mottled body. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma* (*Oligocephalus*) *whipplei* and *E. (Belophlox)* *fricksium*.

E. cragini Gilbert buries its eggs, but *E. boschungi* Wall and Williams and *E. trisella* Bailey and Richards attach their eggs to plants (Boschung 1979; W. C. Starnes personal communication). If the phylogeny based on morphology (Fig. 7) is accurate, *E. boschungi* and *E. trisella* must have evolved egg-attaching behavior independently of one another. The fact that *E. trisella* attaches its eggs to vegetation in headwaters (even seepages) (W. C. Starnes, personal communication) was a major factor in placing it in the subgenus *Ozarka* with *E. boschungi*, which has essentially the same spawning requirements and behavior (Boschung 1979; Williams & Robison 1980). Independent derivation of this behavior in the two species weakens the argument for their close relationship to one another.

The breeding behaviors of too few species of the subgenus *Etheostoma* are known to compare their distributions with a phylogeny based on morphology. However, it is interesting that the two known buriers [*E. variatum* Kirtland and *E. tetrazonum* (Hubbs and Black)] are in the *E. variatum* species group [including also *E. euzonum* (Hubbs and Black), *E. osburni* (Hubbs and Trautman), and *E. kanawhae* (Raney)], and the only known attacher, *E. blennioides* Rafinesque, is a member of the second major lineage [including *E. rupestre* Gilbert and Swain, *E. inscriptum* (Jordan and Brayton), *E. thalassinum* (Jordan and Brayton), *E. swannanoa* Jordan and Evermann, *E. blennius* Gilbert and Swain, and *E. histrio* Jordan and Gilbert], all of which eventually may be shown to be egg attachers. *E. sellare* (Radcliffe and Welsh), the sole member of the third major lineage in the subgenus, is a highly distinctive (Knapp 1976; Page 1981) species on the verge of extinction. It has a flattened genital papilla (Knapp 1976) similar to those of egg-clumping and egg-clustering species (Page & Swofford 1984). If *E. sellare* is found to belong to one of these latter behavioral groups, it could be of major significance in efforts to protect

the species from extinction. Suitable spawning sites may be a limiting factor for the only extant population of *E. sellare*.

Clumping

Egg clumping was first reported in 1939 for *E. maculatum* Kirtland (Raney & Lachner 1939) but was unreported for other darters until observed in 1981 in *E. aquali* Williams and Etnier and *E. microlepidum* Raney and Zorach (Page et al. 1982). In preparation for spawning, the male selects a cavity under a large rock as a territory and future nesting site. Ultimately, a female swims into the cavity being guarded by the male, wedges herself into the interface between the stone and the gravel substrate beneath the stone, and deposits eggs. As she does so, they are fertilized by the male. After spawning, the female leaves, and the male remains to guard the clump of eggs (Fig. 8). The adhesive eggs adhere to both the nest stone and the underlying substrate material; if a stone is lifted from the water, a clump of adhesive eggs remains attached to it (Fig. 9).

Egg clumping is known only among species of the subgenus *Nothonotus* of *Etheostoma*.

Clumpers

Etheostoma (Nothonotus) maculatum
(Raney & Lachner 1939)

E. (N.) aquali (Page et al. 1982)

E. (N.) microlepidum (Page et al. 1982)

Egg clumping is almost certainly a direct derivative of the egg-burying behavior (Page et al. 1982) characteristic of other species of *Nothonotus* [known in *E. juliae* Meek, *E. rufilineatum* (Cope), *E. camurum* (Cope), and *E. tippecanoe* Jordan and Evermann]. The transition from burying in some species of *Nothonotus* to clumping in others requires only that the male establish a territory beneath a stone and that a female deposit her eggs in the interface area between the stone and the underlying substrate.

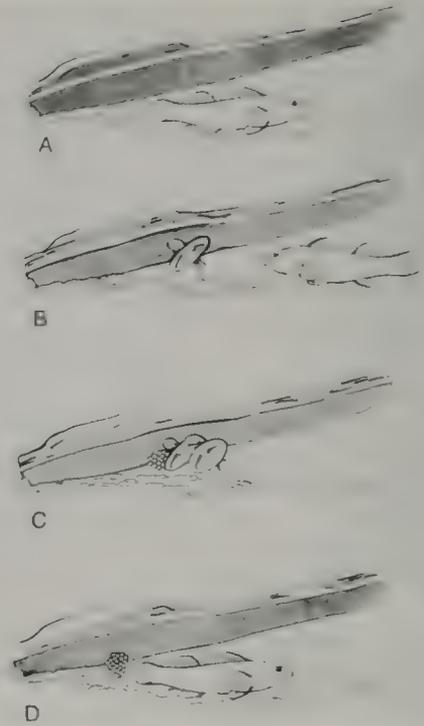


Fig. 8. — Egg-clumping behavior. (A) The male establishes a territory centered under a large stone. (B) The female enters the territory and wedges herself between the stone and the underlying substrate. (C) The male positions himself next to the female and fertilizes eggs as they are released by the female. (D) The male remains to guard the clump of eggs.

With 14 described and 1 undescribed species, the subgenus *Nothonotus* is one of the two largest subgenera of darters, and intrasubgeneric relationships are unclear. The egg-clumping species are members of the *E. maculatum* lineage within the subgenus (Fig. 10), but it is unknown at present at what point on the lineage egg clumping arose. *E. rufilineatum* has been observed to bury its eggs (Stiles 1972), and although spawning was not observed, Bryant (1979) felt confident that *E. acuticeps* Bailey also buries its eggs. Spawning behavior data on *E. rubrum* Raney and Suttkus and *E. moorei* Raney and Suttkus should pinpoint the origin of egg clumping in *Nothonotus*.

Although *Etheostoma sanguiflum* (Cope) has been considered a subspecies of *E. maculatum* Kirtland by some



Fig. 9. — A male *Etheostoma microlepidum* and his clump of eggs on the underside of a stone removed from East Fork Stones River, Rutherford County, Tennessee, on 6 May 1981. The male was guarding the eggs prior to their removal from the stream.

authors (Zorach & Raney 1967; Williams & Etnier 1978), the distinctive pigmentation of the first dorsal fin (especially the bright red spots at the front and rear of the fin) of the male of *E. sanguifluum* is shared with *E. aquali* Williams and Etnier but is absent in all other species of the subgenus *Nothonotus*. Recognition of a closer relationship between *E. sanguifluum* and *E. aquali*, than of either taxon to *E. maculatum* (Fig. 10), requires the elevation of *E. sanguifluum* to specific status. The form heretofore known as *E. maculatum vulneratum* (Cope) also possesses the distinctive dorsal fin pigmentation and should be named *E. sanguifluum vulneratum* (Cope).

Clustering

The first report of egg-clustering behavior in darters was by Seal in 1892 in a report on *E. olmstedii* Storer. Since then it has been documented in an

additional 15 species in the subgenera *Boleosoma* and *Catonotus* of *Etheostoma* listed below.

The male of an egg-clustering species establishes a territory centered about the cavity under a large (usually flat) stone. The cavity and the underside of the stone are cleared of silt and debris by fin-wagging activities of the male. A ripe female enters the cavity and, following courting by the male, rolls to one side and, once inverted, rises and lays eggs on the underside of the stone. The male inverts and fertilizes the eggs, which are arranged by the female in a single-layer cluster (i.e., eggs are rarely laid on top of one another) on the stone. The female leaves; other females sequentially may add eggs to the nest. The male remains and guards the eggs to hatching (Fig. 11). In species of *Boleosoma*, a log may be substituted for a stone.

Egg clustering is similar to egg clumping in that eggs are amassed under a stone and guarded by the male.

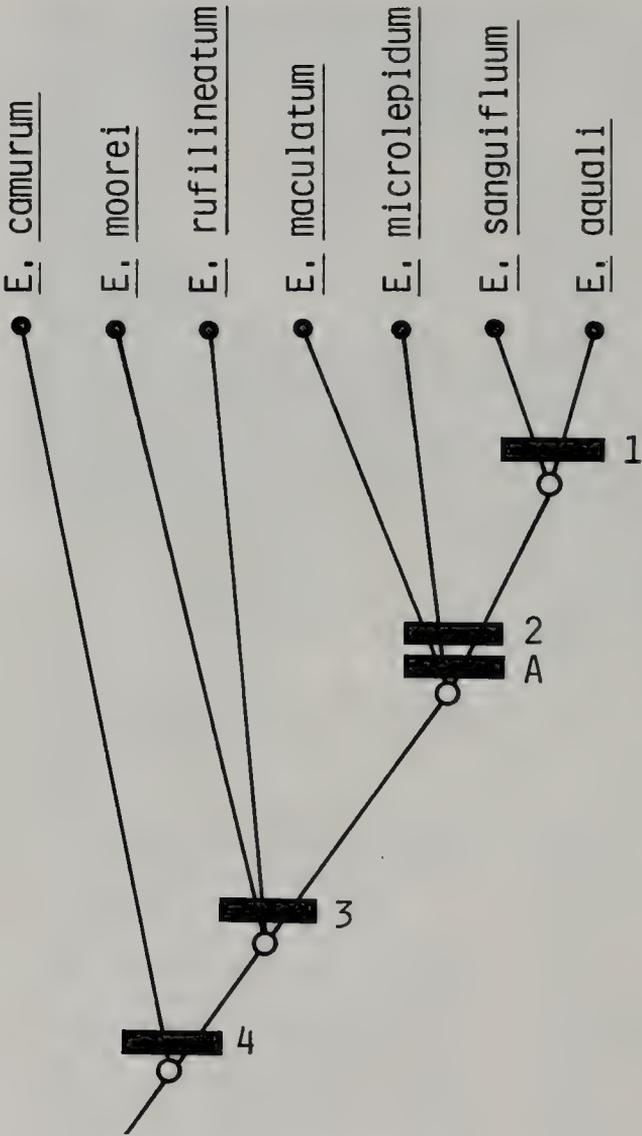


Fig. 10. — Hypothesized phylogenetic relationships among some of the species of *Nothotus*. Synapomorphies (black rectangles) are (1) dorsal fin with two red spots at the front, one red spot at the rear, (2) haloed red spots on the side of the male, (A) egg-clumping behavior, (3) black spots on fins of the female, and (4) red spots on the side of the body. Synapomorphous Character states were identified by outgroup comparisons to *Etheostoma* (*Nothotus*) *tippecanoe*, *E. (N.) juliae*, and *E. (N.) acuticeps*.

It is dissimilar, and appears to be "perfected," in that every egg is exposed and can be tended to individually by the guarding male (Fig. 12).

The derivation of egg clustering from darters which attach their eggs to stones requires only that (1) eggs are laid on the underside rather than the tops and sides of rocks, (2) eggs are clustered in close proximity to one another rather than distributed over a broad area, and (3) the male remains and guards the eggs. Laying eggs on the underside rather than on more ex-

posed areas of rocks probably exposes them to fewer predators although some potential predators, e.g., crayfishes and caddisflies (Brigham et al. 1982:9.6), are common under rocks. Once the eggs under the stone are guarded by the male, the survival rate undoubtedly increases dramatically, and such a concentration of eggs is quickly selected for.

Variation in behavior divides egg-clustering species into three groups: (A) those in which both male and female invert only long enough to lay

Clusterers

Group A. Female and male briefly invert
E. (Catonotus) squamiceps (Page 1974)
E. (C.) olivaceum (Page 1980)
E. (C.) neopterum (Page & Mayden
 1979)^a

Group B. Female only has prolonged
 inversion

E. (C.) flabellare (Winn 1958)
E. (C.) sp. = Duskytail darter (Etnier
 personal communication)^a
E. (C.) kennicotti (Page 1975a)
E. (C.) obeyense (Page et al. 1981)^a
E. (C.) virgatum (Kornman 1980)^a
E. (C.) smithi (Page & Burr 1976)
E. (C.) striatulum (Page 1980)^a
E. (C.) barbouri (Page et al. 1982)^a

Group C. Female and male have pro-
 longed inversions

E. (Boleosoma) olmstedti (Atz 1940)
E. (B.) nigrum (Winn 1958)^a
E. (B.) podostemone (Jenkins 1980)^a
E. (B.) perlongum (Lindquist et al.
 1981)
E. (B.) longimanum (Page et al
 1981)^a

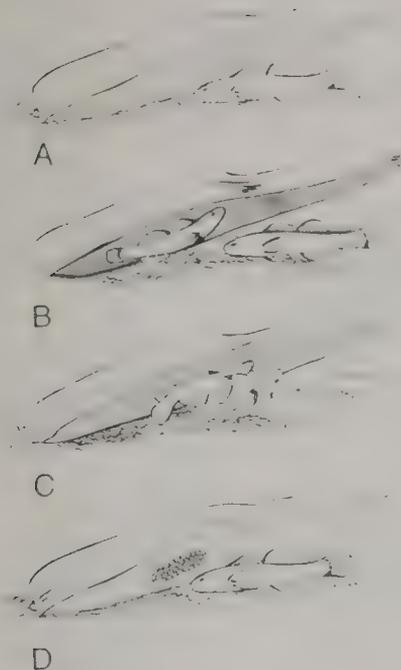


Fig. 11. — Egg-clustering behavior. (A) The male establishes a territory centered under a large stone. (B) The female enters the territory and selects a site for egg deposition on the underside of the stone. (C) The female inverts, rises, and deposits eggs on the stone; as she does so, the male follows and fertilizes the eggs. (D) The male remains to guard the cluster of eggs.

and fertilize each release of eggs (usually 1-5 eggs); (B) those in which the female, once inverted, remains inverted for a prolonged period of egg laying (several minutes to a few hours) but the male only briefly (a few seconds) and periodically inverts; and (C) those in which both male and female remain inverted for an extended period. Obviously, group B represents an advancement over group A, and group C represents an advancement over group B. Group A includes the primitive species of the subgenus *Catonotus*; B, the advanced species of *Catonotus* (Page 1975b); and group C, species of the subgenus *Boleosoma*. Winn (1958) distinguished between behavior types B and C.

^a Although known to be a clusterer, group assignment is predicted from the behavior of closest relatives and is not based on actual observations.

The phylogenetic sequence of breeding behaviors among *Catonotus* is concordant with a phylogeny of the subgenus based on morphology in that three synapomorphies unite the *E. flabellare* Rafinesque lineage as advanced and apart from the *E. squamiceps* Jordan species group (Fig. 13).

Both *Catonotus* and *Boleosoma* must have evolved from egg-attaching precursors. Although egg clustering itself could be considered a synapomorphy uniting these two subgenera, they differ markedly in their morphology and do not appear to be sister groups (Page 1981). *Boleosoma* shares derived characteristics with other groups of *Etheostoma* (Fig. 14) and almost certainly had an origin independent from that of *Catonotus*. It appears to be most closely related to *E. (Ioa) vitreum* (Cope), an

egg-attaching species. The sister-group of *Catonotus* should first be sought among egg-attaching species; however, if the attaching precursor now is extinct, an egg-burying group may be the closest extant relative.

EVOLUTION OF PERCID SPAWNING BEHAVIORS

Combining the evolutionary sequences discussed above produces the phyl-



Fig. 12. - Male *Ettheostoma neopterum* and his cluster of eggs on the underside of a stone removed from Birdsong Creek, Benton County, Tennessee, on 15 April 1978. The male was guarding the eggs prior to their removal from the stream.

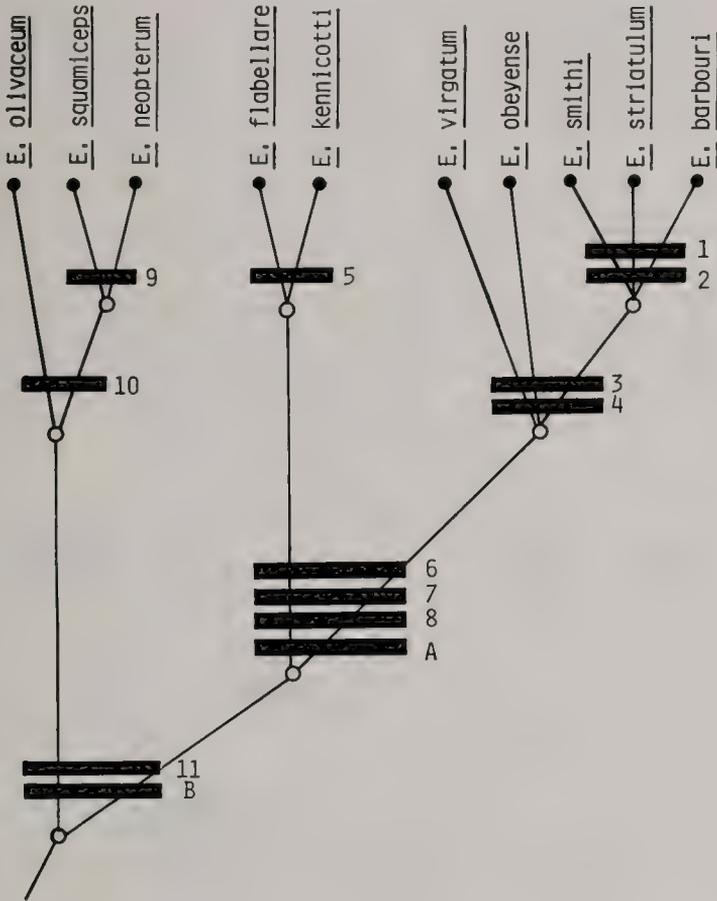


Fig. 13. – Hypothesized phylogenetic relationships among species of *Catonotus*. Synapomorphies (black rectangles) are (1) four infraorbital pores, (2) maximum standard length less than 50 mm, (3) bar pattern on the cheek, (4) blue-edged red fins on the breeding male, (5) large gold knobs on the first dorsal fin, (6) nape unscaled, (7) prepectoral area unscaled, (8) infraorbital canal widely interrupted, (A) type B clustering behavior (the female remains inverted during spawning), (9) infraorbital canal narrowly interrupted, (10) caudal peduncle with three black spots, (11) broad, flat nonbifurcate genital papilla on the female, (B) egg-clustering behavior. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma (Psychromaster) tuscumbia* and *E. (Fuscatelum) parvipinne*.

ogy depicted in Fig. 15. There appear to be no reasonable alternatives to any of the transitions depicted. However, each type of behavior could have arisen, and in some instances almost certainly did arise, more than once. For example, although gamma clustering results from a modification of beta clustering, it does not mean that the only extant gamma-clustering group of darters (*Boleosoma*) arose from the only extant beta-clustering group (i.e., the *flabellare*

group of *Catonotus*); rather, all alpha and beta precursors of *Boleosoma* are extinct.

The phylogeny (Fig. 15) supports the contention that darters, the most primitive of which are buriers, are derivatives, and probably the sister group, of *Stizostedion*. This position disagrees with the conclusions of Collette (1963) based on osteology, but it agrees with those of Hubbs (1971) based on the survival of intergroup percid

hybrids. A phylogenetic classification necessitates the recognition of the subfamilies Etheostomatinae (containing the tribes Luciopercini, Etheostomatini, and Romanichthyini) and Percinae (Table 1).

Each step in the evolution of spawning behaviors represents, for the species in which it evolved, a survival advantage over its precursor. Pit broadcasting concentrates the eggs in an area subsequently guarded by the male

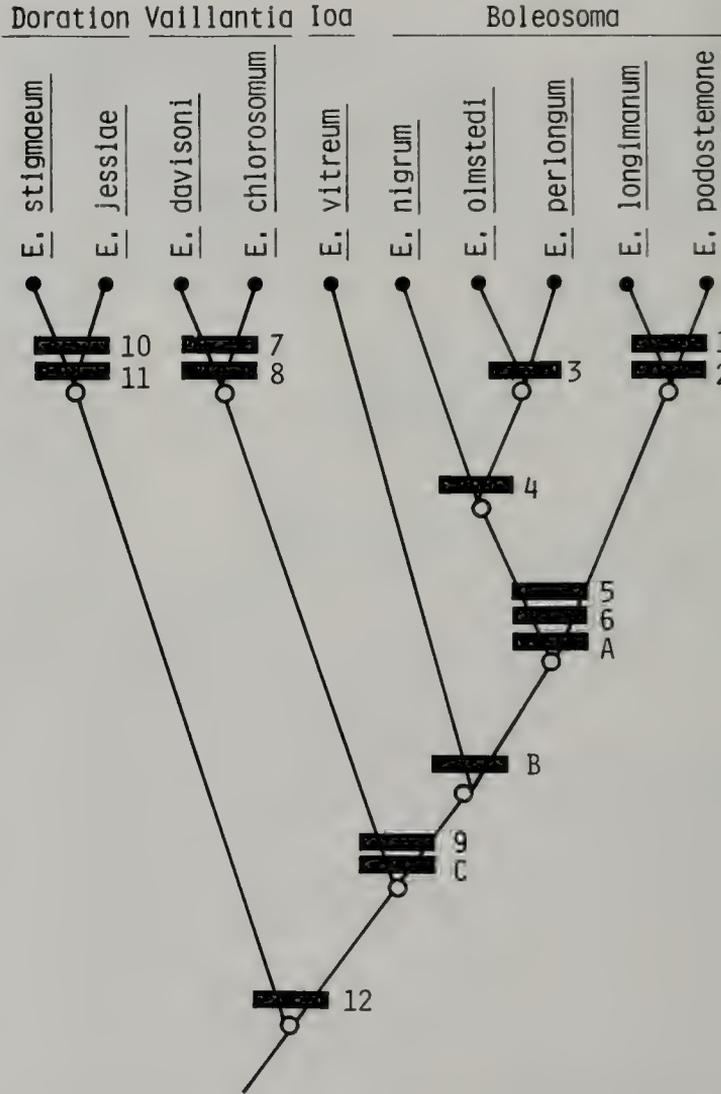
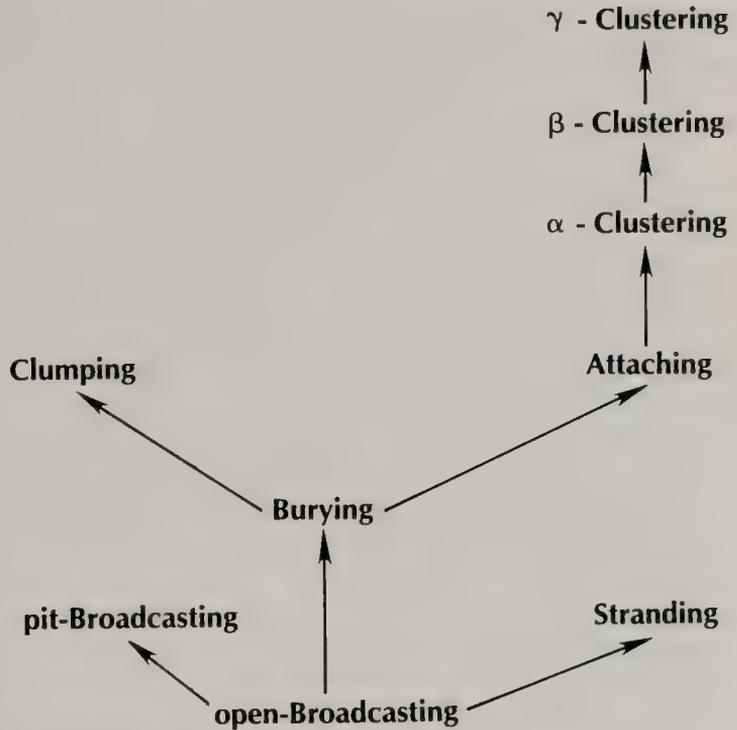


Fig. 14. - Hypothesized phylogenetic relationships among species of the subgenera *Boleosoma*, *Ioa*, *Vaillantia*, and *Doration*. Synapomorphies (black rectangles) are (1) broad branchiostegal membrane connection, (2) red-orange spots on the breeding male, (3) elongated second dorsal fin on the breeding male, (4) overall dusky breeding male, (5) bifurcate genital papilla on the female, (6) white knobs on paired fins, (A) egg-clustering behavior, (B) eggs attached to rocks, (7) black bridle around the snout, (8) extremely short second dorsal fin, (9) spatulate genital papilla on the female, (C) egg-attaching behavior, (10) blue bars on the adult male, (11) blue and red bands in the first dorsal fin of the adult male, (12) brown-black x/w marks on the body. Synapomorphous character states were identified by outgroup comparisons to *Etheostoma* (*Psychromaster*) *tuscumbia* and *E. (Litocara) nianguae*.

Fig. 15. — Hypothesized evolutionary relationships among percid breeding behaviors.



and thus increases the probability of their survival by reducing predation. Also, *S. lucioperca* males fan the eggs, presumably to prevent them from being covered by silt, and thereby reduce mortality due to anoxia.

Burying eggs reduces exposure to predators and probably to parasites, enhancing survivability. However, eggs can be buried only in flowing water habitats, usually in gravel but sometimes in sand, where burying does not subject the eggs to especially low oxygen levels such as would occur if eggs were buried in slow-flowing or standing water. Buriers are constrained behaviorally to flowing water and coarse substrates. Consequently, stream modifications, such as impoundments and channelization, prevent successful spawning by these species.

In the primitive state, species of *Nothonotus* bury their eggs in the sand-gravel mixture on the downstream side of a large stone in fast water. Clumping, as discussed above, evolved in a species of *Nothonotus* which buried its

eggs under a partially elevated stone, thereby enhancing crypticity. The advantage of male egg guarding followed.

The derivation of attaching from burying (or from any other behavior) is difficult to envision. However, the presence of both behaviors within several (at least three) subgenera of *Etheostoma* leaves no doubt that one is derived directly from the other. The strong positive correlation between primitive morphology and burying (e.g., all species of *Percina* are buriers) and between advanced morphology and attaching (e.g., in the subgenus *Boleichthys*) clearly indicates that the direction is from burying to attaching. For darters living in slow-flowing or standing water (e.g., *Boleichthys* species), the advantage of attaching is obvious; with demersal and adhesive eggs, the only alternatives to attaching are burying eggs in an oxygen-poor substrate (often rotting vegetation and mud) or migrating to suitable habitats for burying. Similarly, species living in bedrock pools [e.g., *E. simoterum* (Cope)] where

little suitable egg-burying substrate exists, were probably better fit after they changed to egg attaching (Page & Mayden 1981). That so many species have converted from burying to attaching (at least 9 of the 13 subgenera of *Etheostoma* for which the spawning behavior of at least one species is known, are known to contain egg-attaching species) seems to reflect the fact that few alternatives exist. Clumping is an alternative, but it was available evolutionarily only to species which bury their eggs near (and eventually under) large stones. Among darters, clumping evolved only in *Nothonotus*; other fishes with behavior similar to egg clumping in darters are species of *Cottus* (Smith 1923) and *Noturus* (Mayden & Burr 1981). The evolution of egg attachment permitted groups of darters to invade new habitats (e.g., bedrock pools, sand and mud bottomed pools, swamps) that otherwise could have been invaded only with periodic (presumably annual) emigrations into other habitats suitable for egg burying. This emigration would be difficult for advanced darters, which lack gas bladders. A few darters have followed the latter strategy [e.g., *Percina cymatotaenia* (Gilbert and Meek), a primitive darter which has a gas bladder and lives in vegetated backwaters, moves into riffles to spawn (Pflieger 1975: 299)]; however, the groups which live and spawn in the same habitat have been most successful in diversifying (e.g., *Boleichthys*, *Nanostoma*).

Clustering darters are sophisticated attachers which concentrate their eggs in a hidden space and then guard them through hatching. The single-layer arrangement of eggs permits the guarding male to tend each egg. Although the close proximity of the eggs promotes the spread of infection, and of predation if a predator succeeds in gaining access to the nest, the advantages of clustering apparently outweigh the disadvantages. Furthermore, males of both egg-clustering darters and egg-clustering minnows

(*Pimephales*) develop swollen flesh on the head and nape during the breeding season. The swollen flesh is thought to have a secretory, presumably fungicidal or bactericidal, function related to protecting the eggs during nest guarding (Cross 1967; Smith & Murphy 1974). Clustering darters and minnows are some of the most widespread and abundant fishes [e.g., *Etheostoma nigrum* Rafinesque, *E. olmstedii*, *E. flabellare*, *Pimephales notatus* (Rafinesque), and *P. promelas* Rafinesque] in North America.

Two earlier discussions on the diversity and evolution of percid reproductive behaviors were those of Winn (1958) and Balon et al. (1977). The latter assigned percids to seven reproductive "guilds" that conceptually encompassed both spawning and ontogenetic characteristics. Species that herein are classified as open substrate broadcasters, stranders, and attachers are variously classified by Balon et al. (1977) as open substrate lithophils (rock spawners), phytophils (plant spawners), and phyto-lithophils. Buriers are termed brood hiding lithophils, and clumpers and clusterers are nest spawning speleophils (cave spawners). McElman (1983) argued subsequently that *S. vitreum* and *S. canadense* should be classified as litho-pelagophils because of the buoyancy, positive phototaxis, swimming ability, and surface suspension properties of their newly hatched young, and that *S. lucioperca* should be termed a phyto-pelagophil because of the swimming ability of its newly hatched young. Page & Swofford (1984) argued that Balon et al. (1977) assigned some darters [i.e., *P. caprodes* (Rafinesque), *E. blennioides*, *E. vitreum*, and possibly *P. shumardi* (Girard) and *Ammocrypta* spp.] to guilds incorrectly.

Winn (1958) dealt exclusively with darters and concentrated primarily on the 14 species for which he presented original data. He recognized the least complex behaviors as primitive and the most complex (especially clustering) as derived, and discussed these evolution-

ary trends: development of territoriality; use of substrates other than gravel for spawning; occupation of smaller streams; maturation of fewer, larger eggs; decrease in promiscuity; development of parental care; an increase in sexual dimorphism (including a relative increase in the size of the male); a decrease in body size; and a decrease in the age of sexual maturity from 2–3 years to 1 year. With data now available on many more species, these trends still seem accurately to characterize darter evolution, except that the only darters thought to be nonterritorial (and the only species in which females are larger than males) are species of advanced (i.e., *Ozarka* and *Boleichthys*), not primitive, subgenera, and sexual dimorphism in color is most extreme among egg buriers (Page 1983; Page and Swofford 1984), behaviorally the most primitive darters.

LIFE HISTORY CORRELATES OF REPRODUCTIVE SPECIALIZATIONS

Some of the morphological correlates of the various reproductive behaviors of darters are discussed by Page & Swofford (1984). Life history characteristics also show trends correlated with reproductive specialization. Some trends are in the direction of r-selected characteristics, and some are in the direction of k-selected characteristics (MacArthur & Wilson 1967; Pianka 1978:122).

One dramatic trend accompanying the evolution of percids is to lay fewer, larger eggs (a k-selected trait). Species of *Stizostedion* lay up to 2,500,000 eggs (Filuk 1962) averaging 0.55–1.10 mm in diameter (Kryzhanovshy et al. 1953). Species of *Percas* lay up to 210,000 eggs averaging 1.0–2.1 mm (Thorpe 1977). Darters lay only up to a few thousand eggs averaging 0.7–2.7 mm (Page 1983:162). The largest eggs among percids are those of the highly evolved egg-clustering species in which parental

care of the eggs warrants a large expenditure in the production of each egg.

Incubation periods seem to have changed little. *Stizostedion* and darters take about 25–30 days to hatch at 10°C and 8–10 days at 20°C (Marshall 1977; Page 1983:168).

In a more r-selected mode, advanced percids (darters) reproduce early (most at 1 year, a few at 2 years), whereas species of *Stizostedion* do not reach maturity until 2–6 years in the male and 3–6 years in the female (Marshall 1977). Longevity (r-selected) ranges from 20 years in *S. vitreum* (Scott & Crossman 1973:772) to only 1.5 years in several species of *Etheostoma* (Page 1983:169). Some of the most advanced species of darters have become semelparous; they mature at 1 year, reproduce, and die before a second spawning season (Page 1983:169). Semelparous species include egg attachers [*E. microperca* Jordan and Gilbert and *E. proeliare* (Hay)] and egg clusterers (*E. striatulum* Page and Braasch).

Some darters exist in large dense populations – to 33 individuals per square meter (Page 1983:170–171); the larger piscivorous percids exist in much smaller populations.

Decreasing body size (r-selected) has been a pervasive element of percid evolution and was discussed at length for darters by Page & Swofford (1984). In brief, darters feed on small benthic organisms and have become more efficient consumers by becoming smaller. Constraints on decreasing body size include living in gravel runs (correlated with egg burying); the smallest darters are pool inhabitants, including many egg-attaching and egg-clustering species. *S. vitreum* reaches a maximum length of about 107 cm and a maximum weight near 11.5 kg (Colby et al. 1979). Those values are 30 times the maximum length and 19,000 times the maximum weight of *E. fonticola* (Jordan and Gilbert), the smallest species of darter at a maximum length of 3.5 cm and weight of 0.6 g (Page & Burr 1979).

SUMMARY

About one-fifth of all North America freshwater fishes are percids (the walleye, sauger, yellow perch, and 148 species of darters). In addition to being diverse, percids often occur in large populations and are important in determining the ecological characteristics of North American streams and lakes. Elsewhere percids occur only in temperate Eurasia (14 species). Knowing the reproductive requirements of these fishes is fundamental to understanding their positions in aquatic environments, protecting them, managing them, and predicting the impacts of proposed environmental alterations, such as impoundments and dredging.

Accompanying the evolution of a large diversity of percids has been the evolution of a variety of reproductive strategies. Among the 71 species of percids for which spawning behaviors are known, six types of behavior are recognized: broadcasting (including pit broadcasting), stranding, burying, attaching, clumping, and clustering (including alpha beta, and gamma clustering).

Broadcasting is the discharging of large numbers of eggs and sperm, usually over rocks or plants. It is the most primitive type of reproductive behavior among fishes and is characteristic of especially primitive percids (*Stizostedion vitreum*, *S. canadense*, and probably *S. marinum* and *Percarina demidoffi*). In pit broadcasting, found in *S. lucioperca*, eggs are broadcast over a pit constructed and guarded by the male.

Stranding is the unique habit of encasing eggs in long gelatinous strands. Stranding appears to be a derivative of broadcasting and is known in *Perca* and *Gymnocephalus*.

Burying is a derivative of, and is similar to, broadcasting, except that eggs are released just below rather than above the surface of the substrate. Among percids burying is restricted to darters. Among darters it is the primitive reproductive behavior and is known

in 12 subgenera of *Percina* and *Etheostoma*.

Attaching behavior involves depositing eggs individually on plants or rocks over a wide area. It is derived from burying and, among percids, is known only in the genus *Etheostoma*. Attaching is found in at least nine subgenera and obviously has evolved independently several times.

Clumping is amassing eggs under a large stone, which subsequently is guarded by the male. It also is derived from burying but has evolved only within the subgenus *Nothonotus*. At present it is known in *E. maculatum*, *E. aquali*, and *E. microlepidum*.

Clustering is found in two unrelated subgenera, *Boleosoma* and *Catonotus*, of *Etheostoma*. It is a highly evolved derivation of attaching behavior in which eggs are concentrated in a single-layer cluster on the underside of a stone and are guarded by the male. Clustering evolved independently in *Boleosoma* and *Catonotus*.

Estimating the evolutionary history (phylogeny) of reproductive behaviors results in a better understanding of the relationships among percids. The phylogeny of breeding behaviors supports the contention that darters, the most primitive of which are buriers, are derivatives of, and among the species discussed here, probably the sister group of *Stizostedion*. A phylogenetic classification necessitates recognition of the subfamilies Etheostomatinae (containing the tribes Luciopercini, Etheostomatini, and Romanichthyini) and Percinae. The unique pigmentation of the first dorsal fin (bright red spots at the front and rear of the fin) of males of *Etheostoma sanguifluum* (Cope) and *E. aquali* Williams and Etnier is a synapomorphy indicating that the two are sister taxa. Thus, *E. sanguifluum* cannot remain a subspecies of *E. maculatum* Kirtland and is recognized here as a species. The subspecies known as *E. maculatum vulneratum* (Cope) becomes *E. sanguifluum vulneratum* (Cope).

Life-history correlates of reproductive specialization among percids include the production of fewer, larger

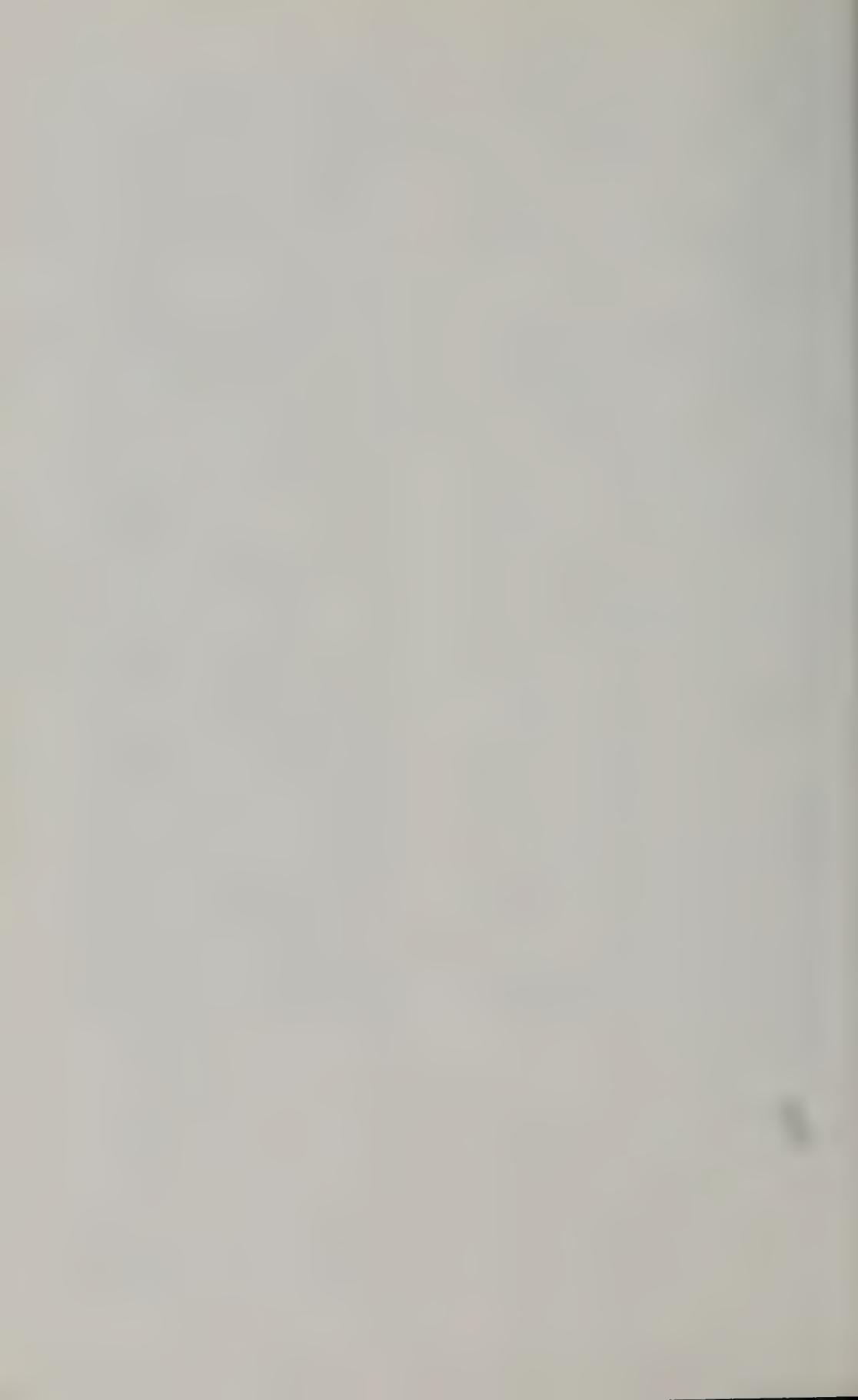
eggs; earlier reproduction; semelparity; reduced longevity; denser populations; and reduced body size.

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Wind Drift and Migration of Thrushes: a Telemetry Study

William W. Cochran and Charles G. Kjos

ABSTRACT

Nocturnal migratory flights of four species of thrushes (*Catharus* spp.) that migrate through Illinois were investigated by radiotelemetry. Winds aloft were measured by theodolite and weather balloon during the birds' migratory flights. Analyses of the migratory flights of individual birds as they encountered different wind conditions indicated that individuals maintained a constant heading and airspeed regardless of the speed and direction of the wind, cloud cover, or landmarks. Lateral wind drift was mitigated and ground speed was maintained above about 6 m/s by the selection of flight altitudes where winds were more favorable. When winds were extremely unfavorable, birds landed. Path deviations caused by variable winds mask the remarkable ability of thrushes to maintain particular headings. Thus, unless winds are scrupulously accounted for, radiotelemetry, radar, and other observations of natural migration are of limited value in the study of orientation.

The spectacular nocturnal migrations of songbirds between breeding and wintering areas separated by many thousands of kilometers have inspired several decades of research that seem to have produced more questions than answers. A persistent question concerns how migrants respond to winds, particularly winds capable of blowing them off course, and another question concerns the effects of overcast skies. This paper is about how migrating thrushes (*Catharus* spp.) respond to wind and overcast skies.

Thorpe (1949) described a migratory journey as consisting of a start, a body, and a termination with each part representing different orientation problems for the migrant. The spring and fall destinations of thrushes passing through the area of this study were

many hundreds to 1 or 2 thousand kilometers distant, and we consider the 200- to 700-km flights reported here representative of the "body" of thrush migrations. These flights were nocturnal, typically about 300 km in length, and usually separated by one or more nights without flight.

Allen (1939) pointed out that the motion of a bird over the ground is the sum of the bird's motion relative to the air and the motion of the air relative to the ground (wind). Although researchers have differed greatly about how birds react to winds, they have accepted the physical reality stated by Allen. The question has never been whether or not birds are affected by the wind but rather what, if anything, they do about it?

Data are presented for Swainson's thrushes [*C. ustulatus* (Nuttall)], veeries [*C. fuscescens* (Stephens)], gray-cheeked thrushes [*C. minimus* (Lafresnaye)], and hermit thrushes [*C. guttatus* (Pallas)]. Graber et al. (1971) delineate the wintering and breeding ranges of these species as well as their occurrence and

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progress through Illinois during migration.

METHODS

Radio-tagged thrushes were followed by means of direction-finding equipment carried in an automobile. Approximations of the thrushes' flight paths were obtained by plotting on U.S. Geological Survey maps (scale 1:250,000) the places and times where thrushes crossed roads. We refer to a line between two plotted road crossings as a *track segment*, the azimuth of a track segment as a *track direction*, the distance represented by a track segment divided by the time difference between two plotted road crossings as a *track segment*, and azimuth of a track segment as a *track direction*, the distance represented by a track segment divided by the time difference between its end points as a *track speed*, and the track direction and speed collectively as the *track vector*. Two or more connected track segments are *estimated flight vector*. Where we refer to the actual path of a bird we use *course*, ground speed, and *path vector* as counterparts to track direction, track speed, and track vector, respectively. Where we refer to actual bird performance, the terms *heading*, *airspeed*, and *flight vector* are used without qualifying them as estimated. Some authors have used *track* to describe the direction of a path, but the correct word is *course*. Therefore, to avoid confusion, we have substituted *path approximation* in those cases where *track* could properly have been used as a noun. Directions are given in degrees, clockwise from true north. Altitudes are referenced to the earth's surface. Times are central standard.

When referring to the behavior of individual thrushes, we often use the term *preferred heading* as a short and convenient substitute for the *mean of a tightly clustered set of measured headings*. In addition, *preferred* implies something special about the direction. Although we do not speculate on what is

special, the preferred headings of thrushes always pointed toward some part of the breeding or wintering area of the species (as seasonally appropriate), but not always away from the wintering area from which an individual could have been coming. Others have used the term similarly to describe the means of sets of headings (usually of different individuals) without implying that particular goals (such as nesting sites) were in the mean direction.

The methods used to determine the geographic (road crossing) points, which define track segments, and to measure or estimate bird altitudes are discussed in the Appendix. Four different methods were used to estimate the headings corresponding to track segments. Occasionally two of the methods were used to estimate a heading for a single track segment. For an extensive discussion of these methods, described briefly below, refer to the Appendix.

Of the 71 heading (and airspeed) estimates in Table 1, 40 were obtained by constructing vector triangles in which an estimated flight vector was the vector difference between the track vector and wind vector. Estimated headings obtained with this method are referred to as *calculated heading estimates*. The method required knowledge of the birds' altitudes and the winds at the birds' altitudes. Winds were measured over increments of altitude. Therefore, the altitude of a bird was required. This method also provides an airspeed estimate.

Six heading estimates were made by the departure method. During the first 100 or so seconds of flight, thrushes climbed through winds from tree level to no more than 150 m altitude. Also, during the period after sunset when migratory flights usually began, the measured winds from surface to 150 m were sometimes light. The departure method is actually a special case of the more general vector triangle method but with a small crosswind component. Therefore, measurement of the initial track direction and confir-

mation of light crosswinds are required. The initial track direction with a small allowance for crosswind provided an estimated heading. One way by which the track direction was measured was to determine the place where a bird crossed over a road within about 2 km of the starting point. The potentially higher track direction error associated with the short track segment was offset by a higher accuracy of the plotted points, i.e., the departure point was known to within 10–20 m and the cross-over point could be determined to within 30–40 m due to the low bird altitude and the reduction of map errors through adequate preparation.

Nineteen heading estimates were determined by the head-null method. This method required measurement of the azimuth of the null plane of the transmitter antenna radiation pattern. In the transmitter attachment method used in this study (Cochran 1972) and in a better method (Raim 1978), the transmitter is mounted on a bird's back, centered between the points where the wings attach to its body (Fig. 1). The 30-cm \times 0.013-mm wire antenna exits the transmitter flush with a bird's back and extends backwards over and beyond the tail. When a bird is in flight, the antenna and the bird's heading are both in the same vertical plane and the antenna is approximately horizontal. No horizontally polarized energy (radio waves) is radiated in this plane. In practice, this arrangement caused the signal to fade completely and then return as the tracking vehicle was driven on a road which passed through this plane. The azimuth of the plane (the bird's heading) was bounded by the azimuth of the last bearing taken as the signal faded and the first taken when the signal returned.

The six remaining heading estimates were made using the cross-polarization method, which required the observer to be positioned approximately under a bird. A receiving antenna pointed up at the bird gave the maximum signal when the antenna elements were aligned parallel with the trans-

mitting antenna and zero signal (a null) when at right angles (cross polarized) to the transmitting antenna. Ranges to overhead birds were equal to their altitudes and thus, never greater than a few kilometers. At such short distances signal maxima were strong and the nulls sharp. When a signal was nulled, the azimuth of the receiving antenna elements was at right angles to the transmitter antenna with the latter in the same plane as the bird's heading, as described above for the head-null method.

Both the head-null and cross-polarization methods resulted in measurements with a 180° ambiguity, because a bird may be headed in either of two azimuths which define the same plane. To resolve the ambiguity, we made flight vector estimates by calculation from the track vector and wind vectors at all conceivable bird altitudes.

Transmitter Bias

It is axiomatic that the weight of the transmitter (approximately 6 percent of a thrush's body weight) affected the flight of the birds we followed, but we do not know whether the effect was faster-than-normal airspeeds (at normal angles of attack with higher-than-normal energy use), normal airspeeds (at higher-than-normal angles of attack and energy use), or slower-than-normal airspeeds (at higher-than-normal angles of attack and normal energy use). The fore-aft centering of the transmitter may have determined which of these effects pertained. We tried to attach each transmitter with its center as near as possible to the places where a bird's wings attach to its body, but in practice the looseness of a thrush's skin and the way in which the bird was held during attachment sometimes resulted in an attachment that was slightly forward of the desired spot. Some of the variability in the airspeeds reported in this paper may have been due to variations in transmitter placement.

The mean of the 17-air-speed sample of Cochran et al. (1967) was 13.1 m/s. Calculations for most of those samples

were made from plots on highway maps, which later were found to have a 7-percent scale error. Adjustment for this error brings their mean airspeed down to about 12.2 m/s, but this is still 20 percent higher than the 10.1 m/s mean for

the airspeed estimates we now report. A species-by-species comparison between the two studies shows the mean airspeeds of Cochran et al. (1967) to be higher by 16, 39, and 25 percent for Swainson's, veery, and gray-cheeked

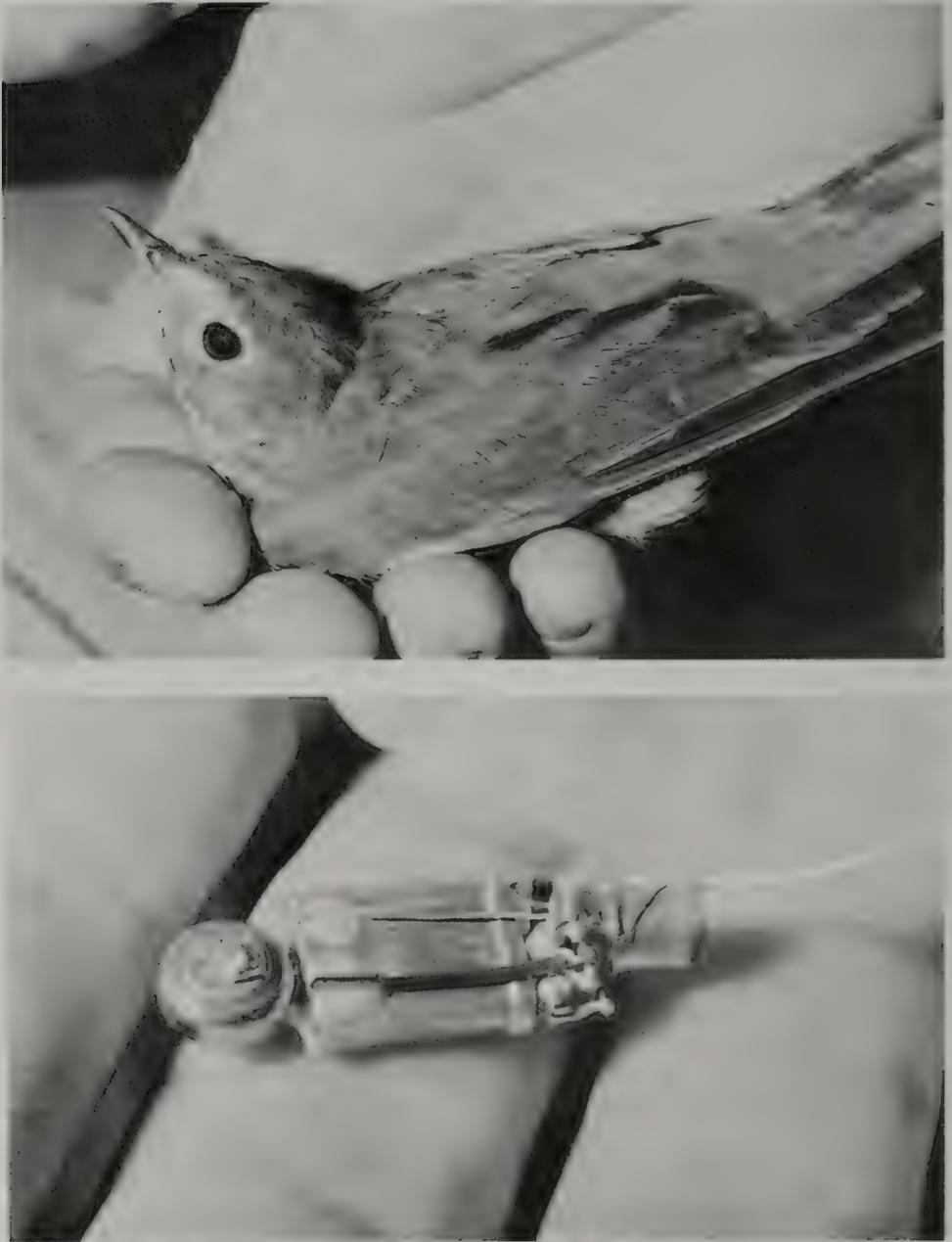


Fig. 1. - (Above) Swainson's thrush carrying a 1.3-g radio transmitter of the type currently in use (Cochran 1980). (Below) a 2.2-g transmitter of the type used in the study reported in this paper.

thrushes, respectively. Therefore, the airspeed difference cannot be attributed to a difference in species mix in the two studies. Most of the birds in this study were fitted with 2.2- to 2.4-g transmitters by C. Kjos, whereas in the study by Cochran et al. (1967), 2.6- to 2.8-g transmitter attachments were about equally divided among R. Graber, W. Cochran, and G. Montgomery. A consistent difference in fore-aft centering of the transmitter is one explanation for the difference between the mean airspeed from the two studies. However, it seems more likely that the heavier transmitters in the earlier study required birds to fly slightly faster to provide additional lift.

Although we believe that thrushes' airspeeds are affected by the attachment of transmitters and that radio-telemetry is not ideal for studying absolute airspeed, the speed analyses in this paper are directed toward finding whether thrushes change their airspeed, altitude, and course direction in response to changes in wind and not toward finding how fast they fly. Analyses of responses to changes in wind are unaffected by the bias discussed above.

It is possible that transmitter attachment left or right of a bird's center of gravity affects the direction of flight. We were more successful in left-right centering of transmitters than we were in fore-aft centering. Furthermore, our analyses are concerned with changes or lack of changes in direction of flight in relation to wind. Therefore, we do not believe that variations in transmitter attachment could have affected our analyses.

The question of the effect of a transmitter, no matter how well centered, on the orientation mechanisms involved in migration is one which we cannot address directly. The migratory flights we observed were within the broad limits of what is generally accepted as normal with regard to progress and orientation toward the breeding or wintering areas. As we will

show, the thrush migrations we observed were, with few exceptions, characterized by headings that were nearly constant regardless of the direction or speed of the wind or the presence or absence of cloud cover. We cannot conceive of how a transmitter could impart to a bird the urge or ability to maintain a particular heading under a variety of wind conditions while depriving it of an urge or ability to behave in some other way.

SUPPLEMENT TO RESULTS OF THE 1965-1966 STUDY (Cochran et al. 1967)

We will first review and discuss the flights of two thrushes reported in Cochran et al. (1967). Although the authors of that paper provided maps showing path approximations, some of which were crooked enough to preclude significant compensation for wind, they did not materially discuss wind drift. The flight numbering they used is retained here, and the path approximations for the two thrushes are shown in their Fig. 7.

For Swainson's #5, Cochran et al. (1967:Table 1) gave only average values for heading estimates and track directions. Detailed data are given here. This Swainson's passed the airport at Springfield, Illinois, when and where winds aloft were being measured by the U.S. Weather Bureau. Several measurements of the bird's altitude and location were made, and from these and the winds-aloft data we calculated estimated headings ($\pm 10^\circ$) and estimated airspeeds (m/s shown in parentheses) of $295^\circ(10.5)$, $298^\circ(12.9)$, and $305^\circ(12.4)$ for track directions and speeds of $220^\circ(9.5)$, $252^\circ(7.8)$, and $286^\circ(7.4)$, respectively. The sky was clear for this entire flight.

The next evening was completely overcast, and the bird was tracked for 83 minutes after it took off. The heading was estimated at $309^\circ (\pm 10^\circ)$ for a track direction of 302° . The spread of

estimated headings for this thrush (295° - 309°) was 14° , less than one-fourth the 82° spread in track directions.

That a single heading, 300° , was within the error range of all estimated headings, that all estimated headings pointed to the breeding range of the species, and that at least one track direction, 220° , pointed well outside the breeding range are consistent with constant-heading behavior. If the differences in estimated headings were not due to measurement errors, it is noteworthy that the greater the deviation of a track direction from a 300° preferred heading, the greater also the deviation of the corresponding estimated heading from 300° . Instead of altering heading to compensate partially for wind drift, this Swainson's may have flown headings which actually increased drift. However, looked at another way, the indicated clockwise heading shifts (295° to 298° to 305°) may have resulted from a slowly altered heading in response to, and to compensate for, the counterclockwise drift in track directions (up to 80°) earlier in the flight.

Cochran et al. (1967:222) mentioned a curvature in the flight path of gray cheek #19. They stated that the change occurred under clear skies but did not elaborate. Detailed data are given here. A 111-minute track segment was in a direction of 314° at a ground speed of 15.8 m/s and was within 35 km of the Peoria, Illinois, airport when winds were being measured there. The altitude of the bird was between 300 and 1,300 m during this segment. Depending on the altitude assumed, estimates varied from 332° to 342° for heading and from 11.3 to 10.1 m/s for airspeed. Later, during the last 53 minutes of the flight, the altitude was between 100 and 300 m with a track direction of 358° and a ground speed of 18 m/s. This portion of the flight was not well situated relative to the schedules and locations of U.S. Weather Bureau windsaloft measuring stations. Fortunately, there were no frontal systems in the

area, and the temporal and spatial variations in wind measured at the various reporting stations followed a consistent pattern, allowing the use of the 2315 CST winds measured at Madison, Wisconsin, about 65 km from the flight. The heading and airspeed estimates were 338° at 10.7 m/s and 348° at 11.5 m/s for altitudes of 300 and 150 m, respectively. Whereas between the earlier and last parts of the flight the track direction shifted 44° , the heading estimates changed less than 17° , and the heading appeared to have been consistent in a direction of 338° - 342° .

The data indicate that as the wind direction shifted clockwise, the heading may have shifted clockwise also. A clockwise heading change, opposite to that which would produce compensation for wind drift, could be called negative compensation. One special case of negative compensation is orientation at a fixed angle to the wind, as suggested by Vleugel (1962). Another special case is downwind orientation as reported by Gauthreaux & Able (1970). Gray-cheeked thrush #19 did not fly downwind nor did it fly a constant angle to the wind, a 100° clockwise shift in winds being associated with only 5° heading change, if any.

Paradoxically, the indicated 5° clockwise heading shift (337° to 342°) may have resulted from a slowly altered heading in response to the early counterclockwise drift (track direction = 314°). This case illustrates, as did the data for Swainson's #5, how the same data may be interpreted as partial negative (instantaneous) compensation behavior or as positive compensation behavior achieved by a slow response.

RESULTS, 1967-1972, ON EFFECTS OF WIND

The flights of 36 thrushes were reviewed in a process of selecting the 14 for which data are presented in Table 1. Of the 22 that were excluded, either winds did not vary significantly during

Table 1. — Continued

Species, ^a Year, ^b Number	Date	Time ^c (CST)	Dur. ^c (min)	Location ^d		Altitude ^e		Track Direction (degrees) (Track Speed) (m/s)	Estimated Heading (degrees) (EAS) ^f (m/s)	Error ^g (± degrees)	Sky ^h	MT ⁱ	MH ^j	
				Lat.	Long.	Min	Max							(meters)
Gc7003	05/08	1955	88	29°13.0'	89°14.1'	250	350	350(15.0)	012(9.0)	7	C	004.0	011.0	
		2208	188	30°18.8'	89°17.7'	100	150	018(16.0)	010(9.0)	8	C			
Sw7005	05/19	2052	49	40°29.7'	88°21.0'	100	300	352(14.4)	330(HN)	5	C	341.0	332.6	
		2210	55	40°53.3'	88°33.4'	200	250	343(9.7)	326(9.8)	4	C			
		2305	50	41° 9.5'	88°39.2'	150	200	353(10.5)	332(9.5)	3	C			
		2355	40	41°26.5'	88°42.2'	200	250	353(9.1)	334(8.8)	4	C			
		0035	67	41°37.8'	88°44.3'	250	300	323(15.1)	340(HN)	6	C			
Ve7008	05/21	0237	64	42°35.1'	89°39.3'	200	250	322(18.3)	335(12.6)	6	C	002.6	352.0	
		2335	49	40° 7.0'	88°17.0'	100	200	025(10.9)	352(9.5)	5	C			
	05/22	2025	38	40°22.8'	88° 8.0'	500	700	017(19.8)	358(10.0)	6	C			
	2223	17	41°15.8'	87°49.5'	250	350	008(10.6)	350(8.1)	6	C-O				
	05/23	0023	15	41°54.8'	87°50.5'	<200		305(7.0)	315(8.0)	6	O			
	0038			Landed in rainstorm										
	05/28	2011	1	41°56.0'	87°54.5'	<30		350(D)	350(D)	3	C			
	2025	123	42° 3.0'	87°57.0'	600	1500	333(23.0)	350(10.0)	10	C				
Sw7012	09/24	2033	5	40° 7.9'	88° 8.1'	200	500	083(14.6)	150(HN)	4	O	107.4	150.2	
		2043	8	40° 8.0'	88° 4.8'	600	700	090(14.4)	148(8.4)	5	O			
		2051	44	40° 8.0'	87°59.0'	500	600	097(14.0)	150(10.6)	5	O			
		2238	58	39°46.0'	87°14.0'	30	100	142(9.5)	153(9.7)	4	O			
		0032	116	39°11.0'	86°32.0'	150	200	125(9.8)	150(8.1)	6	O			
He7015	10/24	1935	1	40° 8.3'	88° 8.1'	<30		190(D)	190(D)	3	O	213.2	189.2	
		1950	24	40° 5.4'	88°12.1'	150	250	228(9.2)	190(10.4)	5	O			
		2017	10	39°59.7'	88°20.4'	300	450	245(12.2)	192(9.8)	6	O			
		2100	85	39°47.3'	88°33.1'	100	200	213(7.1)	189(9.0)	3	O-C			
		2240	6	39°28.0'	88°47.2'	<50		190(10.0)	185(HN)	4	O			

Species, ^a Year, Number ^b	Date	Time ^c (CST)	Dur. ^c (min)	Location ^d		Altitude ^e		Track Direction (degrees) (Track Speed) (m/s)	Estimated Heading (degrees) (EAS) ^f (m/s)	Error ^g (± degrees)	Sky ^h	MT ⁱ	MH ^j		
				Lat.	Long.	Min (meters)	Max (meters)								
He7018	10/28	1901	9	40° 8.3'	88° 8.1'	100 - 200		165(9.0)	190(8.0)	5	O	185.7	193.0		
				39°47.5'	88°10.9'	500 - 1500		202(13.5)		193(HN)	5	O			
				39°29.6'	88°18.0'	1000-2000		190(13.2)		196(CP)	4	O			
Ve7103	05/08	1955	39	40° 7.0'	88°17.0'	250 - 350		346(9.7)	317(10.1)	5	C	352.0	318.3		
				40°27.3'	88°21.8'	200 - 400		000(13.8)		320(HN)	4	C-O			
				40°50.0'	88°20.0'	<150		210(19.0)		(210 < head < 270)		O			
				Landed in rainstorm											
				2012	41° 5.7'	88°34.0'	>1300		009(16.3)		320(HN)	4	C		
2059	41°31.0'	88°29.9'	<1000		333(17.9)		316(HN)	5	C						
Sw7118	05/29	1958	2	40° 8.4'	88° 8.1'	<100		343(D)	343(D)	5	C	332.0	339.7		
				40°27.6'	88°30.5'	2000-2500		318(11.2)		345(HN)	4	C			
				41° 7.4'	89°12.1'	1500-1800		335(10.4)		341(9.8)	5	C			
				42°13.7'	89°49.5'	150 - 300		355(10.6)		336(9.0)	6	C			
				2120	43° 9.8'	90°41.8'	1000-2000		331(16.3)		338(CP)	6	C		
				0126	44°34.3'	91°28.5'	1000-1500		356(15.0)		335(CP)	4	C-O-C		
0350	46° 0.0'	92° 3.0'	<200		286(?)		340(CP)	6	C						
Gc7207	05/16	2005	26	40° 1.3'	88°15.1'	100 - 1000		312(11.3)	348(CP)	4	C	338.3	352.0		
				40°29.1'	88°39.2'	200 - 500		345(12.6)		353(CP)	4	C			
				41°46.2'	88°51.5'	<100		358(9.4)		355(HN)	6	C			

^a Letters identify species as veery (Ve), gray cheek (Gc), hermit (He), or Swanson's thrush (Sw).

^b Year is year of flight and number is an identification number.

^c Time refers to start (CST) and Dur. to the duration (minutes) of track segment.

^d Location refers to the start of the track segment.

^e Altitude is given in meters above earth's surface.

^f EAS is estimated air speed in meters per second; accuracy is typically ± 5 percent, or identifies a method which does not yield airspeed, i.e., heading null (HN), cross-polarization (CP), and departure (D) methods.

^g Error refers to estimated heading.

^h Sky refers to cloud cover during track segment:

C (clear or partly cloudy) and O (100 percent cloud).

ⁱ MT is mean of track segments.

^j MH is mean of estimated headings.

the period of observation, or wind measurements were not available sufficiently near the flight path to permit analyses (e.g., see Fig. 2). For the 14 selected thrushes, track direction data were available for flight in winds differing

significantly (1) during a single night's flight, (2) between different nights, or (3) during ascent or descent. From the numerous track segments measured for each of the 14 individuals, we selected (for analysis and presentation)

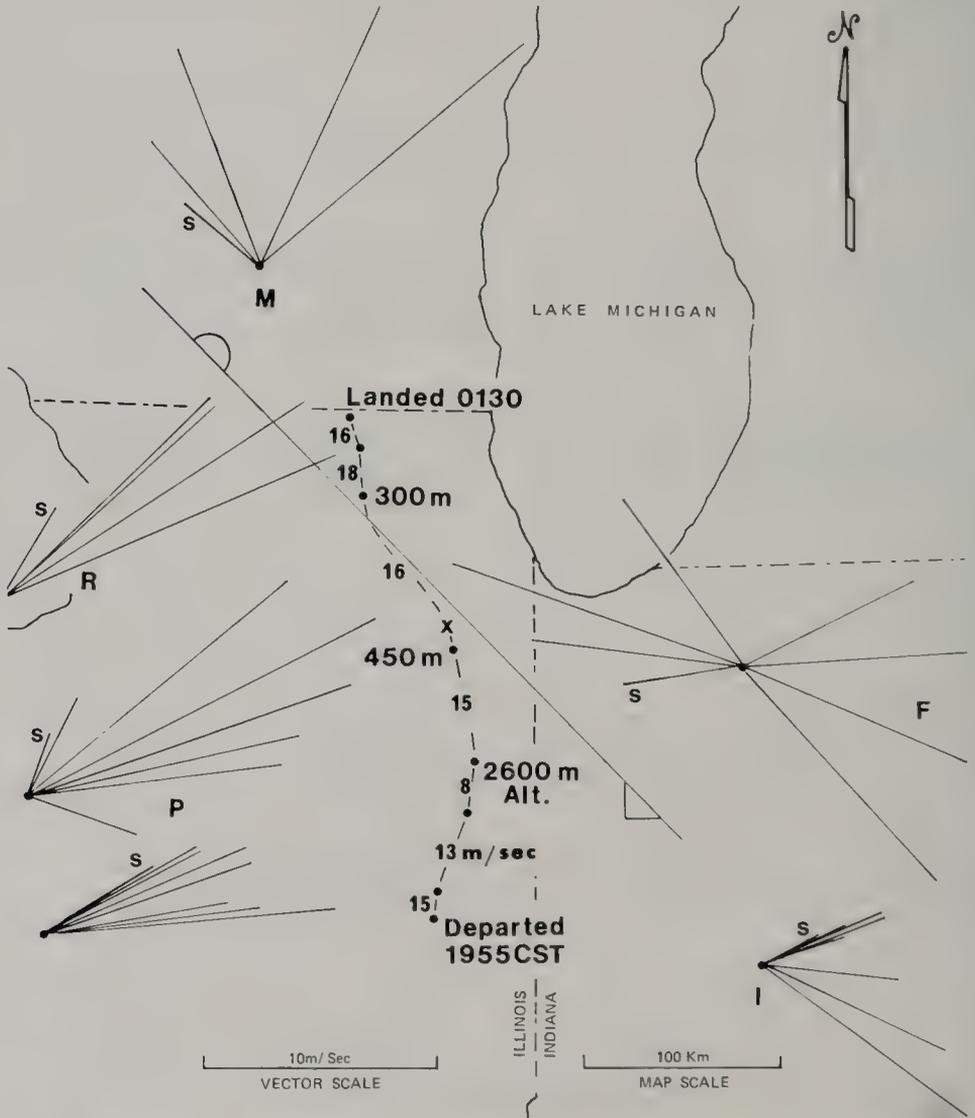


Fig. 2. — Track of veery 6705, area winds aloft, and the position of a weak front. Winds aloft data are by the U.S. Weather Bureau (USWB) for 2315 CST, 25 May 1967, except for P, where the lower set of winds is for 1730 CST. Letters P, R, M, F, and I are the geographic locations of the places where the USWB measured winds aloft (drawn nearby). Winds are for increasing altitudes, going clockwise from surface wind (marked S) to 150, 300, 800, 1,300, 1,800, 2,300, and 2,800 m. The position of the front was taken from the USWB surface chart for midnight, 25 May. Track speeds (one- or two-digit numbers between points marking the bird's path) were computed from straight-line distances between points. Bird altitudes shown are ± 20 percent. X is the position of the bird at 2315 CST and also the approximate position of the warm front at that time.

segments for which headings could be estimated with minimal error by vector subtraction of winds aloft measured close to the bird's paths and near their altitudes or by the head-null or cross-polarization methods.

Track directions and heading estimates for each individual bird were normalized about their respective means so that the data for all birds (Table 1) could be pooled to examine the relationship between courses and headings (Fig. 3). When the use of two methods resulted in two heading estimates for a single track direction, as indicated by a double entry in the heading estimate column in Table 1, the mean of the two estimates was used in constructing Fig. 3.

Course-heading plots are useful, because constant-course (complete compensation for wind) and constant-heading (no compensation for wind) behaviors, in variable crosswinds, would produce distributions along the vertical and horizontal axes, respectively. Distributions representing headings which partially compensate for lateral wind drift, or which are at a constant non-zero angle to the wind, are difficult to interpret in course-heading plots. However, the point is moot for the thrush data, because heading estimates are distributed along the horizontal axis.

The actual data do not consist of courses and headings but of approximations to these, namely, track directions and heading estimates. For simplicity, track direction versus heading estimate plots (e.g., Fig. 3) will be called TD-HE plots. Track directions were better estimates of courses ($\pm 1^\circ$ or 2°) than heading estimates were of headings ($\pm 3^\circ$ - 10°). This fact biases against track variations the impression given by a TD-HE distribution unless the variations are significantly greater than the error range of heading estimates. It is for this reason that flights were excluded from the analysis, as mentioned above, if wind variations were too small to alter courses by an amount greater than the probable error range in estimated headings.

The other consequence of the 6° - 20° error range in heading estimates is that small heading changes, whether in response to wind or for other reasons, are masked. Some of the vertical scatter of points in the TD-HE plot (Fig. 3) may thus represent real heading changes which are small compared with corresponding variations in track directions.

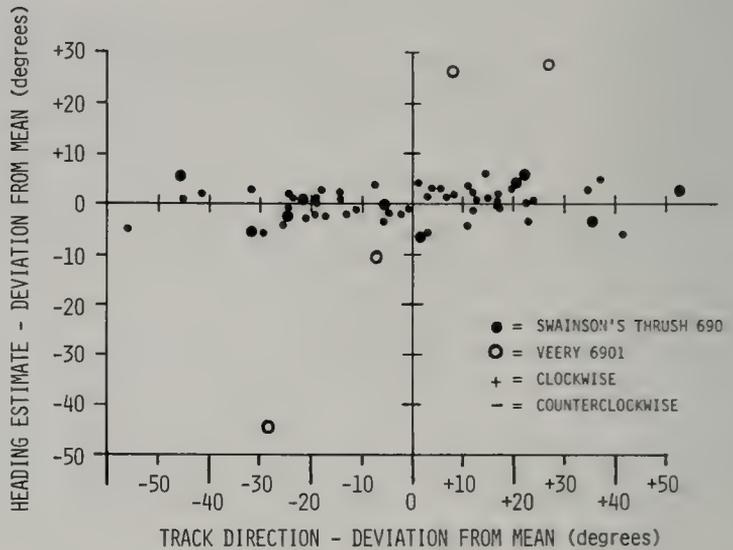
Swainson's Thrush 6905 — An Example

The flight of Swainson's 6905 was chosen as an example for discussion because it was observed flying in winds which varied from night to night, during the same night, and significantly and rapidly with altitude on one night. Track directions and heading estimates for this bird are distinguished by a separate symbol in Fig. 3.

Swainson's 6905 was netted at 1130 on 15 May in a 0.5-ha woods located on the west edge of Champaign, Illinois. It weighed 36.7 g. A 2.4-g transmitter was attached, and the bird was released within 25 minutes of its striking the net. It remained in the woods until the evening of 23 May, when it departed on a flight which ended the next morning in a park near the center of Galesburg, Illinois. It departed that evening, flew all night, and landed at twilight in a 40-ha woodlot about 18 km southeast of Waterloo, Iowa, where it was renetted on the same morning for the purpose of replacing the transmitter with one having a fresh battery. It weighed 34.7 g, not including the transmitter weight. The transmitter was not replaced, because the adhesive held it so firmly that the bird might have been wounded had the transmitter been pulled off. The bird was released in the woodlot and was monitored in the woodlot until the battery failed 2 days later.

The heading estimates for track segments T1, T2, and T3 (Fig. 4) show a progressive clockwise shift totaling 9° into winds coming from the bird's right side. Similarly, the heading estimates for T4 and T5 indicate an 11°

Fig. 3. — Plot of deviations of track directions and estimated headings, for individual thrushes, from the respective mean value of track direction and estimated heading. Data are from Table 1.



counterclockwise shift into winds with a component coming from the bird's left side. Also, the airspeed estimate for T5 was greater than that for T4. These changes are consistent with a compensatory response to lateral wind drift by a gradually altered heading and airspeed or by partial negative compensation.

During the first 40 minutes of the second night's flight (Fig. 5) the track direction changed by more than 90° . The bird departed while we measured winds aloft 5 km west of the bird. The first two bearings to the bird were taken from this place 1 and 5 minutes after the bird took off. Subsequently, seven additional bearings were taken as the tracking vehicle was driven on a circuitous route under and around the path of the bird. These bearings, and the times and places from which they were taken, are shown on the maps of Fig. 6. Although bearings were taken continually, only those above, taken carefully while the vehicle was stopped at known map points, could be used for analysis. Between 21 and 26 minutes after the bird's takeoff, while stopped, we made repeated attempts to measure the elevation angle to the bird but failed because the angle was below 30° , where ground reflections cause erratic readings.

The series of bearings and the times, coupled with the winds measured in the same airspace as the bird, provided data for evaluation of computer simulated paths of a bird's hypothetical constant-heading, constant-air-speed ascent through the winds aloft that we measured. The process was iterative, a matter of computing paths for different headings, airspeeds, and ascent rates and noting which combination best fit the observed bearing-time data. Sixty iterations revealed that a 290° heading, 8.1-m/s airspeed, and 0.66-m/s ascent rate fit all bearing-time data within 5 percent. Fig. 6A, 6B, and 6C illustrate that headings of 280° and 300° , airspeeds of 7.2 and 9.0 m/s, and ascent rates of 0.56 and 0.81 m/s, respectively, cause poor fits to the bearing-time data.

To understand this analysis, it is important to note that there is no guarantee, no matter how many parameter combinations are tried, that a particular model will produce a path that will match (fit) the bearing-time data. If we had tried all combinations of headings, airspeeds, and ascent rates in increments of 1° , 0.1 m/s, and 0.01 m/s, respectively, and had found none which, with the constant parameter model, produced a path which nearly

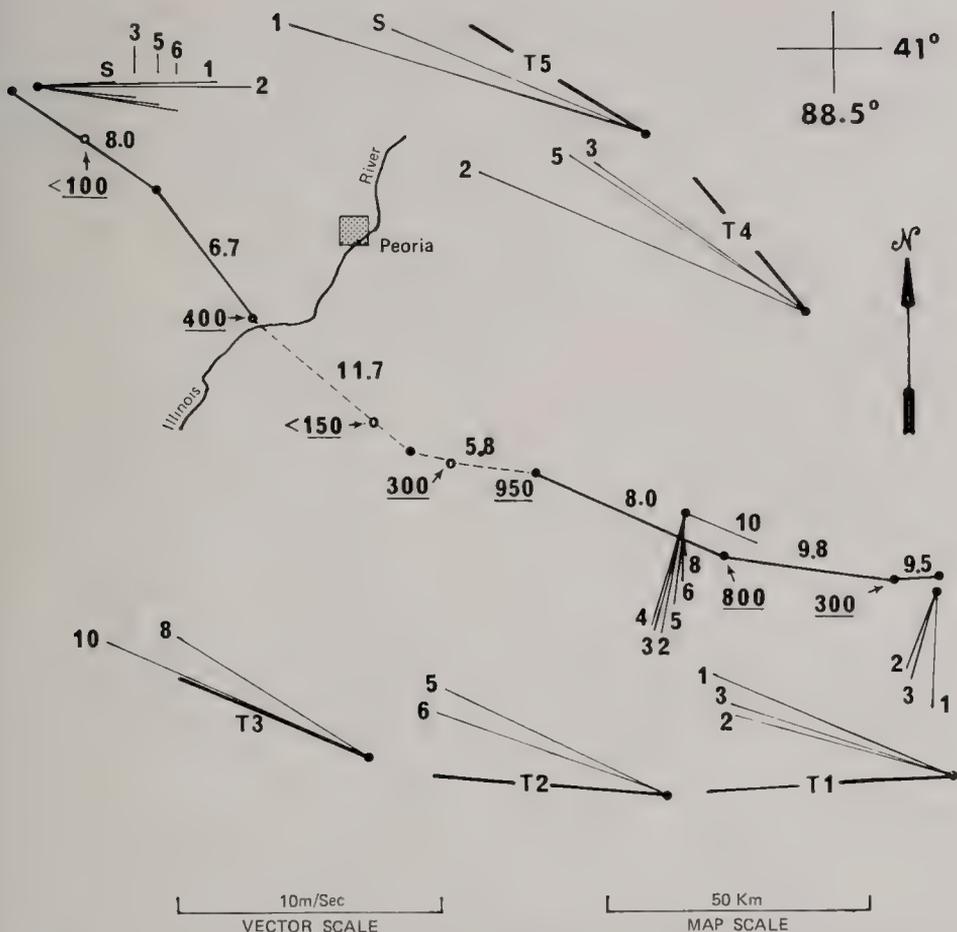


Fig. 4. — The approximate 23–24 May path of Swainson’s 6905, winds aloft vectors measured along the path (shown near where measured), and vector representation of estimated headings (light lines) and track vectors (heavy lines with “T” designators). Track speeds (numbers along lines connecting solid points) are in meters per second for the straight-line distance between points. Bird altitude measurements (underlined) are in meters above the surface and are accurate to ± 20 percent, or better. Vector plots are for track segments drawn as solid lines and are labelled chronologically T1, T2, etc. Winds aloft vectors are labelled with altitude in 100’s of meters (S = surface). Each estimated heading in the vector plots (light lines) is labelled with the altitude (in 100’s of meters) of the wind used for its computation, and corresponding wind vectors are shown to the same scale separately with the wind vector sets. T1 and winds taken at departure go together, estimated heading vectors shown for T2 and T3 are from the second set of winds, taken along the path, and the vectors for T4 and T5 use the last set of winds, taken just after the bird landed.

fit the observed directions and times, we would have been required to reject the model, our bearing-time data, our wind data, or some or all of these. Similarly, had the model provided a fit only for unbelievable parameters, e.g., an airspeed of 40 m/s, a rejection would have been required. We could then have constructed more complicated behavi-

oral models ad nauseum in hopes of finding one which fit the bearing-time-wind data. That the simplest model (constant behavior, i.e., constant heading, airspeed, ascent) produced a path consistent with our bearing-time-wind data and that the airspeed, heading, and ascent rate required to produce the fit were close to those observed for this

bird in other portions of its migration, constitute powerful support for both model and parameters. Of course, there are numerous other models, involving variable parameters, which can produce fits to our bearing-time-wind data,

but we reject these on grounds of simplicity in hypothesis (Barker 1957: Chapter 5).

Later in the flight, as the bird descended in the vicinity of the Mississippi River, the track direction again

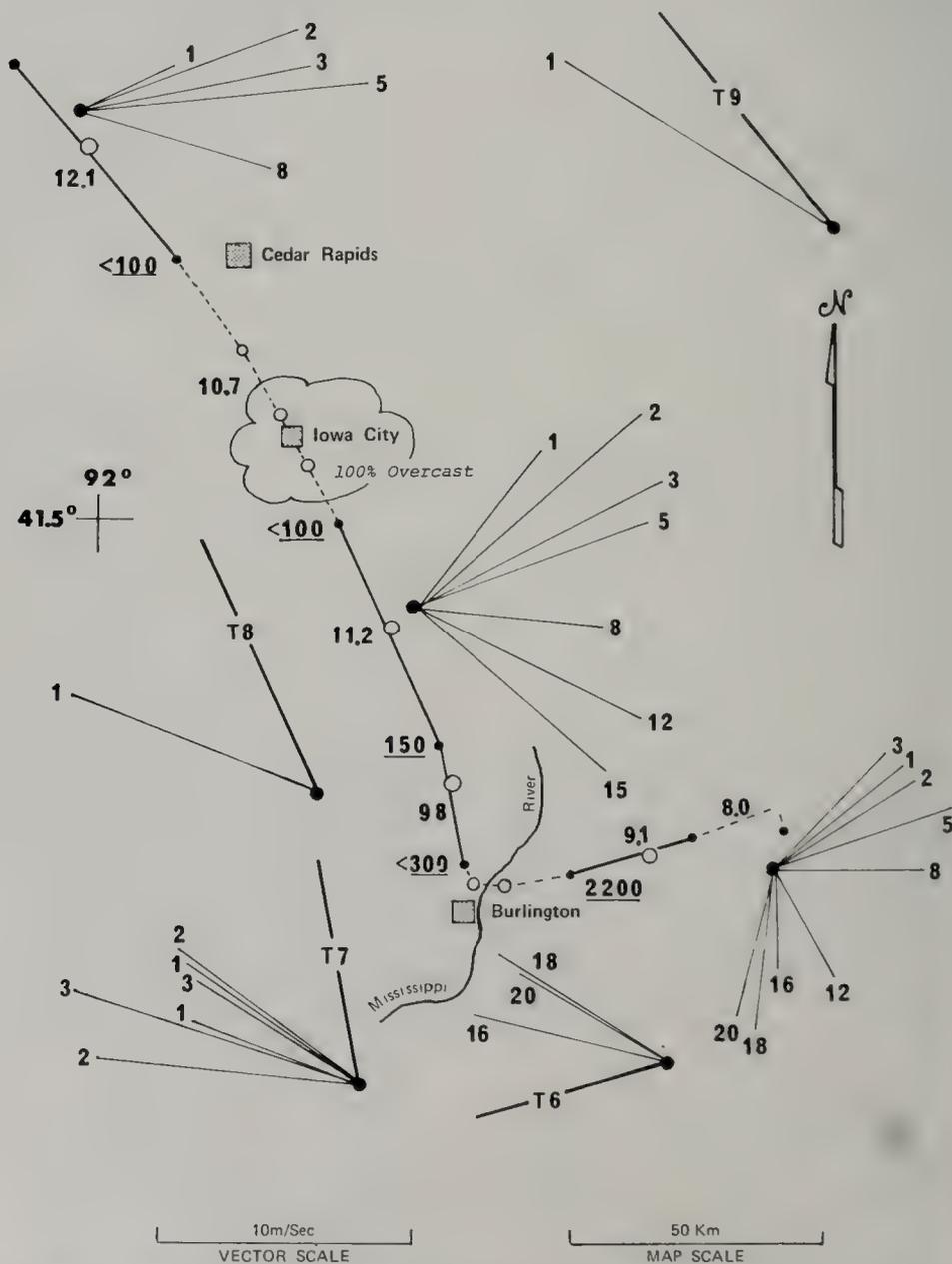


Fig. 5. - The approximate 24-25 May path of Swainson's 6905. Other information is shown as in Fig. 4, except that two sets of estimated headings are shown for T7, the upper set for winds measured at departure and the lower set for winds measured immediately to the north.

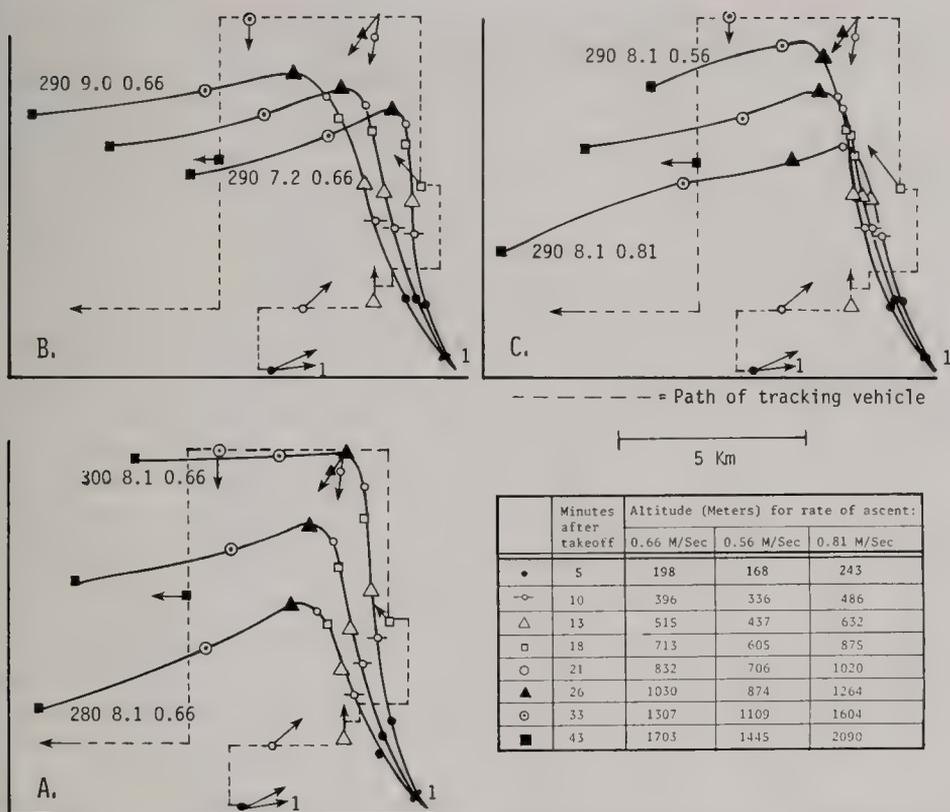


Fig. 6. — Computer simulated paths of a hypothetical bird ascending (at different rates, airspeeds, and headings), through winds aloft measured during the departure of Swainson's 6905 on 25 May (Fig. 5). Time-bearing data from the tracking vehicle and the route of the tracking vehicle are also shown. The central paths, in 6A, 6B, and 6C have the same 290° heading, 8.1 m/s airspeed, and 0.66 m/s ascent rate and thus are drawn identically. They nominally fit the observed time-bearing data. Alternate paths illustrate the effects of other values of these parameters. Arrows are bearings taken from the tracking vehicle. All times are in minutes after the bird took off. North is up. The take-off point and the position shown for minute 21 are the first two points plotted in the overall track of Fig. 5.

changed by 90° or more (Fig. 5). A simulation during this period would appear similar to Fig. 6 turned upside down, but the data during this period were sufficient only to indicate that the descent was more rapid than the prior ascent.

It is interesting to examine the options open to Swainson's 6905 on a heading of 290° at an airspeed of 8.1 m/s. Courses and ground speeds were calculated for the winds measured at altitudes reached by the bird (Table 2). These are the same as those used in the simulated plot of Fig. 6, but without the smoothing effect of interpolation of

winds, which would cause Table 4 to be several pages long. Except for very near the surface, no altitude had winds that were favorable for flight on a course of 290°. At 950 m, lateral drift was near zero, but ground speed was reduced to about 2.2 m/s. The bird flew for about 60 km at altitudes above 950 m and incurred a 48° counterclockwise drift, but at a respectable ground speed of about 9 m/s. Later it chose near-surface flight with about a 50° clockwise drift, again at about 10 m/s ground speed. The bird appears to have preferred (or at least to have chosen) lateral drift to loss of ground speed.

Table 2. — Track directions and speeds calculated for real wind data (Table 4) and a bird with heading 290° and airspeed 8.1 m/s

Altitude (meters)	Track Direction (degrees)	Direction Relative to 290°	Track Speed (m/s)
Surface	299	+9	7.8
31	316	+26	7.5
90	341	+51	7.4
170	343	+53	6.6
270	337	+47	8.3
370	358	+68	4.5
470	349	+59	5.7
570	348	+58	5.9
665	340	+50	5.0
760	343	+53	3.0
855	319	+29	3.3
950	299	+9	2.2
1,045	252	-38	3.6
1,135	250	-40	5.6
1,230	254	-36	6.1
1,320	253	-37	6.1
1,410	256	-34	7.9
1,500	270	-20	7.3
1,635	259	-31	7.0
1,820	247	-43	9.3
2,000	245	-45	9.3

We observed only 12 cases of thrushes confronted by a choice between less lateral drift with lower ground speed and more lateral drift with higher ground speed. Although the results from a variety of analytical methods are similar, we present here an analysis of the component of track speed in the direction of the mean estimated (preferred) heading (progress speed) instead of the track speed. Progress speed is a measure of progress in the heading direction. Although the sample is small (Fig. 7), thrushes consistently "accepted" considerable lateral drift in avoiding progress speeds below about 6 m/s, choosing altitudes that resulted in reductions in lateral drift provided that progress speed was not reduced below about 10 m/s. An expected result of this selective behavior is the compression of the range of progress speeds (and ground speeds), a result reported in numerous radar studies. However, as will be shown, such a compression, for thrushes, is not significantly contributed to by altered airspeed.

We have indicated that Swainson's 6905 may have reduced drift by increasing airspeed during the latter part of its flight of 23 May (Fig. 4). An increase in airspeed may also have occurred on the flight of 24 May (Fig. 5). However, the increases (about 2 m/s or 20 percent) are of the same magnitude as the uncertainty in our estimated airspeeds. We examined airspeed data for the entire sample of Table 1. There appears to be no relationship (Fig. 8) between estimated airspeed and the deviation of track direction from the estimated heading (a measure of drift). Nor do we see a relationship between track speeds and airspeeds (Fig. 9), as has been indicated in several radar studies (see Larkin & Thompson 1980). Ground speeds for thrushes (Fig. 9) not listed in Table 1 tend to be high, because these thrushes flew mostly in tail winds (small or only slightly changing side winds) and, as has been mentioned, were for this reason among those not analyzed for drift. We believe the data show that if thrushes alter airspeed in response to lateral drift or to head or tail wind components, the response is limited to the order of 1 or 2 m/s.

CHANGES DURING A FLIGHT — DRIFT REDUCTION

For the other thrushes tracked, with the possible exception of Swainson's 7012, insufficient data or winds that were less variable precluded modelling and detailed discussion like that presented for Swainson's 6905. However, it is useful to compare track directions near the beginnings and ends of flights with the preferred (mean estimated) heading (Table 3). In all but 1 of 16 flights, the difference between track direction and heading decreased during the night. The average difference was halved. The average rate at which the difference decreased was 5.5° per hour.

Several factors are not taken into account in this beginning-and-end an-

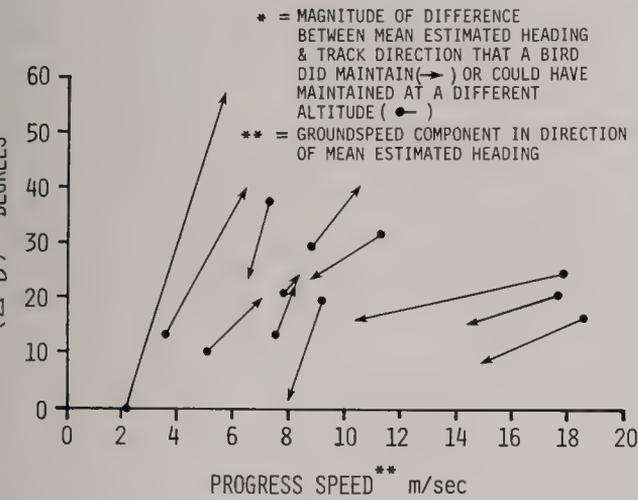


Fig. 7. — Twelve thrush choices between low progress speed with small deviation of course from a preferred heading and high progress speed with a larger deviation of course from a preferred heading. The dot is the option rejected, and the arrowhead is the option chosen. In each case the bird passed through the altitude where the wind provided the rejected option and levelled off at the altitude providing the chosen option.

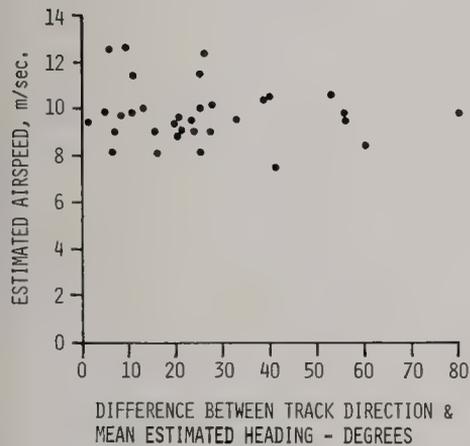


Fig. 8. — Estimated airspeed versus difference between track direction and mean estimated (preferred) heading. Data are from Table 1.

alysis. Birds were usually presented with different wind profiles near the beginnings and ends of flights. These differing wind profiles and the lack of accurate, continuous heading and speed data make it impossible to apportion the observed drift reduction among such possibilities as the winds becoming more favorable, the birds selecting altitudes with more favorable wind, or perhaps the birds slowly changing headings. The effect of changing wind is demonstrated by the first night's flight of Swainson's 6905 (Fig. 4). Unfortunately, we do not know exactly where the wind change occurred, but

Table 3. — Track direction, relative to mean heading estimate, for an early and a late track segment in the same night's flight.

Species, Year Number	Interval ^a (minutes)	Early Segment	Later Segment
		Deg ^b (TS) ^c	Deg ^b (TS) ^c
He6910	136	-89 (22)	-47 (24)
Sw6902	98	+23 (14.5)	+6 (13.7)
Sw6905	370	-28 (9.5)	+7 (8.0)
	334	-41 (8.0)	+26 (10.7)
Gc7003	183	-21 (15)	+7 (16)
Sw7005	353	+19 (14.4)	-11 (18.3)
Ve7008	113	+25 (19.8)	+18 (10.6)
	86	-21 (23)	-8 ^d (28) ^d
Sw7012	257	-53 (14)	-25 (9.8)
He7015	161	+38 (9.2)	+1 (10)
He7018	128	-28 (9.0)	-3 (13.2)
Ve7103	63	+28 (9.7)	+42 (13.8)
	51	+51 (16.3)	+15 (17.9)
Sw7118	360	-23 (11.2)	+14 (10.6)
	265	-21 ^d (19.3) ^d	+16 (15)
Gc7207	288	-40 (11.3)	+6 (9.4)
Mean	203	34.3 ^e 14.1	15.8 ^e 14.3

^a Between the midpoints of the two compared track segments.

^b Difference in degrees between track direction and mean estimated heading; plus indicates track direction clockwise from the mean estimated heading, minus counterclockwise.

^c Track speed in meters per second.

^d Data from track segment not given in Table 1.

^e Mean of the absolute value of differences, sign ignored.

at an altitude of about 800 m the bird had achieved a track direction (seg-

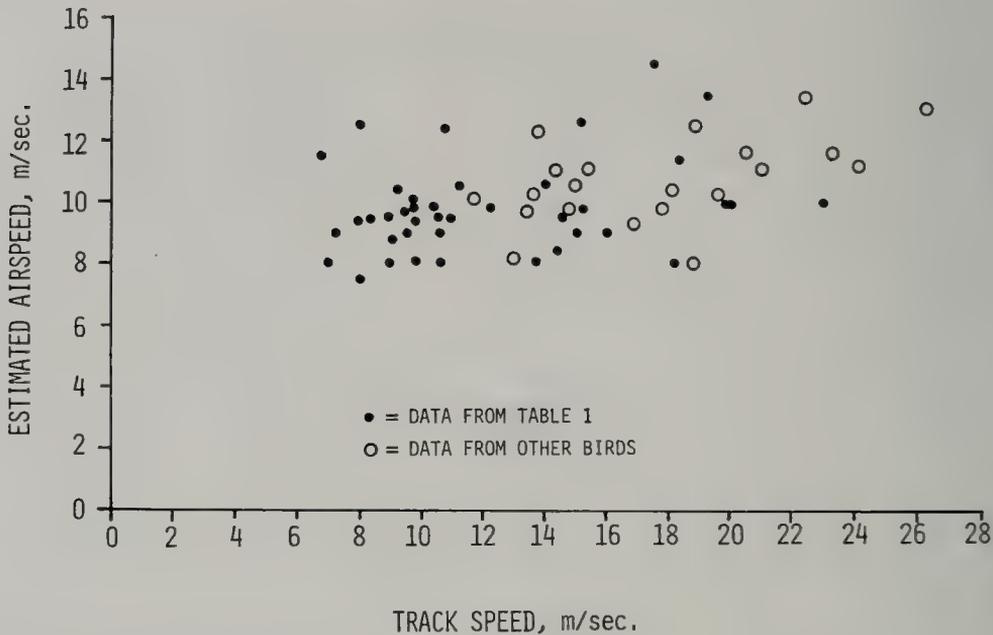


Fig. 9. — Estimated airspeed versus track speed.

ment T3) closed to its preferred heading. Then, presumably upon encountering changing wind, it reduced its altitude, and the track direction and speed changed markedly. A little later, at a still lower altitude, the difference between track direction and mean estimated heading was again reduced. It is tempting to assume that the process of finding an optimal altitude takes time and that, when different, less favorable, winds are encountered, a bird must repeat the process. If a bird repeats the process when less favorable winds are encountered, changing winds would tend to hinder a bird's efforts to find an altitude with winds optimal for its preferred heading and would tend to negate the compensatory effects of slowly altering its heading. Thus, the analysis derived from Table 2 probably understates thrushes' ability to reduce lateral drift. However, the data of Table 2 suggest that thrushes reduce drift over a period of time, that such reduction is accomplished without sacrifice of ground speed, and that the main method employed is altitude selection rather than change in heading or airspeed.

ATYPICAL BEHAVIOR

Of the 36 thrushes tracked, veery 6901 was the only one to make a large heading change not attributable to storms. Data for it are included in Table 1 even though the wind varied little during the 3.5 hours the bird was tracked. The data plotted for this bird in Fig. 3 are given a special symbol. The veery did not maintain a constant course, a constant heading, or a constant heading relative to the wind direction. Instead, the bird turned clockwise (a heading change of at least 60°), as evidenced by both track directions and heading estimates. The turn could not have been an attempt to fly downwind, because the heading continued to change by 30° or more past the downwind direction. A delayed response to lateral wind drift is ruled out, because the indicated heading change was in the wrong direction. The sky was cloudless throughout the flight. We offer no explanation for the behavior of this veery.

Veeries 7008 and 7103 encountered thunderstorms and landed after changing heading away from head winds.

Table 4. — Theodolite measurements and computed winds aloft for the start of the 24 May flight of Swainson's thrush 6905.

Minutes After Release	Balloon		Computed Wind		
	Elevation (meters)	Azimuth (degrees)	Elevation Angle (degrees)	Blowing Toward (degrees)	Speed (m/s)
0.25	61	41.5	49.0	41.5	3.5
0.5	116	47.5	37.5	50.7	6.6
1.0	216	53.0	31.75	57.2	6.6
1.5	315	49.0	30.0	42.0	6.6
2.0	414	57.0	28.75	76.5	7.6
2.5	513	59.0	28.0	66.1	7.1
3.0	612	60.0	27.5	64.6	7.0
3.5	707	61.5	27.5	71.0	6.2
4.0	801	65.0	27.5	89.4	6.7
4.5	895	67.5	28.0	92.1	5.4
5.0	990	71.0	28.5	106.7	5.9
5.5	1,080	75.5	29.5	133.0	5.7
6.0	1,170	80.0	31.0	153.4	5.2
6.5	1,260	84.0	32.5	159.5	4.7
7.0	1,350	88.0	33.75	159.1	4.9
7.5	1,440	92.0	35.5	180.7	4.7
8.0	1,529	94.5	37.0	175.8	3.0
8.5	1,620	98.0	38.0	167.1	4.4
9.0	1,710	101.5	39.5	189.4	4.2
9.5	1,798	106.5	41.0	195.6	6.0
10.0	1,889	112.0	41.5	180.9	7.1
10.5	1,979	117.0	42.0	186.2	6.6
11.0	2,070	122.0	42.25	187.2	7.0

Data for the short track segments are listed in Table 1 but were not included in the TD-HE plot or in the means of the other track directions and heading estimates for these birds. Veery 7008 was approaching violent thunderstorms (frequent lightning was visible from the ground) between 2342 and 0038 CST but landed before encountering heavy rain. During this period the track direction and estimated heading shifted 45° and 35°, respectively. At the time the bird landed, the wind was blowing toward the south up to an altitude of at least 200 m, where the weather balloon disappeared into the cloud layer. Veery 7103 encountered a squall line with the surface wind blowing toward 170° at 7–11 m/s. We were north-northwest of the bird, awaiting its passage when these strong winds came up within a few minutes. Between 2148 and 2204 CST, we moved

twice to the east and twice to the west to obtain bearings for triangulation and a heading estimate by the head-null method. Triangulation indicated that the bird was nearly stationary relative to the ground; heading estimates were 320° at 2152 and 2201 CST. While we drove back south to investigate, a sudden increase in signal strength indicated that the bird had changed heading. During the next 9 minutes the track direction was to the south-southwest until the bird landed in a dense woods just as the rain became a downpour.

EFFECTS OF OVERCAST

Track directions and heading estimates for individual thrushes under clear, partly cloudy, and completely

overcast skies provided tests for the effect of cloud cover.

Veeries 7008 and 7103, Swainson's 7118, and hermit 7015 (Table 1) collectively made eight transitions between clear and overcast skies. Similarly, Swainson's 6905 passed through a region with complete overcast (Fig. 5). Swainson's #5 and gray cheek #19 (Cochran et al. 1967) were observed under clear and overcast. In addition to these, three thrushes not included in Table 1 were observed under clear and overcast skies. These represent 15 transitions between clear and overcast sky, none of which was associated with a heading change. None of the 34 thrushes tracked during this study or the 21 thrushes studied by Cochran et al. (1967) was observed to alter heading during changes in cloud cover.

Migration was initiated under overcast skies by Swainson's 7012 and hermits 7015 and 7018 and by Swainson's #5, gray cheek #19 (Cochran et al. 1967), and one of the three thrushes observed under overcast in this study but not included in Table 1. We believe that the data show that thrushes are not affected by overcast skies present at the initiation of, or encountered during, migratory flight.

Griffin (1973) reported oriented flight of small birds in, above, and in between cloud layers. We were able to measure the altitude of flight and cloud ceiling for 12 thrushes tracked when there was a solid cloud layer. Of these 12, including the 10 discussed above, all flew below the clouds. A veery (Cochran 1972:Fig. 6) may be an exception. It was about 30 km east of the west shore of Lake Michigan at daybreak. The western lakeshore region was shrouded in heavy fog, but we could not tell how far the fog extended over the lake. The veery may have been flying over the fog, but certainly was unable to see the western shore even had it been high enough for line-of-sight viewing. The veery's track direction over Lake Michigan was within 10° of that observed during the pre-

ceding 560 km of flight, and it thus seems probable that this veery was well oriented in the absence of cues in the same sense that Griffin suggests for birds over clouds at more typical cloud altitudes.

DISCUSSION

Wind drift is an important factor in the study of the orientation and navigation of migratory birds. In a practical sense, the responses of birds to wind determine the kinds of observations needed and how these should be interpreted. If individual birds maintained constant courses, a knowledge of their orientation behavior could be obtained directly, because track directions are measurable by most techniques. However, few of the many radar and visual studies give precise wind-altitude data, and none provides rigorous proof that individual birds maintain a constant course in variable winds. Analyses in all but a few of these studies have relied on assumptions about mean goals (intentions) of mixtures of unknown species (the radar swarm) arranged into sets flying in different winds. Even if species could be identified, assumptions about the goals of observed individuals could seldom be more precise than a quadrant. No matter how rigorous the mathematical and statistical treatment of models, radar observations, or visual observations, the validity of any conclusions can never exceed that of the underlying assumptions.

The constant-heading hypothesis finds partial support in several radar studies (Richardson 1976; Williams et al. 1977; Emlen & DeMong 1978). However, a majority of radar studies, at least 26 according to Alerstam (1976), indicate that the drift of the swarm is less than passive, i.e., there is partial compensation or no drift at all. If partial compensation is a reality for "average" behavior, we point out that it may result from mixes of individuals and species behaving differently, for exam-

ple, some compensating completely; some partially; some flying downwind; and some, like the thrushes, flying a preferred heading. Bloch et al. (1981), in a study of European migrants, emphasize the mixture aspect but state that "Songbirds compensate drift due to a side wind at least partly by altering their heading; large individuals appear to be more successful in this than small individuals." Their separation of radar targets into five classes by echo signature and size analyses, although useful for some purposes, required assumptions about goal directions as in less sophisticated radar studies. However, the goal directions of migrants in Europe may be far more restricted than those of the western hemisphere thrushes, which as species breed and winter over a wide range of longitude.

In reference to radar studies in Illinois, Bellrose (1967:305) states that "all our evidence indicates that they correct within a few degrees for wind drift." It is difficult to reconcile our thrush data with this conclusion about the seasonal average behavior of the average trans-Illinois migrant. That thrushes select altitude for favorable winds would have shown up in radar data as pseudo drift (Nisbet & Drury 1967; Alerstam 1976), which increases apparent drift in the analysis of radar data and would add to rather than account for the discrepancy between our findings and Bellrose's findings. Graber et al. (1971) consider thrushes to be common migrants in Illinois, and both tower-kill data (Graber 1968; Seets & Bohlen 1977) and flight-call data (Graber & Cochran 1960) indicate that thrushes are among the most common migrants through Illinois in May and September. Therefore, thrushes should have been well represented in Bellrose's radar samples. Thrush species might be among the few that do not compensate totally, and it may be that their inclusion in Bellrose's averages was responsible for the "few degrees" of drift allowed for the average bird.

We have shown that thrushes reduce lateral drift as a night's flight progresses and that the reduction is accomplished primarily by the selection of an altitude with the least unfavorable wind and secondarily, if at all, by small, slowly implemented changes in heading and/or airspeed. Our data also suggest that when cross and opposing winds are the only options, keeping progress speed above about 6 m/s takes precedence over reduction of lateral drift, the latter having first priority only when progress speed exceeds 10 m/s. Thrushes landed when winds provided no options other than a progress speed of less than 2 m/s.

The ascent rates we measured for thrushes, between 0.3 and 0.7 m/s, are much less than the climbing capability of up to 4.4 m/s reported for passerines by Able (1977). Although high rates of ascent may not be as aerodynamically efficient as lower rates, the overall efficiency during a night's flight – in terms of distance covered per unit energy – would be improved for birds that quickly find the best winds available. If energy efficiency is improved by finding the best winds available as quickly as possible, and if thrushes are capable of faster ascents than those we observed, then their relatively slow ascent may indicate that the "measurement" process by which thrushes assess the effects of winds is an integrative one requiring a significant amount of time. This idea finds additional support in the considerable time (20–50 minutes) taken by thrushes 6809, 6810, and 7103 to respond (by landing) to extremely unfavorable winds and possibly in thrushes slowly altering their headings, as discussed below.

Some of our data suggest that if the optimal wind has a significant cross-wind component, as it often does, thrushes respond by slowly altering their heading and perhaps airspeed as well. We reject the alternate interpretation, negative compensation, because there is no apparent benefit in a bird's increasing its lateral drift. Our data

are not accurate or continuous enough for precise analysis, but they do rule out rates of change greater than a few degrees per hour. Corrections at such small rates could produce significant compensation for drift on long overwater flights in consistent wind but would be of limited benefit in the variable wind of the midwestern United States, particularly in spring, and for typical 6-hour overland thrush flights. We speculate that the ultimate degree of correction sought by slowly altering heading or airspeed may be set at limits imposed by progress speed, as suggested for corrections achieved by the selection of altitude for optimal wind.

Some of the thrushes we observed ascended, during the first hour or so of flight, through a variety of unfavorable winds and then descended to an altitude with winds more favorable than those encountered at higher altitudes. Some remained at a higher altitude with a wind no better than one encountered at a lower altitude. Still others ascended for a shorter period and levelled off at an altitude with an acceptable wind without testing higher altitudes for more acceptable winds. We note also that the ascent at the initiation of migratory flight is not repeated later in flight even if winds change significantly. Instead, after the initial ascent, altitude selection is restricted to descent or to small upward adjustments. These observations are consistent with a strategy of seeking a tolerable compromise through minimum effort rather than continuously seeking the most favorable wind available at all times. We believe that the energy expenditure required for major ascents, coupled with the low probability that major wind changes will occur during a night's flight, represent an energy-cost-to-wind-benefit ratio which favors the acceptance of a satisfactory compromise at hand as opposed to the continual seeking of a better compromise.

That lateral drift is reduced, by whatever means, and that low progress (or ground) speed results in the termin-

ation of flight, suggest that thrushes are aware of some aspects of their path vector, can assess the speed and direction of the wind relative to their heading, or some combination of both. Bruderer (1982:11) states that the ground is the "most simple and probable" reference by which the course is estimated. Bellrose (1967:306) speculated that birds may be capable of obtaining information about both speed and direction of wind, relative to their heading, from the "gust-form of air." If small scale accelerations of air (gusts) were used by thrushes to evaluate wind, it would seem that the evaluation could be done more quickly than our data indicate. For this reason and also because linear landscape features appear to be responsible for faster-than-usual course evaluation, as discussed below, we favor the explanation that thrushes use the ground as a reference for evaluating their situation much as a man might use objects on shore when paddling a canoe in a strong current.

Chicago (population about 7 million) and nearby Lake Michigan did not influence the flight headings of thrushes. Veery 7008 flew for 20 km over south and central Chicago before changing course and landing after encountering a thunderstorm. Two thrushes (gray cheek #7, Cochran et al. 1967; a veery, Cochran 1972: Fig. 6) flew essentially straight paths over Chicago and then out over Lake Michigan. Four others, not reported here because their flights were in unchanging winds, had straight paths over the Chicago metropolitan area. Unfortunately, none of these thrushes could be shown to be on courses markedly different from their preferred headings; therefore, we cannot dismiss the possibility that a bird flying in a strong crosswind as it encountered Chicago or Lake Michigan would use these major land features as references for course evaluation or correction, as is shown below for thrushes crossing major rivers.

Of nine thrushes that we have tracked across the Mississippi River, the course of only one, Swainson's 6905 (Fig. 5), changed in the vicinity of the river. The change in course is entirely attributable to the bird's descent to an altitude having a markedly different wind. The river and nearby Burlington, Iowa (population about 33,000), were prominent landscape features which may have enabled the bird to determine quickly that its precrossing course of about 254° was well off its approximately 295° preferred heading. Later in the same night, this thrush passed directly over Iowa City, Iowa (population about 35,000), and near Cedar Rapids, Iowa (population about 85,000), on a course that was 20° - 30° to the right of its preferred heading without noticeably responding. However, during this time the bird was already flying so low that it could not have safely responded by descending. The paths of the other eight thrushes did not vary in the vicinity of the river, but their courses were within 20° of their preferred headings when they crossed it.

Of 17 thrushes that we have tracked crossing the Illinois River, Swainson's #5 (Cochran et al. 1967) was the only one whose course changed in the vicinity of the river. Its approximately 250° course prior to encountering the river was well off its 300° preferred heading. A descent was detected near the river. The course shift could have been entirely due to a change in winds at the lower altitude, but altitude data were too crude to preclude other possibilities.

The observations of Swainson's 6905 and #5 suggest that features of large rivers may provide better ground reference than the relatively featureless intervening landscape, despite a profusion of lighted small towns and cities. Perhaps cities are too bright or too new on an evolutionary time scale, or perhaps thrushes respond to linear landscape features only (e.g., rivers), as suggested by Bruderer (1982), but not to point features (e.g., cities), as proposed

by Rabol (1974). Bingman et al. (1982:49) hypothesized "that migrants could utilize the Hudson River as a topographical reference by which to perceive wind drift from a preferred track and correct at least partially for these effects." However, they concluded that the birds altered their headings to achieve courses closely paralleling the river. That rivers are not followed by thrushes, even temporarily, is contrary to their conclusions and in agreement with James (1955).

Cochran et al. (1967:224) state, "Flights of less than an hour's duration sometimes occur during or before thunderstorm activity. These flights are downwind at low altitudes." Data gathered since 1966 do not support the downwind aspect of their conclusion. Instead, upon encountering a storm or squall line, thrushes adopted a heading that precluded upwind flight (and therefore was sometimes downwind) and always landed after changing heading, sometimes within minutes and sometimes after as long as an hour. We have not yet analyzed all the data bearing upon the question of thrush behavior in inclement weather and wish here only to remove any suggestion that downwind headings are specifically chosen.

However, regardless of wind direction, flights of radio-tagged wood thrushes [*Catharus mustelina* (Gmelin)] observed in Illinois during the last phase of spring migration to their nest sites were flying approximately downwind and at low altitude (Cochran unpublished data). At times and geographic localities where a low-altitude mix of radar or visual "targets" consisted of a considerable proportion of birds in the site-search phase, downwind distributions of track directions similar to those reported by Gauthreaux & Able (1970) might be observed.

Cloud cover had no effect on the headings of individual thrushes, whether encountered before or during flight. In this regard our thrush observations are consistent with the radar

observations reported by Bellrose & Graber (1963). Able (1982) discussed the growing body of evidence for well-oriented flight under (and in) overcast and briefly reflected on what this may mean regarding orientation mechanisms. He concluded that "we appear no closer to understanding the mechanism by which this is accomplished than when Griffin (1973) discussed the problem nearly a decade ago." The data presented here add to the evidence for oriented migratory flight under overcast skies but do not reveal the mechanisms involved.

How can thrushes find their way between specific nesting and wintering areas separated by thousands of kilometers if they are largely at the mercy of the wind? We do not know, but winds do not make the feat as difficult as one might conclude at first glance. For example, we followed three thrushes for more than one night's flight and more than 400 km total distance each. The path of Swainson's 6905 was as serpentine as any we have observed, with track directions which varied more than 100° . Yet, after two nights of flight its azimuth from where we began observations at Champaign, Illinois, to near LaPorte City, Iowa, where we left it, was 308° , only 13° different from its preferred 295° heading. The overall path of Swainson's 7118 was 335° , only 5° different from its preferred heading of 340° ; that of veery 7008 was 350° , not measurably different from its 352° preferred heading.

Long migrations made up of many shorter single night's flights are subject only to net drift according to the prevailing wind components of the various geographic areas traversed. The effects of weather systems will tend to cancel one another. Prevailing winds would necessarily shape any evolved system of navigation. The surprise in our data was that the net drift was remarkably small for such short path distances as 400–700 km in spite of the fact that the birds selected for presentation here drifted more than most of those that we observed.

Thrushes' constant-heading behavior, with wind drift mitigated by their seeking an altitude with, at worst, a not-too-unfavorable wind, represents a long-distance migratory strategy that, in view of the probability that net drift is negligible, is more conservative of energy than strategies involving complete or partial compensation for wind. We point out that nothing short of nearly perfect compensation for wind drift, especially for long migrations, can substantially reduce a distance-time penalty incurred by a bird in a homing process near the end of a migratory journey. Factors in addition to energy conservation are probably important in successful migratory strategies. For example, partial-compensation behavior may have an advantage over both complete-compensation and constant-heading behaviors on long overwater flights. Perhaps the advantages of partial-compensation behavior versus complete-compensation and constant-heading behaviors on long overwater flights could be examined on theoretical grounds, but we have not done so. We only speculate that the slow altering of heading, subject to restrictions on minimum acceptable progress speed, may have survival value for long overwater flights. Such behavior had such a small effect during short overland flights that we cannot be certain we observed it; therefore, if thrushes do alter headings and air-speeds slowly, the significance of such behavior would seem to lie elsewhere in their migratory journeys.

CONCLUSIONS

1. Individual thrushes do not maintain a constant track direction (path over the ground) unless the wind they are flying in is also constant.

2. Individual thrushes maintain a constant heading during a night's flight and from night to night to an accuracy equal to or better than the $\pm 3^\circ$ precision of our best measurements, liable to the exceptions in 3 and 4 below.

3. Thrushes may change their heading in response to lateral wind, but if they do so, it is at a rate of change of less than about 3° per hour.

4. If thrushes alter their airspeeds to reduce lateral drift, they do so by less than about 2 m/s.

5. Thrushes' airspeeds (mean = 10.1 m/s, SD = 1.6) are independent of and less variable than their ground speeds (mean = 13.7 m/s, SD = 4.6).

6. Thrushes turn to avoid a headwind component (prior to landing) when they encounter thunderstorms.

7. Thrushes mitigate the effects of lateral winds by flying at altitudes where winds are not too unfavorable (see 8 and 9). After takeoff, thrushes ascend until they find suitable winds, but if these are not found below 2 or 3 km, they descend and either land or accept a compromise at a lower altitude, never below about 75 m. As winds change during a night's flight, thrushes adjust their altitude accordingly, usually by descending and rarely by ascending – but never to the altitude reached during the initial ascent.

8. If winds at all altitudes above about 75 m have unfavorable head and side components so that progress speed cannot be maintained above 2 or 3 m/s, thrushes land.

9. Thrushes choose winds for minimum lateral drift provided progress speed does not fall below about 6 m/s. When the choice is between lateral drift (up to about 60°) and progress speed (below about 6 m/s), thrushes accept the lateral drift.

10. The ascent rate of thrushes at the beginning of flight is usually in the range of 0.5–1.0 m/s. This rate is less than their climbing capability and may reflect the time needed for assessment of winds aloft.

11. Primarily because of (7) above and secondarily because of (3), (4), and the fact that wind speed typically declines during the night, thrushes' track directions become closer to their preferred headings toward the end of a night's flight.

12. Thrushes initiate and maintain constant (preferred) headings during migratory flights under, and during transitions between, clear, partly cloudy, and completely overcast skies, but they seldom, if ever, fly above the lowest unbroken cloud layer.

13. By implication from (7) above, thrushes either directly sense information about wind speed and direction (e.g., from anisotropies of small-scale turbulence), or they evaluate some aspect(s) of their progress over the ground, or both.

14. Prominent linear landscape features, such as large rivers, may enable thrushes to more effectively sense information about their progress over the ground.

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APPENDIX

DETERMINING LOCATIONS OF FLYING THRUSHES

Cochran et al. (1967:214) describe a method of determining the locations

of flying thrushes by driving a tracking vehicle under them. This and other location methods require that the observers get close to a flying bird. From a knowledge of the approximate track speed and direction of a flying bird, a forward extrapolation of its flight path was plotted on a highway map. The places and times where the bird was likely to cross roads were noted. One of these road crossover places was selected by considering the average speed the vehicle could be expected to make in reaching the chosen place and the need to get there before the bird. Each new location of the bird was used to update the projected path and select the next crossover place. A general discussion of tactics and strategy are given in Cochran (1972:53-58). We point out here that tactics for keeping up with a bird are considerably different and more easily accomplished than those for making the repeated close passes necessary for gathering the best data.

Cochran et al. (1967: Fig. 4) employed a horizontally aimed eight-element yagi receiving antenna rotatable through 360° of azimuth. The antenna was equipped for reception of both horizontal and vertical polarization. This antenna provided horizontal directivity to a bird if the elevation angle to the bird was less than about 45° . For elevation angles less than 45° the signal was strongest (a peak) when the antenna was directed at the bird's azimuth, and it gradually weakened for azimuths on either side of the peak, reaching the minimum for azimuths in the vicinity of 90° from the peak. A second, much weaker peak occurred when the antenna was pointed directly away from the bird. As a bird entered a "cone" above the vehicle (elevation angles greater than about 45°), the relation between signal strength and antenna azimuth could not be interpreted, peaks and nulls appearing at numerous and varying azimuths. As a bird left the overhead "cone of uncertainty," the familiar relationship between antenna azimuth and signal strength returned. Position-

ing the vehicle for such an overhead passage (crossover) required selecting a place along the bird's projected path, as discussed above. At this place (ahead of the bird), the bearing to the bird was approximately 180° different from the bird's previously plotted track direction. In practice, the process of positioning the vehicle was iterative. The first location where the vehicle was stopped was only approximately correct. As the bird moved closer, bearing changes were noted, and the vehicle was moved forward or backward in an effort to place the vehicle directly in the oncoming bird's path. The process was sometimes frantic during the last moments, requiring rapid turning about or driving at high speeds in reverse. Sometimes the procedure failed, and the bird crossed the road well ahead of or behind the vehicle, a situation which, we will show, evolved into a method for determining both altitude and location.

Here we are interested in how the accuracy of the information gathered in this simple crossover procedure was estimated. In our study we made the receiving antenna moveable in elevation as well as azimuth (Cochran 1972: Fig. 4). With this alt-azimuth antenna mount, the cone of uncertainty was theoretically eliminated. In practice, because of the awkwardness of an alt-azimuth mount when directed in the near-overhead region, a cone of uncertainty remained for elevation angles above about 75° . By simple geometry it can be shown that (1) a bird must pass directly overhead for entry and exit bearings (into and out of the cone of uncertainty) to differ by 180° , and (2) for a bird's passage anywhere through the cone, the assumption that it passed directly overhead can err by no more than the altitude of the bird times the cosine of the elevation angle defining the edge of the cone. For example, for cones defined by 45° and 75° elevation angles and a bird at an altitude of 100 m, the bird must pass over a point on the road within ± 70 and ± 26 m, re-

spectively, of the position of the vehicle. Except on the rare occasions when crossovers were detected while we were within sight of mapped landmarks, our errors in positioning the vehicle on a map were typically ± 50 m due to map plotting and vehicle odometer precision and accuracy limitations. Therefore, for birds flying at 100 m or below, there was little point in worrying about cone entry and exit bearings. This situation was fortunate, because the rapidly changing angles to birds that flew past at low altitudes did not allow us to get more than crude bearings. At higher bird altitudes cone entry and exit bearings are more important. The errors discussed above for a bird at 100 m altitude become 700 and 260 m for a bird at 1,000 m altitude. However, when thrushes were flying high, there was time to take bearings carefully and to position the vehicle so that the bird passed near the axis of the cone. We conservatively estimate that, with the alt-azimuth mounted antenna used in our study, the crossover positions we plotted were never more than 200 m, and usually less than 100 m, from the actual crossing point.

Estimating the time of a bird's passage overhead required taking the mean of the times of its entry into and exit from the cone of uncertainty. A bird flying at a ground speed of 500 m/min (about 8.3 m/s) at an altitude of 1,000 m would pass through a cone defined by a 75° elevation angle in 62 seconds. In practice, these timings were never precise, especially for birds flying high, mainly because the transition into and out of the cone was never as distinct as presented here for purposes of explanation. It usually took five to ten transmitter pulses (about 5–10 seconds) to take a bearing and, failing in this, 10–20 additional seconds to determine that readings made no sense (the bird was in the cone). A similar delay occurred in determining that a bird had left the cone of uncertainty. Therefore, timings were usually late by 20 or 30 seconds. However, be-

cause track speeds were determined between successive crossovers, the systematic errors due to the delays tended to cancel one another. We believe our crossover timing error, as it affected track speed calculations, was rarely greater than 30 seconds, and from limitations imposed by the geometry of a pass, never as great as 1 minute.

The accuracy of the track directions and track speeds, as measured between successive crossovers, is estimated as follows. Assuming a worst-case 300-m error at right angles to a 20-km track segment, the error in computed track direction would be 0.85° . For a 20-km track segment flown at 8.3 m/s ground speed, a 30-second timing error would cause a 0.2-m/s error in computed track speed.

It was possible to measure altitude from two or more elevation and azimuth angles taken before and/or after a bird passed nearly overhead. Geometrically, one side and two angles define a triangle. In this case the length of the side was provided by track speed times the time interval between angle measurements. However, it was difficult to measure accurately the elevation angle to birds approaching head on or receding (tail view), because these aspects gave mixed polarization, which magnified errors caused by signal energy reflected from the ground. Errors in the elevation angle of only 10° – 15° can cause errors of altitude measurement as great as 50 percent. Therefore, we used this triangle method only when circumstances precluded the use of the method described below.

We have mentioned that birds crossing roads ahead of or behind the vehicle provided a way of measuring altitude at the crossover point. The method is described and illustrated in Cochran (1972), but will be briefly recounted here. It requires that the track direction be known, preferably to within 10° , from prior data. The method is best described by example, starting with the tracking vehicle northwest of a bird holding a northerly course. The

tracking vehicle is driven east as if a crossover place were to be determined, but is held back so that the bird will pass in front of the vehicle. While the bird passes in front of the vehicle, the transmitting antenna (and bird) present a side aspect, which gives pure horizontal polarization. Polarization is important, because the best elevation angles are taken when the polarization of the received energy is purely horizontal. When the azimuth to the bird is straight ahead (as the bird crosses the road), the time, odometer reading, and elevation angle to the bird are recorded. The vehicle continues moving east while azimuths are taken, and soon the azimuth is north (a second odometer reading is recorded at this time). Because the track direction is north, the vehicle is now at the place where the bird recently crossed the road (the crossover place is determined). The time of the crossover has already been recorded. The altitude of the bird as it crossed the road is the distance between the two odometer readings times the sine of the previously recorded elevation angle. The method is valid even if the path direction is not at right angles to the road, but the desired side aspect of the bird is, in practice, lost if path-road angles are less than about 45° . The trick is to be at a place on the road (when the bird crosses it) which gives an elevation angle in the useful range of 30° - 70° .

Potential timing and positioning errors are not significantly different for this cross-ahead method from those for the crossover (overhead) method. The primary error in timing a crossing equals the product of the sine of the error in the first (presumed dead ahead) bearing, the distance from the place this bearing was taken to the road-crossing point, and the reciprocal of a bird's track (ground) speed. For a 5° bearing error, a 1-km distance, and an 8-m/s track speed, the timing error would be 10.9 seconds. The error in computing the place of crossing equals the error in distance measurement

plus the product of the sine of the sum of the errors of the assumed track direction and second bearing taken, the track speed, and the time interval between first and second bearings. In the example above, an 80-m distance error, a combined track direction and second bearing error of 10° (these sum algebraically and may cancel), and a time interval of 41 seconds (vehicle speed of 55 mph), would cause a maximum crossover positioning error of 137 m ($80 + 57$). Altitude error equals the product of the difference between the tangents of the true and measured elevation angles and the sum of the distance and the distance error. For the above example, if the bird's actual crossover altitude was 1,000 m, if a 45° elevation angle was erroneously measured as 35° , and if there was an 80-m error in the measured distance the vehicle traveled between measurement points, then the calculated altitude would be 644 or 756 m for vehicle distance short or long, respectively.

The sensitivity of altitude computation to elevation angle error results in highly variable accuracy of altitude estimates (Table 1). We tested the accuracy of radio measurement of elevation angle against optical measurement to a transmitter attached to a kite and found that between 30° and 60° elevation, given time for numerous vertical sweeps of the antenna, errors were less than $\pm 3^\circ$. In practice we seldom noted a consistency of elevation angle measurements which would suggest that their accuracy was within the few degrees indicated by the kite tests. One exception was Swainson's 7005, which had a continuous (instead of pulsed) transmitter that greatly facilitated measurement of elevation angles (and azimuth bearings as well).

The futility of using U.S. Weather Bureau (USWB) winds-aloft data is illustrated by the impossibility of analyzing the flight of Veery 6705 (Fig. 2), which was tracked before we obtained winds-aloft measuring equipment. This veery flew at different altitudes in

winds which varied greatly with altitude, time, and geographic location. The veery descended as it passed through a slowly moving warm front with large shifts of the lower-strata winds north of the front. A case for a variety of behaviors could be made by choosing particular winds-aloft data from those available from the USWB for different times and places. Only constant-course behavior (complete compensation) can be excluded. We invite the reader to apply compass and rule to data of Fig. 2, which is scaled accurately enough for this purpose. Sometimes birds did fly close to USWB stations when winds aloft were being measured, e.g., thrushes #5 and #19 (Cochran et al. 1967) discussed in the text. The probability of this occurring was small in the 1960's and is lower now, because times when and places where the USWB measures winds aloft have greatly decreased. For example, we did not measure winds aloft when Swainson's 6905 passed south of Peoria, Illinois, around midnight (Fig. 4), because we counted on obtaining the 2315 USWB measurements. When we went to the USWB for their data, we were told that they no longer measured winds at 2315 hours, a severe disappointment, as this wind information would have allowed us to analyze the middle portion of the flight. Even when USWB winds-aloft measurements were available for the place and time of a bird's passage, they were of limited use when wind shear was high, because they are computed for increments of about 500 m (above about 800 m). Some USWB wind data we examined showed a 180° shift between two adjacent 500-m levels! We do not imply that USWB personnel were ever less than helpful and cooperative; in fact we found that they would, for cost, given an hour or two of advance notice by telephone, measure winds aloft at times we specified. On several occasions, when we saw that a bird was headed toward one of their stations, we took advantage of this service. The widely distributed network of USWB stations

with its capability for winds-aloft measurement represents a useful and accessible resource.

We calculated winds aloft from the theodolite measurements of elevation and azimuth angles to ascending helium-filled balloons. We took readings at 15, 30, 45, and 60 seconds, and at 30-second intervals thereafter. These intervals provided wind data for altitudes of 30, 100, 150, and 195 m and at about 100-m intervals at higher altitudes. The theodolite was calibrated by sighting the north star or by a corrected magnetic compass sighting when the sky was cloudy. The horizon was established by a bubble level. A light was attached to the balloon for night readings, but this was unnecessary for measurements started 30 minutes after sunset or before sunrise, near the usual beginning and ending times of thrush flights. We tested how accurately balloons conformed to the assumed ascent rate by measurements from two theodolites. For six test ascents actual altitude did not deviate from the standard rates (for a 30-g balloon) by more than 2 percent. Measurements taken at the beginning of the second night of flight of Swainson's 6905 (Fig. 5) are listed in Table 4. Note that we missed the 45-second reading in this set. Missing one of the first few readings was common because of the difficulty in keeping the theodolite pointed at the nearby balloon as the balloon rapidly changed azimuth and elevation. We measured winds aloft before and after flights and as often as circumstances permitted during a flight.

Calculated heading estimates (those with associated track speeds in Table 1) were obtained by using standard trigonometric equations (on a computer) instead of the equally valid but more time consuming graphical method illustrated in Fig. 4 and 5. The accuracy of track and wind vectors we measured was usually good enough for the calculation of approximate path vectors (near where winds were measured) to an accuracy of $\pm 1^\circ$ or 2° and 0.5–1.0

m/s. Unfortunately, altitude measurements were usually too inaccurate to permit an unambiguous choice of winds to use for the calculations. Therefore, lack of accurate altitude data and/or lack of wind data at particular places precluded the use of most of the tracking data gathered during the study. Calculated heading estimates ($\pm 3^\circ$: Table 1) resulted under ideal conditions when wind did not change significantly over the range of altitude estimates. We applied a 3° uncertainty to all heading estimates as a conservative lower limit to the error range for calculations from measurements taken under these ideal circumstances. Appropriate (higher) error ranges were applied when added uncertainty resulted from less than ideal track or wind vector data or when wind varied significantly over the range of altitudes estimated for a bird. Headings were excluded from the data set when the estimated errors exceeded about $\pm 10^\circ$.

TAKING HEADINGS BY METHODS NOT REQUIRING WIND AND ALTITUDE DATA

To understand these methods, it is useful to visualize the aspect, i.e., the projection, of a trailing wire antenna (on a bird) on an observer's plane of vision, as viewed from various places. For purposes of discussion, we consider the antenna wire to be straight and to pass directly over the bird's tail parallel to the earth. Viewed from directly ahead of or behind a bird (at the bird's altitude) the wire is invisible (has a point aspect). Viewed from ahead or behind, but from the ground, the wire appears as a vertical (to earth) line which subtends a smaller viewing angle than if the wire were turned broadside to the viewer (wholly in his plane of vision). This apparent shortening of the wire is called "foreshortening." The maximum amount of energy which can be received from a wire antenna is proportional to the ratio of the foreshortened

aspect to the broadside aspect (the wire in the observer's plane of vision), or simply, to the sine of the viewing angle (V_a), which is 0° from head on and 90° for a broadside view. We say "maximum amount of energy which can be received" because, for an antenna pointed at a bird, the signal actually received depends on the relative orientation between the receiving antenna elements and the aspect presented by the transmitter antenna wire. In the example above (a view from the ground ahead of the bird) the wire antenna on the bird appears foreshortened and vertical. If a receiving antenna with elements vertical to the ground is pointed at the vertically appearing transmitter wire antenna, it will receive all the energy available. Conversely, if the receiving antenna elements are horizontal, none of the available energy will be received. In contrast, viewed from the side there is no foreshortening ($\text{sine } 90^\circ = 1$); so the maximum amount of energy will be received, but only if the receiving antenna is held with elements horizontal to match the horizontal aspect of the wire. Matching polarization maximizes signal and crossing polarization nulls the signal. More concisely, the received signal strength is proportional to the cosine of the angle between the relative aspects of the receiving antenna elements and the transmitting antenna wire, which we call the crossing angle (C_a). Thus, from any point the received signal is proportional to the product of $\text{sine}(V_a)$ and $\text{cosine}(C_a)$. Therefore, received signal strength is maximum when $V_a=90$ and $C_a=0$, and zero when $V_a=0$ or $C_a=90$. We stress the logical use of *and* and *or* in the preceding statement. It is unfortunate for discussion's sake that V_a and C_a cannot in all cases be conveniently expressed in an orthogonal system relative to the earth's surface. However, the following statements are true for head-on, side, and underneath positions of an observer; the special cases where these angles bear an orthogonal relationship to the earth's surface.

1. The strongest signals are received when an observer is to the side ($V_a=90$) using horizontal (to earth) polarization (forcing $C_a=0$).

2. A weaker signal is available from directly ahead of (or behind) a bird ($V_a =$ elevation angle to bird) and is maximized by using vertical polarization (forcing $C_a=0$).

3. A zero signal is received for horizontal (to earth) polarization (forcing $C_a=0$) only when directly ahead of (or behind) a bird.

4. A zero signal is received for a bird overhead (or below) by forcing $C_a=90$.

THE HEAD-NULL METHOD

This method required measurement of the azimuth to the bird while conditions (2) and (3) above apply. Although it is theoretically possible to verify geometrically a directly ahead (or behind) position by noting a finite signal with vertical polarization (2 above) and a zero signal with horizontal polarization (3 above), it is impossible to confirm a zero signal, because no matter how sensitive a receiver is, a signal always disappears into the receiver's background noise before the signal becomes zero. In practice, the head-null method required driving the tracking vehicle across the dead-ahead-of-the-bird position and noting the disappearance and reappearance of the horizontally polarized signal and the corresponding azimuths to the bird (obtained by using the vertically polarized antenna). Dead ahead (of the bird) refers to the bird's heading and not to the projection of its course (probable path). When the tracking vehicle is a small distance (relative to the distance to the bird) on either side of dead ahead of the bird, the strength of signals from both horizontally and vertically polarized receiving antennas is very sensitive to the elevation angle and the angle subtended at the bird by the tracking vehicle and the dead-ahead azimuth. Both of these angles are small and change rapidly as the

distance from the oncoming bird decreases. The net result of the angular asymmetry thereby introduced between points equidistant on each side of the dead-ahead-of-the-bird position, compounded by the difference in distance to the oncoming bird at these two points, is that the azimuth for $C_a=0$ (corresponding to the dead-ahead vehicle position and from which the bird's heading is determined) is not the mean of the azimuths of the disappearance and reappearance of the horizontally polarized signal. The asymmetry and distance problems are compounded on a road which angles toward the bird and are mitigated on a road which angles away from the bird, the degree of compounding or mitigation depending on the angles and distances involved. For these reasons and because it is practically impossible to correct quantitatively for them, this method is best executed at a high vehicle speed which approximately "freezes" the overall geometry while the azimuths of disappearance and reappearance are being measured. This "freezing" is more closely approximated for a bird several kilometers distant, because the angles and distance to the bird are limited to smaller percentage changes during the time required for vehicle movement. Unfortunately, the signals from a more distant bird are weaker due to distance and small V_a and elevation angle, which move the places for signal disappearance and reappearance farther apart and require the vehicle to cover a greater distance during the measurements. Additionally, it is harder to measure bearings accurately when travelling at high speed, and roads which were not at right angles to a bird's heading, as was the usual case, further complicated execution and interpretation. Therefore, the high precision typical of null measurements could not be realized in practice with the head-null method. The error range for the head-null estimates used in this paper (Table 1) was determined from the disappearance and reappearance

ance azimuths, which were definite bounds to the actual heading. We never purposely executed this method by crossing behind a bird, because falling behind was too often associated with permanently losing contact with a bird. An optimal tactic was to cross in front for a head-null estimate of heading and to turn around and obtain a crossover location and an altitude estimate by the means previously discussed.

THE CROSS-POLARIZATION METHOD

The cross-polarization method of obtaining a heading estimate is conceptually simple, a matter of getting under the bird and as in (4) above, rotating the receiving antenna about a vertical axis until a null indicated C_a was equal to 90° . This method was a natural companion to the crossover positioning method described previously. When the bird was in the cone of uncertainty, it was also in position for rotating the vertically pointed yagi antenna to the null position ($C_a=90^\circ$) and reading this position directly on the azimuth compass rose. In practice this maneuver was difficult, especially for birds at lower altitudes, because birds were not in the cone of uncertainty long enough to allow us to take good measurements. Actually, the cone of uncertainty represented a zone of confusion for the antenna operator, and it was not until late in the study that we became skillful in executing the cross-polarization method. We consider $\pm 4^\circ$ to be a sufficiently conservative base error range for these measurements, which were precise to 1° or 2° relative to the azimuth of the vehicle. The major source of error was in the vehicle's azimuth. The three cross-polarization heading estimates for Swainson's 7118 were obtained from an aircraft circling high above the bird. In general, an aircraft would be an excellent platform from which to use the cross-polarization

method if a belly-mounted dipole antenna could be rotated from inside the aircraft. In the case of Swainson's 7118 we used a hastily rented aircraft and pilot and were forced to use an antenna clamped to the footstep. The aircraft had to be circled without banking it (using rudder only) alternately clockwise and counterclockwise, because the antenna was not mounted symmetrically on the airframe. The mean of 10-12 readings, (half taken during clockwise circling), which ranged over 10° in azimuth, was used for each of the estimated headings. Frequent gyroscope calibration was required. Only three heading estimates were obtained because of time taken in navigating, fueling, locating the bird, and determining its altitude by the crude proximity method described in Cochran (1972). The last heading estimate was obtained as the bird descended through a large wind shear, and the associated track segment is without a track speed (Table 1) because the end point of the segment is where we located the bird on the ground without having detected the exact landing time.

IN SUMMARY

The procedures and methods are described above as set-piece operation, the making of a specific measurement at a specific time or when a certain situation pertained. In reality, bird tracking was more chaotic and required the gathering and recording of a large amount of potentially redundant data without knowing beforehand which would be good enough and which would be acquired at the right places and times to be useful for analysis. For example, we mentioned taking an elevation angle when the azimuth to a bird indicated that it was crossing a road ahead of the vehicle. In practice, azimuths and elevations were continually taken and recorded as the vehicle sped toward the bird. As likely as not, no good set of measurements was

available for the dead-ahead position, but was available when the bird was at some small (less than 20°) angle to the right or left of dead ahead. The geometry of all of the methods described is somewhat tolerant of deviations from the ideal situation as long as the deviations are taken into account. More often than not, attempts to execute the various procedures failed. We were fortunate that the data from the relatively small percentage of successful execu-

tions were sufficient to address the question of wind drift in thrushes.

The equipment used in this decade-old study was primitive by the standards of 1983, but the geometries of the methods remain fixed. Today, greater quantities of more accurate data could be obtained by the use of microcomputer control of several vehicle-mounted antenna systems, each specialized for gathering data appropriate to the geometry of a particular method.

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Afternoon Session Summary

James R. Karr

A 50th anniversary symposium or even the centennial meeting only 25 years ago would no doubt have been very different from that held in 1983 to commemorate the 125th anniversary of the Illinois Natural History Survey. Noteworthy differences might include the conceptual context of the scientific questions addressed and, especially, the increased technological dependency of late 20th-century biological science. But commonalities would also be obvious, the most important of which would be the firm foundation in natural history and the use of that knowledge in the interpretation of pattern and process in nature.

Each paper in the afternoon session draws on its own unique combination of these and other factors. Goldman takes his title from the classic paper of Stephen A. Forbes and forges an impressive array of observations and insightful interpretations to account for changes in Lake Tahoe. He demonstrates the importance of long-term research, of the integration of observations of apparently unrelated phenomena, indeed of the perseverance required to accumulate sufficient information to demonstrate pattern in nature and the process that generates and, in this case, degrades natural resources of considerable value.

Goldman's work at Lake Tahoe, like research that led to improvement of the Thames River (Gameson & Wheeler 1977) and Lake Washington (Edmondson 1977), demonstrates that the causes of environmental degradation can be identified. The work at Tahoe

parallels studies of the Illinois River conducted by staff of the Illinois Natural History Survey (Mills et al. 1966; Starrett 1972; Bellrose et al. 1983). The challenge for the Natural History Survey in the future is to do for Illinois streams what Goldman has done for Lake Tahoe. But the lesson of Lake Tahoe is more than "the lake is damaged and may even face ecological destruction" – the land itself may be destroyed as well through erosion and other degradation. In Illinois we must take action to protect rivers *and* the land they drain. Without them even the most innovative technological society faces overwhelming environmental crises.

The second paper of the afternoon session is concerned with very different geographic and biological scales. The concern of Philipp, Kaminski, and Whitt about the genetic integrity of largemouth bass populations develops from a careful integration of natural history, population genetics, and evolution. The application of new technologies to identify genetic traits allows a more sophisticated view of the responsibility of fishery managers and, indeed, of resource managers in a broader context. The folly of mixing gene pools of northern and southern largemouth bass is demonstrated through documentation of the negative effects of careless stocking programs on regionally adapted populations. We see modern technology, allowing sophisticated analysis of pattern, combined with good old-fashioned natural history to yield the potential for more informed management of natural resources. More conventional forms of management techniques, such as habitat manipulation, harvest regulation, propagation, and stocking, must be combined with genetic management.

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Page reviews reproductive behavior and its evolution in about 150 species of percid fishes. Spawning behavior provides the focus for an analysis of an array of life-history attributes that vary in concert with reproductive behavior. The accumulation and integration of detailed information on the biology of many species provide a foundation for the synthesis of theoretical insights and help to define management options and strategies.

With Cochran and Kjos we emerge from the water to explore the biology of bird migration. Specifically, they deal with the problems posed by wind and overcast skies for thrushes on the long voyage between breeding and wintering grounds. I can attest to the precision of these navigational skills because, like others, I have had migrant warblers and thrushes return to the same wintering territory in Panama after annual trips to breed in North America.

Cochran and Kjos document the ability of thrushes to compensate for wind and cloud cover during migration. With an insightful combination of technical sophistication and natural-history wisdom, avian migration is not made simple, but it at least becomes more comprehensible. Cochran and Kjos show that thrushes have preferred flight directions and speeds for accomplishing their navigational feats. They seek winds at a variety of heights that provide for these preferences. When winds are such that flight speeds are reduced to less than 2 m/s, the birds simply land and wait for better conditions.

Throughout this set of papers, natural-history information accumulated laboriously from tedious observations over extended periods combines with sophisticated applications of modern technology and biological theory to yield knowledge of factors that will, when taken collectively, provide the opportunity for better management of natural resources as well as greater understanding of our natural world.

As I listened to these presentations, several general thoughts came to mind. These thoughts involve inherent difficulties in the integration of knowledge from various biological disciplines and the incorporation of that knowledge in a broader societal context.

1. The study of organisms and the interpretation of natural-history data are key responsibilities of the Natural History Survey. The job has been well done in the past but will become more difficult in the future because biologists face the same problem that herbivores face in dealing with plant chemistry while feeding and in avoiding predators. In the evolutionary battle between food and feeder, each is constantly trying to get one step ahead of the other. In a very real sense human society is on the same treadmill in the use of pesticides (evolution of pest resistance) and technology (the inability of biological systems to change rapidly enough to survive the growth of that technology). I am confident that, unless we destroy the biological systems of earth, including ourselves, no long-term panacea will be forthcoming because of the evolutionary process. In the end, *Homo sapiens* as we know the species may simply become extinct through evolutionary processes much as *H. erectus* was replaced.

This continuing evolutionary process is both good and bad. Good because we can continue to enjoy the vitality, excitement, and challenge of biological research; bad because we will always be racing to keep up with insults to the integrity of our planet's thin biological mantle while we try to extract goods and services from that mantle.

2. The biologist's perspective must always be both microscopic and macroscopic. Short-term or local solutions should not be used without careful evaluation of their probable long-term and regional (even national and international) implications. Perhaps the most difficult task facing biologists will be the integration of information obtained over a hierarchy of spatial and

temporal scales. We must simultaneously take a close look at detail while standing back to view systems as integrated wholes.

3. Interactions between basic and applied biologists have often been less than satisfactory. Many theoreticians, often with limited field experience, have looked down upon managers, perhaps because of a disdain for mission-oriented research. Conversely, resource managers have been reluctant to evaluate the merit of recent theoretical developments, perhaps because they are too "esoteric." That the two can effectively merge, indeed depend on each other, is demonstrated by the papers presented here and by the research going on at INHS. The complexity of important resource issues requires the effective merger of the two camps and cooperation to their mutual benefit.

4. As I have noted several times, a substructure of systematic and natural-history information (of inherent value on their own, as are music and art) is essential as a backdrop for virtually all natural-resource decisions. Theoretical

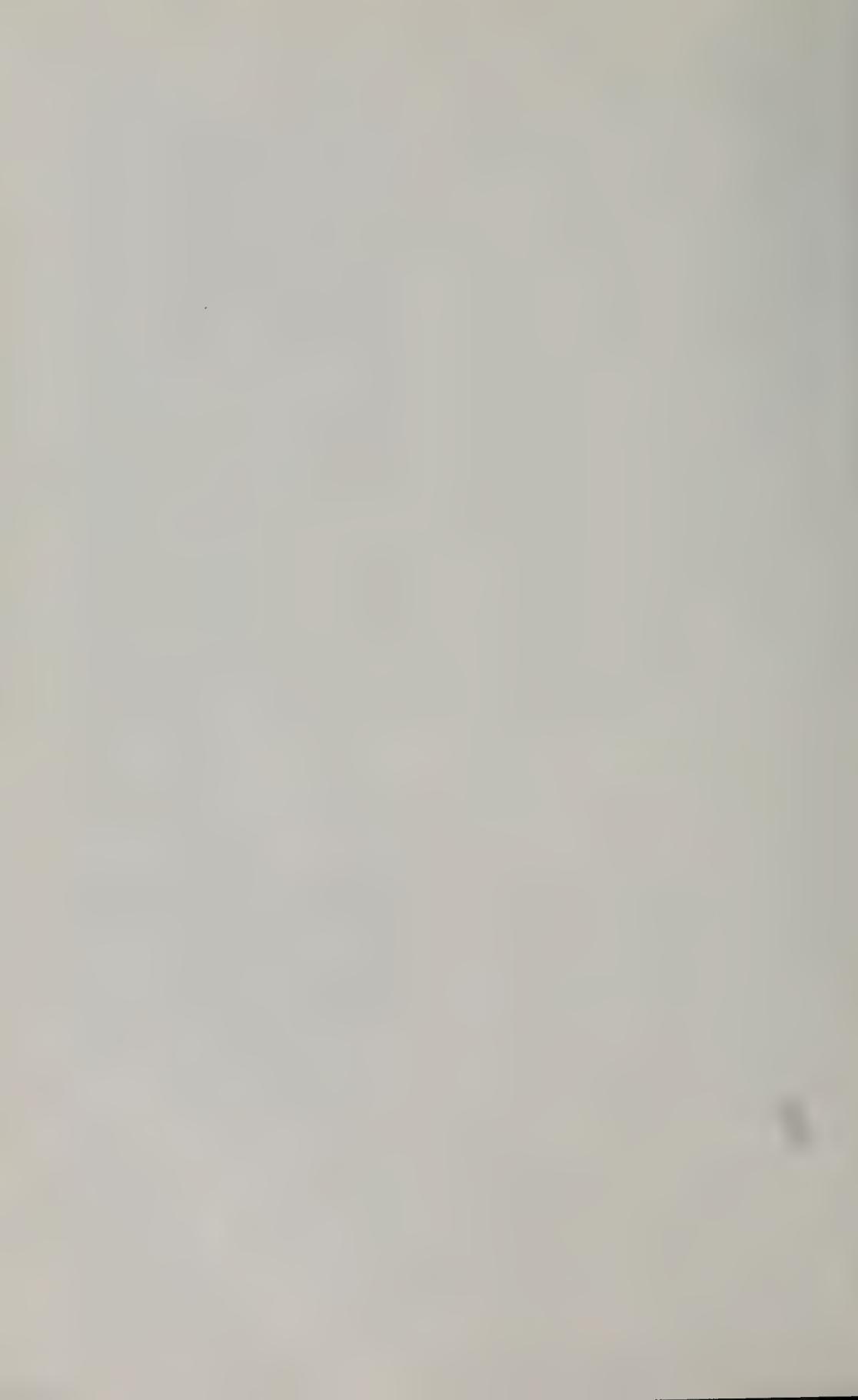
considerations alone are inadequate for informed resource management.

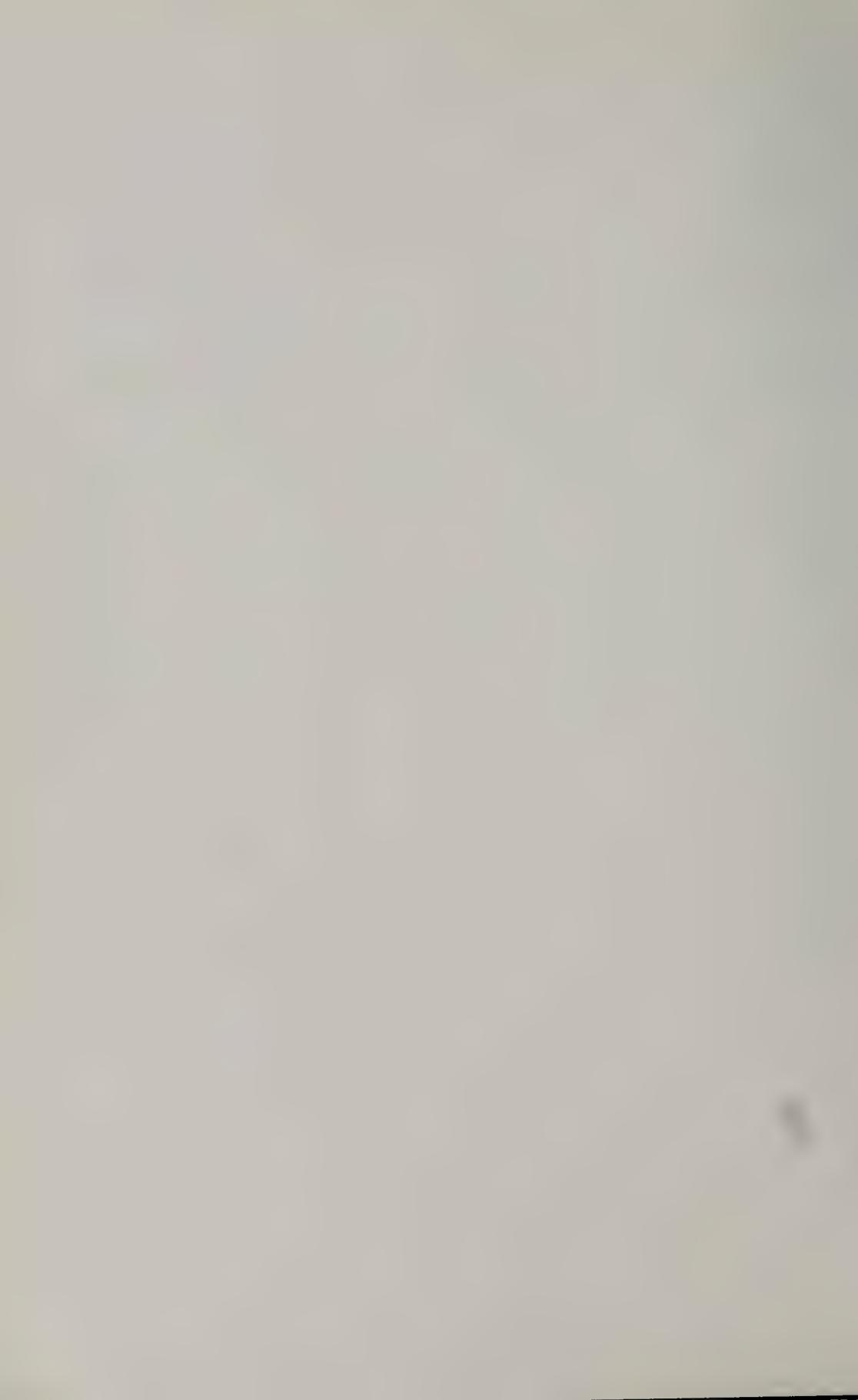
5. Finally, biologists must recognize their insights and integrate them into the social, political, and economic contexts in which societal decisions are made. Biologists can no longer advocate policies that ignore any of these realities. Similarly, economists, politicians, and others cannot ignore long-term trends in the degradation of life support systems as if they were not relevant to current and future conditions for human society. If biologists do not participate as equal partners, biology will be ignored, or perhaps worse, we will continue to base decisions on the input of those not familiar with the facts of biology.

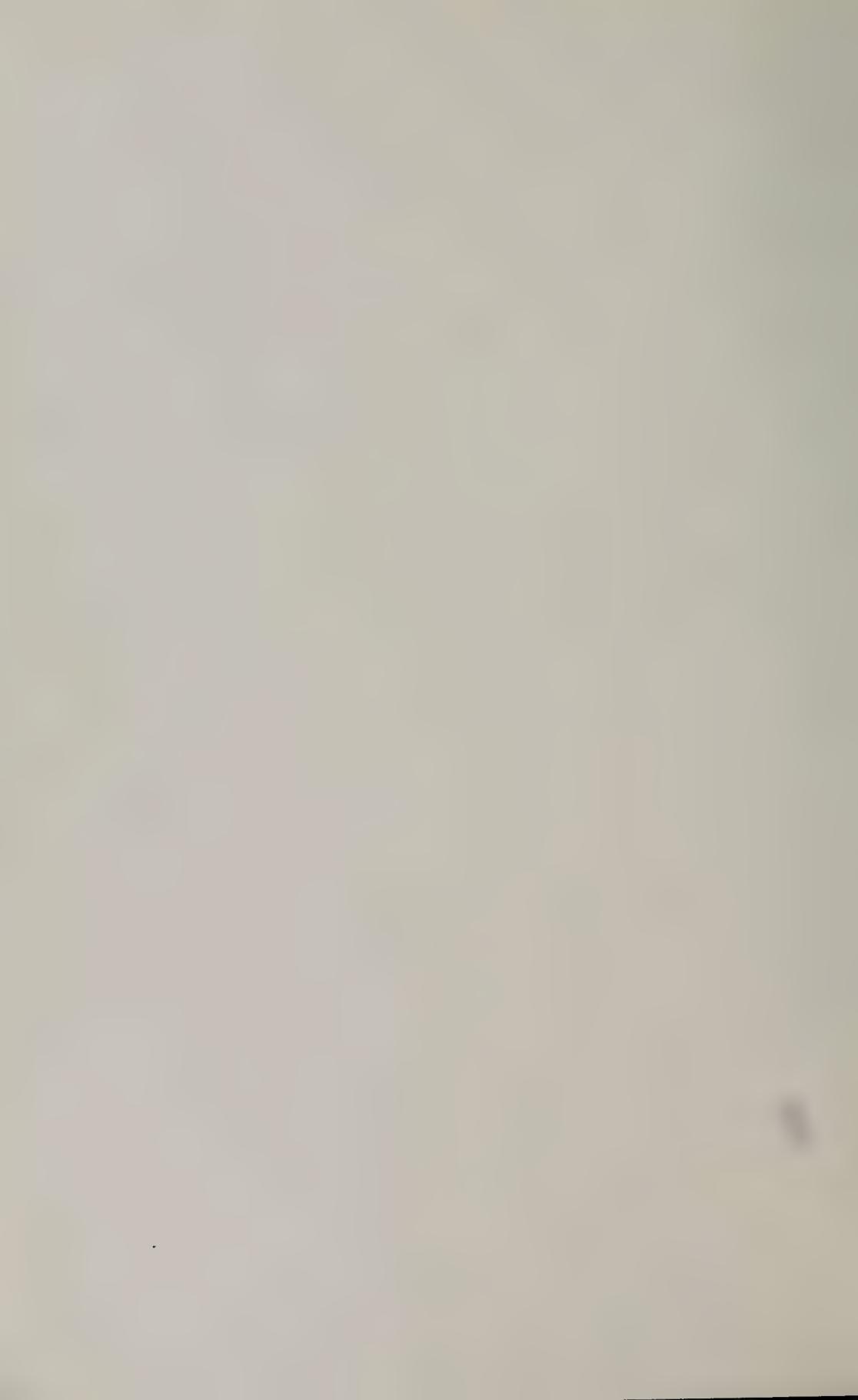
In summary, challenges to biologists for the future are immense. Looking back on the last 25 years, I see growth and intellectual vitality. I expect the future to be even more exciting and look forward to learning more about the growth at the 150th anniversary celebration of the Illinois Natural History Survey.

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ILLINOIS
Natural History Survey
BULLETIN

The Crayfishes and Shrimp
(Decapoda) of Illinois

Lawrence M. Page

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NATURAL HISTORY SURVEY DIVISION
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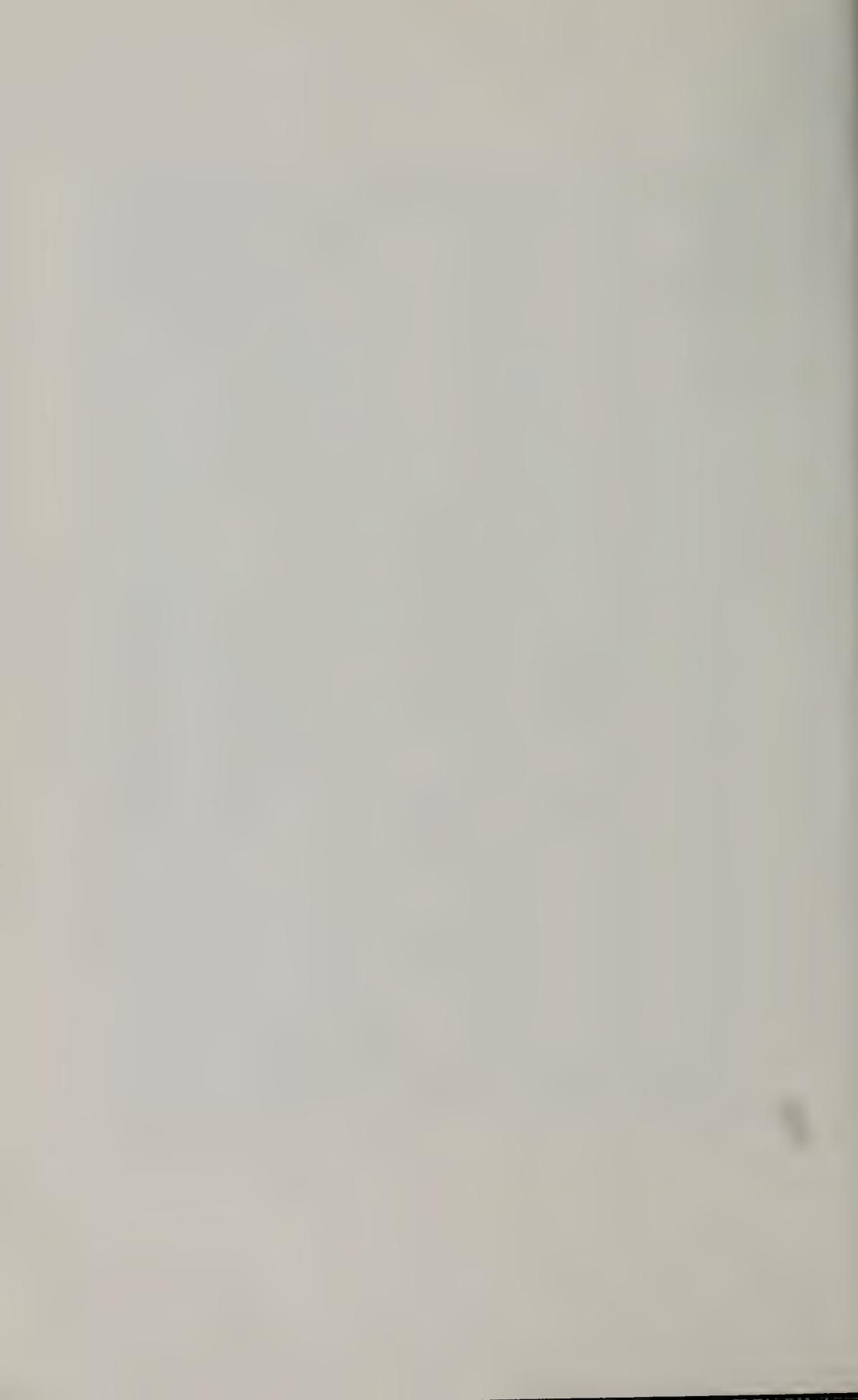


Frontispiece: *Orconectes illinoiensis* form I male from Gibbons Creek, Herod, Pope County, Illinois, 4 March 1973.

This report is dedicated to

MRS. BERNICE SWEENEY

on the occasion of her retirement and in honor of her 22 years of service to the Section of Faunistic Surveys and Insect Identification of the Illinois Natural History Survey. Her numerous helpful contributions to this and other studies are sincerely appreciated.



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The Crayfishes and Shrimps (Decapoda) of Illinois

Lawrence M. Page

Crayfishes and shrimps (Decapoda) are conspicuous components of the aquatic environments of Illinois. Although only 23 species are known to inhabit the state (Table 1), they are among our largest aquatic invertebrates and often are present in large populations.

HISTORICAL STUDIES OF ILLINOIS DECAPODS

Most of the historical information available on crayfishes and shrimps of Illinois is that published by Forbes (1876), Rietz (1912), and Brown (1955). The "List of Illinois Crustacea" was, as Forbes (1876) noted, "a first contribution to the knowledge of our crustacea," and contained the "results of a single season's work." Included in the list were *Macrobrachium ohione*, *Palaemonetes kadiakensis* (as *P. exilipes*), *Procambarus acutus* (including *Cambarus stygius*), *P. gracilis*, *Orconectes immunis*, *O. propinquus*, *O. rusticus* (as *O. placidus*), *O. virilis* (including *O. wisconsinensis*), and *Cambarus diogenes* (as *C. obesus*). Hagen, in his earlier (1870) monograph on North American crayfishes, had noted the occurrence in Illinois of all of the above crayfishes except *P. gracilis*. Hagen erroneously also recorded for Illinois *P. troglodytes*, an Atlantic Coast species.

A bachelor's thesis submitted to the University of Illinois in 1912 (Rietz 1912) and entitled *Ecological Relations of the Crawfishes of Illinois* added to the list of Illinois species *O. indianensis*, *C. robustus* (also listed for Illinois by Faxon 1885), *C. tenebrosus* (as *C. bartoni brevis*), and *Fallicambarus fodiens*

(as *C. argillicola*, also listed for Illinois by Faxon 1890).

A doctoral dissertation submitted to the University of Illinois in 1955, *The Biology of the Crayfishes of Central and Southeastern Illinois* (Brown 1955), was based on extensive collecting (at 410 stations) in the Sangamon, Wabash, and

Table 1.—Classification of the crayfishes and shrimps of Illinois, primarily following Holthuis (1952) and Hobbs (1974b).

Order Decapoda
Family Palaemonidae
Genus <i>Macrobrachium</i>
1. <i>M. ohione</i> (Smith)
Genus <i>Palaemonetes</i>
2. <i>P. kadiakensis</i> Rathbun
Family Cambaridae
Subfamily Cambarellinae
Genus <i>Cambarellus</i>
Subgenus <i>Dirigicambarus</i>
3. <i>C. shufeldtii</i> (Faxon)
Subgenus <i>Pandicambarus</i>
4. <i>C. puer</i> Hobbs
Subfamily Cambarinae
Genus <i>Procambarus</i>
Subgenus <i>Girardiella</i>
5. <i>P. gracilis</i> (Bundy)
Subgenus <i>Ortmannicus</i>
6. <i>P. acutus</i> (Girard)
7. <i>P. viaeviridis</i> (Faxon)
Subgenus <i>Scapulicambarus</i>
8. <i>P. clarkii</i> (Girard)
Genus <i>Orconectes</i>
9. <i>O. illinoiensis</i> Brown
10. <i>O. immunis</i> (Hagen)
11. <i>O. indianensis</i> (Hay)
12. <i>O. kentuckiensis</i> Rhoades
13. <i>O. lancifer</i> (Hagen)
14. <i>O. placidus</i> (Hagen)
15. <i>O. propinquus</i> (Girard)
16. <i>O. rusticus</i> (Girard)
17. <i>O. stamardi</i> Page
18. <i>O. virilis</i> (Hagen)
Genus <i>Fallicambarus</i>
Subgenus <i>Creaserinus</i>
19. <i>F. fodiens</i> (Coutle)
Genus <i>Cambarus</i>
Subgenus <i>Erebicambarus</i>
20. <i>C. tenebrosus</i> Hay
21. <i>C. rusticiformis</i> Rhoades
Subgenus <i>Lacunicambarus</i>
22. <i>C. diogenes</i> Girard
Subgenus <i>Puncticambarus</i>
23. <i>C. robustus</i> Girard

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Ohio river systems. To the growing list of Illinois species, including *Cambar-ellus shufeldtii* and *O. lancifer* reported in the interim by Faxon (1914), Brown added *P. clarkii*, *O. kentuckiensis*, and *O. illinoiensis* (described by Brown in 1956).

Statewide collections made for the present survey have added *Cambarellus puer*, *P. viaeviridis*, *O. placidus*, *O. stannardi*, and *Cambarus rusticiformis* to the list of Illinois species. The list of Illinois shrimps and crayfishes now stands at 23 species.

METHODS

Collecting for the present survey of Illinois decapods spanned a decade (March 1972 to September 1982). Collections were made at 1,294 localities (Fig. 1) in all counties of the state (Fig. 2), but were most heavily concentrated in southern Illinois, where the largest diversities of habitats and species occur. All species of aquatic Malacostraca (Isopoda, Amphipoda, Decapoda) present at each site were collected. A plethora of taxonomic problems among the isopods and amphipods prevent their inclusion in this report. Lewis & Bowman (1981) and Lewis (1982) recently have published distributional studies on the subterranean isopods of Illinois.

A dot on Figure 1 indicates that one or more malacostracans were collected at that locality. Stations sampled at which no species were found are not shown on the map. Although the absence of malacostracans at a site can be informative, it may indicate only that insufficient time was spent in searching. Old records (pre-1972) are included on the species distribution maps when they document significant changes in distribution (e.g., for *Macrobrachium ohione*). A few recently (1984) discovered localities are plotted for *O. rusticus* and *O. stannardi*.

Because ecological analyses were attempted for each species, all individuals encountered usually were preserved; if large numbers were encoun-

tered, only the early portion of the sample was preserved, and subsequently collected individuals were returned to the water.

Specimens usually were collected by dipnetting, minnow seining, or by digging them from their burrows. Malacostraca require cover, and the most successful method of collecting was to place a dip net downstream from, or (in standing water) next to, accumulations of stones, brush, living vegetation, etc., and to kick through the material, thereby dislodging specimens into the dip net. The most successful method of collecting burrowers was to dig into the burrow down to the water table, splash the water, wait for the curious crayfish to investigate the disturbance, and grab it. This worked well in the relatively shallow burrows of *C. diogenes* but less well in the deeper burrows of *P. gracilis*, *P. viaeviridis*, and *F. fodiens*.

Specimens were placed in 10-percent formalin if large, in 70-percent ethyl alcohol if small enough to go into a 3-dram vial. In the laboratory, specimens were washed in water, identified, counted, sexed, and placed in 70-percent ethyl alcohol for permanent storage in the Illinois Natural History Survey collection. Records were kept on the presence of form I males and of females carrying eggs or young.

Measurements of crayfishes are given in millimeters of carapace length (CL). Length-frequency distributions are presented for those species for which no published growth or longevity data are available and of which large collections were made in Illinois. Keys, diagnoses, and descriptions are based on Illinois populations only. Taxa are arranged phylogenetically, except within *Orconectes* where species are arranged alphabetically because of our present lack of understanding of interspecific relationships.

EXTRALIMITAL SPECIES AND STUDIES

Several species of crayfishes not found



Fig. 1.—Localities in Illinois where aquatic Malacostraca were collected between March 1972 and September 1982.

in Illinois live in eastern Missouri and western Kentucky in streams draining directly into the Mississippi and Ohio rivers, and they eventually may be found, presumably as waifs, in Illinois. In Missouri, these are *Orconectes harrisoni*, *O. hylas*, *O. luteus*, *O. medius*, *O. nais*, *O. peruncus*, *P. punctimanus*, *O. quadruncus*, and *Cambarus hubbsi*,

and in Kentucky, *O. bisectus* and *O. tricuspis*. It is more likely, however, that additions to the Illinois fauna will result from human introductions, deliberate or otherwise, and could originate from anywhere.

Regional publications on freshwater decapods of North America are available for Alabama (Bouchard 1976),



Fig. 2.—Counties of Illinois.

Arkansas (Bouchard & Robison 1980), California (Riegel 1959), Colorado (Unger 1978), Florida (Hobbs 1942), Georgia (Hobbs 1981), Indiana (Hay 1896; Eberly 1955), Iowa (Phillips 1980), Kansas (Williams & Leonard 1952), Kentucky (Rhoades 1944a), Louisiana (Penn 1952, 1956, 1959; Penn & Marlow 1959), Maryland (Meredith & Schwartz 1960), Michigan (Pearse 1910; Creaser 1931), Nebraska (Engle 1926), New Jersey (Fowler 1912; Francois 1959), New York (Crocker 1957), Ohio (Turner 1926; Rhoades 1944b), Oklahoma (Creaser & Ortenburger 1933; Reimer 1969), Ontario (Crocker & Barr 1968), Pennsylvania (Ortmann 1906), Texas (Penn & Hobbs 1958), West Virginia (Newcombe 1929), Wisconsin (Creaser 1932), the Cumberland Plateau and Cumberland Mountains (Bouchard 1976), New England (Crocker 1979), the Ozark Plateaus and Ouachita Provinces (Williams 1954), the Southern Appalachians and Cumberland Plateau (Ortmann 1931), and Mexico (Villalobos 1983).

Extremely useful publications on crayfishes are Hobbs' key and checklist to all described crayfishes of North America (Hobbs 1972a, 1974b).

GEOLOGICAL HISTORY OF ILLINOIS AND ZOOGEOGRAPHY OF NATIVE ILLINOIS DECAPODS

Prior to settlement by Europeans, Illinois was covered by oak-hickory forest, maple-basswood forest, and bluestem prairie. Today much of Illinois has been cleared and developed, primarily for agriculture and urbanization.

The oldest prominent physiographic features of Illinois are remnants of the Appalachian Revolution near the close of the Paleozoic. The intense folding and faulting during the formation of the Appalachian Mountains, and the more moderate folding and tilting to the west, created the template for the topographic diversity present today in

southern Illinois (Fenneman 1938). During the Mesozoic, the seas enlarged, and by the Cretaceous they inundated the Coastal Plain as far north as southern Illinois. The subsequent uplifting of the continent in the late Cretaceous exposed much of the Coastal Plain, including the flatlands persisting today as swamps along the lower Ohio River in southern Illinois (Fenneman 1938).

In the late Tertiary the Mississippi River ran along the western edge, and the lowermost Ohio River followed the eastern edge, of Crowley's Ridge (a ridge on the Coastal Plain of southeastern Missouri and northeastern Arkansas). The two great rivers met near where Helena, Arkansas, is now (Fenneman 1938; Fisk 1944). The Ohio River was comparatively small, had its headwaters in southern Indiana and central Kentucky (Wayne 1952), meandered across southern Illinois through the present Cache River valley, and, after being joined by the Cumberland and Tennessee rivers, flowed south to its confluence with the Mississippi. It is uncertain whether the Tennessee River joined the Ohio above the entrance of the Ohio into the Cache lowland or whether it flowed from its present mouth down the present course of the Ohio and Mississippi rivers and joined the Ohio near southern Tennessee.

The Mississippi River followed much of its present course in Minnesota and Wisconsin, then cut through northern Illinois (Willman & Frye 1970), where it was joined by its major tributary, Teays River, and flowed south along the present course of the Illinois River. The Teays River began along the western side of the Blue Ridge Mountains of Kentucky, Virginia, and West Virginia, flowed northward to central Ohio, then turned west across central Indiana and Illinois through the Mahomet Valley to the Mississippi (Horberg 1945; Wayne 1952; Teller 1973); or in Indiana turned south through the present Wabash Valley to the Ohio River (Fidlar 1948). It may be that an early Pleistocene ice advance blocked the original course of

the Teays through the Mahomet Valley and diverted it into the Wabash Valley (Wayne 1952).

In the Pleistocene, continental ice caps advanced in stages and interrupted the progress of post-Tertiary erosion cycles. In glaciated areas, topographic diversity was reduced, valleys were obstructed, and river courses were altered. Areas of low relief, including the Central Lowlands, were covered by deep deposits of drift, forming undulating till plains.

The earliest glacial invasions, the Nebraskan and the Kansan, extended into northern Missouri, southern Illinois, southern Indiana, and southern central Ohio. Streams which formerly had drained northward into Hudson Bay and eastward to the Atlantic Ocean were blocked and diverted to the Mississippi basin. The lower Teays River was eliminated, and its tributaries were diverted into the ancestral Ohio River (Flint 1971; Hocutt, Denoncourt, & Stauffer 1978), greatly increasing the area drained by the Ohio.

To the west of the Mississippi River the Kansan ice cap extended farther south than other Pleistocene glaciers and terminated in Missouri, approximately along the present course of the Missouri River. East of the Mississippi River the Kansan ice cap was exceeded in its southern extent by the later Illinoian glacier, which in some areas reached the present course of the Ohio River. The Illinoian leveled or buried in drift most of Illinois. Because it was the last of the glaciers, drift of the Wisconsinan covers a large area of Illinois (Fig. 3) and its ecological impact is enormous.

As the ice caps retreated, huge quantities of drift were left behind, filling river channels and valleys. Mounds of drift (moraines) sometimes reached heights of 30 m or more and widths of several kilometers. Moraines generally were concentric to one another and, when they formed extensive lakes, lacked drainage outlets. Ultimately, low

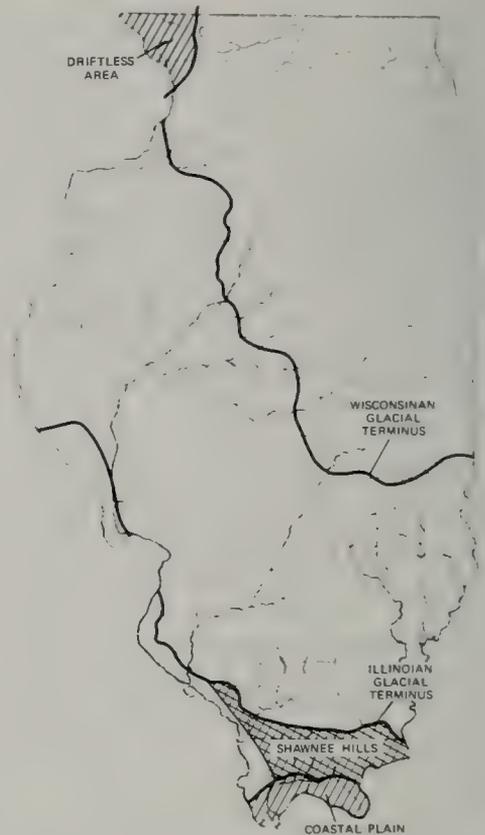


Fig. 3.—Glacial boundaries and major physiographic features in Illinois.

points of the moraines became drainage outlets. Water flowing from one lake to another along the concentric moraines gradually formed streams and, eventually, complete drainage systems. With drainage, the process of erosion began. As sediments were carried into lakes, the coarser particles (sand and gravel) were deposited and the smaller particles (silt and clay) were carried away. Eventually, the lakes became marshes and, later, prairies. Thick layers of sand were sometimes left behind, such as those found today in the Kankakee River system of Illinois and Indiana. Dunes were subsequently formed as the wind piled sand into hills.

Throughout the Pleistocene, an area of southwestern Wisconsin and northwestern Illinois remained unglaciated.

This "Driftless Area" supports a topographic diversity, due in part to recent erosion, absent in the glaciated region. Interglacial periods, the Aftonian, Yarmouth, and Sangamon, were characterized by warmer and drier climates similar to that of today (Braun 1950).

The Wisconsinan ice cap was up to 3 km thick and in some areas, melting, interrupted by periodic advancement, took more than 10,000 years (Clark & Stearn 1960). New drainage systems eroded the glaciated area, and the junction of the Ohio and Mississippi rivers moved progressively northward (Matthes 1933; Fisk 1944). The Great Lakes were formed as water was impounded in the former Laurentian River basin. The present drainages of Illinois (Fig. 4) are discussed in detail by Forbes & Richardson (1908) and Smith (1971).

Pleistocene glaciers that covered most of Illinois had profound effects on the distributions of organisms. The principal zoogeographic effects were the elimination of populations (probably including entire species) and the displacement of species farther south than they had occurred preglacially. Principal postglacial zoogeographic events were the reinvasions of glaciated regions and the crossing of previously insurmountable basin divides through the newly established drainage systems.

The Illinoian glaciation reached within 30 km of the northern boundary of the Mississippi Embayment in southern Illinois (Willman & Frye 1970). A few species may have maintained populations in the surviving uplands, the Shawnee Hills of southern Illinois (Fig. 3).

It must have been easy for animals to invade the new drainages of the glaciated region of Illinois as they became connected to the existing Ohio and Mississippi rivers. Postglacial invasions (or reinvasions) undoubtedly were mostly from the south; i.e., the Ozark Plateau, Mississippi Embayment, Interior Lowland, Appalachian Plateau, and ephemeral drainages along the

southern edges of the glaciers. Because all of northern North America (48° and north) except a large part of Alaska was covered by ice, the only possible non-southern postglacial origins of the decapod fauna of Illinois are east coast drainages (presumably via the Susquehanna Outlet connecting the eastern Great Lakes and the Susquehanna River), the Driftless Area of northwestern Illinois, and the upper Missouri River drainage. Some species may have invaded from more than one refugium.

Species likely, because of their present distributions, to have invaded from the south are *M. ohione*, *P. kadiakensis*, *P. acutus*, *F. fodiens*, and *C. diogenes*. All but *C. diogenes* are sluggish-water inhabitants that probably invaded the low-gradient drainages of Illinois from similar low-gradient streams on the former Mississippi Embayment. *C. diogenes* presumably moved from the Shawnee Hills and other southern areas into new drainages to the north.

P. gracilis, *O. immunis*, and *O. virilis* now occupy western drainages that were unglaciated, principally the upper Missouri, and they probably entered Illinois from the west. The eastward movement of other grassland and plains animals during the recent Xerothermic Period is discussed by Smith (1957).

O. propinquus now occurs only in glaciated areas of eastern North America but is most closely related to species living in streams in unglaciated southern Ohio, eastern Kentucky, West Virginia, and Pennsylvania (Fitzpatrick 1967). It and *C. robustus* probably invaded Illinois from the east. *C. robustus*, as discussed in the species account, has since retreated from Illinois.

O. stannardi does not now occur in areas considered to have been Pleistocene refugia, and it may be autochthonous to the Little Wabash River system of Illinois. Autochthonism would require it to have differentiated from its closest relatives since the Pleistocene.

The present decapod fauna of Illinois

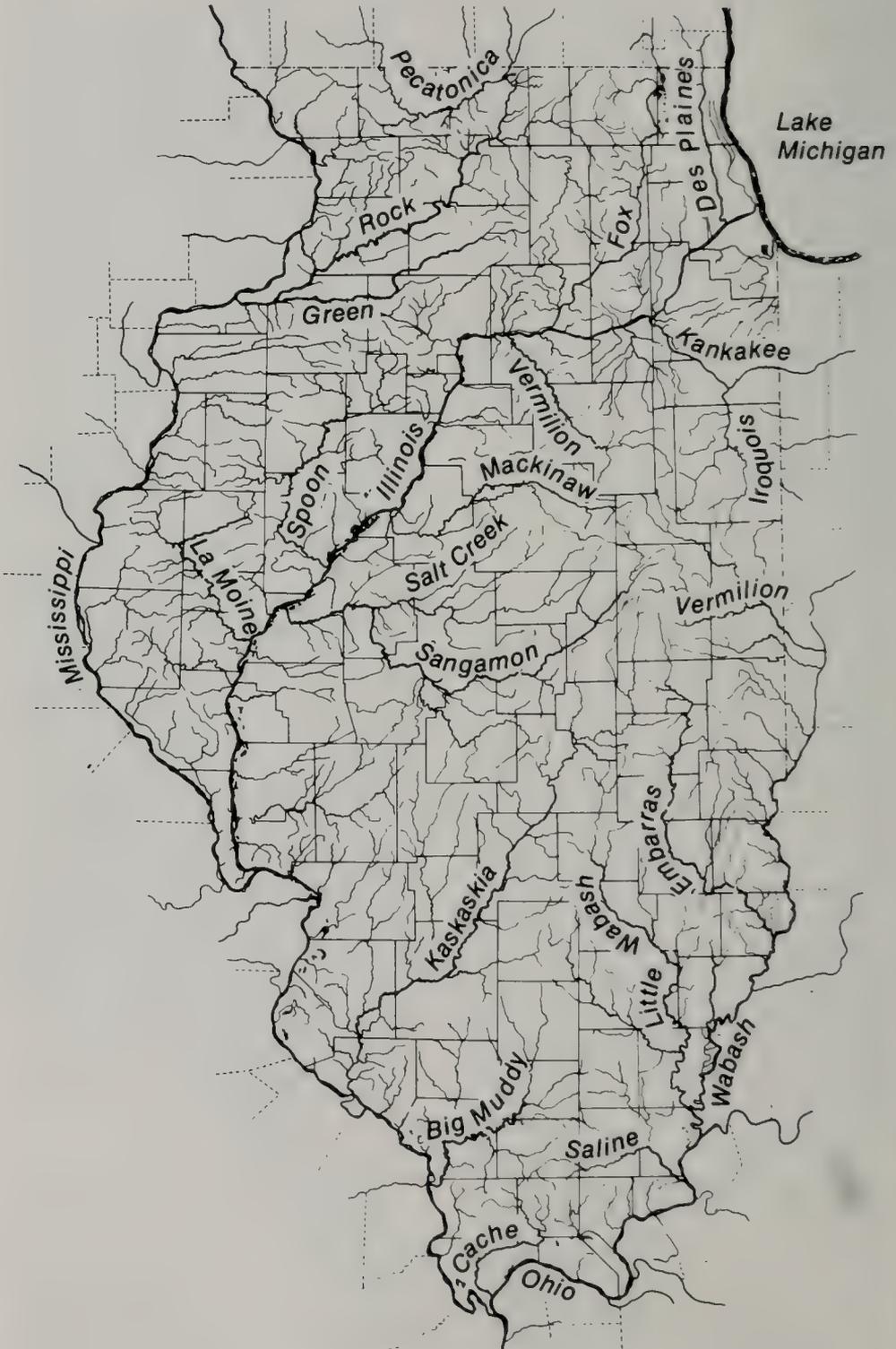


Fig. 4.—Present drainages of Illinois.

Table 2.—Native species grouped according to their distributions among physiographic divisions of Illinois.

Coastal Plain	Shawnee Hills	Lowland	Glaciated Area	Statewide
<i>C. puer</i>	<i>O. illinoiensis</i>	<i>M. ohione</i>	<i>P. gracilis</i>	<i>P. acutus</i>
<i>C. shufeldtii</i>	<i>O. indianensis</i>	<i>P. kadiakensis</i>	<i>O. propinquus</i>	<i>O. immunis</i>
<i>P. clarkii</i>	<i>O. kentuckiensis</i>		<i>O. stannardi</i>	<i>F. fodiens</i>
<i>P. viaeviridis</i>	<i>O. placidus</i>		<i>O. virilis</i> ^a	<i>C. diogenes</i>
<i>O. lancifer</i>	<i>C. tenebrosus</i> ^b		<i>C. robustus</i>	

^aAlso found on the Coastal Plain.

^bAlso found in one locality in east-central Illinois.

may be divided into Coastal Plain, Shawnee Hills, Lowland, Glaciated-area, and Statewide species groups (Table 2). The Statewide species group includes two burrowers (*C. diogenes* and *F. fodiens*) and two sluggish-pool inhabitants (*P. acutus* and *O. immunis*).

Those species found on the Coastal Plain and in the Shawnee Hills presumably have been there for a long time and have undergone little or no post-glacial dispersal. Those in the glaciated regions must have invaded or re-invaded after glaciation (i.e., within the past 10,000–100,000 years) or must have speciated since then. Illinois' endemic decapods, *O. illinoiensis* and *O. stannardi*, and its near-endemics, *O. kentuckiensis* and *O. indianensis*, occur south of the boundary of the Wisconsin glaciation. All except *O. stannardi*, which occurs on Illinoian glacial till, are occupants of the Shawnee Hills.

NATURAL HISTORY

Crayfish Life Cycle

During the mating season, form I males (males in which one or more of the terminal elements on the gonopods [first pleopods] are corneous) actively seek receptive females by grasping other crayfishes with their chelae. When a male or nonreceptive female is grasped, it resists, and the aggressive male releases his catch and continues searching. When a receptive female is grasped, it stretches the antennae, chelae, and walking legs forward, curves the end of the abdomen ventrally and anteriorly,

and becomes motionless. The male turns the female on her back, holds her chelae in his, positions his abdomen over hers (still curved forward), inserts the ischial hooks on his pereopods into the coxal membranes of the pereopods of the female (which locks the two crayfish together), and inserts the tips of his gonopods in the annulus ventralis (seminal receptacle) of the female. Sperm travel from the reproductive openings on the bases of the fifth pereopods along the gonopods to the annulus ventralis, and mating is completed. A waxy sperm plug projecting from the annulus indicates that the female has recently mated.

Frequencies of form I males among Illinois collections of crayfishes indicate that most matings occur between September and March, although considerable interspecific variation occurs. Species of *Cambarellus* have a high incidence of form I males throughout the year.

Sperm are carried by the female until oviposition (egg laying), which in Illinois occurs mostly in March, April, and May but may begin in some species as early as December or January. In preparation for oviposition the female cleans the underside of her abdomen, mostly through brushing motions of the fifth pereopods. During oviposition the female turns on her back, curls the abdomen forward, and from glands on the abdomen secretes a clear, sticky substance (glair) which fills the area between the curled abdomen and the thorax. Sperm and eggs are released



Fig. 5.—Female *Orconectes immunis* with eggs attached ("in berry").

into the glair from the annulus ventralis and external openings of the oviducts, respectively. Following oviposition, the glair hardens and cements the fertilized eggs to the pleopods. With eggs attached to her abdomen, a female crayfish is said to be ovigerous or "in berry" (Fig. 5).

Eggs are carried by the female for 2-20 weeks, depending on the water temperature. When the eggs hatch, the young remain attached to the abdomen and are carried by the female through three instars. The first juvenile instar has extremely large eyes, a yolk-filled carapace, an incomplete abdomen, and hooked chelae. First instars attach to the female with the hooked chelae and by a stalk linking the telson of the instar to the abdomen of the mother. After 2-7 days first instars molt to second instars, which are more adultlike but still lack a fully developed abdomen and cling to the mother's abdomen by their chelae. After another 4-12 days, another molt results in the third instar, which closely resembles the adult and hangs onto the mother with its chelae and pereopods. It may leave the protection of the mother for short periods. Subsequent instars are free living. Growth proceeds through a series of 6-10 molts during the summer, and sexual maturity may be attained by

late summer or early fall. Sexual maturity in the male corresponds to a molt to form I. The first molt following the mating period returns the male to a nonreproductive state (form II) in which the gonopods are without corneous tips. Following copulation, females do not molt until after the young permanently have left. In Illinois, crayfishes appear to survive a maximum of two reproductive seasons.

In nonburrowing Illinois crayfishes, all aspects of their life history occur in surface waters. Burrowing species spend variable amounts of time in surface waters. Adults of *P. gracilis* and *P. viaeviridis* leave their burrows and enter temporary bodies of water to mate. *F. fodiens* leaves its burrows to mate, and females remain out of their burrows during the period in which they carry their eggs and young. Young of these three species remain above ground in temporary water as long as the water remains; as the water table recedes below the surface, they burrow. Adults of *P. viaeviridis* and *F. fodiens* may be found above ground in Illinois only during periods of late winter-to-spring flooding (January to May). Sexually mature *P. gracilis* leave burrows on warm rainy nights but otherwise seldom are found out of their burrows. Adults of *C. diogenes* leave their burrows on the banks

of streams more often than do the species just mentioned, perhaps to forage as well as to mate, but do so more frequently during the mating and egg- and young-carrying seasons.

Freshwater Shrimp Life Cycle

Females carry eggs attached to their pleopods between April and August in Illinois and between February and October farther south. The eggs hatch, and free-swimming larvae pass through

six stages in about 3 weeks, described in detail for *Palaemonetes kadiakensis* by Broad & Hubschman (1963). Larvae and juveniles increase, and adults decrease, in abundance through the summer. Adults disappear in late summer-early fall, corresponding to a maximum life span of about 1 year in *Palaemonetes kadiakensis* and 2 years in *Macrobrachium ohione*. The largest adults mature and reproduce earliest in the year. Observations on copulation apparently are unrecorded.

KEY TO ILLINOIS SPECIES

Morphological characteristics used to describe and identify crayfishes and

shrimps in keys and systematic accounts are illustrated in Fig. 6-9.

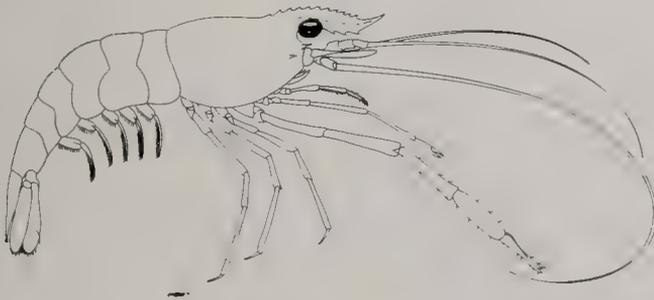
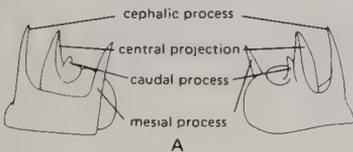
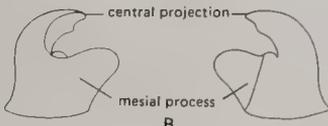


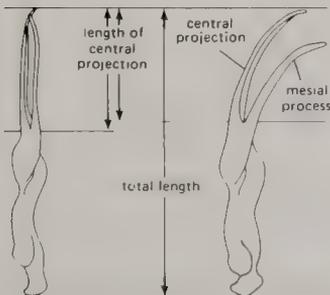
Fig. 6.—Lateral view of *Macrobrachium ohione* (after Holthuis 1952).



A



B



C

Fig. 7.—Morphology of crayfish gonopods (after Hobbs 1972a). (A) Mesial (left) and lateral views of terminal elements of generalized *Procambarus* gonopod. (B) Mesial (left) and lateral views of terminal elements of generalized *Cambarus* gonopod. (C) Generalized *Orconectes* gonopods.

Crayfishes are most easily and accurately identified by using characteristics of the gonopod (first pleopod) of form I (breeding) males, and in geographic areas having many similar species, accurate identifications of specimens other than form I males can be nearly impossible. In Illinois, with only 23 species of decapods, it is possible to identify most free-living specimens (including juveniles) to species. Following are two keys, the first is based on general morphology, the second on characteristics of form I male crayfishes. In both keys, references to crayfish gonopods are to those of form I males.

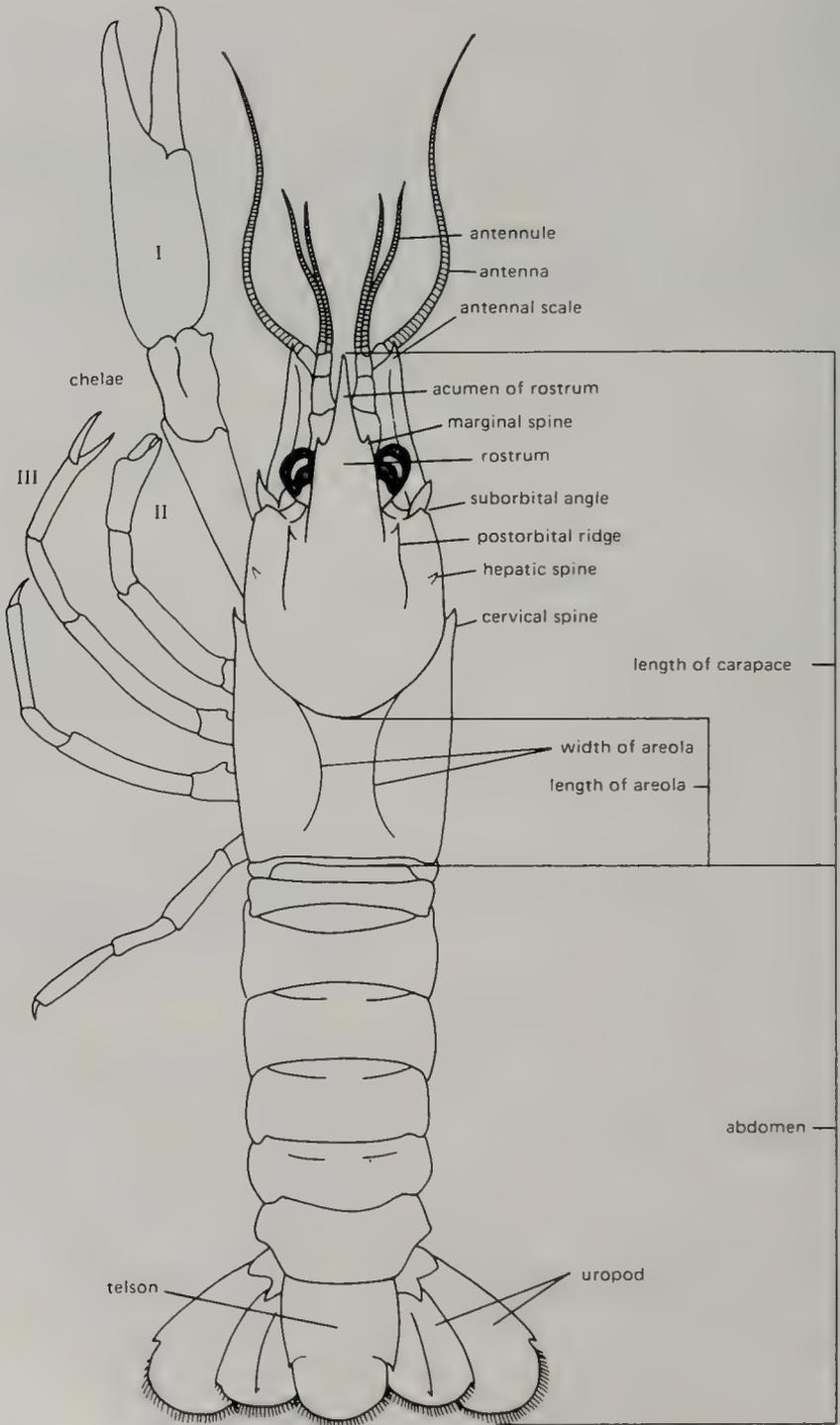


Fig. 8—Dorsal view of crayfish, illustrating features used in keys and descriptions (after Hobbs 1972a)

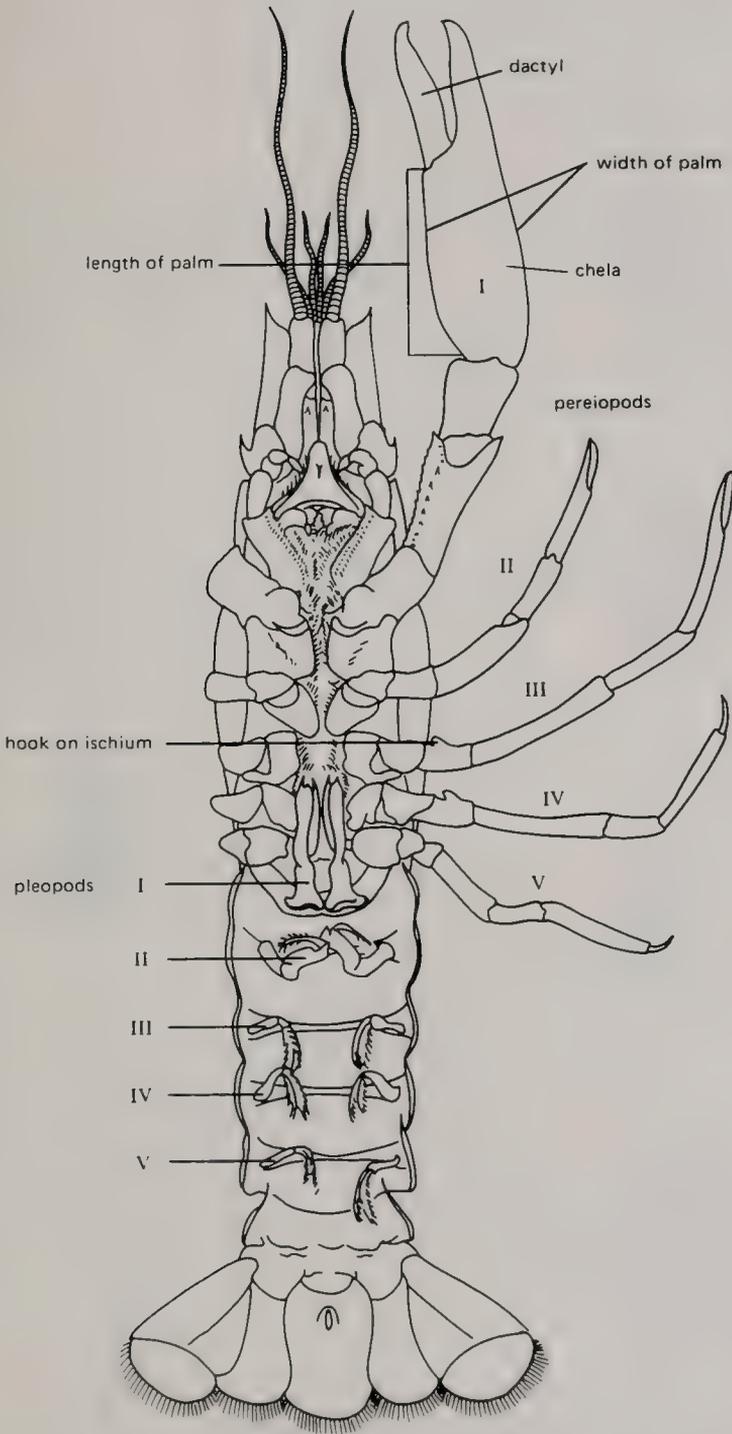


Fig. 9.—Ventral view of crayfish, illustrating features used in keys and descriptions (after Hobbs 1972a).

I. Key to Decapods of Illinois

(Key to form I male crayfishes on page 351)

1. First two pair of legs with chelae; abdomen compressed laterally (Fig. 6)...(Family Palaemonidae)2

1. First three pairs of legs with chelae; abdomen flattened dorsoventrally (Fig. 8)...(Family Cambaridae)3

2. Second pair of legs much longer than the first pair; 9-13 teeth along upper edge of rostrum (Fig. 10) *Macrobrachium ohione* (p. 356)



Fig. 10.

2. Second pair of legs only slightly longer than first pair; 6-8 teeth along upper edge of rostrum (Fig. 11) *Palaemonetes kadiakensis* (p. 359)

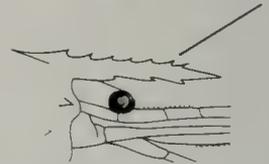


Fig. 11.

3. Areola wide; narrowest width about 20-25 percent of length (Fig. 12); rostrum flat dorsally; small, adult carapace length never more than 16 mm (32 mm total length)...(Genus *Cambarellus*)4



Fig. 12.

3. Areola obliterated to moderately wide but narrowest width never more than 20 percent of length (except in *Orconectes propinquus* and *O. stannardi*); rostrum concave dorsally; maximum carapace length much more than 16 mm5



Fig. 13.

4. Terminal elements of gonopod curved (Fig. 13); margins of rostrum slightly convex, barely converging anteriorly; annulus ventralis extends anteroventrally (Fig. 14) *Cambarellus puer* (p. 366)



Fig. 14.

4. Terminal elements of gonopod straight (Fig. 15); margins of rostrum straight, strongly converging anteriorly; annulus ventralis extends ventrally (Fig. 16)..... *Cambarellus shufeldtii* (p. 363)



Fig. 15.



Fig. 16.

- 5. Areola linear to obliterated (Fig. 17)6
- 5. Areola narrow to wide10

6. Rostrum deeply excavated, with acumen longer than basal margin of rostrum (Fig. 18).....
Orconectes lancifer (p. 400)

6. Rostrum shallowly excavated; acumen much shorter than margin of rostrum7

7. Chela long and narrow, maximum width less than one-third of length (Fig. 19); acumen and marginal spines of rostrum well-developed (Fig. 20); a longitudinal blue stripe along underside of abdomen (fades in preservative)*Procambarus clarkii* (p. 381)

7. Chela wide, maximum width more than one-third of length; small acumen, no marginal spines on rostrum; no blue stripe on abdomen8

8. Areola linear only at midlength (Fig. 21); gonopod terminates in small straight elements (Fig. 22); annulus ventralis subrectangular, elevated laterally *Procambarus gracilis* (p. 370)

8. Areola linear through most of length (Fig. 23); gonopod terminates in two large curved elements (Fig. 24); annulus ventralis wider than long, elevated posteriorly9

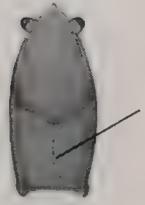


Fig. 17.



Fig. 18.



Fig. 19.



Fig. 20.



Fig. 22.



Fig. 21.



Fig. 23.



Fig. 24.

- 9. Suborbital margin of carapace smooth to slightly angular (Fig. 25); opposable margin of movable finger of chela with deep concavity (absent in regenerated chela) in proximal one-half (Fig. 26) *Fallicambarus fodiens* (p. 422)



Fig. 25.



Fig. 26.

- 9. Suborbital margin of carapace angular (Fig. 27); opposable margin of dactyl of chela without deep concavity (Fig. 28) *Cambarus diogenes* (p. 434)



Fig. 27.



Fig. 28.

- 10. Margins of rostrum without large spines (Fig. 29) 11



Fig. 29.

- 10. Margins of rostrum with large spines (Fig. 30) 15



Fig. 30.

- 11. Carapace laterally compressed; chela long and narrow, maximum width less than one-third of length 12

- 11. Carapace dorsoventrally flattened; chela wide, maximum width more than one-third of length 14

- 12. Gonopod terminates in large curved elements (Fig. 31); annulus ventralis wide, with fossa far to one side (Fig. 32) *Orconectes immunitus* (p. 388)



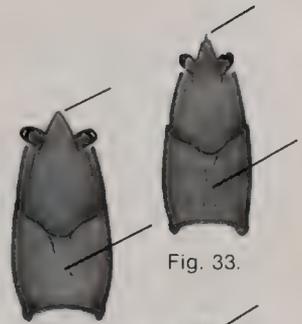
Fig. 31.



Fig. 32.

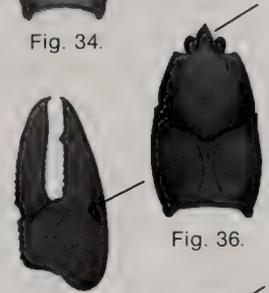
- 12. Gonopod terminates in very short elements; annulus ventralis with fossa more centrally located 13

13. Margins of rostrum elevated, strongly converging to acumen (Fig. 33); narrow areola (Fig. 33) *Procambarus acutus* (p. 376)

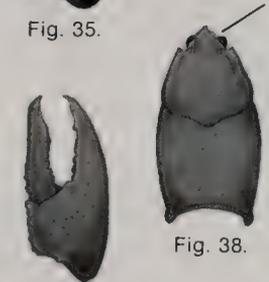


13. Margins of rostrum not elevated; rostrum more rounded anteriorly (Fig. 34); wide areola (Fig. 34) *Procambarus viaeviridis* (p. 378)

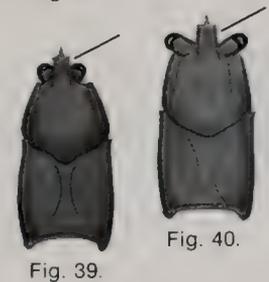
14. Base of fixed finger of chela with deep dorsal and ventral impressions (Fig. 35); margins of rostrum converge anteriorly (Fig. 36) *Cambarus robustus* (p. 439)



14. Base of fixed finger of chela without deep impressions (Fig. 37); margins of rostrum nearly parallel, barely converging anteriorly (Fig. 38) *Cambarus tenebrosus* (p. 428)



15. Margins of rostrum distinctly concave (Fig. 39) 16

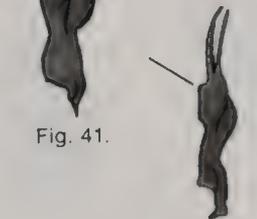


15. Margins of rostrum straight (Fig. 40) 18

16. Central projection of gonopod large and blade-like, curved at right angle to shaft (Fig. 41); annulus ventralis with fossa to side *Cambarus rusticiformis* (p. 432)



16. Central projection of gonopod not large and bladelike; annulus ventralis with fossa centrally located 17



17. Dorsal (cephalic when lifted from body) surface of gonopod with prominent shoulder (Fig. 42) *Orconectes rusticus* (p. 412)

Fig. 42.

17. Dorsal surface of gonopod without prominent shoulder (Fig. 43).....*Orconectes placidus* (p. 404)

18. Areola distinctly narrows just anterior to mid-length (Fig. 44); gonopod reaches coxa of cheliped with abdomen flexed; no black band on fingers of chela *Orconectes virilis* (p. 417)

18. Areola remains fairly wide throughout (Fig. 40); gonopod does not reach coxa of first pair of walking legs; black band (fades in preservative) near tips of fingers of chela19

19. Rostrum deeply excavated medially, with margins distinctly converging anteriorly (Fig. 45)*Orconectes illinoiensis* (p. 386)

19. Rostrum shallowly excavated, margins barely converging anteriorly20

20. Rostrum without median carina (Fig. 46);*Orconectes kentuckiensis* (p. 396)

20. Rostrum with median carina (small in *O. indianensis*) (Fig. 47);21

21. Mesial process of gonopod with spur on caudal surface (Fig. 48)*Orconectes stannardi* (p. 415)

21. Mesial process of gonopod without spur22

22. Rostrum with large median carina (Fig. 49); gonopod with tips of elements barely diverging (Fig. 50);..... *Orconectes propinquus* (p. 406)

22. Rostrum with small median carina (Fig. 51); gonopod with tips of elements strongly diverging (Fig. 52).... *Orconectes indianensis* (p. 394)

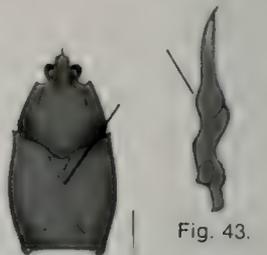


Fig. 43.

Fig. 44.



Fig. 46.



Fig. 45.



Fig. 48.



Fig. 47.



Fig. 50.



Fig. 49.



Fig. 52.



Fig. 51.

II. Key to Illinois Crayfishes Based on Form I Males (i.e., males with corneous terminal elements on the gonopods)

- 1. Ischia of second and third pereiopods with hooks (Fig. 9) . . . *Genus Cambarellus*2
- 1. Ischia of second pereiopods without hooks3
- 2. Terminal elements of gonopod straight (Fig. 53)*Cambarellus shufeldtii* (p. 363)
- 2. Terminal elements of gonopod curved at about right angle to shaft (Fig. 54) *Cambarellus puer* (p. 366)
- 3. Central projection of gonopod large and blade-like, curved at right angle to shaft (Fig. 55) . . . Genera *Fallicambarus* and *Cambarus*4
- 2. Central projection of gonopod not bladelike . . . Genera *Orconectes* and *Procambarus*8
- 4. Areola linear (Fig. 56).....5
- 4. Areola narrow to wide6
- 5. Suborbital margin of carapace smooth to slightly angular (Fig. 57); opposable margin of movable finger of chela with deep concavity (absent in regenerated chela) in proximal one-half (Fig. 58) *Fallicambarus fodiens* (p. 422)
- 5. Suborbital margin of carapace angular (Fig. 59); opposable margin of movable finger of chela without deep concavity (Fig. 60)..... *Cambarus diogenes* (p. 434)
- 6. Base of fixed finger of chela with deep dorsal and ventral impressions (Fig. 61)*Cambarus robustus* (p. 439)



Fig. 53.



Fig. 54.



Fig. 55.



Fig. 56.



Fig. 57.



Fig. 58.



Fig. 59.



Fig. 60.



Fig. 61.

6. Base of fixed finger of chela without deep impressions.....7

7. Margins of rostrum concave, with spines (Fig. 62) *Cambarus rusticiformis* (p. 432)

7. Margins of rostrum straight, without spines (Fig. 63) *Cambarus tenebrosus* (p. 428)

8. Gonopod terminates in two elements (Fig. 64) ... Genus *Orconectes*.....9

8. Gonopod terminates in more than two, very short elements (Fig. 65) ... Genus *Procambarus*18

9. Areola obliterated (Fig. 66); rostrum deeply excavated, with acumen longer than basal margin of rostrum (Fig. 66) *Orconectes lancifer* (p. 400)

9. Areola narrow to wide; acumen much shorter than basal margin of rostrum10

10. Both terminal elements of gonopod curved at right angle to shaft (Fig. 67); annulus ventralis with fossa far to one side (Fig. 68) *Orconectes immunis* (p. 388)

10. One or both terminal elements of gonopod straight or only slightly curved; annulus ventralis with fossa more centrally located.....11

11. Central projection constitutes one-fourth or less of total length of gonopod (Fig. 7).....12

11. Central projection constitutes more than one-fourth of total length of gonopod (Fig. 7)16

12. Terminal elements of gonopod distinctly divergent (Fig. 69 & 70)13



Fig. 62.



Fig. 64.



Fig. 63.



Fig. 65.



Fig. 66.



Fig. 67.



Fig. 68.



Fig. 69.



Fig. 70.

- 12. Terminal elements of gonopod nearly parallel (Fig. 72 & 73).....14
- 13. Terminal elements of gonopod curved (Fig. 69)*Orconectes kentuckiensis* (p. 396)
- 13. Terminal elements of gonopod nearly straight (Fig. 70) *Orconectes indianensis* (p. 394)
- 14. Rostrum with median carina (Fig. 71)15
- 14. Rostrum without median carina..... *Orconectes illinoiensis* (p. 386)

- 15. Mesial process of gonopod with spur on caudal surface (Fig. 72)*Orconectes stannardi* (p. 415)
- 15. Mesial process of gonopod without spur (Fig. 73) *Orconectes propinquus* (p. 406)
- 16. Both elements of gonopod curved (Fig. 74); areola distinctly narrows anteriorly (Fig. 75); no black bands on fingers of chela..... *Orconectes virilis* (p. 417)
- 16. Mesial process of gonopod not curved; areola remains fairly wide throughout; black band (fades in preservative) near tips of fingers of chela17

- 17. Dorsal (cephalic when lifted from body) surface of gonopod with prominent shoulder (Fig. 76)*Orconectes rusticus* (p. 412)
- 17. Dorsal surface of gonopod without prominent shoulder (Fig. 77).....*Orconectes placidus* (p. 404)

- 18. Dorsal surface of gonopod with prominent shoulder (Fig. 78); cephalic process a large lobe (Fig. 78) *Procambarus clarkii* (p. 381)
- 18. Dorsal surface of gonopod without shoulder; cephalic process small.....19



Fig. 71.



Fig. 72.



Fig. 73.



Fig. 74.



Fig. 75.



Fig. 76.

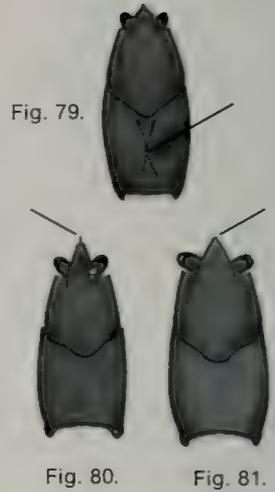


Fig. 77.



Fig. 78.

- 19. Areola linear at midlength (Fig. 79); hooks on ischia of third pereopods only (Fig. 9).....
Procambarus gracilis (p. 370)
- 19. Areola narrow but not linear (Fig. 80 & 81); hooks on ischia of third and fourth pereopods.....20
- 20. Margins of rostrum elevated, converging to acumen (Fig. 80); narrow areola (Fig. 80).....
.....*Procambarus acutus* (p. 376)
- 20. Margins of rostrum not elevated; rostrum more rounded anteriorly (Fig. 81); wide areola (Fig. 81) *Procambarus viaeviridis* (p. 378)



SYSTEMATIC ACCOUNTS

FAMILY PALAEMONIDAE

Both shrimps native to Illinois are members of the family Palaemonidae, which is worldwide in distribution.

Macrobrachium ohione, with 9-13 teeth along the upper edge of the rostrum, is easily separable from *Palaemonetes kadiakensis*, which has only 6-8 (almost always 7) teeth. *M. ohione*, which reaches 100 mm in total length (tip of rostrum to tip of telson), also is much larger than *P. kadiakensis*, which reaches a maximum length of only about 50 mm.

Genus *Macrobrachium* Bate

Macrobrachium Bate 1868

Species of *Macrobrachium*, referred to as river shrimps, differ from species of *Palaemonetes* by possessing a hepatic spine, lacking a branchiostegal spine, and having the second pair of legs much longer than the first pair (in *Palaemonetes* the second pair is only slightly longer than the first pair).

Although *Macrobrachium* contains about 100 species worldwide (35 in the western hemisphere), only four (*M. ohione*, *M. acanthurus*, *M. carcinus*, and *M. olfersii*) are found in the freshwaters of the eastern United States (Hedgpeth 1949; Holthuis 1952). *M.*

ohione is the only species of *Macrobrachium* found in the Mississippi River system.

***Macrobrachium ohione* (Smith)
(Fig. 82)**

Palaemon Ohionis Smith 1874
Palaemon sallei Kingsley 1882

Description.—Holthuis (1952) distinguished *M. ohione* from other American species of *Macrobrachium* by this combination of characteristics: carpus of second legs as long as or longer than merus; telson with a distinct posterior margin (rather than gradually tapering toward a slender tip); second chelae of adult male equal or nearly equal to one another in size (some species are bilaterally asymmetrical with the chela on one side much larger); no tubercles along cutting edges of fingers of second chela of adult male; cutting edges of fingers of large chela of adult male with one or two fairly large teeth proximally; eggs numerous and small (about 0.5 mm in diameter); second pair of legs of adult male with velvety pubescence on some or all joints; rostrum with styliform apex (and no teeth distally).

M. ohione is pale gray with light blue spots and a blue abdomen (Hedgpeth 1947, 1949). Adult females average larger than adult males and have much

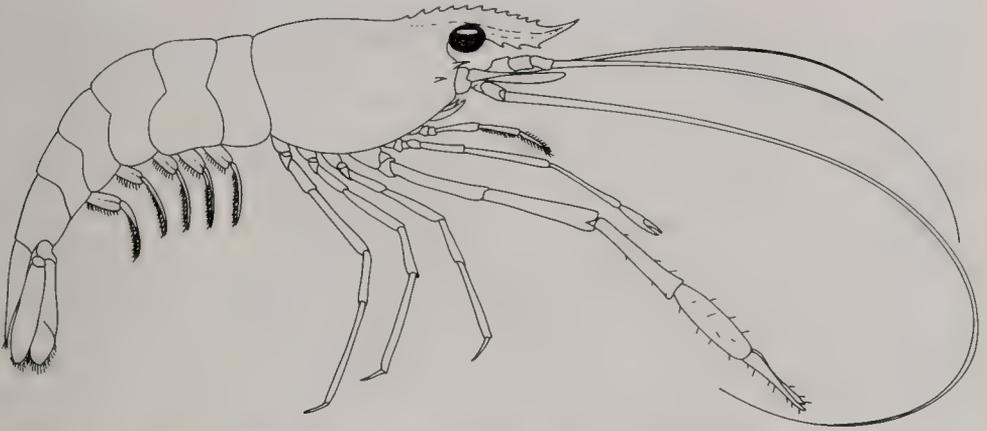


Fig. 82.—Lateral view of *Macrobrachium ohione* (after Holthuis 1952).

longer second legs (Holthuis 1952). Females reach about 100 mm in length, males about 70 mm (Hedgpeth 1949; Truesdale & Mermilliod 1979).

Distribution and Habitat.—*M. ohione* occupies freshwater habitats along the Atlantic coast from Virginia to Florida, along the Gulf Coast from Alabama to Texas, and north in the Mississippi and Ohio river systems to Oklahoma, Missouri, Illinois, Indiana,

and Ohio (Fig. 83). Coastal populations move into estuaries in spring (Gunter 1937; Hedgpeth 1949; Reimer, Strawn, & Dixon 1974).

In Illinois, *M. ohione* has been recorded from Cairo, Alexander County (Forbes 1876); Grand Tower, Jackson County (Forbes 1876); Chester, Randolph County (McCormick 1934); and Shawneetown, Gallatin County (Hedgpeth 1949) (Fig. 84). Although Hedgpeth (1949) and Holthuis (1952) cite Luce (1933) as recording *M. ohione* from the lower Kaskaskia River, Illinois, the reference is actually to its use as fish bait.

Forbes (1876) described *M. ohione* as “abundant at Cairo, where it is frequently eaten” and reported second handedly its presence in the Mississippi River system from St. Louis to New Orleans. It apparently was common in the Mississippi River as recently as the 1930’s, when McCormick (1934) described the successful use of “shrimp sets” at Chester. Shrimp sets were willow or cottonwood branches set along the river’s edge and bent so that their leaves were under water. As shrimp fed on the leaves they were dipnetted by fishermen.

In the Illinois Natural History Survey collection are six series of *M. ohione* from Illinois, including one made by S. A. Forbes at Cairo (undated). The five collections with locality data,



Fig. 83.—Total distribution of *Macrobrachium ohione*.

(Mount Carmel, Wabash County, 1892; Mississippi River, Grand Tower, Jackson County, 1932 and 1944; Mississippi River, Missouri River Station, Madison County, 1944; and Mississippi River, 1 mi S Cairo, Alexander County, 1962) are represented on the distribution map (Fig. 84). No *M. ohione* were found during the present survey (1972–1982). Although perhaps still present in the state, the species obviously has undergone a tremendous reduction in population. Little information on the ecology of the species in Illinois is available, but its decline presumably is attributable to the loss of suitable habitats as a result of the excessive modifications (especially channelization, impoundment, and drainage of bottomland lakes) of Illinois' largest rivers.

Life History.—In the Mississippi River at Chester, McCormick (1934)

counted 8,000 eggs on an 84-mm female and observed that ovigerous females ranged from 34 to 90 mm long. Among Illinois Natural History Survey collections of Illinois *M. ohione* (all made between May and October), ovigerous females are present only in a collection made 13–14 May 1932.

In Louisiana, Truesdale & Mermilliod (1979) found ovigerous females (50–93 mm in total length) from March through September. Five females, ranging from 54 to 80 mm, were carrying 6,273–24,800 eggs. Eggs were about 0.5 mm across, bright orange when first laid, and brown at later stages. Huner (1977) found *M. ohione* at Port Allen, Louisiana, to range from 17 to 92 mm long, to average 30.6 mm ($N = 7,058$), and to live a maximum of 2 years. Ovigerous females ($N = 88$) ranged from 27 to 92 mm and averaged 66 mm.

In the springs of 1969–1971, Reimer, Strawn, & Dixon (1974) studied movements of *M. ohione* into Galveston Bay, Texas. Increased movement was associated with rainfall, and salinities as high as 15 percent seemed to prevent further movement. The first individuals to appear in the bay were males and females without eggs. Females carrying eggs first appeared in late March. Females averaged larger than males, and only the largest females (52–82 mm) bore eggs.

M. ohione feeds on both plant and animal material (McCormick 1934; Gunter 1937; Darnell 1958; Truesdale & Mermilliod 1979) and in turn is fed upon by several predators, including flathead catfish (*Pylodictis olivaris*) and white bass (*Morone chrysops*) (Bryan, Truesdale, & Sabins 1975).

Genus *Palaemonetes* Heller

Palaemonetes Heller 1869

Of the approximately 17 species of *Palaemonetes* (referred to as prawns, glass shrimp, and freshwater shrimp) in the western hemisphere, only *P. kadiakensis* occurs in Illinois. *P. paludosus* is widespread in the eastern United States and along the Gulf Coast



Fig. 84.—Distribution of *Macrobrachium ohione* in Illinois. Large circles = pre-1900 collections, small circles = 1932–1949 collections, black dot = collection made in 1962.

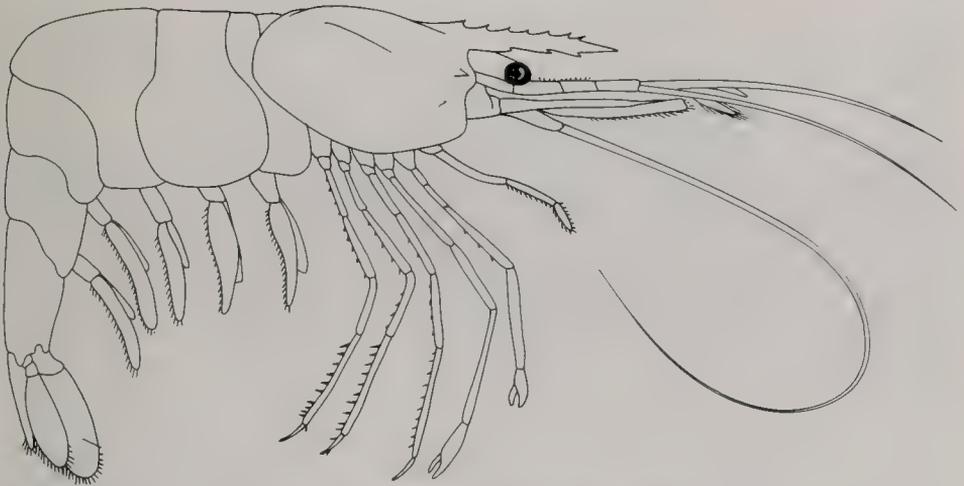


Fig. 85.—Lateral view of *Palaemonetes kadiakensis*.

as far west as eastern Texas, but it does not enter the Mississippi River system. In addition to *P. kadiakensis* and *P. paludosus*, the only freshwater species in the United States are highly localized spring- and cave-inhabiting forms in Texas (*P. antrorum*, *P. holthuisi*, and *P. texanus*) and Florida (*P. cummingsi*) (Strenth 1976).

***Palaemonetes kadiakensis* Rathbun**
(Fig. 85)

Palaemonetes kadiakensis Rathbun
1902

Description.—*P. kadiakensis* is the only species of *Palaemonetes* with three apical setae on the appendix masculina (Fig. 86) occurring in the freshwaters of the United States (Fleming 1969). Rostrum straight; upper margin convex with 6–8, usually 7, teeth; lower margin with 2–3 teeth. Carapace with antennal and branchiostegal spines; branchiostegal spine below branchiostegal groove. Abdomen humped at third segment; sixth abdominal slightly less than twice as long as fifth segment, slightly shorter than telson. Anterior pair of dorsal spines on telson usually distinctly behind middle of length, posterior pair near distal margin. Eyes large, pigmented. Lateral antennular flagellum with rami fused for 11–23 articles; free portion of shorter ramus

with 3–8 articles. Scaphocerite about three times as long as wide, lamella overreaching distolateral tooth.

Living specimens are transparent with green eyes, red-brown antennae, and many very small red-brown specks on the body. The internal organs are readily visible, and a bright green vegetation-filled intestine is often a prominent feature. The species reaches a

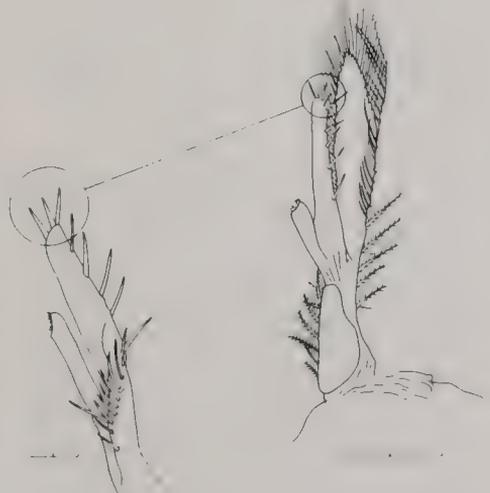


Fig. 86.—Appendices masculina and interna (left) and entire second pleopod (right) of male *Palaemonetes kadiakensis* (after Meehean 1936).

maximum length of about 53 mm total length (Meehen 1936).

Distribution and Habitat.—*P. kadiakensis* occupies sluggish freshwater habitats from Minnesota and the shores of Lakes Ontario, Erie, and Michigan south in the Mississippi River system to the Gulf of Mexico, and Gulf Coast drainages from northeastern Mexico (Nuevo Leon) to northern Florida (Holthuis 1952) (Fig. 87). Although the



Fig. 87.—Total distribution of *Palaemonetes kadiakensis*.

locality given on the label accompanying the type specimen is Kodiak Island, Alaska, it is doubtful that the species ever occurred in Alaska (Holthuis 1952).

P. kadiakensis now occurs throughout the southern one-fourth of Illinois, in backwaters along the Mississippi River, in backwaters of the Illinois River at least as far north as Bureau County, and in Wolf Lake (Lake Michigan drainage) in Cook County (Fig. 88). It abounds in swamps (Fig. 89) and swamplike streams on the Coastal Plain of Illinois and is common in standing- and sluggish-water habitats as far north as Salem. It is uncommon in the Illinois River and in Wolf Lake.



Fig. 88.—Distribution of *Palaemonetes kadiakensis* in Illinois. Open circle = pre-1898 record for the Kankakee River; black dots = 1972-1982 collections.

Forbes (1876) recorded *P. kadiakensis* (as *P. exilipes*) only from the Illinois River but described it as being very common. A specimen in the U.S. National Museum of Natural History documents its former occurrence at Kankakee, Kankakee County (pre-1898, exact date unknown), a locality well outside the present range.

P. kadiakensis almost always is associated with, and is most abundant in, living aquatic vegetation. Its reduction in distribution and abundance in Illinois probably is attributable to increased turbidity and sedimentation and the resultant loss of vegetation. Beds of emergent and submerged vegetation once were common throughout Illinois but now are rarely encountered. The loss of vegetation is also one of the



Fig. 89.—Mermet Swamp, Massac County, Illinois (8 October 1984). Large populations of *Palaemonetes kadiakensis* and *P. clarkii* occur here.

main causes of reductions in populations of Illinois fishes (Smith 1979).

Life History.—Reproduction in Illinois, as indicated by the presence of ovigerous females, occurs from April to August (Table 3). In Louisiana the reproductive period extends from February to October (Meehan 1936; White 1949), and in central Missouri (where the species is introduced) from mid-May to August (Nielsen & Reynolds 1977).

In Illinois collections, ovigerous females range in total length from 30 to 39 mm. Eggs (embryos) on 15 females numbered 22–137 (mean, 86.6) (Table 4). The relationship (Model II regression) between the number of eggs (N) and total length (L) was $N = -230.16 + 9.19L$, $r = 0.674$, and between the number of eggs and the weight of the female (W) was $N = 10.78 + 318.21W$, $r = 0.694$. Nielsen & Reynolds (1977) found that the number of eggs varied from 20 to 76 on females 25–36 mm in length and equalled $-111.43 + 5.29L$, $r^2 = 0.64$. Meehan (1936) found as many as 154 eggs (on a 49-mm female).

Eggs are spherical, orange, and about

1.0 mm in diameter. The egg mass constituted an average of 11.2 percent of the weight of the female (without the eggs) in 15 Illinois females (Table 4). Females may produce more than one brood per season (Broad & Hubschman 1963; Nielsen & Reynolds 1977). The incubation period lasts 24–28 days at 18.5°–24° C. Detailed accounts of lar-

Table 3.—Illinois collections of *Palaemonetes kadiakensis*.

Month	No. of Collections	No. of Collections with	
		Ovigerous Females	Percentage of Collections with Ovigerous Females
January	2	0	0
February	3	0	0
March	2	0	0
April	8	2	20
May	8	6	75
June	11	5	45
July	8	5	63
August	3	1	33
September	16	0	0
October	11	0	0
November	1	0	0
December	1	0	0

Table 4.—Relationship between size of female and the number and weight of eggs (embryos) in Illinois-collected *Palaemonetes kadiakensis*.

Date of Collection	Total Length of Female, mm	Weight of Female ^a w/o Eggs, g	Total Weight of Eggs ^a , g	Number of Eggs
28 April 1976	38	0.334	0.037	125
"	39	0.369	0.052	137
18 May 1973	31	0.162	0.023	61
"	30	0.129	0.027	77
"	31	0.103	0.017	64
29 May 1974	31	0.174	0.027	97
"	33	0.153	0.021	91
"	37	0.210	0.021	97
20 June 1973	37	0.361	0.032	113
"	38	0.345	0.040	112
"	35	0.281	0.020	85
25 July 1973	32	0.234	0.018	73
"	36	0.272	0.013	69
"	37	0.296	0.013	76
10 August 1973	32	0.151	0.012	22

^aAir dried.

val development and postembryonic growth are given by Broad & Hubschman (1963) and Hubschman & Rose (1969).

In Missouri, Nielsen and Reynolds (1977) found growth to be rapid from hatching through fall, slow in winter, and rapid in spring as shrimp matured. Females reached a larger size (to 36 mm) than males. Most individuals of both sexes reproduced at 1 year of age and then died. Sex ratios varied among study areas and among monthly samples, although females usually constituted about 55–60 percent of the sample.

P. kadiakensis feeds mainly on living plants but also may feed on dead plants and living or dead animals (Creaser 1933; Meehean 1936; Nielsen & Reynolds 1975).

FAMILY CAMBARIDAE

Except for species of the genus *Pacifasticus* (which is restricted to Pacific drainages and the headwaters of the Missouri River in Wyoming and Montana), all North American crayfishes are members of the family Cambaridae. Elsewhere the family occurs only in Japan, Korea, and the Amur Basin of eastern Asia (Hobbs 1974a). Included

among North American cambarids are about 300 described and several undescribed species in two subfamilies. Cambarellinae contains only the genus *Cambarellus*; Cambarinae contains 10 genera: *Barbicambarus*, *Bouchardina*, *Cambarus*, *Distocambarus*, *Fallicambarus*, *Faxonella*, *Hobbseus*, *Orconectes*, *Procambarus*, and *Troglocambarus* (Hobbs 1974a, 1977; Hobbs & Carlson 1983).

Cambarid crayfishes differ from crayfishes of the family Astacidae (which occur in Europe and western North America) by possessing cyclic dimorphism in the male (i.e., the alternation between forms I and II) and hooks on the ischia of one or more of the second through fourth pereopods of the male. Astacids lack cyclic dimorphism and ischial hooks. Cambarids have a variety of complex terminal elements on the gonopod, but in astacids the gonopod has a simple cylindrical termination. Astacids lack an annulus ventralis; female cambarids usually have one. In crayfishes of the family Parastacidae (occurring in Australia, New Guinea, New Zealand, Madagascar, and South America), the first pleopod is absent in both sexes, and the telson is never completely divided by a transverse

suture; except in some species of *Falli-cambarus*, the telson always is divided in North American cambarids.

Genus *Cambarellus* Ortmann

Cambarellus Ortmann 1905

Gonopod with three terminal elements; central projection not large and bladeliike. Ischia of second and third pereopods of male with hooks.

Species of *Cambarellus* are distributed throughout the southern United States and Mexico, generally in swamps and other standing- or sluggish-water habitats. They are "dwarf" crayfishes, reaching a maximum total length of about 30 mm. Two of the 17 recognized species of *Cambarellus* occur in southern Illinois. Fitzpatrick (1983) revised *Cambarellus*, proposing the recognition of three subgenera.

Cambarellus shufeldtii (Faxon) (Fig. 90)

Cambarus Shufeldtii Faxon 1884

Description.—Rostrum broad, flat, often deflecting downward anteriorly; margins straight, strongly converging anteriorly, ending in large spines; acumen moderately large. Carapace compressed, with cervical spines; sub-orbital margin angular. Areola wide, narrowest part about 19–24 percent of length. Chela narrow and long, smooth; palm without tubercles. Form I gonopod terminates in three elements, all distally directed (not curved): sclerotized central projection, nonsclerotized mesial process, and nonsclerotized caudal process. Dorsal color variable, from rust red to light brown with two dark brown stripes or rows of spots on either side of the areola extending down the abdomen.

C. shufeldtii appears to have no obviously close relatives, being the only species in the genus with straight terminal elements on the gonopod and the only member of the subgenus *Dirigicambarus* (Fitzpatrick 1983).

Distribution and Habitat.—*C. shufeldtii* occupies bodies of sluggish water, mostly on the Coastal Plain, from

southern Illinois to southwestern Alabama and eastern Texas (Fig. 91). In Illinois, *C. shufeldtii* is known only from Alexander, Jackson, Massac, Pulaski, and Union counties in both the Mississippi and Ohio basins. Most localities are on the former Mississippi Embayment, but the species also ascends the lower Mississippi River Valley and the lower Big Muddy River to about Sand Ridge in Jackson County (Fig. 92).

C. shufeldtii was first collected in Illinois at Cairo by Robert Kennicott (Faxon 1914). Brown (1955) found the species in five sloughs and ditches in Alexander and Massac counties. The 28 collections made in the present survey were from cypress swamps, sloughs, and backwaters. *C. shufeldtii* is especially common in the heavily vegetated LaRue Swamp-Wolf Lake complex in Union County. *C. shufeldtii* and *C. puer* have not been found together in Illinois and apparently compete for suitable habitats. In Gulf Coast streams *C. shufeldtii* is supplanting *C. puer* (see *C. puer* account).

C. shufeldtii was probably more common and widespread in extreme southern Illinois prior to the extensive clearing of swamps and river floodplains. Brown (1955) mentioned an earlier collection of a "dwarf crayfish" near Shawneetown (Gallatin County) but was unable to document the occurrence of *Cambarellus* that far northeast. In view of the occurrence, or former occurrence, of several swamp-inhabiting fishes (*Fundulus dispar*, *Elassoma zonatum*, *Lepomis punctatus*, and *L. symmetricus* [Smith 1979]) that far northeast, or even into the lowlands of the lower Wabash River drainage, the presence of *C. shufeldtii* or *C. puer* in the same area is possible.

In Louisiana, *C. shufeldtii* lives in clear, shallow (less than 40 cm deep), permanent, sun-exposed, mud-bottomed, vegetated bodies of water (Penn 1950). *C. shufeldtii* characteristically does not burrow but may survive periods of drought in subterranean cells (Penn 1950). Apparently the crayfish

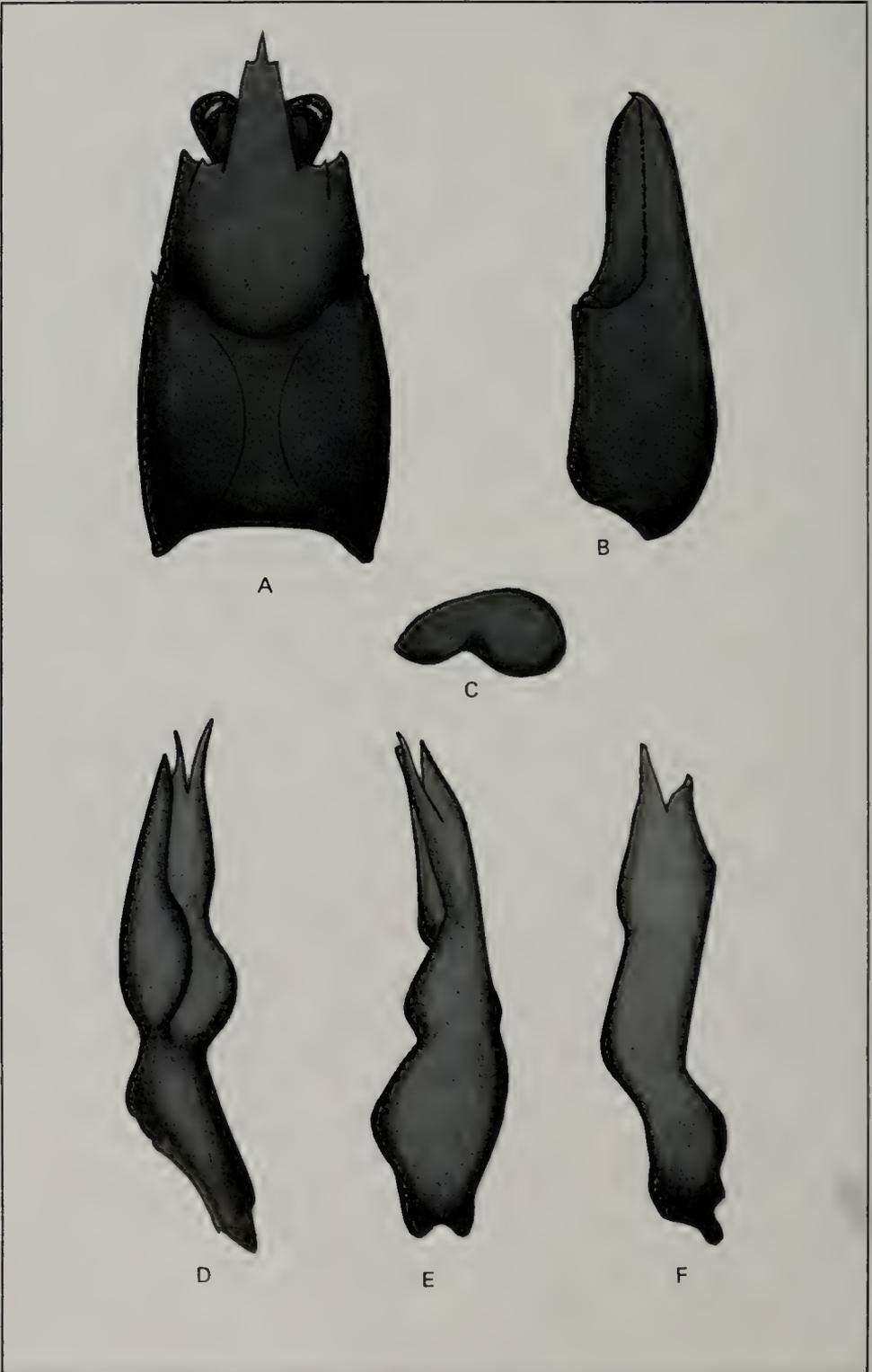


Fig. 90.—*Cambarellus shufeldtii*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 91.—Total distribution of *Cambarellus shufeldtii*.

excavates a chamber in the mud bottom of the slough or swamp as drying occurs and then seals the top of the chamber to prevent desiccation.

Life History.—Form I males are present in Illinois collections (Table 5) during most months and peak in occurrence in December, February, and March. In Louisiana, Penn (1942, 1950) found form I males in all months except September, with peaks in January, February, and July. Presumably, mating in *C. shufeldtii* may occur at anytime but peaks in winter in Illinois and in winter and summer in Louisiana.

Females carrying eggs were found in Illinois from February to May, and peaked in occurrence in March (Table 5); females carrying young have been found in Illinois in April, June (Table 5), and July (Brown 1955). In Louisiana, females with eggs or young are present in every month, with strong peaks in January–March and June–July (Penn 1942, 1950; Lowe 1961), again suggesting two peaks of reproductive activity in the southern part of the range.

Nine Illinois females, 11.6–14.2 mm

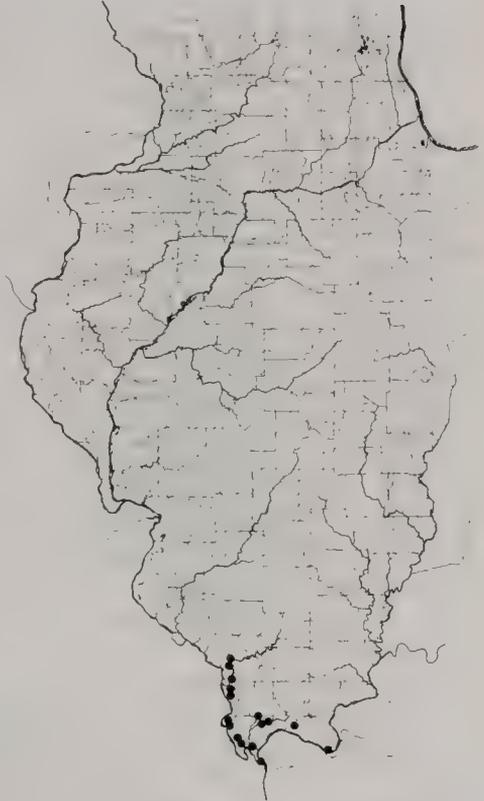


Fig. 92.—Distribution of *Cambarellus shufeldtii* in Illinois; black dots = 1972–1982 collections.

CL, collected in February and March were carrying 47–99 (mean, 80.1) eggs averaging 1.1 mm in diameter. The relationship between numbers of eggs (N) and carapace length (CL) is $N = -539.0 + 558.9 \log CL$, $r = 0.86$. Four females, 12.4–13.5 mm CL, collected in April 1974 were carrying 15–74 (mean, 44.8) young. The decline from an average of 80.1 eggs to an average of 44.8 young suggests a 44 percent mortality during egg and early instar stages. Penn (1942) found the number of eggs or young on a female to increase with the carapace length of the female, with females 8.5 mm averaging 27 offspring and those 11 mm averaging 54 offspring. An overall average of 34 offspring per female ($N = 100$) in Louisiana (Penn 1942) is about one-half the average number of offspring (69.2) per female ($N = 13$) in Illinois; however, the comparison is

Table 5.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Cambarellus shufeldtii*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	2	0	0	0	0	0	0
February	2	2	100	1	50	0	0
March	3	3	100	2	67	0	0
April	2	1	50	1	50	1	50
May	4	2	50	1	25	0	0
June	7	3	43	0	0	1	13
July	2	1	50	0	0	0	0
August	2	0	0	0	0	0	0
September	2	0	0	0	0	0	0
October	4	1	25	0	0	0	0
November	4	1	25	0	0	0	0
December	2	2	100	0	0	0	0

marred by the fact that females tend to carry fewer young than eggs, and the proportion of females with young to females with eggs is unknown for the Louisiana sample.

Of 95 individuals collected in LaRue Swamp-Wolf Lake in February and March 1974, 47 were females and 48 were males. The unimodal size-frequency distribution of the 95 individuals (Fig. 93) suggests that all were from the same year class. Longevity probably seldom exceeds 1 year (Lowe 1961), although an occasional individual may live part of a second year. The largest *C. shufeldtii* from Illinois, a 15.2-mm female collected in Kincaid Creek, Jackson County, 29 November 1973, is larger than any specimen re-

corded for Louisiana (Lowe 1961) and probably was in its second year of life.

Females ($N = 47$, mean = 12.2 mm CL) were significantly (t cal = 11.27, $P < 0.001$) longer than males ($N = 48$, mean = 10.3). In *C. shufeldtii* populations, and in mixed populations of *C. shufeldtii* and *C. puer*, the largest individuals are dominant (Lowe 1956; Penn & Fitzpatrick 1963).

Sixteen (34 percent) of the 47 females were ovigerous and ranged from 11.6 to 14.2 (mean, 12.8) mm CL; non-ovigerous females were generally smaller, ranging from 10.2 to 13.7 (mean, 11.9) mm CL. Of the 48 males, 34 (71 percent) were form I and ranged from 9.1 to 11.9 (mean, 10.5) mm CL; other males were generally smaller and ranged from 8.8 to 11.8 (mean, 9.9) mm CL. In Louisiana, form I *C. shufeldtii* measure 6.7–11.5 mm CL and weigh 64.0–339.4 mg (Black 1966).

Growth is rapid, and sexual maturity may be reached in 2 months in Louisiana (Penn 1950), where 12–13 molts are required to reach sexual maturity and the mean growth increment is 0.45 mm/molt (Black 1966).

Cambarellus puer Hobbs
(Fig. 94)

Cambarellus puer Hobbs 1942

Description.—Rostrum broad, flat, often deflecting downward anteriorly;

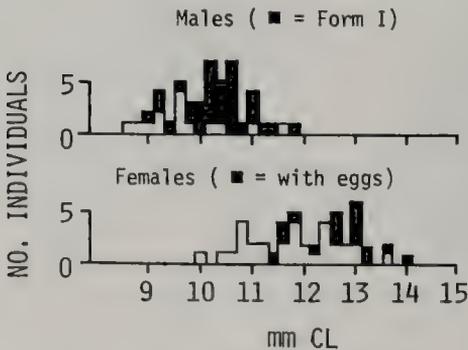


Fig. 93.—Size-frequency distribution of *Cambarellus shufeldtii* collected in LaRue Swamp-Wolf Lake, February, March 1974.

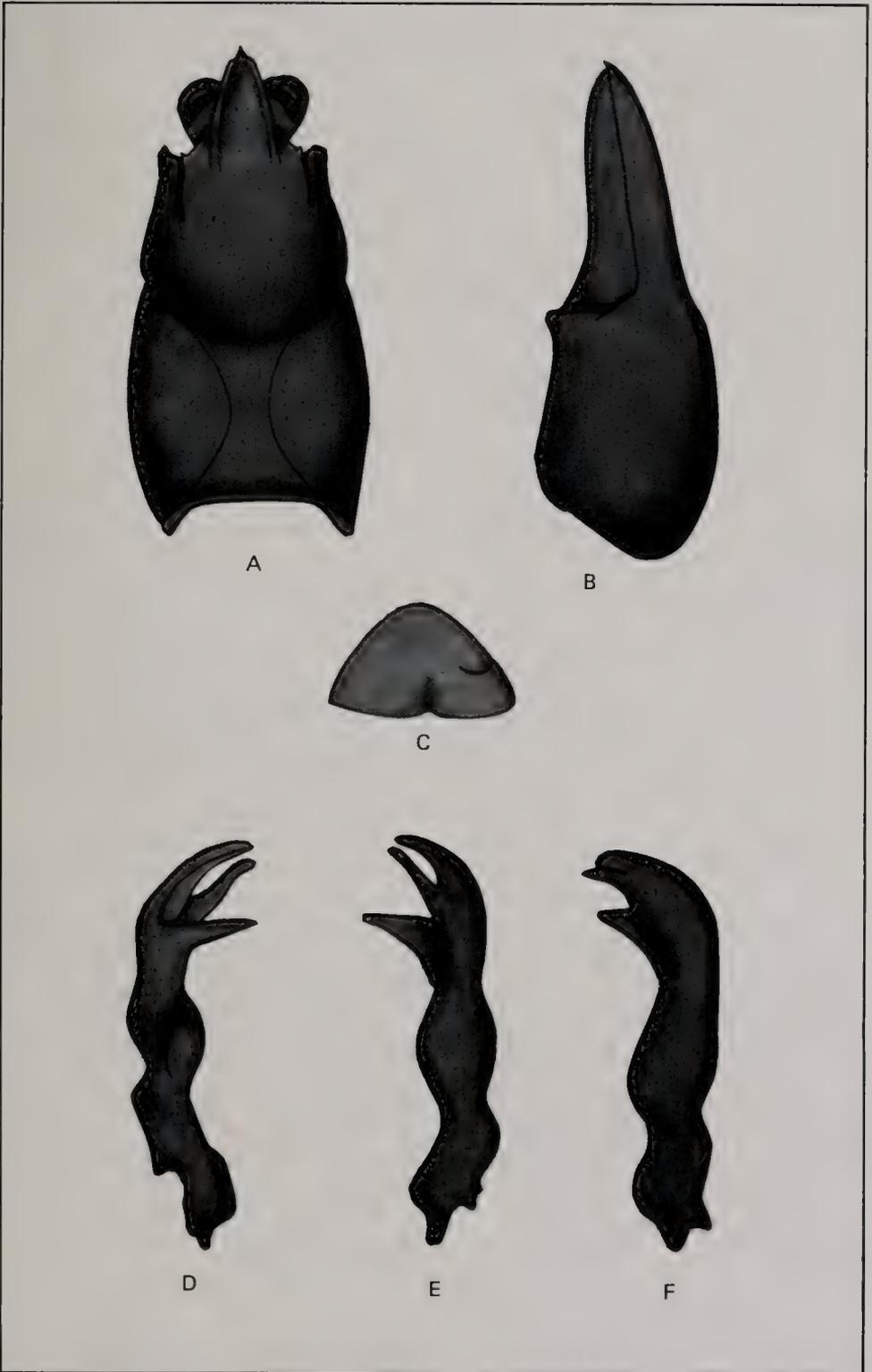


Fig. 94.—*Cambarellus puer*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

margins convex, barely converging anteriorly, ending in large spines; acumen moderately large. Carapace compressed, with cervical spines; sub-orbital margin angular. Areola wide, narrowest part about 25 percent of length. Chela narrow and long, smooth; palm without tubercles. Form I gonopod terminates in three elements: sclerotized central projection, nonsclerotized mesial process, and nonsclerotized caudal process, all curved at sharp angle (about 45°-90°) to principal axis of gonopod. Color as in *C. shufeldtii*.

The closest relatives of *C. puer* are *C. schmitti* and *C. lesliei* (see Fitzpatrick & Laning 1976), two occupants of the Gulf Coastal Plain from Mississippi to Florida. *C. puer*, *C. schmitti*, *C. lesliei*, *C. diminutus*, *C. blacki*, *C. ninae*, and *C. texanus* all are members of the subgenus *Pandicambarus* (Fitzpatrick 1983).

Variation in morphological characteristics of *C. puer* was studied by Chambers, Payne, & Kennedy (1979). Three populations were separable from one another but not given taxonomic status. Illinois populations are part of a larger population extending along the Mississippi River and across southern Louisiana. In general, individuals in the east are larger than those in the west; females are larger and have shorter, broader chelae and shorter rostra than do males.

Distribution and Habitat.—*C. puer* ranges from southern Illinois and southeastern Missouri to the Gulf Coast of Louisiana and the lower Colorado River drainage of Texas (Fig. 95). All populations are on the Coastal Plain. In Louisiana, *C. puer* occurs most frequently in shallow (less than 40 cm deep), clear, permanent, sun-exposed, mud-bottomed, vegetated water bodies (Penn 1950).

C. puer was first found in Illinois in 1973 (Page & Burr 1973) and now is known from seven sites in the Mississippi and Ohio basins in Union, Johnson, and Alexander counties (Fig. 96). In Illinois, it occupies cypress swamps

(Fig. 97), effluent streams, and lowland areas which probably were swamps prior to being cleared. All but one collection from a roadside ditch were made in permanent water bodies, and most specimens were found among living or dead vegetation. *C. puer* may be more widespread on the Coastal Plain of Illinois than present records indicate and almost certainly was more widespread and common prior to the drainage of swamps and lowlands.

C. puer and *C. shufeldtii* were collected at 23 sites in Illinois, mostly in Coastal Plain swamps, but never were collected together. Competitive exclusion among species of *Cambarellus* has been documented in Gulf Coast areas (Penn & Fitzpatrick 1962, 1963) and apparently is operating in Illinois. *C. puer* and *C. shufeldtii* seem unable to coexist and, at least along the Gulf Coast, *C. shufeldtii* has supplanted *C. puer* at several localities within historic times (Penn & Fitzpatrick 1962, 1963). *C. shufeldtii* was found experimentally to be dominant over *C. puer* (i.e., *C. puer* retreats following contact with *C. shufeldtii*) (Penn & Fitzpatrick 1963), suggesting that in nature *C. shufeldtii* aggressively displaces *C. puer* from certain habitats.

Life History.—Louisiana data suggest two reproductive periods (winter and summer) (Penn 1950; Black 1966), although form I males can be found in all months (Black 1966). Illinois data are seasonally incomplete (Table 6), but two reproductive periods, somewhat later (i.e., late winter-spring and fall) than in Louisiana, may also occur in Illinois. In Louisiana, form I males peak in occurrence from December to March (about 60-95 percent of all males) and from July to August (about 45-75 percent) (Penn 1950; Black 1966). In the available Illinois collections (Table 6), form I males are present February-May and in October. In Louisiana, form I *C. puer* males measure 7.2-12.0 mm CL and weigh 75.4-112.1 mg (Black 1966). Thirteen or 14 molts are required to reach sexual maturity, with a mean



Fig. 95.—Total distribution of *Cambarellus puer*.



Fig. 96.—Distribution of *Cambarellus puer* in Illinois; black dots = 1972-1982 collections.

growth increment of 0.45 mm/molt (Black 1966). Sixteen form I males collected in Illinois ranged from 7.7 to 12.8 and averaged 10.4 mm CL.

In Louisiana, females carrying eggs or young occur January–April, and August–September (Penn 1950). In Illinois, females carrying eggs were collected March–May, and females carrying young have been collected in May (Table 6). Ten Illinois females carrying eggs (collected March–May) ranged from 11.0 to 14.6 mm and averaged 12.2 mm; five females carrying young (in May) ranged from 10.6 to 11.5, and averaged 10.9 mm CL.

Six Illinois females, 11.0–14.6 mm CL, had 52–98 (mean, 82.3) eggs averaging 1.1 mm in diameter. Five females, 10.6–11.5 mm CL, had 15–48 (mean, 30.8) young attached; the young on the female with 48 young were first instars, the 15–36 young on the other females were later instars, suggesting a high mortality while they are carried by the mother.

Of the 60 *C. puer* collected in Illinois, 30 were males (16 were form I), and 30 were females. Longevity is 15–18 months (Black 1966).

Genus *Procambarus* Ortmann

Procambarus Ortmann 1905

Paracambarus Ortmann 1906

Ortmannicus Fowler 1912

Gonopod terminates in three or four (sometimes two in species occurring outside of Illinois) very short elements. Ischia of third, or third and fourth, pereopods of male with hooks.

Illinois harbors four species of *Procambarus*, a genus of 148 species (Hobbs 1981) reaching its greatest diversity in the southern United States and extending as far south as Cuba and Honduras. The four species in Illinois are sluggish-water inhabitants, as are most species of the genus. Illinois species are in the subgenera *Girardiella* (*gracilis*), *Ortmannicus* (*acutus* and *viaeviridis*), and *Scapulicambarus* (*clarkii*).

***Procambarus gracilis* (Bundy)**
(Fig. 98)

Cambarus gracilis Bundy 1876

Description.—Rostrum broad, deeply excavated, with short acumen, no median carina; margins barely converge anteriorly, without tubercles or spines. Carapace compressed, lacking cervical spines; suborbital margin angular.

Areola extremely narrow, almost linear. Chela large, heavily punctate; palm with one row or large tubercles on mesial margin; dactyl with shallow concavity on basal half of opposable margin. Form I gonopod terminates in four short elements: a sclerotized, curved central projection; a curved mesial process; a straight cephalic process;

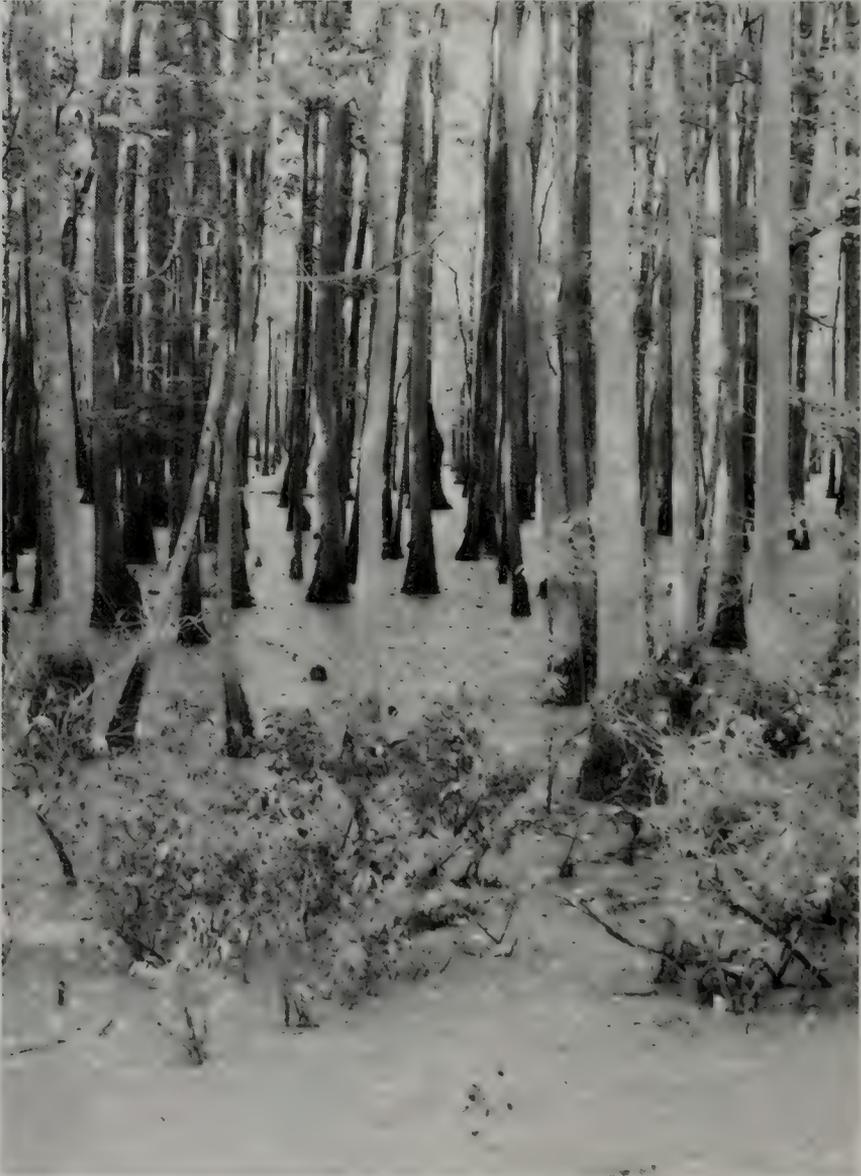


Fig. 97.—Bell Pond, east of Grantsburg, Johnson County, Illinois (8 October 1984), supports large populations of *C. puer* and *P. clarkii*.

Table 6.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Cambarellus puer*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
February	1	1	100	0	0	0	0
March	3	2	67	1	33	0	0
April	1	1	100	1	100	0	0
May	1	1	100	1	100	1	100
August	1	0	0	0	0	0	0
October	1	1	100	0	0	0	0

and a large sclerotized caudal process. Adults have a bright red thorax and abdomen, are red brown elsewhere; young are red brown overall.

Bundy (in Forbes 1876) described *Cambarus gracilis* (= *P. gracilis*) from Normal, McLean County, Illinois, and Racine, Racine County, Wisconsin. Hobb (1974b) restricted the type locality to Normal. *P. gracilis* is a member of the subgenus *Girardiella* (see Hobbs 1972b) and has its closest relationships to *P. liberorum* and *P. reimeri* (Fitzpatrick 1978a; Hobbs 1979).

Distribution and Habitat.—*P. gracilis* is a burrower occupying grasslands and former grasslands from eastern Indiana and southeastern Wisconsin to southeastern Nebraska, eastern Kansas, Oklahoma, and northeastern Texas (Fig. 99). It is generally distributed throughout the glaciated area of Illinois, i.e., north of the Shawnee Hills, although it appears to be absent in the Big Muddy-Lower Kaskaskia drainage area and is uncommon in northern Illinois and in the Kankakee River basin (Fig. 100).

P. gracilis is found in low, poorly drained areas usually with a silt or clay substrate and covered with grasses or other prairie plants. Where tracts of prairie remain in Illinois, *P. gracilis* often is present in large populations. Unfortunately, few large tracts of prairie remain, and populations of *P. gracilis* more typically are small and isolated in such habitats as roadside ditches (Fig. 101) and field drainage ditches. Although appearing to retain

little of the original characteristics of prairies, when flooded these ditches will be found to harbor *P. gracilis*.

P. gracilis spends most of the year underground in burrows (Fig. 102) that may reach 2 m in depth (Creaser 1932) and end in an enlarged resting chamber beneath the water table (Creaser & Ortenburger 1933; Phillips 1980). During periods of heavy rainfall, usually late winter and spring, the ditches and prairies flood, and *P. gracilis* can be found above ground. Usually only small individuals are found. During the present survey, few adult *P. gracilis* were encountered; in fact, judging from the individuals collected, most populations seemed to consist only of juveniles. Apparently even during periods of flooding, large individuals stay underground. Large individuals are more likely to leave the burrows on warm rainy summer nights and walk above ground.

Life History.—Because so few adult *P. gracilis* were collected during the present survey, little new life history information can be added. Of the 101 collections of Illinois *P. gracilis* procured during the present study, only five contained form I males, and none contained females with eggs or young attached. Form I males ($N = 7$) were present in June, July, and October collections (Table 7) and ranged from 30.2 to 34.4 mm CL (mean, 32.7 mm CL). The largest female (from Bugaboo Creek, Lawrence County, 12 April 1979) was 34.8 mm CL.

Rietz (1912) found form I males in

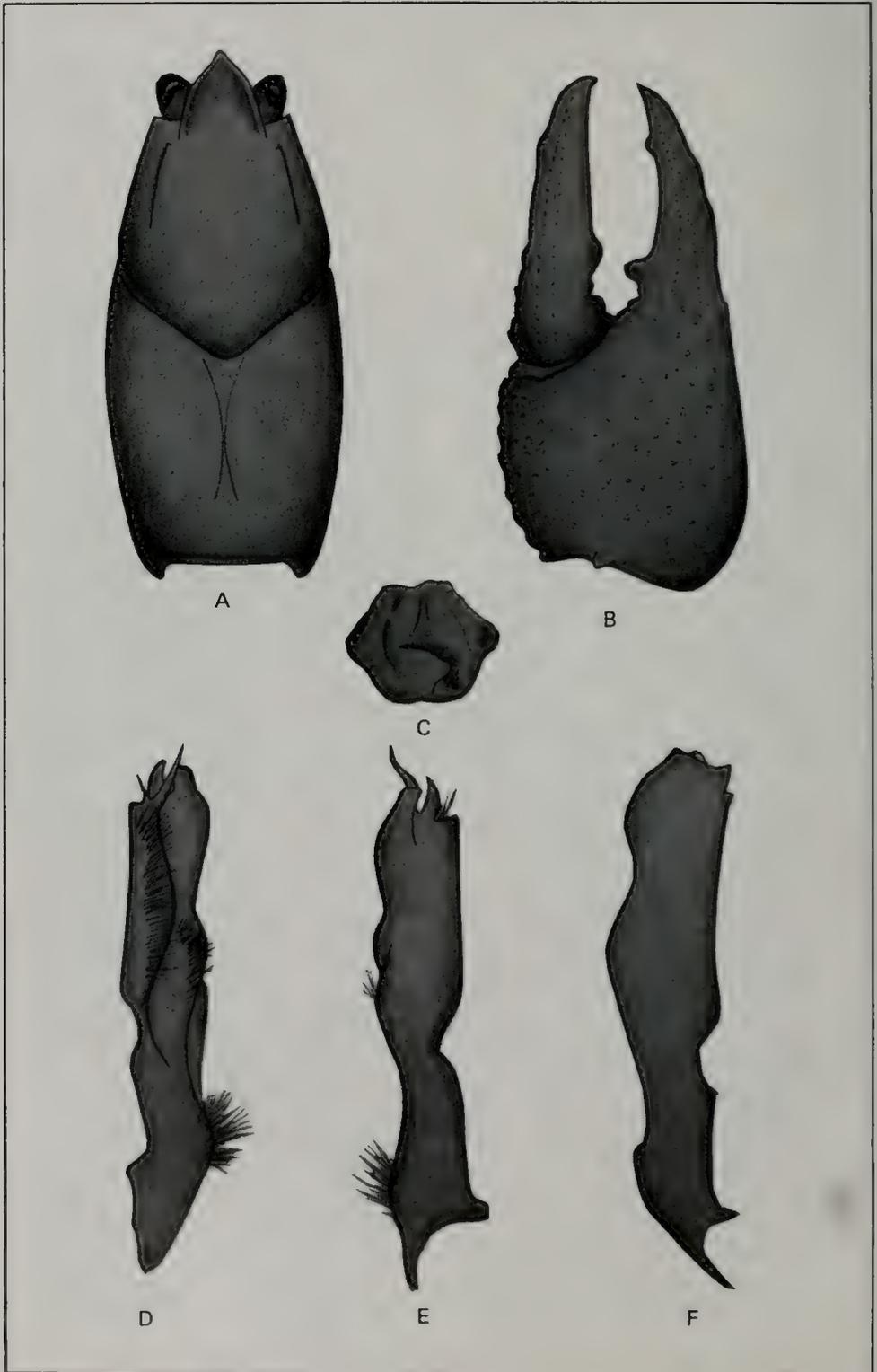


Fig. 98.—*Procambarus gracilis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 99.—Total distribution of *Procambarus gracilis*. The eastern limit of its range is unknown.



Fig. 100.—Distribution of *Procambarus gracilis* in Illinois. Open circle = 1922 record for the Kankakee River; black dots = 1972-1982 collections.

Illinois in February, March, April, and May. Brown (1955) found form I males in Illinois in August and October and females with young attached in March, April, and October. Brown's largest form I male was 39 mm CL, and his largest female was 47 mm CL. Williams & Leonard (1952) found young attached to many of the females collected in early spring in Kansas. Creaser (1932)

noted that "females with young attached are taken in Missouri as late as October."

Among all specimens collected in the present study, males outnumbered

Table 7.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Procambarus gracilis*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males	Ovigerous Females	Females with Young	Form I Males	Ovigerous Females	Females with Young
February	3	0	0	0	0	0	0
March	13	0	0	0	0	0	0
April	17	0	0	0	0	0	0
May	16	0	0	0	0	0	0
June	12	3	25	0	0	0	0
July	6	1	17	0	0	0	0
August	2	0	0	0	0	0	0
September	16	0	0	0	0	0	0
October	13	1	8	0	0	0	0
November	3	0	0	0	0	0	0



Fig. 101.—Roadside ditch, ½ mi. W Winterrowd, Effingham County, Illinois, 3 May 1977; typical habitat for *Procambarus gracilis*.



Fig. 102.—Capped entrance to burrow of *Procambarus gracilis* in a field in Des Plaines, Cook County, Illinois, 15 June 1972.

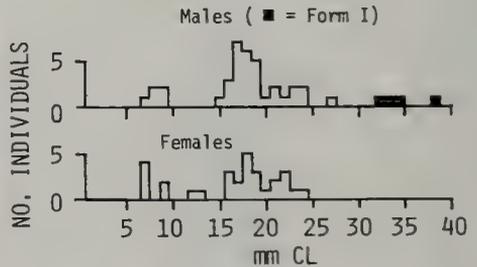


Fig. 103.—Size-frequency distribution of *Procambarus gracilis* collected in northeastern Illinois, June 1972.

females 182 to 157 (1.16:1). Very small specimens (< 10 mm CL) were collected as early as February 28 and as late as October 7. Length-frequency data on June-collected samples from northeastern Illinois suggest that males live to a third year (i.e., are 2+ years old); form I males were the largest males in the collection (Fig. 103). The lengths of larger females collected elsewhere in Illinois suggest that they also live to a third summer (i.e., to 35 mm CL) and maybe even to a fourth (to 47 mm CL).

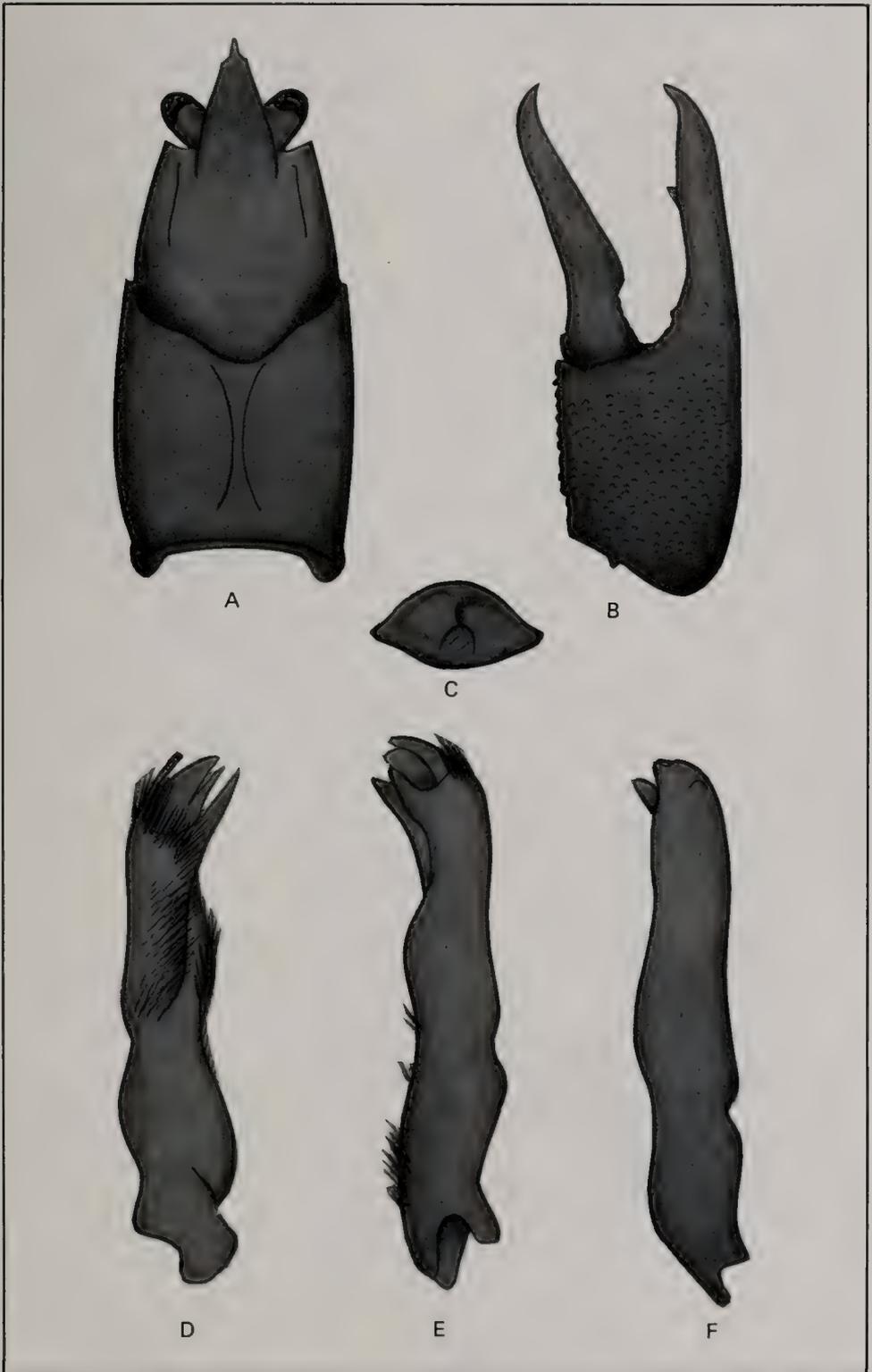


Fig. 104.—*Procambarus acutus*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

***Procambarus acutus* (Girard)**

(Fig. 104)

Cambarus acutus Girard 1852*Cambarus stygius* Bundy 1876

Description.—Rostrum broad posteriorly, strongly converges anteriorly, excavated, no median carina, marginal spines or tubercles small to absent (largest on small individuals). Carapace compressed, cervical spines present; suborbital margin angular. Areola narrow, narrowest part about 5–8 percent of length. Chela long and narrow, heavily punctate; palm with row of large tubercles on mesial margin, one or two adjacent rows on dorsal and ventral surfaces. Form I gonopod terminates in four elements, all more or less directed caudodistally and variously obscured by a mass of setae originating on the caudal knob: a relatively large sclerotized central projection, an unsclerotized slender mesial process, a sclerotized cephalic process, and a sclerotized caudal process. Dorsal color individuals dark red with a black rectangle on each abdominal segment.

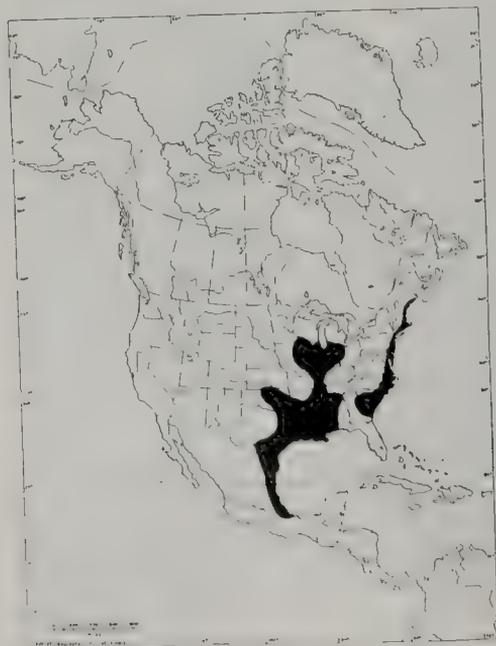


Fig. 105.—Total distribution of *Procambarus acutus*.

P. acutus is a member of the *P. blandingii* species group of the subgenus *Ortmannicus* (Hobbs 1962, 1972b). Two subspecies of *P. acutus* are recognized. *P. a. cuevachicae* occupies San Luis Potosi and Puebla and intergrades with *P. a. acutus* in northern Mexico and Texas. *P. a. acutus* occupies the rest of the range of the species (Hobbs 1972a), as described below. Hobbs (1981) noted the existence of several regionally restricted "variants" of *P. a. acutus* and suggested that some may deserve taxonomic recognition.

Cambarus stygius was described by Bundy (in Forbes 1876) from specimens found, following a storm, on the shore of Lake Michigan at Racine, Wisconsin, (Bundy 1882) and listed by Forbes (1876) as an Illinois species. Creaser (1932) declared *Cambarus stygius* to be a synonym of *Cambarus blandingii acutus* (= *Cambarus acutus* Girard).

Distribution and Habitat.—*P. acutus* has a disjunct range. In the east it occurs along the Atlantic Slope from Maine to central Georgia (Altamaha River system) and to the west (Great Lakes and Mississippi River basins) it ranges from southern Michigan and western Indiana west to southeastern Minnesota and south to Alabama, western Oklahoma, and along the Gulf slope into Mexico (Fig. 105).

P. acutus has been counted among the Illinois fauna since 1870 (Hagen 1870), and Forbes (1876) stated that it was very common in central Illinois. Rietz (1912) found the species (as *Cambarus blandingii*) to be widely distributed and generally abundant and documented its occurrence in 32 Illinois counties. Brown (1955) found it in 36 counties drained by the Sangamon, Wabash, and Ohio river systems and reported it especially common in the Sangamon system. Populations in Illinois were generally referred to as *P. blandingii* until Hobbs (1962) restricted the range of *P. a. blandingii* to North and South Carolina.

Presently *P. acutus* occupies most, perhaps all, drainages of the state, but

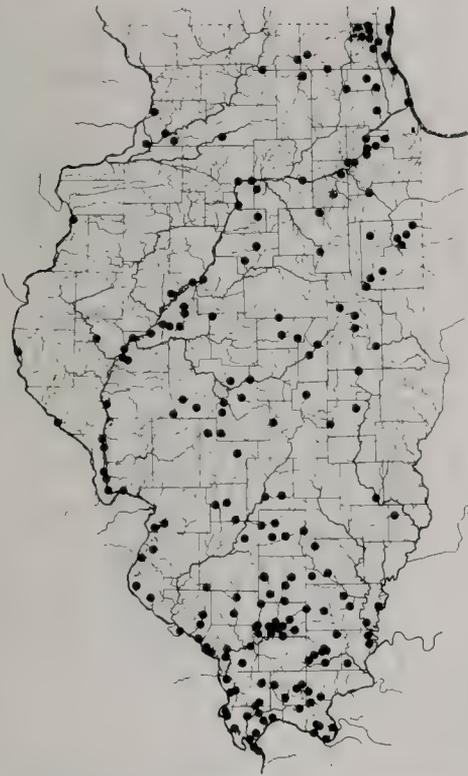


Fig. 106.—Distribution of *Procambarus acutus* in Illinois; black dots = 1972–1982 collections.

records are absent from the Spoon and other small rivers in western Illinois and from the Pecatonica and other streams in northwestern Illinois (Fig. 106). It is most common in the sluggish streams

of southern Illinois, especially in the Big Muddy drainage and in streams on the Coastal Plain. Being a relatively deep water species, *P. acutus* is somewhat more difficult to capture than are shallow water crayfishes, and it may be more common in Illinois than present records suggest.

In Illinois, the species is most common in permanent standing water bodies, especially those with luxuriant vegetation, and also is found in stream pools and slowly flowing runs with mud or sand bottoms. Elsewhere, the species occupies similar habitats but also may rarely be found in swiftly flowing streams (e.g., Williams 1954; Brown 1959; Hobbs 1981).

A burrow may be constructed and inhabited when water bodies reach below-normal levels (Cralley 1932; Creaser & Ortenburger 1933), adults may burrow during cold weather, and females sometimes sequester themselves in burrows when carrying eggs and young (Cralley 1932; Penn 1956; Hobbs 1981). The sequestering behavior could explain the extremely small number of ovigerous females found in Illinois and elsewhere (see below). In the Reel-foot Lake area, Hobbs & Marchand (1943) found burrows of *P. acutus* to be shallow excavations, usually under logs and consisting of a single passage-way extending only a few inches under-

Table 8.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Procambarus acutus*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	7	2	29	0	0	0	0
February	6	1	17	0	0	0	0
March	13	2	15	0	0	0	0
April	28	4	14	0	0	0	0
May	37	2	5	0	0	0	0
June	33	10	30	0	0	0	0
July	17	8	47	0	0	0	0
August	13	3	23	0	0	0	0
September	18	5	28	0	0	0	0
October	23	0	0	0	0	0	0
November	11	0	0	0	0	0	0
December	6	1	17	0	0	1	17

ground. A burrow 60 cm deep was found along the margin of a drainage ditch in Iowa (Phillips 1980).

Life History.—In the present survey of Illinois, 212 collections of *P. acutus* were made. Form I males were found every month except October and November (Table 8). They peaked in relative abundance in June–September and, secondarily, in January. Cralley (1932) found form I males in Illinois in June and July, and Brown (1955) from April to July and in September. Form I males have been found in June and July in western Tennessee (Hobbs & Marchand 1943); in August and September in the Ozark-Quachita region (Williams 1954); from February to July and in September in Texas (Penn & Hobbs 1958); from May to August in Iowa (Phillips 1980); in April, August, and “the fall” in Georgia; in March, April, June, July, and September in Alabama; in April and May in Florida; and in all months except May in South Carolina (Hobbs 1981).

No females were found carrying eggs, and only one (49.3 mm CL), collected in December, was carrying young ($N = 30$). In other Illinois surveys, Rietz (1912) reported a female collected with young in April, Cralley (1932) reported ovigerous females collected in July, and Brown (1955) found a female with eggs in August and one with young attached in April. All females with eggs and young found by Cralley and Brown were taken from burrows.

Few females with eggs or young have been collected elsewhere, probably because of their sequestering behavior (Penn 1956; Hobbs 1981). In the southeastern United States, no females with eggs and only one female with young (from Alabama in September) have been collected (Hobbs 1981). Turner (1926) reported eggs and young on *P. acutus* in Ohio and Indiana in March, July, and September, and Penn (1956) found females with young attached in October and January in Louisiana.

In the present survey males slightly outnumbered females, 523 to 513. The

largest Illinois specimen is a 54.1-mm CL female collected on 20 February 1974 in the Maeystown Creek system, Monroe County. The largest male is a 54.0 mm-CL form I collected in 1974 in the Mississippi River, Whiteside County. Hobbs (1981) recorded a 58.9-mm CL form I male from Georgia. The smallest form I male from Illinois is 30.8 mm CL and was collected in the Mississippi River, Randolph County, on 24 March 1975.

Procambarus viaeviridis (Faxon)

(Fig. 107)

Cambarus viae-viridis Faxon 1914

Description.—Rostrum flat, deflecting downward anteriorly; margins converge anteriorly to short acumen, without spines or tubercles; no median carina. Carapace compressed, lacking cervical spines; suborbital margin barely angular. Areola narrow, narrowest part about 4–7 percent of length. Chela long and narrow, heavily punctate; palm with row of 7–9 long tubercles on mesial margin, 2–3 adjacent rows of smaller tubercles. Form I gonopod terminates in four short elements: a sclerotized mesial process, a sclerotized central projection, a cephalic process, and a large setae-covered caudal knob on cephalic surface. Adults are deep rust red dorsally with the abdomen somewhat lighter in color than the carapace.

P. viaeviridis is a member of the *P. blandingii* species group of the subgenus *Ortmannicus* (Hobbs 1962, 1972b).

Distribution and Habitat.—*P. viae-viridis* occupies standing water bodies and sluggish streams on the former Mississippi Embayment and Gulf Coastal Plain from southern Illinois south to northern Louisiana and central Alabama (Fig. 108).

P. viaeviridis is restricted in Illinois to cypress swamps and floodplains along sluggish streams in the extreme southern part of the state (Fig. 109). First reported for Illinois by Page and Burr (1973), the species now is known

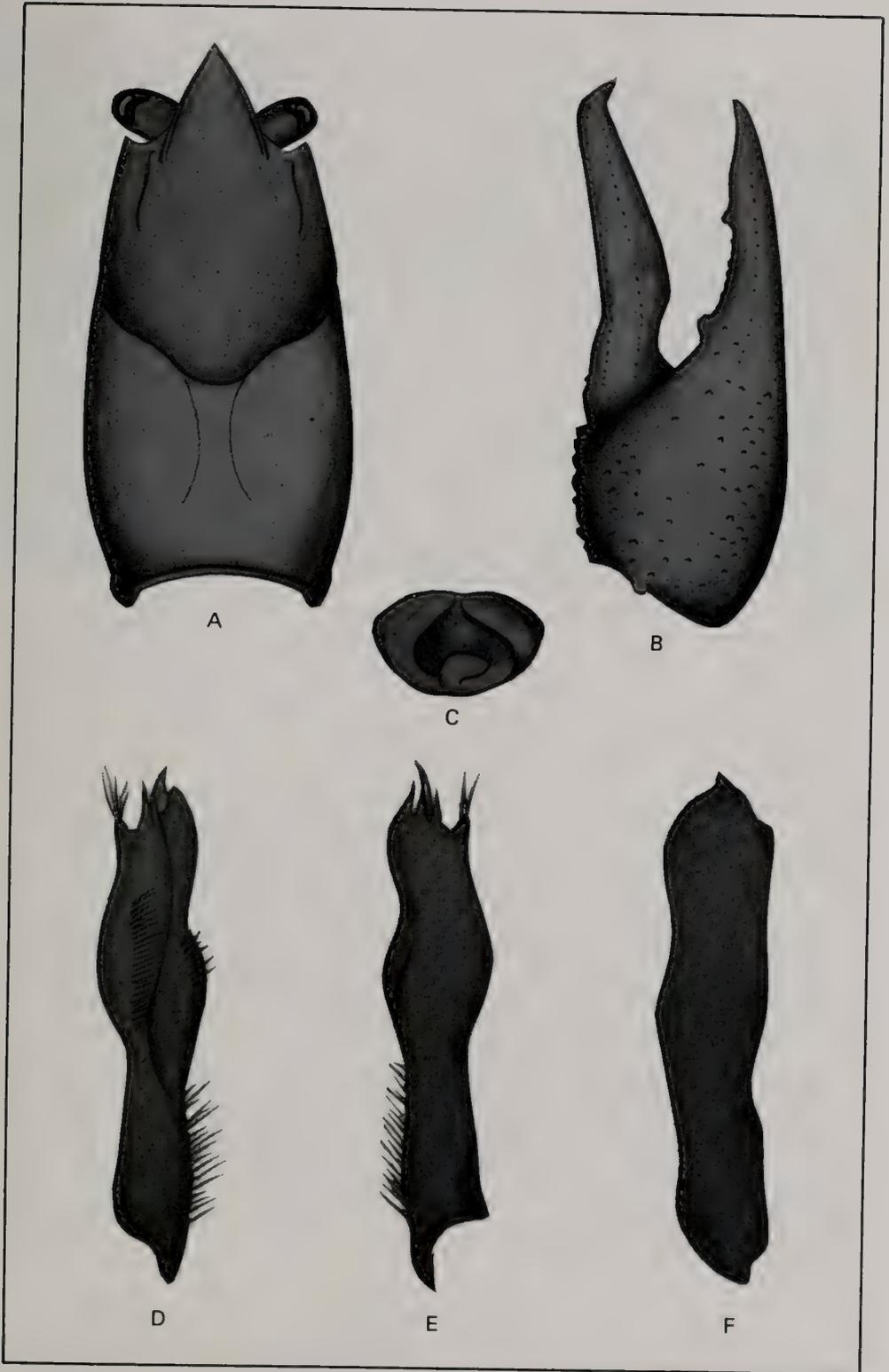


Fig. 107.—*Procambarus viaeviridis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

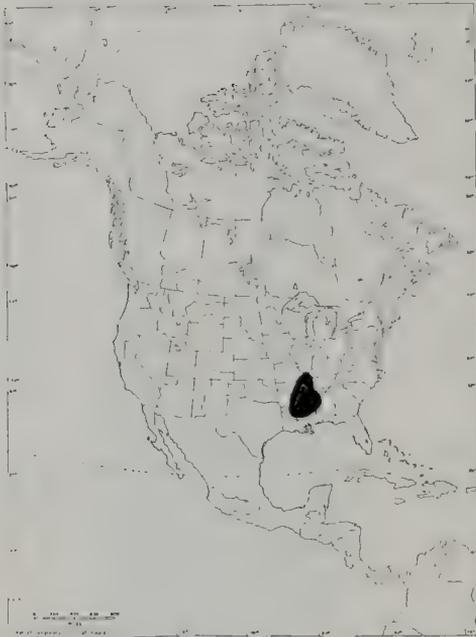


Fig. 108.—Total distribution of *Procambarus viaeviridis*.

from localities in the Ohio River drainage in Alexander, Johnson, Massac, Pope, and Pulaski counties. The largest populations are in cypress swamps (especially Heron Pond-Little Black Slough and Bell Pond) in Johnson County.

Life History.—Other than brief comments on its affinity for sluggish and standing bodies of water, nothing appears to have been published on the ecological characteristics of *P. viaeviridis*. During the present study, 16 collections of the species were made, all from December through May (Table 9).

Table 9.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Procambarus viaeviridis*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	1	1	100	0	0	0	0
February	2	0	0	0	0	0	0
March	2	0	0	0	0	0	0
April	5	0	0	0	0	0	0
May	5	2	40	0	0	0	0
December	1	0	0	0	0	0	0



Fig. 109.—Distribution of *Procambarus viaeviridis* in Illinois; black dots = 1972-1982 collections.

During this period, water levels in southern Illinois are generally high, and *P. viaeviridis* can be found on flooded floodplains, in some roadside ditches, and in swamps. Periodically flooded areas appear to be the preferred habitat of *P. viaeviridis*, and when they dry, the crayfish burrows underground. In April, specimens were dug from burrows 15-30 cm deep on the floodplain



Fig. 110.—Floodplain of Max Creek at the Route 147 bridge, Johnson County, Illinois, 8 October 1984. *Procambarus viaeviridis* can be found here above ground during flooding and can be dug from burrows during periods of low water. *P. viaeviridis* persists here even though the formerly forested floodplain now is covered with grasses.

of Max Creek, Johnson County (Fig. 110). In December and January, 1975–76, crayfish were active in water 1°C under a cover of ice. The usual absence of floodwater in southern Illinois from June through November accounts for the lack of Illinois collections during this period (Table 9); however, more extensive effort presumably would

reveal that the species may be found in permanent swamps even during this period.

Form I males were present in collections made in January and May (Table 9). Among the four form I males collected, the smallest was 24.1 mm CL, and the largest was 29.9 mm CL. The largest Illinois specimen of *P. viaeviridis* is a 32.3-mm CL female collected in Heron Pond on 30 March 1973. No females with eggs or young attached were collected. The smallest individuals (about 5–10 mm CL) were collected in January and February.

The length-frequency distribution of individuals collected in Bell Pond in May ($N = 50$) suggests that the species, at least in Illinois, lives 2 years (Fig. 111). The sex ratio in this collection was 1.4 males: 1 female.

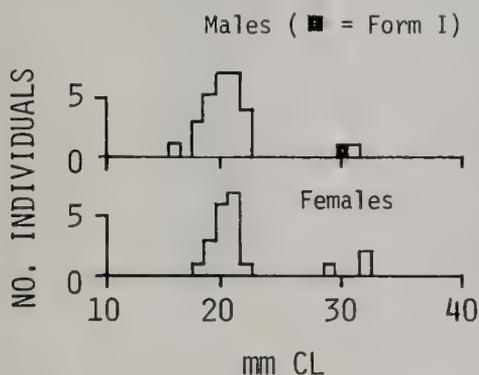


Fig. 111.—Size-frequency distribution of *Procamburus viaeviridis* collected in Bell Pond, Johnson County, Illinois, 19 May 1973.

***Procamburus clarkii* (Girard)**
(Fig. 112)

Cambarus Clarkii Girard 1852

Description.—Rostrum deeply ex-

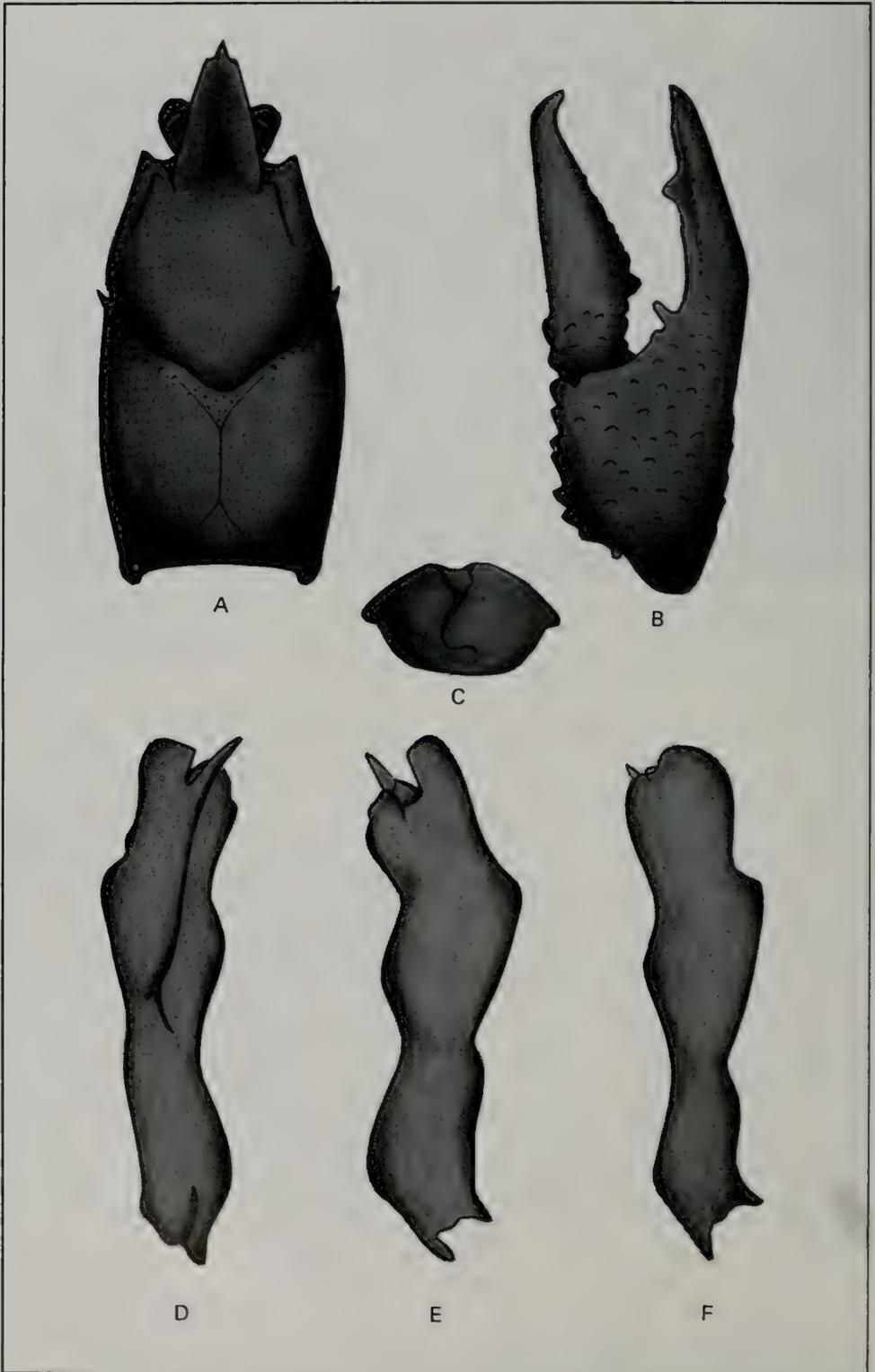


Fig. 112.—*Procambarus clarkii*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

cavated; margins converge anteriorly, terminating in small to large spines; acumen long; no median carina. Carapace compressed, with cervical spines; suborbital margin angular. Areola extremely narrow, sometimes obliterated at midlength. Chela long and narrow, punctate; palm with row of 6-8 tubercles on mesial margin, 2-3 adjacent rows of smaller tubercles. Form I gonopod with a large angular shoulder on cephalic surface, a large lobiform sclerotized cephalic process, small mesial process, and small sclerotized central projection. Light to dark red dorsally and laterally; white ventrally with blue stripe along middle of abdomen.

P. clarkii is a member of the subgenus *Scapulicambarus* (Hobbs 1972b), an assemblage of six species confined to the Atlantic and Gulf Coastal Plain of the United States and Mexico (Hobbs & Grubbs 1982).

Distribution and Habitat.—*P. clarkii* is an abundant inhabitant of standing water bodies and slowly flowing streams on the Gulf Coastal Plain from the

Florida panhandle to northern Mexico and up the former Mississippi Embayment to southern Illinois (Fig. 113). It is the crayfish commonly harvested for human consumption in the eastern United States.

In Illinois, *P. clarkii* occurs in swamps, vegetated ponds, and stream pools in the extreme southern part of the state (Pope, Johnson, Massac, Union, Pulaski, and Alexander counties) (Fig. 114). Most localities are in the Ohio River drainage, although some are in the Mississippi River drainage. It remains common, especially in Mermet Swamp (Fig. 89), Bell Pond (Fig. 97), LaRue Swamp, Horseshoe Lake, and parts of the Cache River system but undoubtedly was more common prior to the drainage of much of the southern Illinois wetlands. *P. clarkii* is taken often with *P. acutus* but is more common than *P. acutus* in the cypress-



Fig. 113.—Total distribution of *Procambarus clarkii*. The southwestern limit of its range is unknown.



Fig. 114.—Distribution of *Procambarus clarkii* in Illinois; black dots = 1972-1982 collections.

Table 10.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Procambarus clarkii*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
February	3	0	0	0	0	1	33
March	2	0	0	0	0	0	0
April	3	1	33	0	0	0	0
May	10	1	10	0	0	0	0
June	3	1	33	0	0	0	0
August	1	0	0	0	0	0	0
September	1	1	100	0	0	0	0
October	4	0	0	0	0	0	0
November	2	0	0	0	0	0	0
December	1	0	0	0	0	0	0

tupelo swamps in which it reaches its greatest abundance.

Brown (1959) compared the habitat characteristics of *P. clarkii* and *P. acutus* in Illinois and Louisiana and concluded that *P. clarkii* is found more often in standing turbid water over mud; *P. acutus* is found more often in running water over a variety of substrates, but also usually over mud.

In Louisiana, Penn (1956) estimated that most collections of *P. clarkii* were made in marshes, then swamps, lakes and ponds, ditches, and, finally, slow streams (especially bayous). The species prefers shallow (less than 40 cm), permanent, static water exposed to full sunlight and usually is collected in mud-bottomed habitats with abundant vegetation (Penn 1956). *P. clarkii* feeds on vegetation (Viosca 1931).

Life History.—The life history of *P. clarkii* in Louisiana has been studied

by Viosca (1939, 1953) and Penn (1943). Females carry eggs and young from June through early September. Juveniles leave the females and live in open water, grow slowly through fall and winter, grow rapidly in spring, and reach sexual maturity by May. Most 1-year-old males are form I during the summer, and copulation apparently occurs through September. The smallest form I male recorded in Louisiana was 24 mm CL. The smallest ovigerous female was 29 mm CL. Adults spend the winter in shallow burrows in marshes and swamp bottoms. Burrows, usually shallow but sometimes reaching 60 cm deep, also may be constructed to escape the drying of the habitat. In the Reelfoot Lake region of western Tennessee, Hobbs & Marchand (1943) found many individuals in burrows in June and July.

Among the 30 collections and 267 individuals (125 males: 142 females) of *P. clarkii* collected in the present survey, form I males were found from April to June and in September (Table 10). The smallest was 34.7 mm CL and was collected in the Cache River, Pulaski County, on 27 April 1976. Brown (1955) found form I males in Illinois in July, August, and September.

In the present survey, the only female with eggs or young attached was a female ca. 47 mm CL (the rostrum was damaged) collected on 18 February 1981 with 43 young attached. Brown (1955)

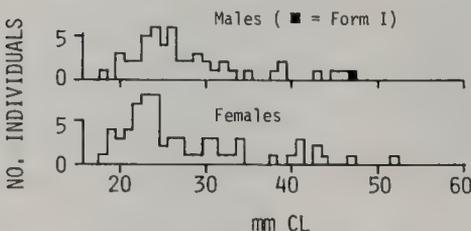


Fig. 115.—Size-frequency distribution of *Procambarus clarkii* collected in Bay Creek, Pope and Johnson counties, Illinois, 19 May 1973.

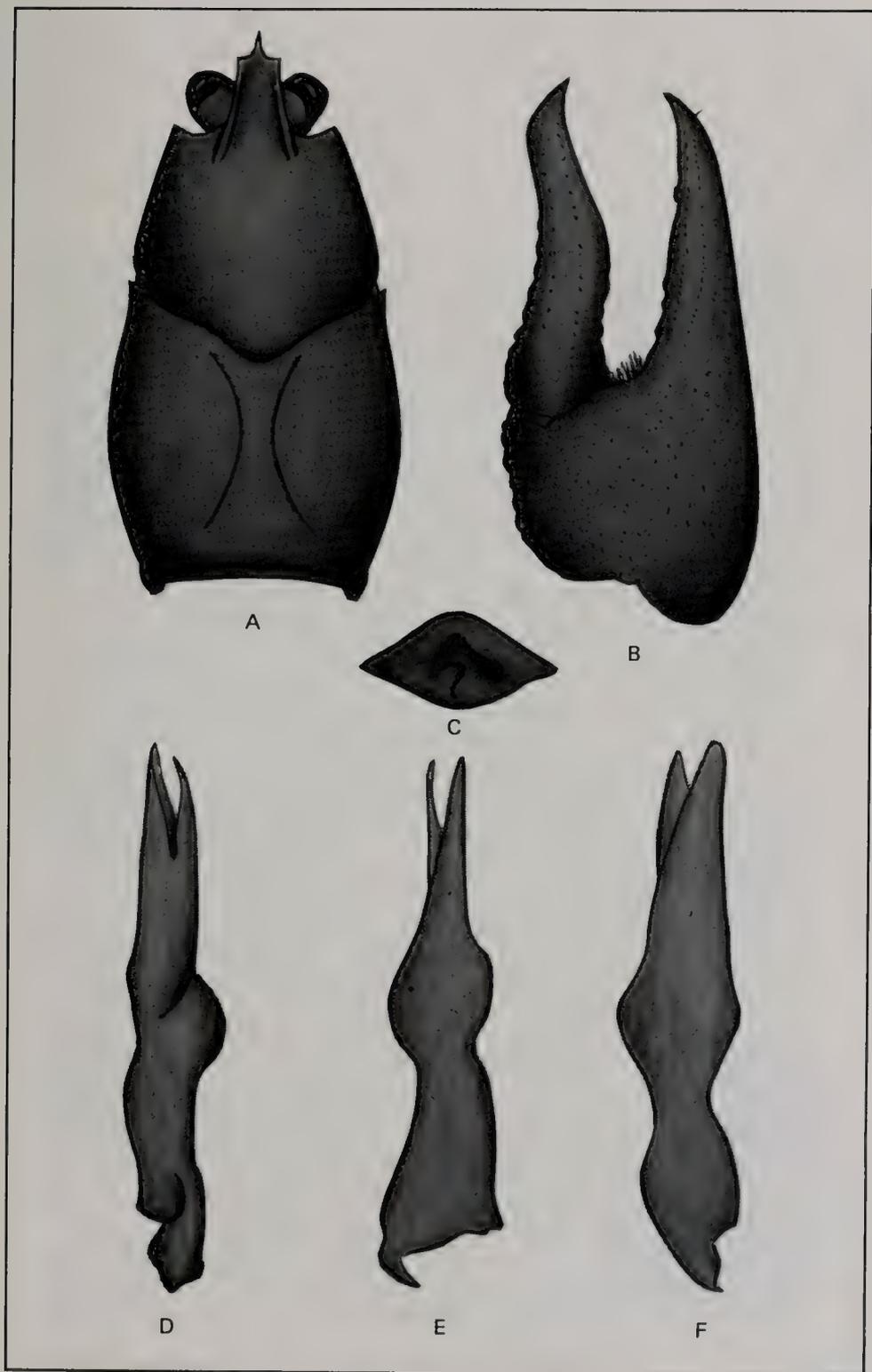


Fig. 116.—*Orconectes illinoiensis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

found two females with eggs and three with young attached in Illinois on 6 September 1954; all were dug from burrows. Penn (1943) found a female only 30.5 mm CL carrying young in Louisiana.

The largest Illinois specimen is a 60.7-mm CL female collected in Horseshoe Lake, Alexander County, on 20 June 1973; the largest male, from the same collection, is a 51.7 mm CL form I. Brown (1955) recorded a 54-mm CL form I male from Illinois.

The size-frequency distribution of 116 individuals collected in the Bay Creek system on 19 May 1973 suggests that individuals of both sexes live a maximum of about 2 years (Fig. 115), although the largest female mentioned above, at 60.7 mm, may have been 3 years old.

Genus *Orconectes* Cope

Orconectes Cope 1872

Faxonius Ortmann 1905

Gonopod with two terminal elements; central projection not large and bladelike. Ischium of third pereopod with hook.

Ten of the 65 recognized species of *Orconectes* (Hobbs 1981) occur in Illinois. Species of *Orconectes* are, with few exceptions, open stream inhabitants and they, more than other crayfishes, have found Illinois suitable for occupation.

Orconectes illinoiensis Brown

(Fig. 116)

Orconectes illinoiensis Brown 1956

Description.—Rostrum deeply excavated, deflecting downward anteriorly; long acumen; margins thick, converging anteriorly, straight to slightly concave, terminating in spines; no median carina. Carapace flattened dorsoventrally, with large cervical spines; suborbital margin smooth to slightly angular. Areola moderately wide, narrowest part about 13–15 percent of length. Chelae large, heavily punctate; fingers often very long; palm

with row of 8–9 tubercles on mesial margin; 1–2 adjacent rows of tubercles on dorsal surface. Form I gonopod terminates in two short, straight elements: a sclerotized central projection and an unsclerotized mesial process. Dorsally light to dull red brown; fingers of chelae with red tips, subdistal black bands.

O. illinoiensis is a member of the *Propinquus* group of *Orconectes* (Fitzpatrick 1967). The closest relative in Illinois is *O. propinquus*.

Distribution and Habitat.—*O. illinoiensis* is endemic to southern Illinois. It was recognized first by Brown (1955) as a distinct species and formally described by him in 1956. During the present survey it was found to occupy rocky riffles and pools of streams in the Ohio and Big Muddy (Mississippi River drainage) systems of Hardin, Pope, Johnson, Massac, Pulaski, Alexander, Union, Williamson, and Jackson counties (Fig. 117). Most of the known



Fig. 117.—Distribution of *Orconectes illinoiensis*; black dots = 1972–1982 collections.

localities (Fig. 118) are in the Shawnee Hills, but a few populations occupy rocky streams on the Coastal Plain and in the region just north of the Shawnee Hills. Some populations may have been eliminated or reduced in recent decades through stream desiccation or other recent perturbations, but the distribu-

tion of the species today probably approximates its prehistoric distribution. Many populations are large, especially in upland streams in Pope County.

Brown (1956) recorded a collection of *O. illinoensis* from Cypress Ditch near Junction in Gallatin County. This is in the Saline River drainage, from



Fig. 118.—Gibbons Creek, Herod, Pope County, Illinois, (8 October 1984) provides habitat for *Orconectes illinoensis*.

Table 11.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes illinoiensis*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
March	2	1	50	1	50	0	0
April	2	1	50	1	50	1	50
May	7	0	0	0	0	1	14
June	4	0	0	0	0	0	0
July	4	1	25	0	0	0	0
August	12	0	0	0	0	0	0
October	7	4	57	0	0	0	0
November	4	3	75	0	0	0	0

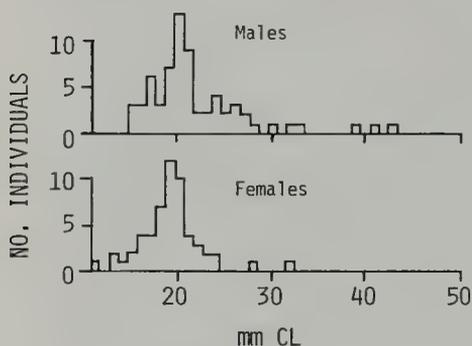


Fig. 119.—Size-frequency distribution of *Orconectes illinoiensis* collected in April and May.

which no other collections of *O. illinoiensis* have been made. Although the specimens cannot now be located and re-examined, it seems likely that they were misidentified *O. indianensis*. Attempts to collect in Cypress Ditch during this survey produced no *Orconectes*.

Life History.—Among the 263 specimens in the INHS collection, 132 are males and 131 are females. The largest specimen is a 42.6-mm CL form II male collected in Gibbons Creek, Pope County, on 2 May 1972. The largest female, 41.6 mm CL, is from Dutchman Creek, Pope County, collected on 14 October 1974.

Form I males collected during the present survey ranged from 18.5 to 42.4 mm CL (the largest has a right chela 55.5 mm in length) and were collected in March, April, July, October, and

November (Table 11). Brown (1955) collected form I males from July to November.

Three females in two collections (Table 11) were ovigerous: a 26.1-mm CL female collected on 26 March 1975 with 175 eggs, a 21.5-mm CL female collected on 8 April 1978 with 84 eggs, and a 31.3-mm CL female collected on the latter date with 110 eggs. Eggs are spherical and average 2.0 mm in diameter. Two females, a 20.0-mm CL female collected on 28 April 1976 and a 27.1-mm CL female collected on 19 May 1973, had 57 and 34 young attached, respectively.

April- and May-collected specimens ($N = 122$) were modally 19–20 mm CL (Fig. 119), and most of these specimens were presumably 1 year old. The few especially large males (39–43 mm CL) were probably 3 years old and represent the maximum longevity of the species.

***Orconectes immunis* (Hagen)**
(Fig. 120)

- Cambarus immunis* Hagen 1870
- Cambarus signifer* Herrick 1882
- Cambarus immunis spinirostris* Faxon 1884
- Faxonius (Faxonius) immunis pedianus* Creaser 1933

Description.—Rostrum excavated; acumen moderately long; margins convex, converging anteriorly, without terminal spines, sometimes with small terminal tubercles; no median carina. Carapace compressed, with cervical

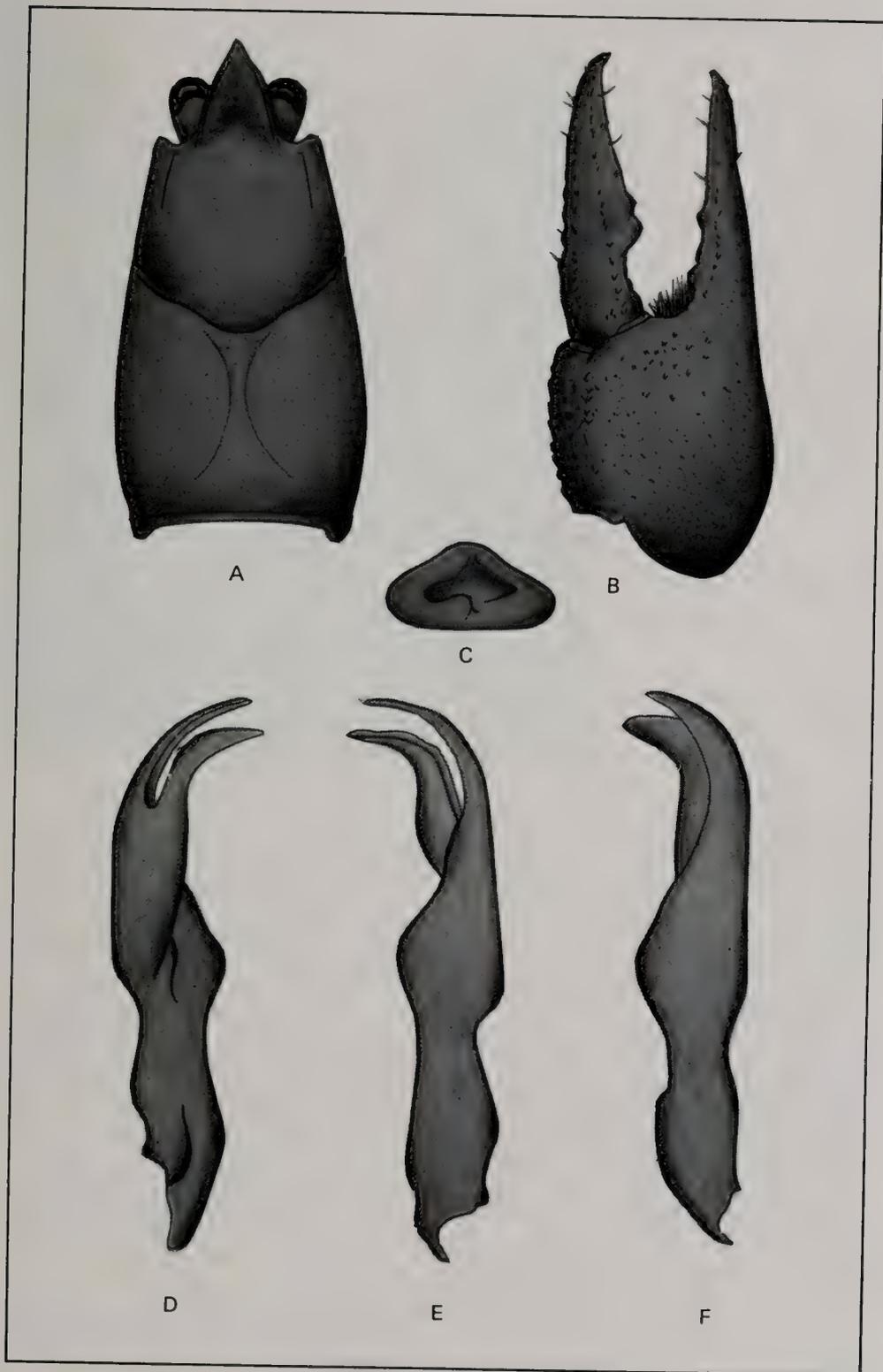


Fig. 120.—*Orconectes immunis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 121.—Total distribution of *Orconectes immunis*.

spines; suborbital margin bluntly angular. Areola narrow, constricted anteriorly, narrowest part about 10 percent of length. Chelae moderate in size, heavily punctate; palm with 2-3 rows of small tubercles on dorsomesial margin. Form I gonopod terminates in two fairly short (central projection about 23 percent of total length of gonopod) elements curved at 90° angle to main axis; a sclerotized central projection and an unsclerotized mesial process. Annulus ventralis distinctive, with fossa far to one side. Dorsal color highly variable, from uniformly red brown to light green with dark brown mottling; fingers of chelae without bright red tips and subdistal black bands.

O. immunis is a member of the *Virilis* group of *Orconectes* and is most similar to *O. alabamensis*, *O. rhoadesi*, and *O. validus*, species inhabiting the Cumberland, Tennessee, and Mobile Bay drainages. Some populations of the wide-ranging *O. immunis* have been considered sufficiently distinct to warrant taxonomic recognition (see syn-

onymy above), and Bovbjerg (1952) referred to northeastern Illinois populations as "*O. immunis* x *pedianus*." However, Williams & Leonard (1952) found that the characteristics which had been used to distinguish subspecies varied clinally and could not be used to diagnose geographically limited populations. No subspecies were recognized by Hobbs (1974b).

Distribution and Habitat.—*O. immunis* ranges from southern Quebec, Maine, and Connecticut west through the Great Lakes (except Lake Superior), to eastern Wyoming and eastern Colorado (Fig. 121). The southern edge of the range approximates the southern limit of Pleistocene glaciation but extends farther south into western Kentucky and Tennessee and farther west into the Great Plains. An isolated population in Muddy Creek (Canadian-Arkansas River drainage), Okfuskee



Fig. 122.—Distribution of *Orconectes immunis* in Illinois; black dots = 1972-1982 collections.



Fig. 123.—Little Wabash River, 2 mi. WSW Mattoon, Coles County, Illinois, 25 October 1983. This and other sluggish weedy streams in Illinois often contain large populations of *Orconectes immunis*.

County, Oklahoma, (Creaser & Ortenburger 1933) is far south of other populations and may have been introduced.

The species occurs throughout Illinois except in the unglaciated northwest (Fig. 122). It appears to be rare in extreme western Illinois, although Rietz (1912) found it in several western counties (Fulton, Hancock, Henderson, and Mercer) for which recent records are unavailable. Elsewhere in the state it is generally common, and local populations sometimes consist of thousands of individuals. It undoubtedly was even more common and widespread when Illinois had large expanses of undrained prairies. In fact, Forbes (1876) referred to *O. immunis* as "the commonest species of central Illinois," and "especially frequent in the muddy ponds of the prairies, where it may be drawn by the hundreds with a small seine."

O. immunis lives in slowly flowing pools, usually with soft bottoms, of headwaters, creeks, and small to large rivers (Fig. 123). It also is found in standing-water bodies but, at least in Illinois (and in the Reelfoot Lake region of Tennessee, Hobbs & Marchand 1943), is primarily a stream species. It frequents intermittent streams and temporary ponds, burrowing down to the water table as drying occurs. *O. immunis* can be found under rocks in drying streams, and burrows are constructed as a means of escaping desiccation. Burrows usually are simple structures, although they may have chimneys and occasionally are relatively elaborate. Brown (1955) described the burrows as up to 2 feet deep and ending in an enlarged pocket below the water table.

Tack (1941) made observations on the

Table 12.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes immunis*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	5	1	20	2	40	0	0
February	4	3	75	2	50	0	0
March	13	7	54	4	31	0	0
April	28	6	21	4	14	4	14
May	26	5	19	0	0	1	4
June	39	5	13	0	0	1	3
July	51	14	27	0	0	0	0
August	36	5	14	0	0	0	0
September	20	3	15	0	0	0	0
October	15	7	47	0	0	0	0
November	5	1	20	0	0	0	0

habits and activities of a pond population of *O. immunis*. On bright sunny days some individuals could be seen moving about and others were partially buried in the mud, but most were hidden under stones or in burrows and came out only at dusk. Most activities occurred at night, including overland movements on rainy nights.

Because *O. immunis* often is found in turbid, sluggish-water bodies, it sometimes is considered more pollution-tolerant than are other crayfishes. It probably is more tolerant of low oxygen conditions associated with certain types of pollution, channelization, and impoundments, which so drastically alter the biotic characteristics of streams, than are inhabitants of clear-water streams. Thus, these conditions have a less detrimental effect on populations of *O. immunis* than they have on clear-water stream inhabitants. However, no data exist to show a greater tolerance to toxic chemicals than that found in other species.

Life History.—In ponds near Ithaca, New York, mating occurred from mid-June to mid-October and peaked in August (Tack 1941). After mating, females retreated to burrows and laid their eggs in October and November. First-year females ($N = 31$) laid from 4 to 170 eggs (mean, 84), and second-year females ($N = 6$) laid 38–289 eggs (mean, 195), with the number increasing with

the length of the female ($r = 0.642$). Eggs hatched in May, and young grew to 13–29 mm CL by late September. Females reaching at least 23 mm CL produced eggs in their first fall, and males were sexually mature at about 20 mm CL; however, most individuals did not reach these lengths until their second summer. Little or no growth occurred during winter. Most individuals die during their second year; a few (mostly females) may live to 3 years.

In northeastern Iowa, Caldwell & Bovbjerg (1969) found that copulation could occur anytime from June through April except during winter, when crayfish were torpid; that eggs were laid in October in burrows or in April and hatch in April, May, and June; that young remain attached to the female for 7–19 days; and that some individuals mature in their first year and die the next but that others do not mature until their second year and live 2 full years. In Iowa, Phillips (1980) found females in berry and with young attached in April and May.

In Illinois, form I males have been found from January through November (Rietz 1912; Cralley 1932; Brown 1955; Table 12). Elsewhere form I males have been found in June and July in Tennessee (Hobbs & Marchand 1943) and from April through September in New York (Crocker 1957). The smallest Illinois form I male recorded was 40 mm

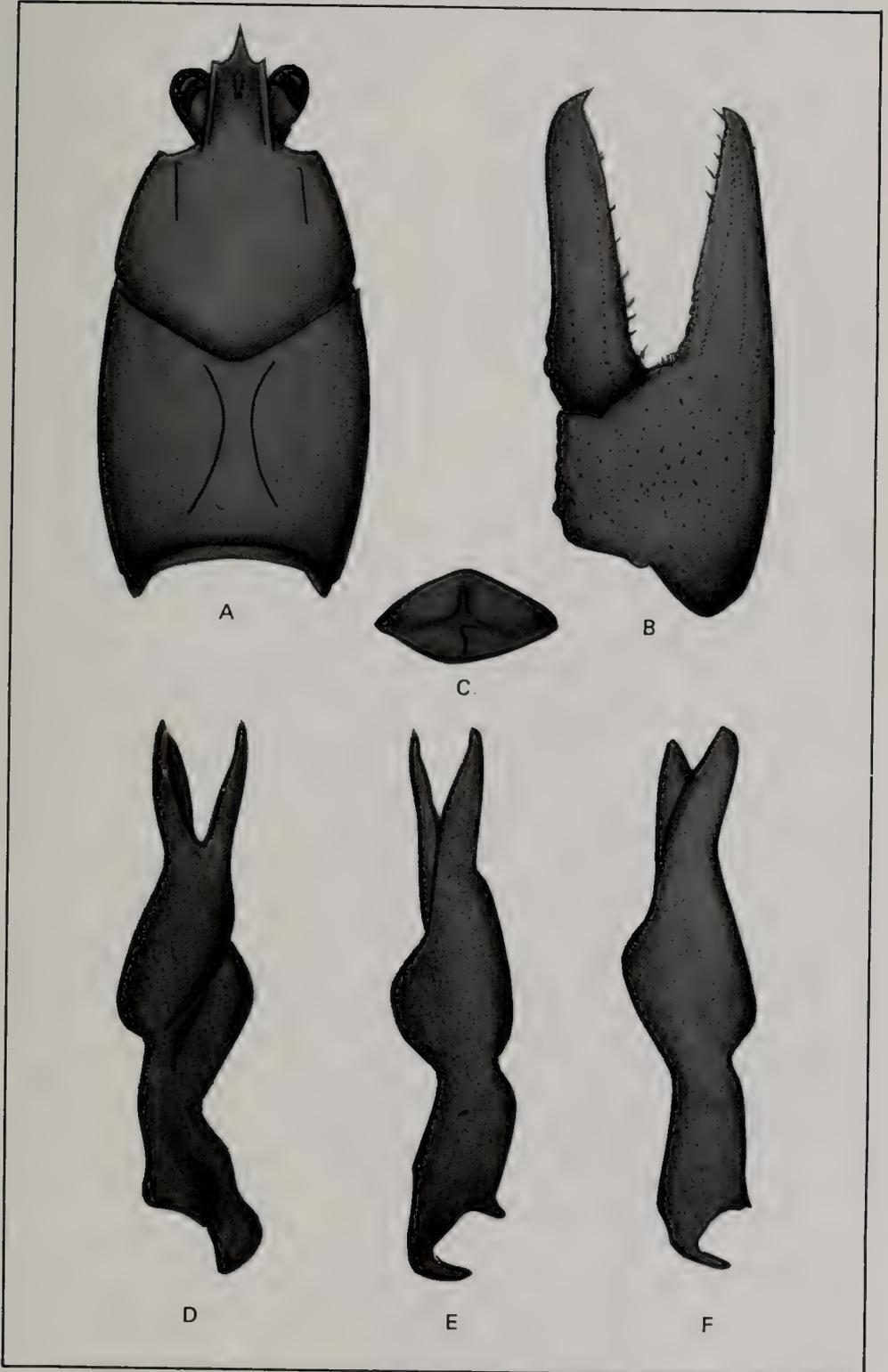


Fig. 124.—*Orconectes indianensis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

total length (about 20 mm CL) (Rietz 1912).

Females carry eggs in Illinois from January through April and carry young from April through June (Rietz 1912; Brown 1955; Table 12). The smallest ovigerous Illinois female is 22 mm CL (collected in Richland County, 12 April 1979), the same length as that reported by Tack (1941) in New York.

Elsewhere, eggs have been noted in April and November in Michigan (Herrick 1896; Pearse 1910); April, May, and October in Iowa (Caldwell & Bovbjerg 1969; Phillips 1980); March and April in Indiana (Williamson 1907); April in Kansas (Harris 1902); April and October in Nebraska (Engle 1926); June in North Dakota (Creaser & Ortenburger 1933); and October–November and April–May in New York (Tack 1941; Crocker 1957). Young are carried in May in New York and Ontario (Tack 1941; Crocker 1957; Crocker & Barr 1968) and from April through June in Iowa (Caldwell & Bovbjerg 1969; Phillips 1980).

Seven Illinois females collected during the present study (21.8–35.9 mm CL) were carrying 102–285 (mean, 168.9) eggs. Eggs averaged about 1.7 mm in diameter. Three females (26.6–35.5 mm CL) carried 58–184 (mean, 120.3) young.

The largest individual encountered during the present survey was a 41.9-mm CL form II male collected in Bennett Creek, Crawford County, on 30 April 1973. Brown (1955) collected a 46-mm CL female from Illinois, and Crocker (1957) recorded a 49-mm CL female from New York. The ratio among all Illinois specimens collected was 505 males: 513 females.

***Orconectes indianensis* (Hay)**
(Fig. 124)

Cambarus indianensis Hay 1896

Description.—Rostrum excavated, slightly deflected downward anteriorly, with long acumen; margins converge slightly anteriorly, ending in small

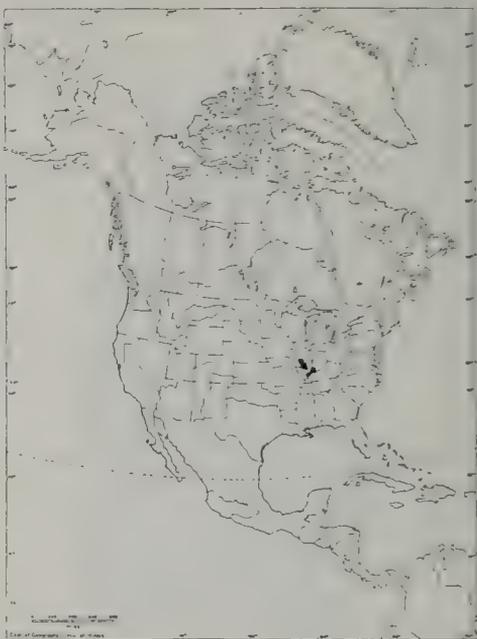


Fig. 125.—Total distribution of *Orconectes indianensis*.

spines; small median carina. Carapace flattened dorsoventrally, with large cervical spines; suborbital margin barely angular. Areola moderately wide, narrowest part 15–20 percent of length. Chela large, heavily punctate; palm with row of 7–9 tubercles on mesial margin, 2–3 adjacent rows of smaller tubercles on dorsal surface. Form I gonopod terminates in two short, distally tapering and strongly diverging elements: a sclerotized central projection and an unsclerotized mesial process. Overall dark brown dorsally, except thorax yellow brown; fingers of chelae with red tips and subdistal black bands.

O. indianensis is most similar, and perhaps most closely related, to *O. wrighti*, a species known only from Hardin County, Tennessee (Hobbs 1974b).

Distribution and Habitat.—*O. indianensis* lives in rocky riffles and pools of small to medium-sized streams in the Wabash River drainage of southwestern Indiana and in the Saline River and Honey Creek systems (both tributary to

the Ohio River) in southeastern Illinois (Fig. 125). This species uses stones as cover and often constructs a short tunnel with a terminal pocket under a stone as a resting place (Brown 1955).

Recent Illinois collections of *O. indianensis* are available from the Saline drainage of Gallatin, Saline, Williamson, Pope, and Johnson counties, and from Honey Creek in Hardin County (Fig. 126). Most collections in the Saline system are from that part of the system draining the Shawnee Hills. The northern part of the system, draining the Mount Vernon Hill Country (Central Lowland Province) seems to be devoid of *O. indianensis*. Honey Creek, also in the Shawnee Hills, is the first large stream south of the Saline River.

Brown (1955) documented essentially the same distribution in Illinois as did the present survey, but his record for *O. illinoiensis* in Cypress Ditch, near Junction, Gallatin County was probably based on *O. indianensis*. Rietz (1912) had more widespread records, but some of them probably (because of the localities) were based on misidentifications of the then undescribed *O. illinoiensis* and *O. stanndardi*. Rietz's record for Grand Pierre Creek, Pope County, and two records for Bay Creek, Pope and Johnson counties were surely based on *O. illinoiensis*. Her record for Skillet Fork, Wayne County, was probably based on *O. stanndardi*. The Little Fox River, White County, record may have been based on *O. propinquus*. However, her records for South Fork



Fig. 126.—Distribution of *Orconectes indianensis* in Illinois. Open circles = pre-1912 records (Rietz 1912); black dots = 1972-1982 collections.

Saline River and, more interestingly, for the North Fork Saline River must have been for *O. indianensis*. No similar species occurs or ever has been recorded for the Saline system. The North Fork records are interesting because *O. indianensis* no longer is found there. The North and Middle forks of the

Table 13.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes indianensis*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
March	1	1	100	1	100	0	0
April	2	0	0	2	100	0	0
May	2	0	0	0	0	1	50
July	1	0	0	0	0	0	0
August	2	1	50	0	0	0	0
September	2	2	100	0	0	0	0
October	3	3	100	0	0	0	0

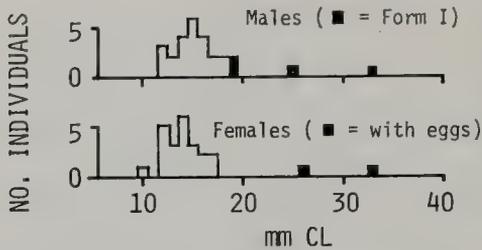


Fig. 127.—Size-frequency distribution of *Orconectes indianensis* collected in Honey Creek, Hardin County, on 23 March 1973.

Saline are badly polluted. They suffer from strip-mine and oil-field pollution, siltation, and desiccation (Smith 1971) and are among the most damaged and abused streams in Illinois. In many areas of these streams little aquatic life of any kind can be found.

Life History.—Apparently the only ecological information on *O. indianensis* is that presented by Brown (1955) and that from the present survey.

Brown (1955) found no ovigerous females and collected form I males only in September and November. In the present study, collections were made from March through October (except June), and form I males were present in March, August, September, and October (Table 13). The smallest form I male was 17.7 mm CL, and the largest was 33.4 mm CL.

Ovigerous females were found in March and April (Table 13). One hundred twenty-one eggs were counted on a 26.3-mm CL female, 148 eggs on a 27.7-mm CL female, and 178 eggs on a 32.2-mm CL female. Eggs averaged about 1.8 mm in diameter. The only female with young attached was 35.0 mm CL and was collected on 19 May 1973. Attached to her were 132 young and 21 unhatched eggs.

The largest Illinois specimens examined were the above-mentioned 35.0-mm female and 33.4-mm form I male. The size-frequency distribution of 51 specimens collected in Honey Creek, Hardin County, on 23 March 1973 (Fig. 127) suggests a 2-year life span, with 1-

year-old males averaging 15.2 mm ($N = 25$), 1-year-old females averaging 13.4 mm ($N = 22$), and 2-year-olds ($N = 4$) ranging from 25 to 33 mm CL. Of the 219 specimens of *O. indianensis* collected during the present survey, 104 were males and 115 were females.

Orconectes kentuckiensis Rhoades (Fig. 128)

Orconectes kentuckiensis Rhoades 1944

Description.—Rostrum excavated, deflected downward anteriorly, with long acumen; margins barely converge anteriorly, ending in tubercles or small spines; lacks median carina. Carapace flattened dorsoventrally, with large cervical spines; suborbital margin barely angular. Areola wide, narrowest part about 18 percent of length. Chela large, heavily punctate; palm with row of 7–9 tubercles on mesial margin; 1–2 adjacent rows of smaller tubercles on dorsal surface. Form I gonopod terminates in a short, thick, distally directed, sclerotized central projection, and a short, caudodistally directed, unsclerotized mesial process. Dorsally dark brown (with yellow brown thorax) to red brown; fingers of chelae with red tips, subdistal black bands.

The gonopod of *O. kentuckiensis* most closely resembles that of *O. sloanii* in southern Indiana and Ohio and *O. harrisonii* in southeastern Missouri. Although the relationships of these species have not been investigated, *O. sloanii* and *O. harrisonii* probably are the closest relatives of *O. kentuckiensis*.

Distribution and Habitat.—*O. kentuckiensis* occurs only in small streams in a small area of southeastern Illinois and northwestern (Crittenden, Livingston, and Union counties) Kentucky (Fig. 129). In Illinois, it occurs only in Big, Hosick, and Peters creeks, three spring-fed, rocky, direct tributaries of the Ohio River in Hardin County (Fig. 130). Its distribution in the headwaters of Big Creek (Fig. 131), by far the largest of the three streams, complements the downstream distribution of *O. placidus*

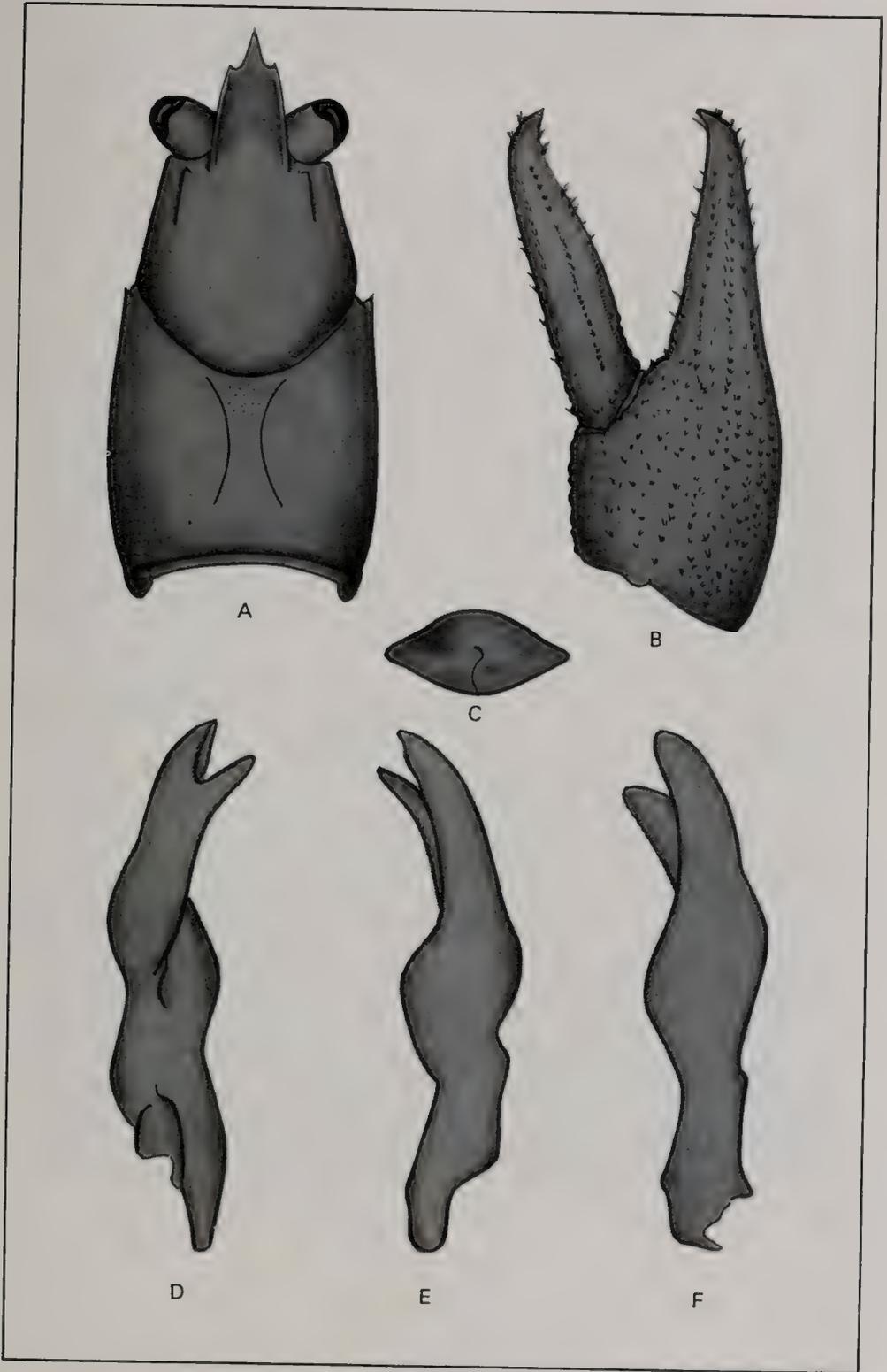


Fig. 128.—*Orconectes kentuckiensis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male, F, lateral view of gonopod of form II male.

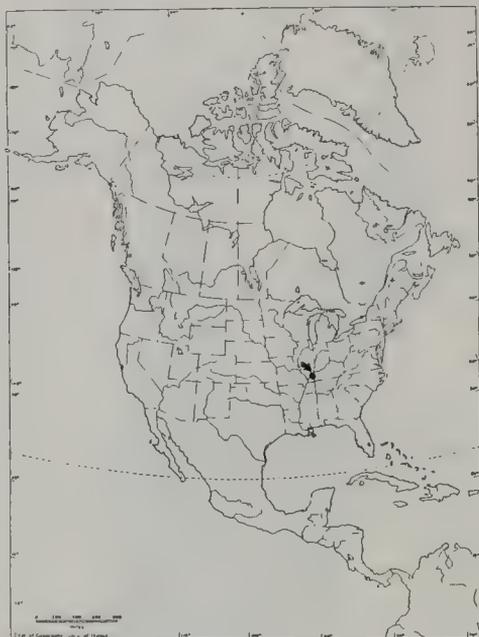


Fig. 129.—Total distribution of *Orconectes kentuckiensis*.

(Boyd & Page 1978). No record of its occurrence in Illinois predates those of Brown (1955). *O. kentuckiensis* probably was never more widespread in Illinois than it is today.

O. kentuckiensis is most common in shallow, rocky pools of small streams (Boyd & Page 1978), where large rocks are used as cover, although Rhoades (1944a) collected specimens in accumu-

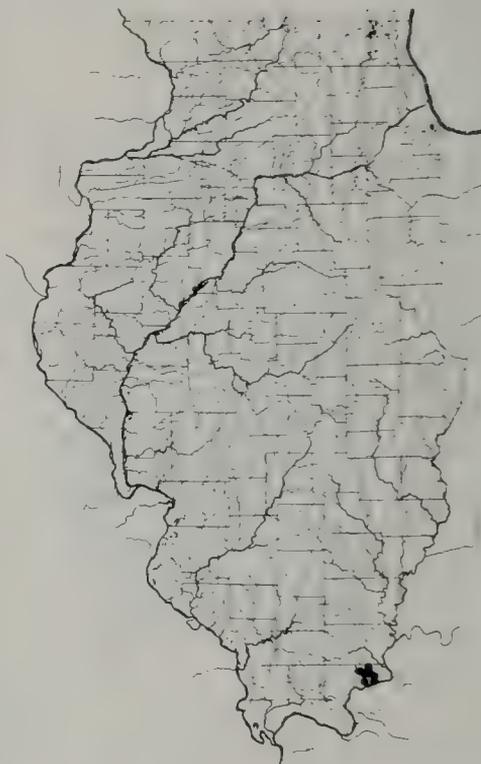


Fig. 130.—Distribution of *Orconectes kentuckiensis* in Illinois; black dots = 1972-1982 collections.

lations of brush over mud. This species does not burrow but may bury itself in loose gravel 2-4 cm below the surface of a dry stream bed (Boyd & Page 1978).

Life History.—The life history of *O.*

Table 14.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes kentuckiensis*.

Month	Number of Collections	Number and Percent of Collections with				
		Form I Males	Ovigerous Females	Females with Young		
January	5	4	80	0	0	0
February	1	1	100	0	0	0
March	10	7	70	3	33	0
April	5	2	40	3	60	0
May	9	0	0	1	11	0
June	16	0	0	0	0	0
July	5	2	40	0	0	1
August	4	1	25	0	0	0
September	9	7	78	0	0	0
October	11	6	55	0	0	0
November	4	4	100	0	0	0
December	3	3	100	0	0	0



Fig. 131.—Headwaters of Big Creek, 2 mi E Karbers Ridge, Hardin County, Illinois, support large populations of *Orconectes kentuckiensis*.

kentuckiensis in Big Creek was studied by Boyd & Page (1978). The species was active at temperatures of 6°–32°C and dissolved oxygen levels of 3.5–14.4 ppm. Most individuals were found in water 5–61 cm deep. The species lived a maximum of 2+ years, had a 1:1 sex ratio, fed on vascular plants and arthropods (amphipods, isopods, crayfishes, caddisflies, and midges), and was preyed upon by fishes.

Form I males (15.9–37.5 mm CL) were present from July through April and peaked in occurrence in November, December, and February; females carrying eggs or young were present in March, April, May, and July (Table 14) and measured 14.8–32.8 mm CL. Fifteen females were carrying 49–248 (mean, 110) eggs. Eggs were spherical and averaged 1.9 mm in diameter. The relationship between the number of eggs (N) and the female's weight in grams (W) was $N = 49.809 + 25.310 W$, $r = 0.807$, and that between N and the female's carapace length (L) was $N = -0.43611 + 1.8516 \log L$, $r = 0.859$. Counts of ovarian eggs in 15 females were 59–249 and averaged 109. Numbers of eggs, ovarian and abdominal, increased significantly with carapace length. The growth of first-year crayfish occurred during a period of 4.5 months, of adult males during spring and summer molts, and of adult females during a summer molt.

The largest *O. kentuckiensis* from Illinois is a 37.5-mm CL form I male collected on 25 April 1975; the largest female is 36.2 mm CL, collected on 30 September 1975. Both are from Big Creek.

Orconectes lancifer (Hagen)
(Fig. 132)

Cambarus lancifer Hagen 1870

Cambarus faxonii Meek 1894

Description.—Rostrum deeply excavated; acumen longer than basal margin of rostrum, turning upward anteriorly; no median carina; margins convex, diverging anteriorly, terminating in spines. Carapace slightly flattened

dorsoventrally, with large cervical spines; suborbital margin angular. Areola narrow, obliterated anteriorly. Chela long and narrow, setose, without tubercles. Form I gonopod terminates in two short, spatulate elements: a sclerotized central projection and an unsclerotized mesial process. Mottled overall in shades of red, brown, and green; fingers of chelae without bright red tips and without black bands subdistally.

O. lancifer is a highly distinctive crayfish with no obviously close relatives.

Distribution and Habitat.—*O. lancifer* is an inhabitant of the Gulf Coastal Plain and is known to occur in Louisiana, Mississippi, Tennessee, eastern Texas, Arkansas, and extreme southern Illinois (Fig. 133). It lives in deep water of oxbows, bayous, and large streams (Black 1972) and, as a result is rather poorly represented in collections.

O. lancifer has been found at only two localities in Illinois. Robert Kennicott, an early naturalist, collected a female at Cairo in the middle 1800's (Faxon 1914), and Page & Burr (1973) recorded a collection of eight individuals from Horseshoe Lake. Both localities are in the Mississippi River drainage of Alexander County (Fig. 134). Four additional collections of *O. lancifer* recently have been made at Horseshoe Lake, where the species probably is common but difficult to collect. Horseshoe Lake (Fig. 135) is an old, relatively deep oxbow of the Mississippi River supporting stands of bald cypress and many species of Coastal Plain animals that are rare in Illinois (Evers & Page 1977). Few oxbows of the Mississippi River exist in southern Illinois, and *O. lancifer* is unlikely to be found elsewhere in the state. Wolf Lake in Union County appears to offer suitable habitat for *O. lancifer*, but several searches there have failed to document its presence.

In Louisiana, *O. lancifer* lives in deep (more than 40 cm), clear, permanent

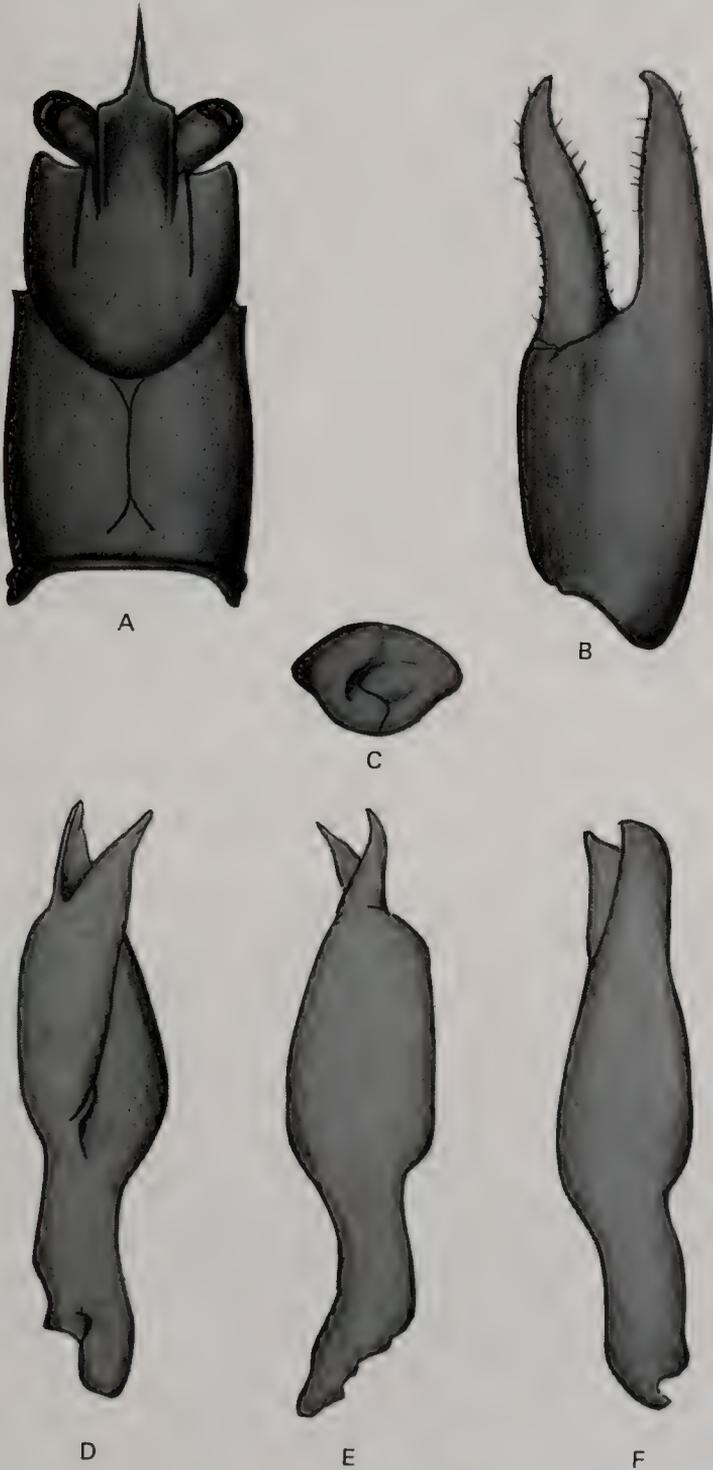


Fig. 132.—*Orconectes lancifer*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 133.—Total distribution of *Orconectes lancifer*.



Fig. 134.—Distribution of *Orconectes lancifer* in Illinois. Open circle = collection made in the mid-1800's (Faxon 1914); black dots = 1972-1982 collections.



Fig. 135.—Horseshoe Lake in Alexander County is the only known locality in Illinois still supporting a population of *Orconectes lancifer*.

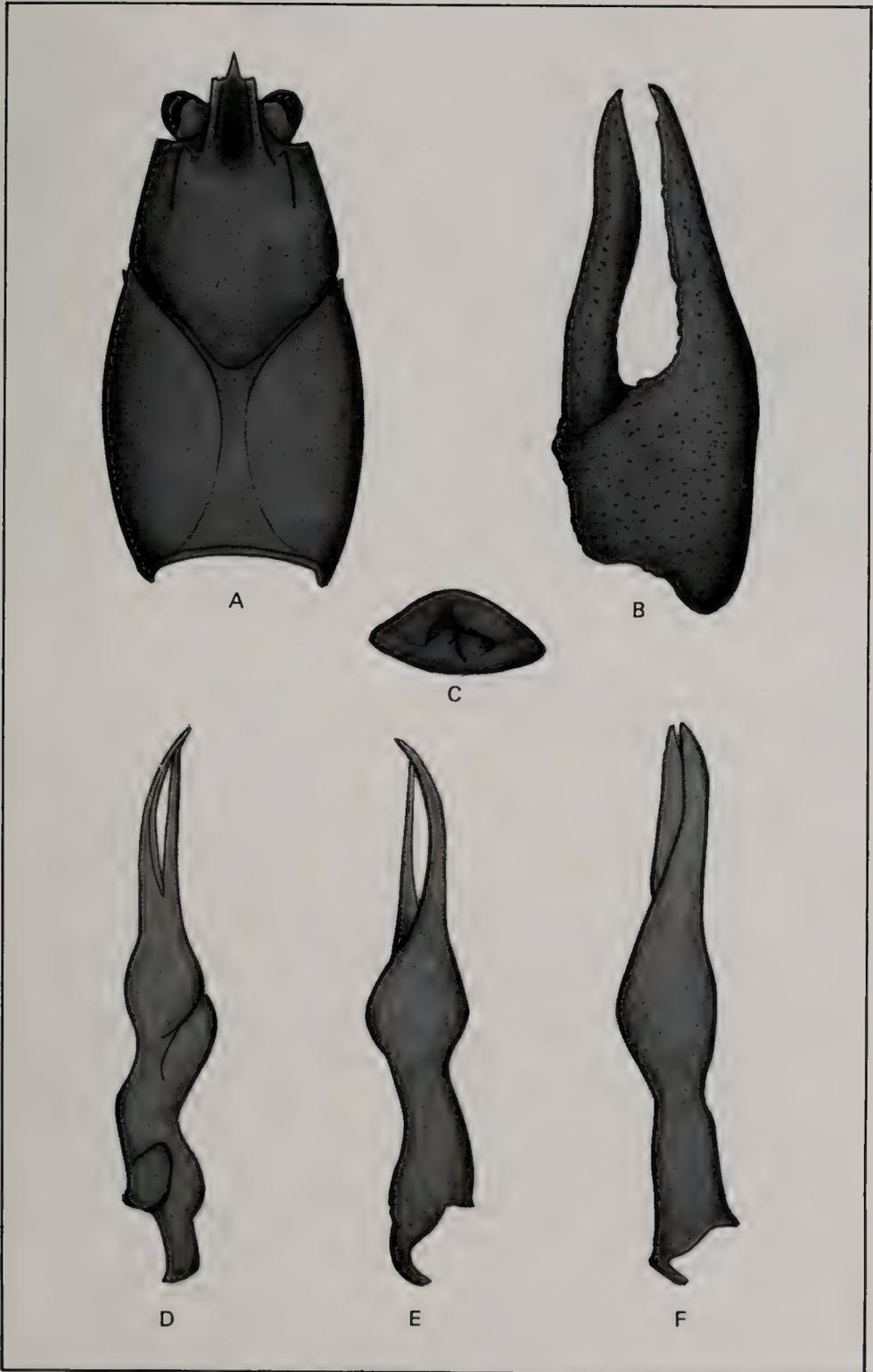


Fig. 136.—*Orconectes placidus*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

water over mud or mixed mud and sand with little aquatic vegetation present (Penn 1952). This description fits Horseshoe Lake fairly well except that the lake is heavily vegetated.

Life History.—Black (1972) summarized the scant life history data available on *O. lancifer*: form I males have been collected from August through November; females carrying eggs or young have been found only in February; juveniles predominate in May, June, and July.

Among the collections made in Illinois are two made in June and one each in July, September, and October. The September and October collections contain a total of three form I males (30–32 mm CL). Also in the Illinois Natural History Survey collection is a 40-mm female from Cheniere Lake, Ouachita Parish, Louisiana, collected on 18 February 1977, with 570 eggs attached. The eggs average 1.5 mm in diameter. These additional observations agree with Black's (1972) description of an autumnal breeding season and winter egg-laying season.

***Orconectes placidus* (Hagen)**
(Fig. 136)

Cambarus placidus Hagen 1870

Description.—Rostrum excavated, no (or low) median carina, long acumen; margins thick, straight to slightly concave, barely converging anteriorly, terminating in spines. Carapace flattened dorsoventrally, with large cervical spines; suborbital margin smooth. Areola moderate, narrowest part about 11–15 percent of length. Chelae large, heavily punctate; palm with 2–3 rows of tubercles along mesial margin. Form I gonopod terminates in a long sclerotized central projection curved at tip and a slightly shorter unsclerotized mesial process; cephalic surface smooth or with broadly rounded (not angular) shoulder. Dorsally red brown; fingers of chelae with red tips, subdistal black bands.

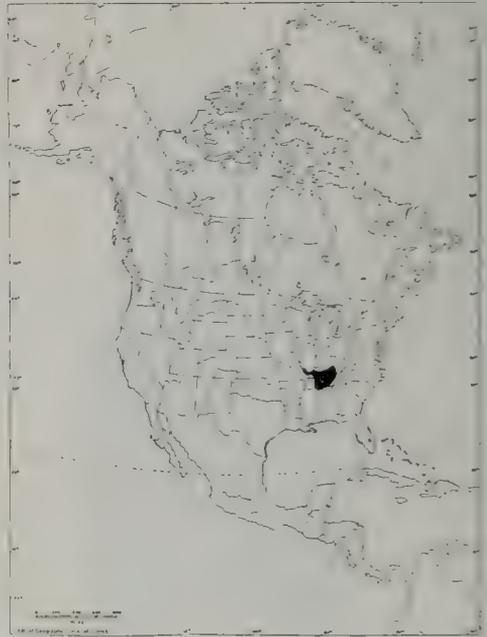


Fig. 137.—Total distribution of *Orconectes placidus*.

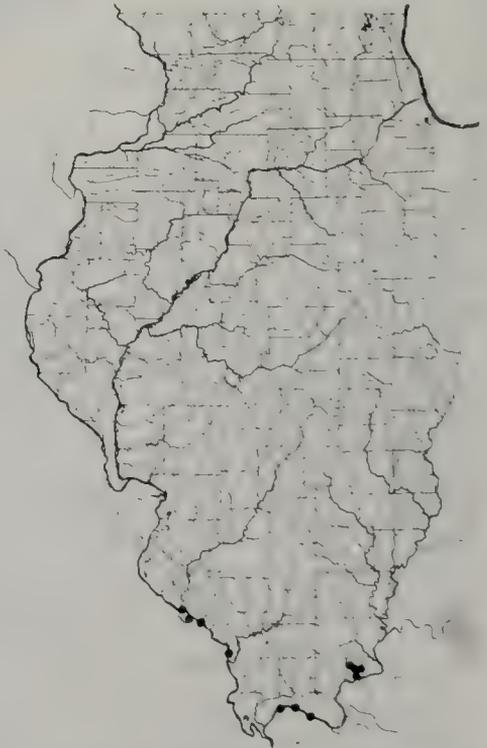


Fig. 138.—Distribution of *Orconectes placidus* in Illinois; black dots = 1972–1982 collections.



Fig. 139.—Gravel riffles in the lower portion of Big Creek, Hardin County, Illinois (10 March 1976) provide the best habitat in Illinois for *Orconectes placidus*.

Among the crayfishes of Illinois, populations herein assigned to *O. placidus* are the most troublesome taxonomically. The only large population is that in Big Creek in Hardin County; other populations are small, highly localized ones inhabiting rocky areas along the banks of the Ohio and Mississippi rivers. Although all are assigned to *O. placidus*, these populations show variations usually indicative of specific distinctiveness in *Orconectes*. The gonopod of the form I male lacks any hint of a shoulder on its dorsal surface in Big Creek specimens but has a definite shoulder (although not as pronounced and angular as in *O. rusticus*) in Mississippi River specimens (no form I males from the Ohio River are available). Big Creek specimens always lack a carina on the rostrum; those from the Ohio and Mississippi rivers may or may not have one. In general, western populations differ the most from typical *O. placidus* occupying the Cumberland and Tennessee river systems in Kentucky and Tennessee (Hobbs 1974b).

Variation in *O. placidus* and its relatives is badly in need of study.

Distribution and Habitat.—*O. placidus* occupies streams of the Cumberland, Tennessee, and lower Ohio rivers in Kentucky, Tennessee, and Illinois (Fig. 137). It lives in rocky riffles and pools, using cavities and interstices as hiding places.

Recent Illinois records exist for Big Creek, Hardin County, the Ohio River, Massac and Pulaski counties, and the Mississippi River, Randolph and Jackson counties (Fig. 138). Most of the large-river collections were made along rocky banks or in rocky backwater areas. In the Big Creek system, *O. placidus* is found mainly in downstream gravel and rubble riffles (Fig. 139), and *O. kentuckiensis* is found mainly in upstream shallow rocky pools (Boyd & Page 1978). As discussed below for *O. rusticus*, Hagen's (1870) and Forbes' (1876) reference to "*C. placidus*" at Quincy is thought to refer to a waif of the Missouri populations of *O. cf. rusticus*. Brown's (1955) discussion of "*O.*

Table 15.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes placidus*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	3	2	67	0	0	0	0
February	1	0	0	0	0	0	0
March	6	5	83	1	17	0	0
April	2	0	0	1	50	0	0
May	6	0	0	0	0	0	0
June	19	0	0	0	0	0	0
July	3	0	0	0	0	0	0
August	1	0	0	0	0	0	0
September	7	5	71	0	0	0	0
October	8	7	88	0	0	0	0
November	4	3	75	0	0	0	0
December	1	1	100	0	0	0	0

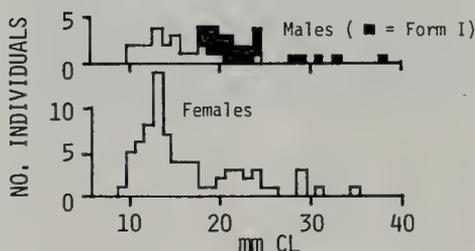


Fig. 140.—Size-frequency distribution of *Orconectes placidus* collected in October in Big Creek, Hardin County.

rusticus” refers to the Big Creek population of *O. placidus*.

Life History.—During the life-history study of *O. kentuckiensis* (Boyd & Page 1978), a large number (61) of collections of *O. placidus* were made. The following observations are based on those collections.

Form I males were present in collections from September through January and in March (only one collection was made in February) (Table 15). Brown (1955) found form I males in Big Creek in November.

Ovigerous females ($N=3$) were found only in March and April (Table 15); they were 15.7, 20.5, and 27.2 mm CL, with 12, 88, and 134 eggs attached, respectively. Eggs were spherical and averaged 2.1 mm in diameter. No females with young attached were found.

The largest preserved Illinois male is a 45.6-mm form II; the largest female is 41.7 mm CL. Both were collected in May and, compared with the size-frequency distribution of October-collected specimens (the largest sample), were probably 2 or 3 years old (Fig. 140). The largest form I male (39.6 mm) has extremely large chelae (right chela = 46.1 mm long). Among the Big Creek specimens were 344 males and 387 females (a ratio of 1:1.13).

Among a combined total of 506 stripe-tail and spottail darters (*Etheostoma kennicotti* and *E. squamiceps*) examined, the ingested remains of crayfishes were found in the stomachs of 4 *E. squamiceps* (Page 1974a, 1975). Considering the relative abundances of crayfishes in Big Creek, these were almost certainly *O. placidus* or *O. kentuckiensis* (Boyd & Page 1978).

Orconectes propinquus (Girard) (Fig. 141)

Cambarus propinquus Girard 1852
Orconectes iowaensis Fitzpatrick 1968

Description.—Rostrum excavated, deflecting downward anteriorly; well-developed median carina; long acumen; margins thick, straight or slightly concave, barely converging anteriorly, terminating in spines or large tubercles. Carapace flattened dorsoventrally, with

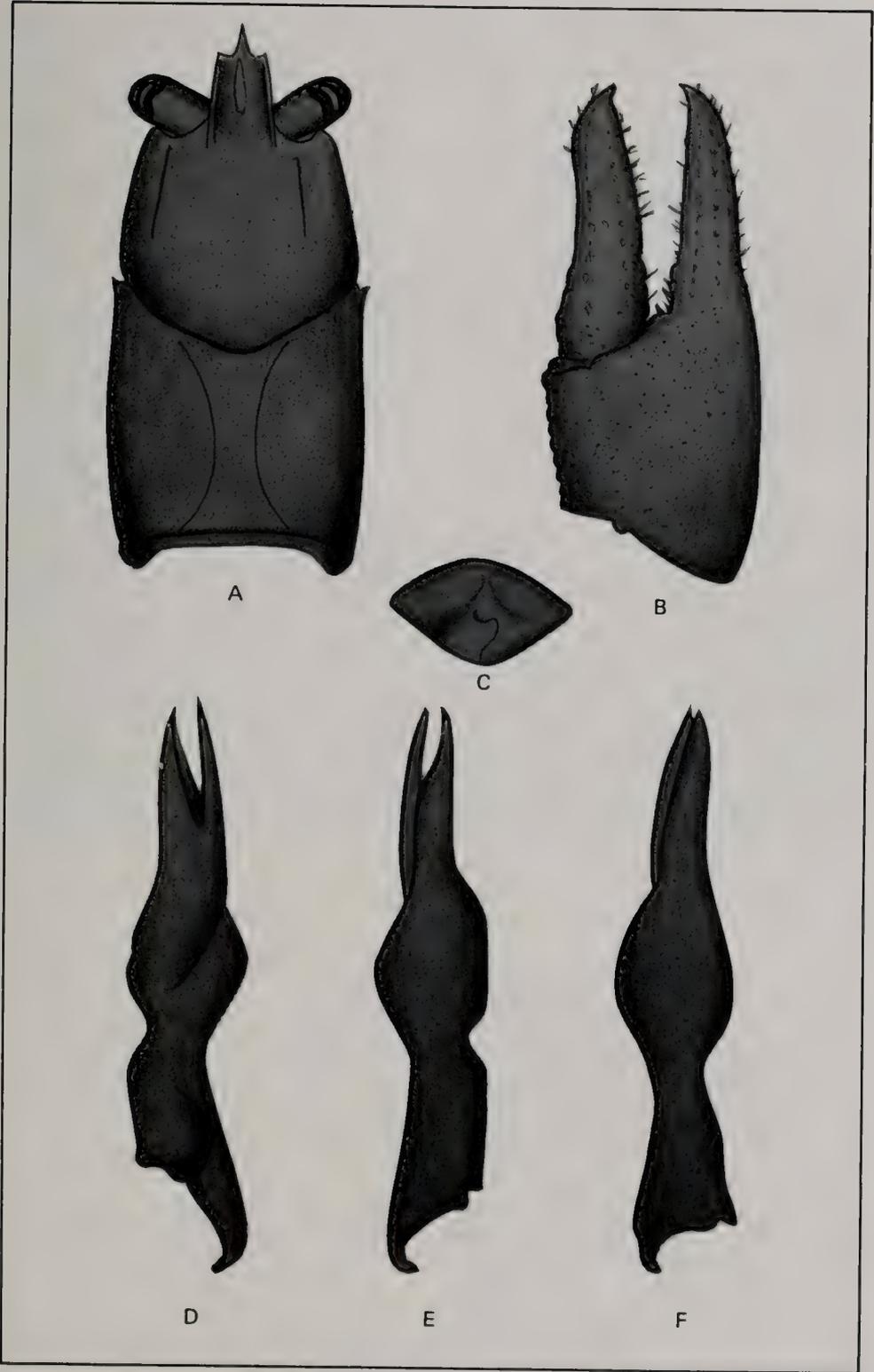


Fig. 141.—*Orconectes propinquus*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

cervical spines; suborbital margin smooth. Areola wide, narrowest part about 19–25 percent of length. Chelae large, heavily punctate; palm with 2–3 rows of tubercles on mesial margin. Form I gonopod terminates in two short, straight elements: a sclerotized central projection and an unsclerotized mesial process. Dorsally green to red brown; fingers of chelae with red tips, subdistal black bands.

Fitzpatrick (1967) found *O. propinquus* to be the most variable species among the *Propinquus* group of species but also to lack taxonomically recognizable subspecies. "*O. iowaensis*," previously thought to be a parapatric relative of *O. propinquus* occupying areas of Iowa adjacent to Illinois (Fitzpatrick 1968), has been relegated to the synonymy of *O. propinquus* by Page (1985).

Distribution and Habitat.—*O. propinquus* ranges from southern Ontario and Quebec south to Illinois, Indiana, Ohio, northern Pennsylvania, New York, and Massachusetts. To the west, its range extends into eastern Iowa and southeastern Minnesota (Fig. 142).

In Illinois, *O. propinquus* occurs in Lake Michigan and in the Wabash, Illinois, Rock, Mississippi, and extreme upper Kaskaskia drainages (Fig. 143). In the Wabash drainage, it extends as far south as White County, is widespread in the Embarras River, but is absent in the Little Wabash River system. In the Illinois and Mississippi rivers, it occurs as far south as Calhoun and Rock Island counties, respectively.

Throughout its range in Illinois, *O. propinquus* is the most common crayfish in clean rocky riffles (Fig. 144). In the fast, rubble and gravel riffles characteristic of the Vermilion, Kankakee, and upper Rock drainages, *O. propinquus* often is abundant. Its absence in most of western and central Illinois presumably is due to the absence of suitable habitat; its absence in southern Illinois apparently is due to the presence there of other species of



Fig. 142.—Total distribution of *Orconectes propinquus*. The northeastern limit of its range is unknown.

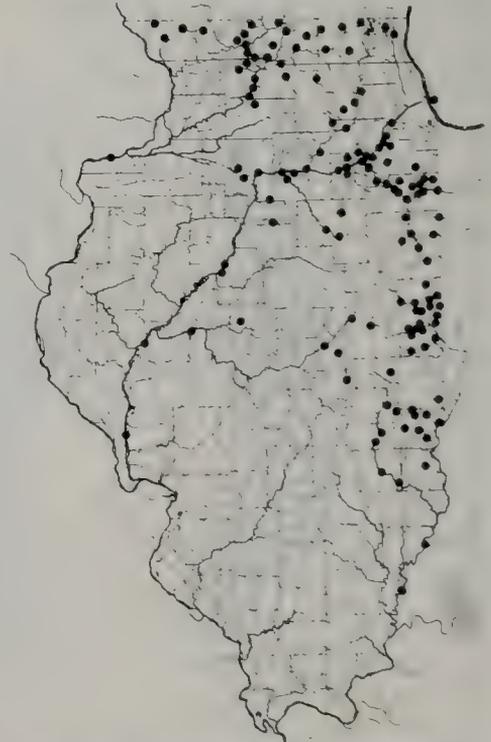


Fig. 143.—Distribution of *Orconectes propinquus* in Illinois; black dots = 1972–1982.



Fig. 144.—Middle Fork Vermilion River, near Collison, Vermilion County, Illinois, provides abundant habitat for *Orconectes propinquus*.

rocky stream-inhabiting species of *Orconectes*.

O. propinquus may dig under stones on the stream bed to escape desiccation (Bovbjerg 1952; Brown 1955) or occasionally into stream banks (Hay 1896; Cralley 1932). Young often are found in vegetation along the margins of a stream. Although primarily an inhabitant of rocky streams, it can become established in lakes (Bovbjerg 1952).

O. propinquus remains widespread and locally common, even abundant, in some areas but probably was more widespread and common prior to the extensive modification of the Illinois

landscape. It does best in clean, clear streams and presumably has suffered population declines as stream siltation has progressed during the last few decades. Among the widespread crayfishes of Illinois, it is probably the best indicator of environmentally healthy streams.

All earlier records of *O. propinquus* in Illinois fall within, or almost within, the present distribution. The record for the Kaskaskia drainage, near Humboldt, Coles County (Rietz 1912), is one county to the south of recent records. This record is significant in documenting the fact that the presence of the

Table 16.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes propinquus*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	1	1	100	0	0	0	0
February	1	0	0	0	0	0	0
March	6	5	83	0	0	0	0
April	2	0	0	2	100	0	0
May	4	1	25	2	50	0	0
June	14	0	0	0	0	0	0
July	14	3	21	0	0	0	0
August	37	8	22	0	0	0	0
September	31	12	39	0	0	0	0
October	14	9	64	0	0	0	0
November	2	1	50	0	0	0	0

species in the Kaskaskia is not an especially recent event, even a recent introduction, as the restricted distribution in the upper portion of the drainage might otherwise suggest. The record for the Mississippi River at Quincy, Adams County (Rietz 1912), also is south of the present range.

Rietz's (1912) record for "*O. propinquus*" in Big Muddy Creek at the Richland-Clay county line and Brown's (1955) records for Clay, Effingham, Marion, Shelby, and White counties (all Little Wabash drainage) are probably based on misidentifications of *O. stansfordi*, as discussed below.

Life History.—The following information is from a life-history study of *O. propinquus* conducted at Urbana, Illinois, 1932-1934 (Van Deventer 1937). Free-swimming young (about 5 mm CL) appear in May and June. They reach 12-27 mm CL during the first growing season and most become sexually mature at about 20 mm. Most individuals reach maturity by fall, and copulation takes place in late fall or early spring. Growth ceases during winter. Eggs are laid in March and April and are carried 4-6 weeks. Those individuals which reach maturity in the fall of their first year and produce young in the following spring die as yearlings. Those which do not mature until their second growing season usually

live 2 years, and a very few individuals live to a third year.

Cralley (1932) found form I males in Champaign County from June through August and recorded seeing copulations in September and October. Van Deventer (1937) found form I males (as small as 12.6 mm CL) in Illinois in September, October, November, and March. Brown (1955) found form I males June-September. During the present survey, form I males (14.6-31.5 mm CL) were found in every month except December, February, and April, when too few collections were made to be meaningful, and June. The data suggest a peak of activity from fall to early spring (Table 16). Form I males have been recorded in August in New England (Crocker 1979) and April-October in New York (Crocker 1957).

In Illinois, females carry eggs in April and May and carry young in May and June (Rietz 1912; Cralley 1932; Van Deventer 1937; Bovbjerg 1952; Brown 1955; Table 16). Van Deventer (1937) found 4-250 eggs on females 16-36 mm CL, with larger females carrying more eggs. Counts of eggs on recently collected females ($N = 5$; 27-32 mm CL) were 175, 192, 228, 229, and 277.

Females carry eggs in April-July in Ontario (Crocker & Barr 1968), eggs in April and May and young in June in New York (Crocker 1957), eggs in April

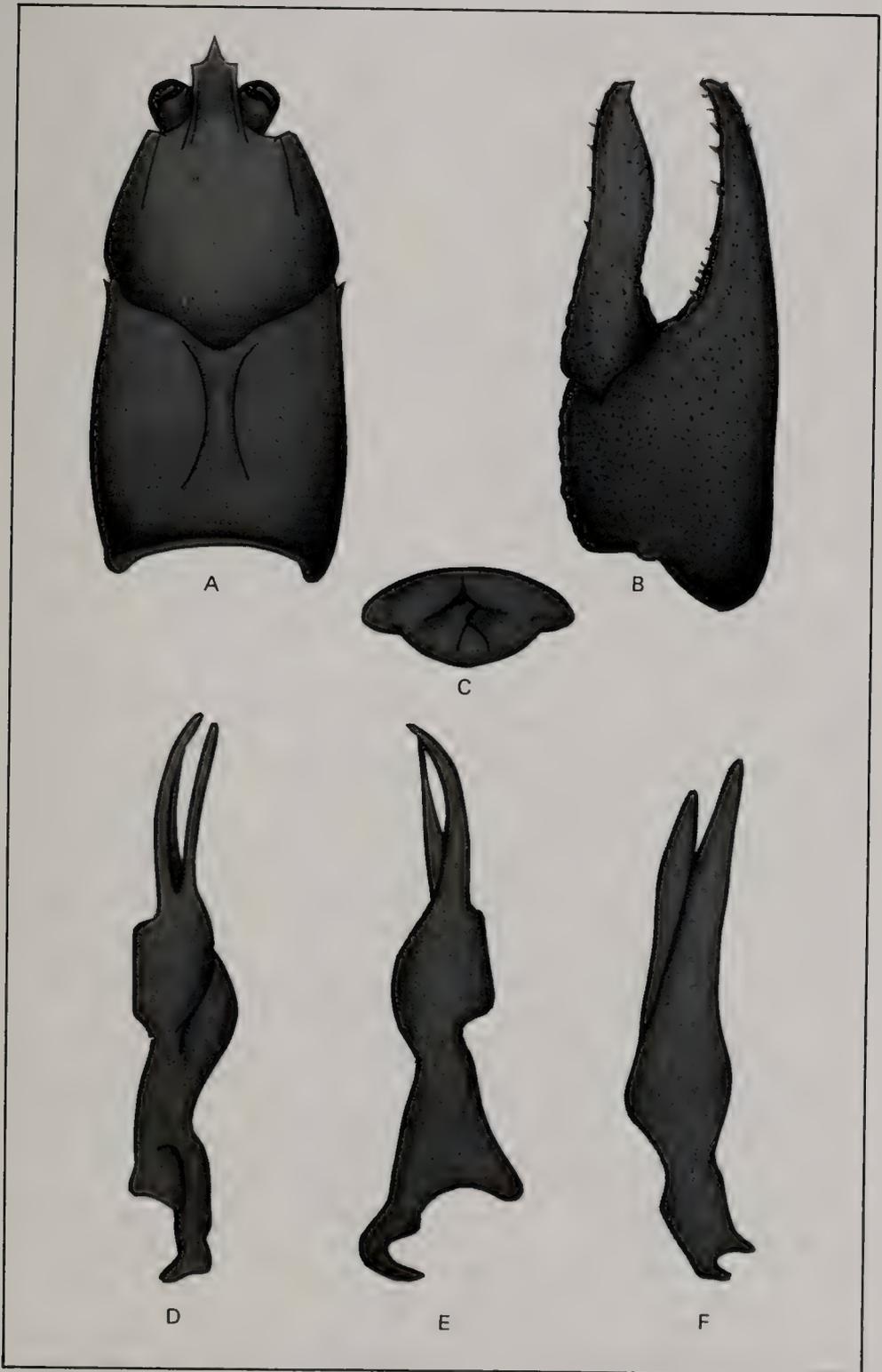


Fig. 145.—*Orconectes rusticus*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

and May in Iowa (as *O. iowaensis*, Phillips 1980), and eggs and young in April–June in Michigan (Pearse 1910; Creaser 1931). Females with eggs and young may be as small as 16 mm CL (Crocker 1957; Berrill 1978). Eggs are spherical and average about 1.9 mm in diameter.

The ratio of males to females among recent Illinois collections is 334:335. The largest specimen collected during the present survey is a 39.3-mm CL female; the largest male is a 31.5-mm form I. Van Deventer (1937) and Brown (1955) each recorded a 40-mm male; Cralley (1932) recorded a 90-mm TL (about 45-mm CL) male and a 90-mm TL female from Champaign County.

O. propinquus is omnivorous, feeding on plant materials and insect larvae (Bovbjerg 1952).

***Orconectes rusticus* (Girard)**
(Fig. 145)

Cambarus rusticus Girard 1852

Cambarus juvenilis Hagen 1870

Description.—Rostrum excavated; no median carina; long acumen; margins thick, concave, terminating in spines. Carapace flattened dorsoventrally, with cervical spines; suborbital margin smooth. Areola moderate, narrowest part about 10–15 percent of length. Chelae large, heavily punctate; palm with two rows of tubercles on mesial margin. Form I gonopod with an angular (90° to axis of gonopod) shoulder on dorsal surface, terminating in two long elements: a sclerotized central projection curved at its tip, and a slightly shorter unsclerotized mesial process. Dorsally green brown to rust red; often a large red spot surrounded by light brown on side of carapace; fingers of chelae with red tips, subdistal black bands.

Close relationships to *O. rusticus* are not readily apparent. Species often confused with, and at times considered related to, *O. rusticus* include *O. forceps*, *O. placidus*, *O. putnami*, *O. spinosus*, and until synonymized with



Fig. 146.—Presumed native distribution of *Orconectes rusticus*.

O. rusticus by Bouchard (1977), *O. juvenilis*.

Distribution and Habitat.—*O. rusticus* now occurs in New England, Ontario, Michigan, Ohio, Indiana, Kentucky, Tennessee, Illinois, Wisconsin, Minnesota, Iowa, Missouri, and New Mexico. It has been widely introduced, presumably through use as fishing bait, and the boundaries of its native range (Fig. 146) now are difficult to determine. However, at least its occurrences in New England (Crocker 1979), Ontario (Crocker & Barr 1968), Wisconsin (Capelli & Munjal 1982), New Mexico (Bouchard 1977), and Illinois are certainly the results of introductions. Once introduced, *O. rusticus* successfully displaces native species and expands its range, apparently because it is a large and aggressive species able to thrive in impoundments and other disturbed habitats (Berrill 1978; Capelli 1982; Capelli & Munjal 1982; Capelli & Magnuson 1983). Its continued use as a live bait species is therefore unwise.

Taxonomic confusion about *O. rus-*



Fig. 147.—Distribution of *Orconectes rusticus* in Illinois. Open circle = Adams County locality given by Hagen (1870) for "*Cambarus placidus*;" black dots = 1972-1984 collections.

ticus and its relatives has reigned since their descriptions. "*Cambarus wisconsinensis* Bundy," found at Normal (Forbes 1876), is a synonym of *O. virilis* (Hobbs 1972a) and is not a reference to *O. rusticus*, as thought by Rietz (1912) and Page (1974b). Brown's (1955) records for "*O. rusticus*" all were for Big Creek in Hardin County and are treated herein as *O. placidus*.

"*Cambarus placidus* Hagen" was recorded from Quincy by Hagen (1870) and Forbes (1876) and considered by Rietz (1912) to represent a record of *O. rusticus*. Quincy is directly across the Mississippi River from the Fabius River system of Missouri which supports a population of *O. rusticus* or a closely related undescribed species. The Quincy record probably represents a waif from the Fabius River population

of *Orconectes* and is plotted on the *O. rusticus* map (Fig. 147).

In Illinois, *O. rusticus* has been found recently in Peoria Lake, Tazewell County (in 1973 and 1974), Powder Horn Lake, Cook County (1975), Wolf Lake, Cook County (1975, 1978, 1980), Eagle Creek, Lake County (1975), Kent Creek, Winnebago County (1977), Nippersink Creek, McHenry County (1979), in a backwater of Fox River at Oak Point State Park, Lake County (1982), and in Lake Michigan, 1 mile east of Burnham Harbor, Cook County (1984). All of these localities are heavily used by fishermen or are near such areas, and the presence of *O. rusticus* in Illinois is surely the result of bait-bucket introductions. Except for Lake Michigan and Wolf and Powder Horn lakes, which are in the Lake Michigan drainage, and Kent Creek, which is a tributary of the Rock River, all localities are in the Fox-Illinois River system (Fig. 147).

O. rusticus is reproducing in Illinois (at least in Wolf Lake, where specimens as small as 16 mm CL have been found) and probably is supplanting native species, as it is in southern Ontario (Berrill 1978) and Wisconsin (Capelli & Munjal 1982). Hybridization between *O. rusticus* and *O. propinquus* and between *O. rusticus* and *O. limosus* has been recorded in Wisconsin and Massachusetts (Capelli & Capelli 1980; Smith 1981) and appears to represent an intermediate step in the displacement by *O. rusticus* of these native species. In Illinois, it appears to be hybridizing with *O. virilis* in Wolf Lake. *O. rusticus* lives in rocky riffles, pools, and along wave-swept lake margins.

Life History.—In fish ponds in Ohio, Langlois (1935) found mating to occur in September and October; following copulation, the females burrow into banks. Oviposition occurs in a few females in October, but mostly in April and May, when females are 1 year old. Eggs hatch in about 20 days and remain attached to the female for about 5 days. Sexual maturity is reached in the fall

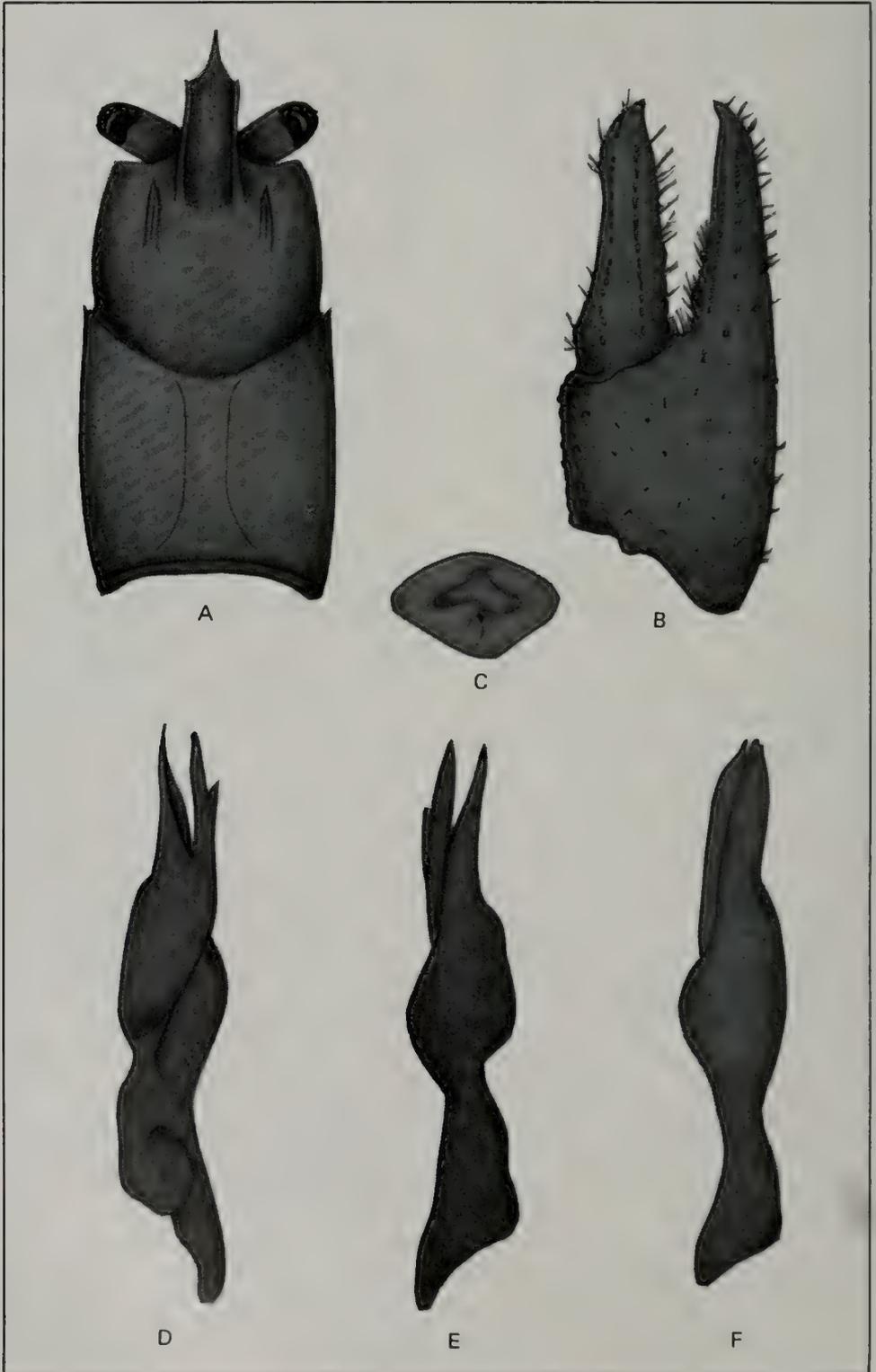


Fig. 148.—*Orconectes stannardi*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

following one summer's growth.

Prins (1968) studied *O. rusticus* in a stream in Kentucky and found that mating peaks in September and October, females oviposit from February through June at about 22–24 months, eggs hatch in May after being carried by the female for 4–6 weeks, young remain attached to the mother for 3 weeks (through April and May), sexual maturity is reached at about 15 months (about 18 mm CL), the sex ratio among juveniles is 1:1, and the species reaches a maximum longevity of about 3 years and a maximum CL of 45 mm. Counts of ovarian eggs in 43 females ranged from 54 to 357. The smallest female with eggs attached (55 eggs) was 17 mm CL; the largest, with 231 eggs, was 38 mm CL. The relationship between the number of eggs (N) and carapace length (L) of 49 females was $N = -91.49 + 8.31L$, with $r = 0.86$. The species feeds mainly on plants and detritus and has been observed feeding out of water along the banks. During winter, *O. rusticus* typically burrows into stream banks and into interstices in the substrate.

Form I males have been found in July and August in Ontario (Crocker & Barr 1968), in June in Maine (Crocker 1979), and in July and September in Iowa (Phillips 1980). Females in berry were collected in April in Iowa (Phillips 1980). Busch (1940) found that it took 20 days for eggs to hatch at 20°–22° C.

Among the nine Illinois collections (made from May through September), form I males (20.5–34.0 mm CL) are present in August and September. No ovigerous females were found. Some Illinois specimens approach the maximum size recorded for the species; the largest Illinois male (form II) is 40.5 mm, and the largest female is 41.5 mm CL.

Orconectes stannardi Page

(Fig. 148)

Orconectes stannardi Page 1985

Description.—Rostrum excavated; well-developed median carina; long acumen; margins moderately thick,

subparallel, slightly converging medially, terminating in spines. Carapace flattened dorsoventrally, with cervical spines; suborbital margin weakly angular. Areola moderately wide, narrowest part about 15–25 percent of length. Chela large, heavily punctate; palm with two rows of tubercles on mesial margin. Form I gonopod terminates in two short, straight elements: a sclerotized central projection and an unsclerotized mesial process with spur about middle of caudal surface; shoulder on cephalic surface at base of central projection. Olive green to light brown and usually heavily speckled with dark brown dorsally; fingers of chelae with red tips, subdistal black bands.

Distribution and Habitat.—*O. stannardi* is a member of the *O. propinquus* species group that is endemic, and



Fig. 149.—Distribution of *Orconectes stannardi*. Open circles = localities given by Rietz (1912) and Brown (1955) for "*O. propinquus*" and "*O. indianensis*;" black dots = 1972–1984 collections.



Fig. 150.—*Orconectes stannardi* is most common along rocky stream margins such as this one on the Little Wabash River, 3.5 mi NNW Louisville, Clay County, Illinois (8 October 1984).

possibly autochthonous, to the Little Wabash River system of Illinois. The region drained by the Little Wabash was glaciated during the Illinoian (about 100,000 y.b.p.) but not the Wisconsinan (about 10,000 y.b.p.) advances,

suggesting that the species originated sometime within the past 100,000 years (Page 1985). All collections made since 1972 are from the Little Wabash River proper (Fig. 149).

Rietz (1912) and Brown (1955) re-

corded localities for *O. propinquus* and *O. indianensis* in the Little Wabash River system that almost certainly were based on misidentified *O. stannardi* (Page 1985). Data collected during the present survey suggest that *O. propinquus*, *O. indianensis*, and *O. stannardi* occur allopatrically and that neither *O. propinquus* nor *O. indianensis* occurs in the Little Wabash River system. Unfortunately, the collections made by Rietz and Brown cannot be located and re-examined.

Although all collections of *O. stannardi* that have been made since 1972 are from the Little Wabash River proper, some of the collections of Rietz (1912) and Brown (1955) were from tributaries. Collections of Rietz (1912) were made in Big Muddy Creek between Richland and Clay counties and in Skillet Fork at Wayne City, Wayne County; the former was identified by Rietz as *O. propinquus* and the latter as *O. indianensis*. Collections cited by Brown (all as *O. propinquus* but which must have been of *O. stannardi*) were made in Dismal Creek, 2¼ mi N Iola, Clay County; Salt Creek, 1 mi SE Effingham, Effingham County; Blue Point Creek, 2½ mi S Shumway, Effingham County; Lost Fork, 1½ mi E Omega, Marion County; branch of Little Wabash River, 1¼ mi SW Trowbridge, Shelby County; and Little Wabash River, 4 mi NE Shumway, Effingham County.

Most individuals were found in shallow riffles composed of large flat stones (Fig. 150). A few were found in deeper water but always in association with stones or accumulations of sticks and other debris. The preference of *O. stannardi* for rocky riffles is typical of the *Propinquus* group of *Orconectes*, the members of which typically hide under stones and among debris. *O. stannardi* is locally common in the Little Wabash River.

Life History.—All seven collections of *O. stannardi* presently available (from November 1973, November 1983, May 1984, and August 1984) contain form I males, and one (May 1984) con-

tains two ovigerous females. All 20 males collected in November, 5 of 11 collected in August, and 1 of 25 collected in May are form I. The two ovigerous females collected in May 1984 were 20.7 mm and 28.9 mm CL and carried 124 and 184 eggs, respectively. Eggs average 1.9 mm in diameter. The largest specimen is a 38.3-mm CL female collected on 22 August 1984; the largest male, from the same collection, is a 30.5-mm form I.

Orconectes virilis (Hagen)

(Fig. 151)

Cambarus virilis Hagen 1870

Cambarus debilis Bundy 1876

Cambarus wisconsinensis Bundy 1876

Cambarus couesi Streets 1877

Description.—Rostrum excavated; moderately long acumen; no median carina; margins thick, straight, barely converging anteriorly, with terminal spines. Carapace flattened dorsoventrally, with cervical spines; suborbital margin bluntly angular. Areola narrow, constricted anteriorly, narrowest part about 6–7 percent of length. Chelae large, heavily punctate; palm with two rows of tubercles on dorsomesial margin. Form I gonopod terminates in two long, caudodistally directed elements: a sclerotized central projection and a shorter unsclerotized mesial process. Dorsally light brown to dark green-brown; fingers of chelae without bright red tips and subdistal black bands.

O. virilis occasionally occurs as a blue color morph in Illinois and elsewhere. Sugar Creek, a tributary of the Sangamon River in McLean County, contains a large number of blue *O. virilis*. The upper reaches of Sugar Creek are highly modified and receive a large amount of pollution from Bloomington-Normal, and the large number of blue crayfish may somehow be related to the degradation of the stream. Anderson (1975) described a 41-mm CL female *O. virilis* from the Kishwaukee River at De Kalb, Illinois, that was "chalky white" overall except

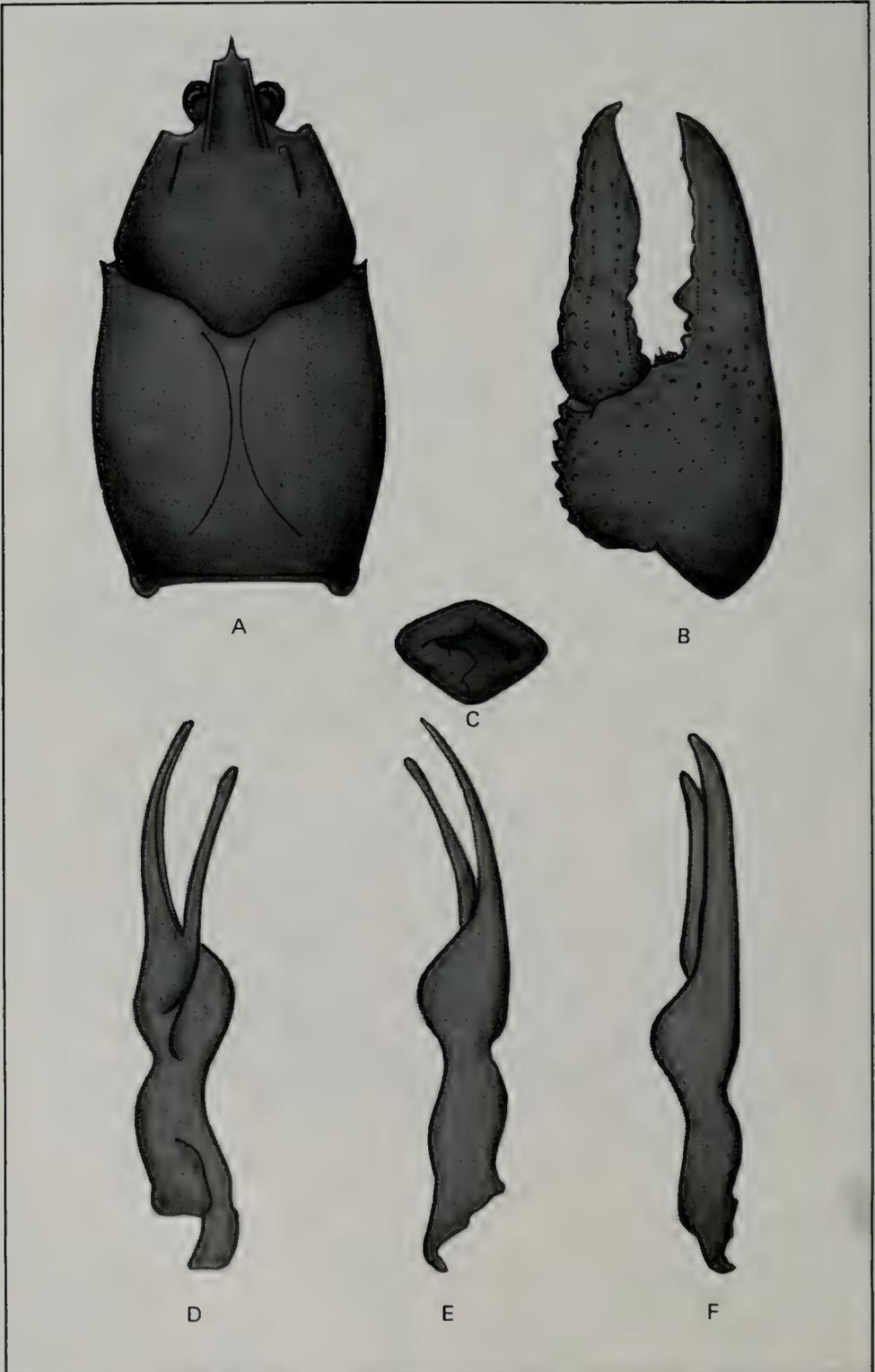


Fig. 151.—*Orconectes virilis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 152.—Total distribution of *Orconectes virilis*. The northern limits of the range are unknown.

for darkly pigmented eyes.

The closest relatives of *O. virilis* are *O. causeyi*, which may be conspecific with *O. virilis* (Hobbs 1974b), and *O. nais*. *O. nais* is very similar to *O. virilis* morphologically but is distinct serologically (Pryor & Leone 1952). An area of intergradation between *O. virilis* and *O. nais* may be present in southwestern Iowa (Phillips 1980).

Distribution and Habitat.—*O. virilis* ranges from New England across southern Canada to the Continental Divide in Montana, southeastern Wyoming, and northeastern Colorado, and south to the Ohio River in Ohio, Indiana, and Illinois, the Missouri River in Missouri, and the Platte River in Nebraska (Fig. 152). The northern limits of its range are unknown (Crocker & Barr 1968), but it occurs farther north than does any other North American crayfish.

O. virilis is the most common crayfish in Illinois and, in some streams, exists in huge populations. It occurs

naturally throughout the state except in the Saline River system and in streams draining the Shawnee Hills and the eastern Coastal Plain (Fig. 153). It is common to abundant over much of its Illinois range, but less so in the lower-gradient streams characteristic of much of western and southeastern Illinois. In the past, its abundance led to its large-scale consumption by humans (e.g., Creaser 1932), but this no longer appears to be true, at least in Illinois.

Although absent from the Shawnee Hills, *O. virilis* occupies Clear Creek and Mill Creek, both of which drain the Ozark Plateaus Province in Union and Alexander counties. Habitats in the "Illinois Ozarks" appear similar to those in the Shawnee Hills, but several animals occupy the Ozark Uplift and not the Shawnee Hills, e.g., the snow scorpionfly, *Boreus brumalis*; the



Fig. 153.—Distribution of *Orconectes virilis* in Illinois; black dots = 1972-1982 collections.



Fig. 154.—*Orconectes virilis* lives in a variety of habitats but usually is found in rocky areas or accumulations of logs and debris such as this logjam on the Little Wabash River, 2.5 mi W Watson, Effingham County, Illinois (8 October 1984).

slender madtom, *Noturus exilis*; the fantail darter, *Etheostoma flabellare*; and the green water snake, *Nerodia cyclopion* (Webb, Penny, & Marlin 1975; Smith 1961, 1979).

A recent record for *O. virilis* in an impoundment in the Saline River system (Berkel Lake, Saline County, 9 October 1977) is almost certainly the result of a recent introduction. The record is based on two individuals, one of which is small (16.3 mm CL), suggesting that the species is reproducing in the lake.

In Illinois, *O. virilis* occupies rocky streams (Fig. 154) and lake margins. It usually occurs in moderate current but is less common in swift riffles (where, throughout much of Illinois, it is replaced by *O. propinquus*) and in sluggish pools (where *O. immunis* predominates). The largest populations are found in areas where large flat stones provide a preponderance of hiding places. In lakes, *O. virilis* may occur as deep as 9 m (Crocker & Barr 1968).

Cralley (1932) found numerous burrows belonging to *O. virilis* opening just above the water line along the banks of the Kaskaskia River in Champaign County. Brown (1955) found a few burrows of *O. virilis* in Illinois and described them as being simple, with an enlarged pocket at the lower end and only one surface opening. Phillips (1980) found a burrow in Iowa about 30 cm deep with two terminal chambers and a chimney about 5 cm tall. Hazlett et al. (1974) found *O. virilis* burrowing extensively along a stream and pond in Michigan; burrows frequently had two entrances, often one above the water level. Rarely during the present survey was *O. virilis* found in burrows, and it appears to be much more common for *O. virilis* to hide under rocks, even in winter, than to burrow; however, as discussed below, ovigerous females may habitually burrow.

Life History.—The wide-ranging and often abundant *O. virilis* has been the subject of numerous studies. In both

Table 17.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Orconectes virilis*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	5	1	20	0	0	0	0
February	4	0	0	0	0	0	0
March	5	3	60	0	0	0	0
April	13	1	8	3	23	0	0
May	27	5	19	2	7	0	0
June	90	6	7	0	0	0	0
July	99	9	9	0	0	0	0
August	101	11	11	0	0	0	0
September	86	28	33	0	0	0	0
October	52	22	42	0	0	0	0
November	21	10	48	0	0	0	0

sexes maturity is usually reached in summer and fall of the third year (Momot 1967), although some females bear eggs during their second year (Momot 1978), and some males become form I in their second year (Weagle & Ozburn 1972). Photoperiod and temperature control ovarian maturation, and increased water temperature triggers egg laying in the spring (Aiken 1969). Form I males may be present during any month but usually peak in abundance in fall. Egg laying occurs from mid-March through July. Threinen (1958a, 1958b) believed that most adult males die after mating, and most adult females die after producing young. Momot (1967) found the maximum longevity to be 3+ years. *O. virilis* feeds on algae and "aufwuchs" in marl lakes (Momot 1967) and probably on a variety of plants and animals, both dead and alive, elsewhere (Caldwell & Bovbjerg 1969).

In Michigan, males at 1 year of age average 31.2 mm CL, at 2 years average 36.5 mm, and at 3 years average 40.8 mm; females average 29.5 mm at 1 year and 36.4 mm at 2 years (Momot 1967).

In Illinois, form I males have been found in all months except February and December (Rietz 1912; Cralley 1932; Brown 1955; Table 17). In the present study, they predominated in March and September–November (no collections

were made in December). Females carrying eggs have been found in March, April, and May, and females with young attached have been found in May and June (Rietz 1912; Brown 1955; Table 17).

Among the 1,182 female *O. virilis* collected in the present survey, only 5 had eggs, and none had young attached. This extremely small number of ovigerous females suggests that they sequester themselves, probably in burrows, when carrying offspring. Although no direct evidence was gathered during the present survey, Cralley (1932) found a female with eggs attached in a burrow in Champaign County, and Hazlett, et al. (1974) noted that, along a stream in southeastern Michigan, ovigerous females tended to stay in burrows.

Egg counts on the five ovigerous females (35.5–49.7 mm CL) collected during the present survey ranged from 385 to 490 (mean, 449), with the largest female carrying the most and the smallest the fewest eggs. The other three females, all 40.0 mm CL, carried 452, 452, and 466 eggs. Weagle & Ozburn (1972) found a mean number of 214 eggs per female ($N = 16$; 26–36 mm CL) in northwestern Ontario, and egg count averages ranged from 98.9 ($N = 22$ females, size range not given) to 150.3 ($N = 46$ females) on females collected

in several Ontario lakes (Momot 1978). Momot & Gowing (1977) found much lower egg counts among high-density populations of *O. virilis* in Michigan lakes. The number of attached eggs on 402 females (22–35 mm CL) averaged only 91.9. These females were smaller than those found in Illinois. Also, fecundity in these lakes was thought to be related to density-dependent processes, i.e., as the density increased the number of eggs carried by females decreased (Momot & Gowing 1977).

Elsewhere, form I males have been found in April and June–October in New England (Crocker 1979), May and August in New York (Crocker 1957), June–August in Ontario (Crocker & Barr 1968), and July–April in Iowa (Caldwell & Bovbjerg 1969). Form I males may be as small as 25 mm CL (Berrill 1978; Weagle & Ozburn 1972).

Females carrying eggs have been found in April and May in Iowa (Caldwell & Bovbjerg 1969; Phillips 1980), April and May in Michigan (Pearse 1910; Momot & Gowing 1977) and New Hampshire (Crocker (1979), May in Rhode Island (Crocker 1979), and May–July in Ontario (Crocker & Barr 1968). Females with young attached have been collected in May in Iowa (Phillips 1980) and in June in Maine (Crocker 1979).

Some Illinois specimens appear to be among the largest recorded, although Creaser (1932) noted that in Wisconsin the species “frequently attains a size of over eight inches” (about 100 mm CL). The largest Illinois specimens are from reservoirs: a 59.5-mm CL female from Dawson Lake, McLean County, collected on 25 September 1972, and a 59.2-mm CL form I male from Baldwin Lake, Randolph County collected on 2 November 1972. *O. virilis* is an aggressive crayfish and, with its large size giving it an advantage, actively excludes the often syntopic *O. immunis* from desirable hiding places (Bovbjerg 1970). Intraspecific dominance was examined by Bovbjerg (1953). The sex ratio among specimens col-

lected during the present survey was 1,243 males:1,182 females.

Genus *Fallicambarus* Hobbs

Fallicambarus Hobbs 1969

Gonopod with two large terminal elements curved at about 90° angle to shaft; central projection large and bladeliike. Ischium of third pereopod of male with hook. Opposable margin of dactyl of chela with deep concavity.

Only *F. fodiens* of the 14 recognized species of *Fallicambarus* (Hobbs 1981) occurs in Illinois. *F. fodiens* is assigned to the subgenus *Creaserinus* and is most closely related to *F. hedgepethi* (see comment below) and *F. uhleri* (Hobbs 1973).

Fallicambarus fodiens (Cottle)

(Fig. 155)

Astacus fodiens Cottle 1863

Cambarus argillicola Faxon 1884

Description.—Rostrum broad, excavated, with short acumen, lacking marginal spines and tubercles, lacking median carina. Carapace compressed, lacking cervical spines; suborbital margin smooth (not angular). Areola obliterated. Chela large, punctate; palm with one to three rows of tubercles on mesial margin; dactyl with deep concavity on basal half of opposable margin. Form I gonopod terminates in two elements, both curved at an angle of about 90° to the principal axis of the gonopod: a distally rounded sclerotized central projection and a short proximally thick mesial process with a peglike tip. Dorsal color variable, usually olive brown with dark brown blotches, but often a uniform light brown to rust red.

Distribution and Habitat.—*F. fodiens* is the most wide-ranging species in its genus, extending, in the Great Lakes (except Lake Superior) and Mississippi River drainages, from southern Ontario to western Kentucky (Fig. 156). South of Kentucky it is replaced by the closely related, and probably conspecific (Burr & Hobbs 1984; H. H. Hobbs

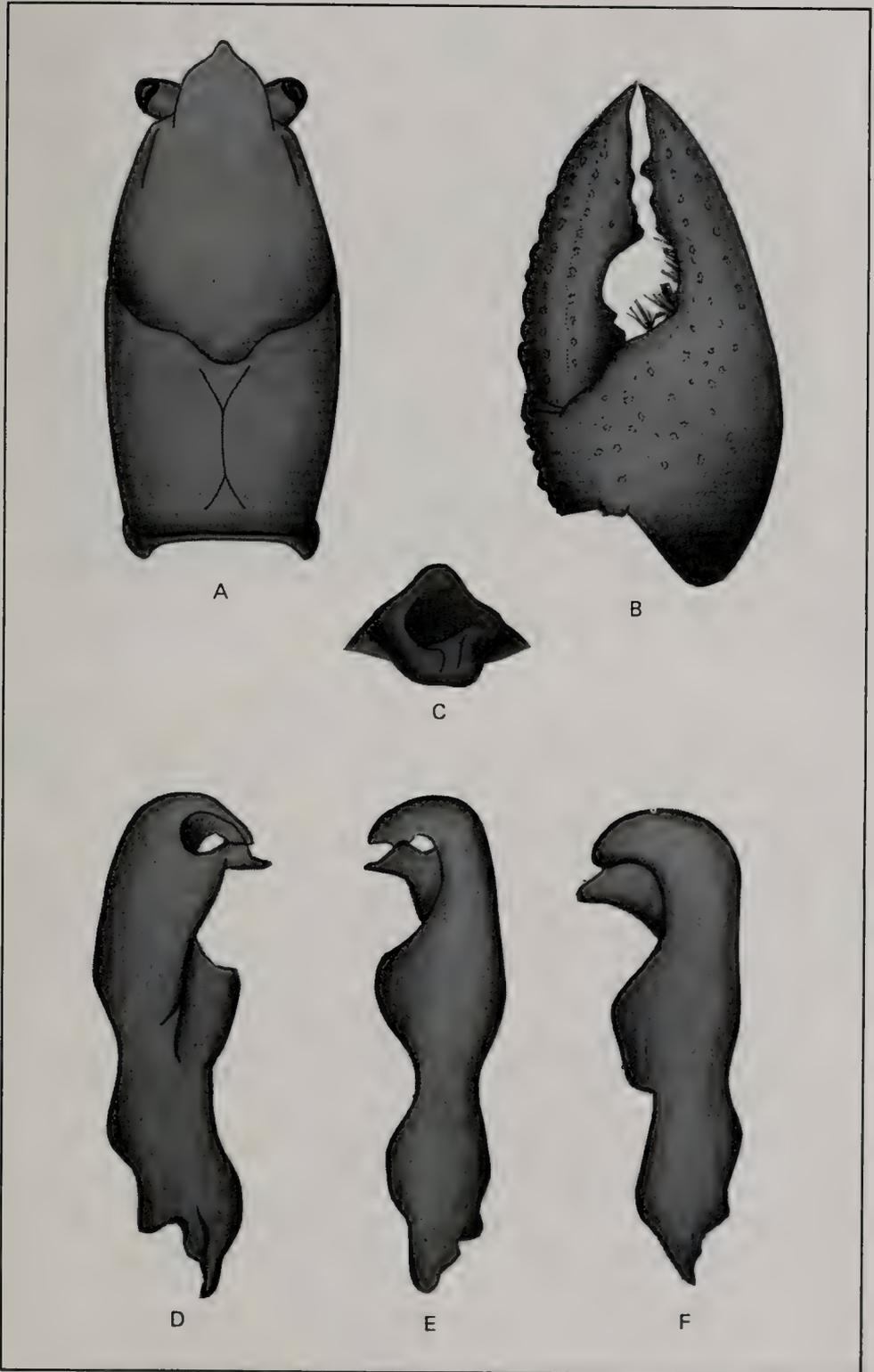


Fig. 155.—*Fallicambarus fodiens*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 156.—Total distribution of *Fallicambarus fodiens*. The southern limit of its range is unknown.



Fig. 157.—Distribution of *Fallicambarus fodiens* in Illinois. Large circles = 1890-1901 collections; small circles = collections made in the 1950's; black dots = 1972-1982 collections.

personal communication), *F. hedgepethi*, which ranges to the Gulf Coast and into Gulf drainages from Georgia to Texas.

In Illinois it is known from the Ohio (including the Wabash), Big Muddy, Sangamon, Illinois, and Lake Michigan drainages (Fig. 157). It appears to be absent from western and extreme northern Illinois and is rare in central Illinois. Although difficult to collect because of its burrowing habits, present records suggest that it remains common in southern Illinois in the Ohio, Big Muddy, Saline, and Little Wabash systems.

During the present survey, *F. fodiens* was collected in central Illinois only on the Sangamon River floodplain at Allerton Park in Piatt County; however, historical records suggest that the species was formerly more common in central and northern Illinois. The northernmost records shown in Fig. 157 are based on a collection at the Illinois Natural History Survey labelled

"Ottawa, LaSalle Co., Ill., Sept. 1901," on Bovbjerg's (1952) study of *F. fodiens* and *O. propinquus* in the Lake Michigan drainage of southern Cook County, and Bovbjerg's (1952) mention of the presence of *F. fodiens* in Dead River at Zion, Lake County, also a tributary of Lake Michigan. Brown (1955) found *F. fodiens* in a woodland pond (Sangamon River system) 2.5 km SW Langleyville, Christian County.

In Illinois, *F. fodiens* lives on wooded floodplains (Fig. 158) or where wooded floodplains formerly occurred. It lives in deep burrows and is in surface waters (usually floodplain ponds) only during floods; 27 of 31 collections of *F. fodiens* made in Illinois since 1972 were made from February through May, the period of late winter-spring flooding, although specimens also have been caught above



Fig. 158.—Lower Simmons Creek, 5 mi N Golconda, Pope County, Illinois (26 October 1983). *Fallicambarus fodiens* is common in burrows along the stream banks and, during floods, in the stream.

ground in June, July, August, and September. As floodwaters recede and floodplain ponds dry, *F. fodiens* burrows underground. In southern Illinois, chimney-topped burrows on wooded floodplains usually are those of *F. fodiens*. Stands of river birch (*Betula nigra*) are especially good indicators of the likely presence of *F. fodiens*. In Ontario, *F. fodiens* inhabits marshes, drainage ditches, and ponds (Crocker & Barr 1968).

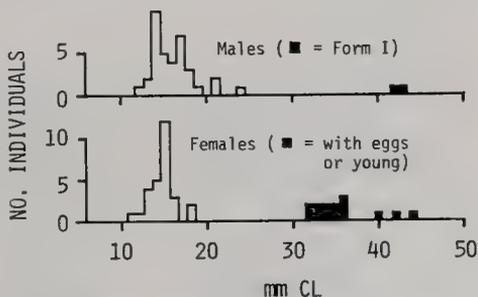


Fig. 159.—Size-frequency distribution of *Fallicambarus fodiens* collected in April in southern Illinois.

Table 18.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Fallicambarus fodiens*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
February	4	0	0	1	25	1	25
March	4	0	0	2	50	1	25
April	15	2	13	0	0	4	27
May	4	0	0	0	0	0	0
June	1	0	0	0	0	0	0
July	1	0	0	0	0	0	0
August	1	0	0	0	0	0	0
December	1	0	0	0	0	0	0

Burrows constructed by *F. fodiens* typically have one to three entrances, often capped by chimneys, leading to an oval resting cavity (Faxon 1885) and leading down from the cavity 30–60 cm is a narrow escape tunnel (Crocker & Barr 1968). Soils having a high clay content are probably necessary for the deep burrows constructed by *F. fodiens* (Crocker & Barr 1968).

Life History.—In a study in southern Cook County, Illinois, Bovbjerg (1952) found juveniles and gravid females in woodland ponds as early as March. By June the adults had disappeared, presumably into burrows, and only young remained in the ponds. By 2 weeks prior to the drying of the pond, all crayfish had disappeared from the pond, either by burrowing or emigrating. Individuals were found (one at a depth of 1.2 m) throughout the summer by digging in the dry pond bed down to the water table. The refilling of the pond in the fall was followed by a reinvasion of *F. fodiens*, which was active in the pond in November under a 5-cm ice cover.

F. fodiens can survive out of water (at 20.5°C and 66 percent relative humidity) for about 12 hours (Bovbjerg 1952), and overland migrations of *F. fodiens* on warm (>5°C) humid nights in March–May were documented by Cummins (1921). *F. fodiens* is omnivorous, and in northern Illinois specimens, stomach contents included plant fragments (especially grass seeds), insect fragments, crayfish appendages, an isopod, and a salamander larva (Bovbjerg 1952).

Sexually mature (form I) males occur in March and April in Michigan (Cummins 1921) and in April (Table 18), August, and October (Brown 1955) in Illinois. The two form I males collected during the present survey had carapace lengths of 42 and 43 mm.

In Michigan, females have been found with eggs in March and April and with young in April and May (Pearse 1910; Cummins 1921; Creaser 1931), in Indiana with eggs and young in April (Hay 1896; Williamson 1907),

in Ontario with eggs in March and April and young in May (Crocker & Barr 1968), and in Illinois with eggs in February and March and young in February, March, and April (Table 18). Brown (1955) dug a female with attached young from a burrow in southern Illinois in October.

In the present survey, three females with eggs and 24 females with attached young were collected. The females with eggs were 22, 28, and 35 mm CL, with 48, 68, and 162 eggs, respectively. Eggs on the two smaller females, one collected each in February and March, averaged 2.2 mm in diameter; those on the largest female, collected in March, averaged 2.5 mm. Seven females collected in February and March (30–44 mm CL) had 96–201 (mean, 132.1) young attached.

The size-frequency distribution of southern Illinois, April-collected *F. fodiens* suggests that the species reaches sexual maturity and dies in its second year. Only males over 40 mm CL (second year) among the individuals collected were form I, and all females over 30 mm CL (second year) were carrying young. All smaller males and females were immature (Fig. 159). The sex ratio among the combined April samples was 44 males:42 females.

Genus *Cambarus* Erichson

Cambarus Erichson 1846

Bartonius Ortmann 1905

Gonopod with two large terminal elements curved at about 90° angle to shaft; central projection large and bladelike. Ischium of third pereopod of male with hook. Opposable margin of dactyl of chela without deep concavity.

Cambarus contains about 77 species (Hobbs 1981), of which four occur in Illinois. Two of the Illinois species (*tenebrosus* and *rusticiformis*) belong to the subgenus *Erebicambarus*, one (*diogenes*) to *Lacunicambarus*, and one (*robustus*) to *Puncticambarus*. The wide-ranging *C. diogenes* appears to be a complex of species (Hobbs 1974b),

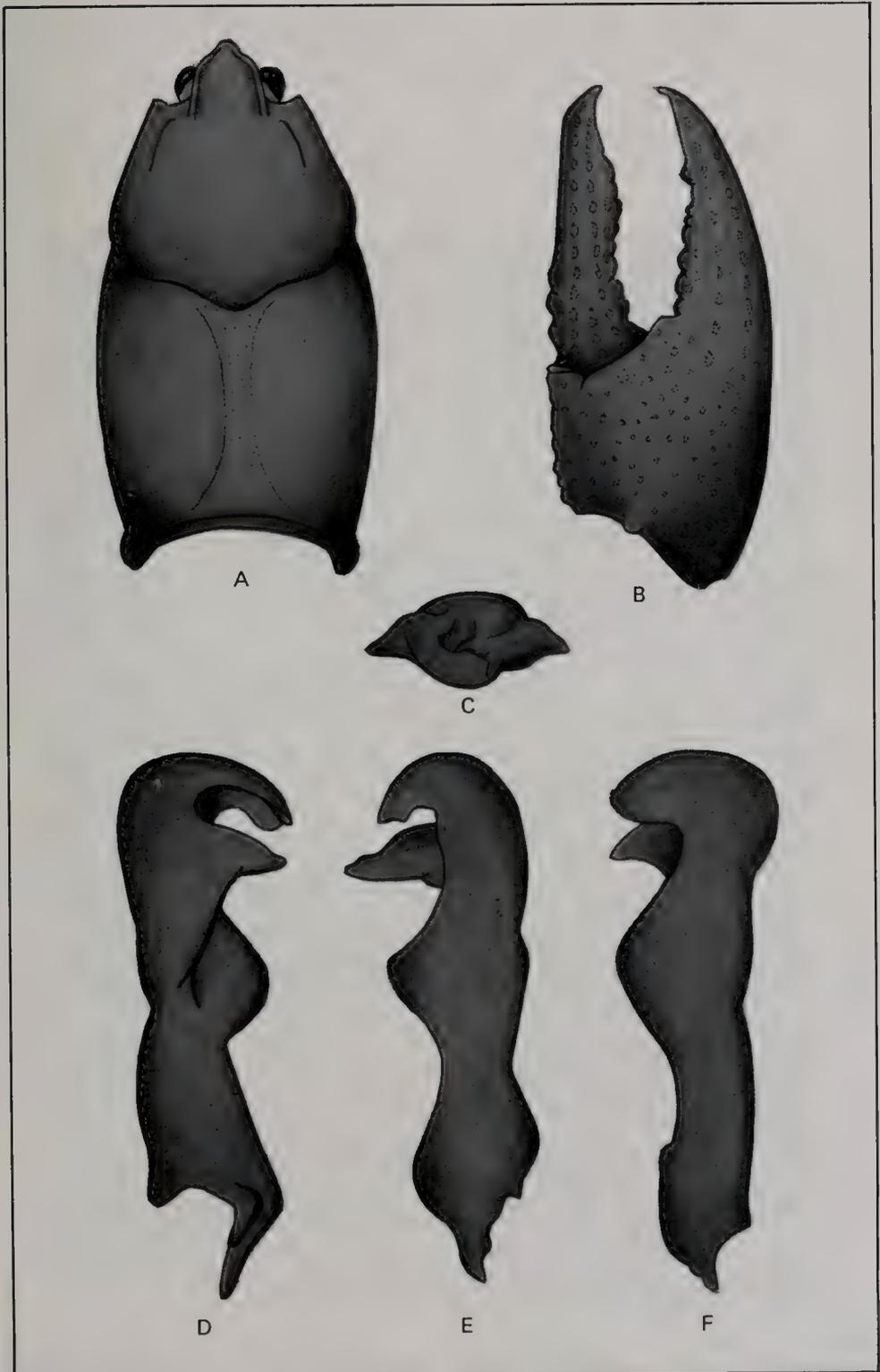


Fig. 160.—*Cambarus tenebrosus*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

more than one of which may occur in Illinois, as discussed in the species account below.

Cambarus tenebrosus Hay
(Fig. 160)

Cambarus bartoni tenebrosus Hay 1902
Cambarus bartoni laevis Faxon 1914

Description.—Rostrum broad, shallowly excavated, lacking median carina; margins slightly converging anteriorly, lacking terminal tubercles or spines; acumen short. Carapace dorsoventrally flattened, cervical spines absent (northern population) or present (southern population); suborbital margin gently angular. Areola moderately wide, narrowest part about 13–14 percent of length, with at least four punctations across. Chela large, heavily punctate; palm with one or two rows of tubercles on mesial surface. Form I gonopod terminates in two elements, both curved at an angle of more than 90° to the principal axis of the gonopod: a distally rounded sclerotized central projection, and a large tapering to broadly rounded mesial process. Dorsally rust red overall, with abdomen slightly browner than carapace.

In a discussion of the distribution and phylogeny of species of *Cambarus*, Hobbs (1969) depicted the range of *C. (Erebicambarus) laevis* as occurring mostly north of the Ohio River and that of the consubgeneric *C. tenebrosus* as being south of the Ohio River. Hobbs (1974b) separated the two species on the relative width of the areola (“at least 4 punctations across narrowest part” in *C. tenebrosus*; “no more than 3 punctations across narrowest part” in *C. laevis*) and the shape of the mesial process of the gonopod (“broadly rounded distally” in *C. tenebrosus*; “strongly tapered, often subacute” in *C. laevis*).

Populations of the subgenus *Erebicambarus* occurring in southern Illinois have been referred to as *C. bartoni brevis* (Rietz 1912), *C. bartoni laevis* (Brown 1955), *C. laevis* (Hobbs 1968,

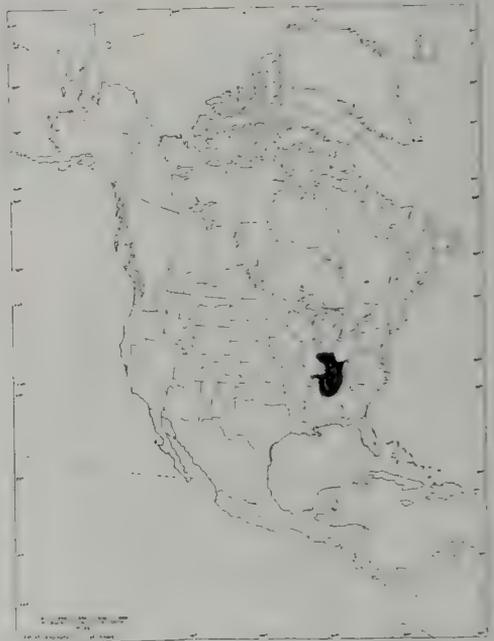


Fig. 161.—Total distribution of *Cambarus tenebrosus*.



Fig. 162.—Distribution of *Cambarus tenebrosus* in Illinois; black dots = 1972–1982 collections.

1969, 1972a; Page 1974b; Peck & Lewis 1977), *C. ornatus* (Peck & Lewis 1977), and *C. tenebrosus* (Peck & Lewis 1977). It now appears that the correct name for the southern Illinois populations is *C. tenebrosus*. Populations extend across

the Shawnee Hills of southern Illinois, into the Cumberland River drainage of western Kentucky, and into the general range of *C. tenebrosus* with no noticeable morphological discontinuities.

In Vermilion County in east-central



Fig. 163.—Spring emptying into Big Creek in Hardin County, Illinois (8 October 1984). This and other springs in the Shawnee Hills provide the best habitat in Illinois for *Cambarus tenebrosus*.

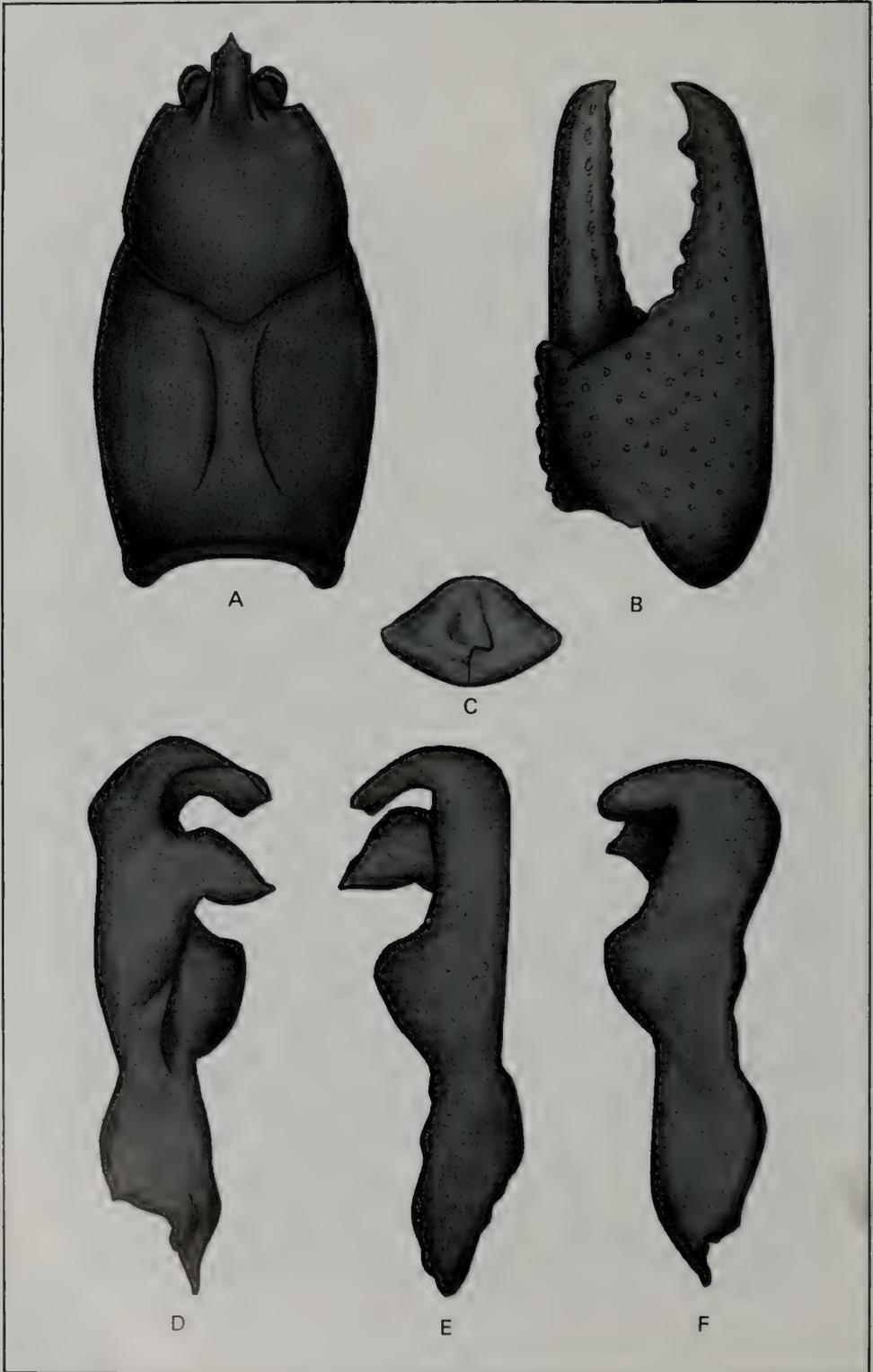


Fig. 164.—*Cambarus rusticiformis*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

Illinois is a population of *Erebicambarus* discovered in 1977. It differs from *C. tenebrosus* in southern Illinois by having a narrower areola and by lacking cervical spines (although tubercles often are present). No form I males have been found. If *C. laevis* is a valid species, the Vermilion County population is morphologically and geographically (*vide* Hobbs 1969) referable to that taxon. However, the absence of discontinuities in the geographic variation in morphology among populations assignable to the *C. tenebrosus*-*C. laevis* complex suggests a lack of reproductive isolation among populations and that only one species is recognizable. Individuals in the northern part of the range of the species have narrower areolae, lack cervical spines, and apparently have more tapered mesial processes on the gonopods. H. H. Hobbs, Jr. (personal communication 1983) suggests that "when adequately studied, *laevis* will prove to be a synonym of *tenebrosus*." Pending such a study, all Illinois populations are referred to as *C. tenebrosus*.

Distribution and Habitat.—*C. tenebrosus* occurs in central and southeastern Indiana, the Vermilion River system in east-central Illinois, the Shawnee Hills of Illinois, western and central Kentucky, central Tennessee, and northern Alabama (Fig. 161). It appears to be absent in southwestern Indiana.

In Illinois and elsewhere, *C. tenebrosus* occupies rocky springs and spring-fed headwaters and creeks. It hides under stones, sometimes forming shallow excavations in the stream bed. Brown (1955) cited "small piles of mud at the edge of rocks" as an indicator of the presence of the species. Its affinity for spring-fed headwaters often results in its occupancy of caves.

In southern Illinois, *C. tenebrosus* is restricted to the Ohio River drainage of Hardin, Pope, Johnson, and Union counties (Fig. 162). It is most common in Big Creek, a moderate-sized stream in Hardin County fed by numerous



Fig. 165.—Total distribution of *Cambarus rusticiformis*.



Fig. 166.—Distribution of *Cambarus rusticiformis* in Illinois; black dot = 1975 collection.

springs (Fig. 163). Elsewhere in Illinois it has been found only in Willow Creek (Vermilion River system) in Vermilion County, Illinois (Fig. 162), where it presumably is distributionally contiguous with the Indiana population.

The Illinois and total ranges of *C. tenebrosus* are quite similar to those of the zigzag salamander (*Plethodon dorsalis*) although the salamander has dispersed into Clear Creek, a tributary of the Mississippi River, in Alexander, Union, and Jackson counties (Smith 1961).

C. tenebrosus, first recorded in Illinois (as *C. bartoni brevis*) by Rietz (1912), probably has essentially the same distribution now as it had prior to the arrival of man. However, the water table of southern Illinois has been lowered within historic times, and some springs may have disappeared or at least are smaller than before, reducing the habitat available for *C. tenebrosus*. Such reductions in habitat have caused some spring-inhabiting fishes (*Phoxinus erythrogaster*, *Rhinichthys atratulus*) to disappear from southern Illinois (Smith 1979).

Life History.—Prins (1968) studied *C. tenebrosus* in a stream system in Kentucky and found it to be most common in constant-temperature headwaters. Most adults were found in burrows or under large rocks, but young and subadults were found in open-stream environments. The diet consisted primarily of vascular plants, especially fallen leaves from the riparian habitat, and filamentous algae. Other food items included detritus, aquatic insects, and crustaceans. Hatching occurs in July and August after eggs have been carried by the female for at least 25–30 days. Growth continues throughout the year, including winter, and sexual maturity is reached at about 20–22 months and 40 mm CL. Mating occurs in winter and spring. Mature females oviposit in June and July at about 22–23 months and probably again at 34–35 months. Egg counts on seven females (44–52 mm CL) ranged from 186 to 266. Maximum

CL was found to be about 65 mm and maximum longevity about 36–38 months. The sex ratio among 3,235 specimens was 1 male:1.03 females.

No form I males or females carrying eggs or young were present among the 40 collections of Illinois *C. tenebrosus* made during the present survey (all months except September). Brown (1955) reported collecting form I males in August and October and a female with attached young in October. All of Brown's collections were made in Hardin and Pope counties, Illinois. A 46.6-mm CL female from Big Creek is the largest Illinois specimen.

Cambarus rusticiformis Rhoades (Fig. 164)

Cambarus rusticiformis Rhoades 1944

Description.—Rostrum narrows anteriorly; margins elevated, concave, and tipped with large knobs; acumen moderate, elevated anteriorly; median carina lacking. Carapace dorsoventrally flattened, with large cervical spine, small suborbital angle. Areola moderately wide, narrowest part 16–18 percent of length. Chela large, heavily punctate; palm with single row of flattened tubercles along mesial surface. Form I gonopod terminates in two elements, both directed caudally at an angle greater than 90° to the principal axis of the gonopod: a distally rounded, sclerotized central projection and a large distally tapering mesial process.

Distribution and Habitat.—*C. rusticiformis* occupies the Cumberland River drainage and the Barren River system (Green River drainage) of Kentucky and Tennessee (Bouchard 1976) and, judging from one Illinois collection, the lower Ohio River (Fig. 165). Two juvenile males (11.7 and 14.6 mm CL) were collected in a rocky backwater of the Ohio River near Lock and Dam 53, 4 km NE Olmsted, Pulaski County, Illinois, (Fig. 166) on 16 July 1975. Several later attempts to find *C. rusticiformis* at the same and other sites on the lower Ohio River were unsuccessful.

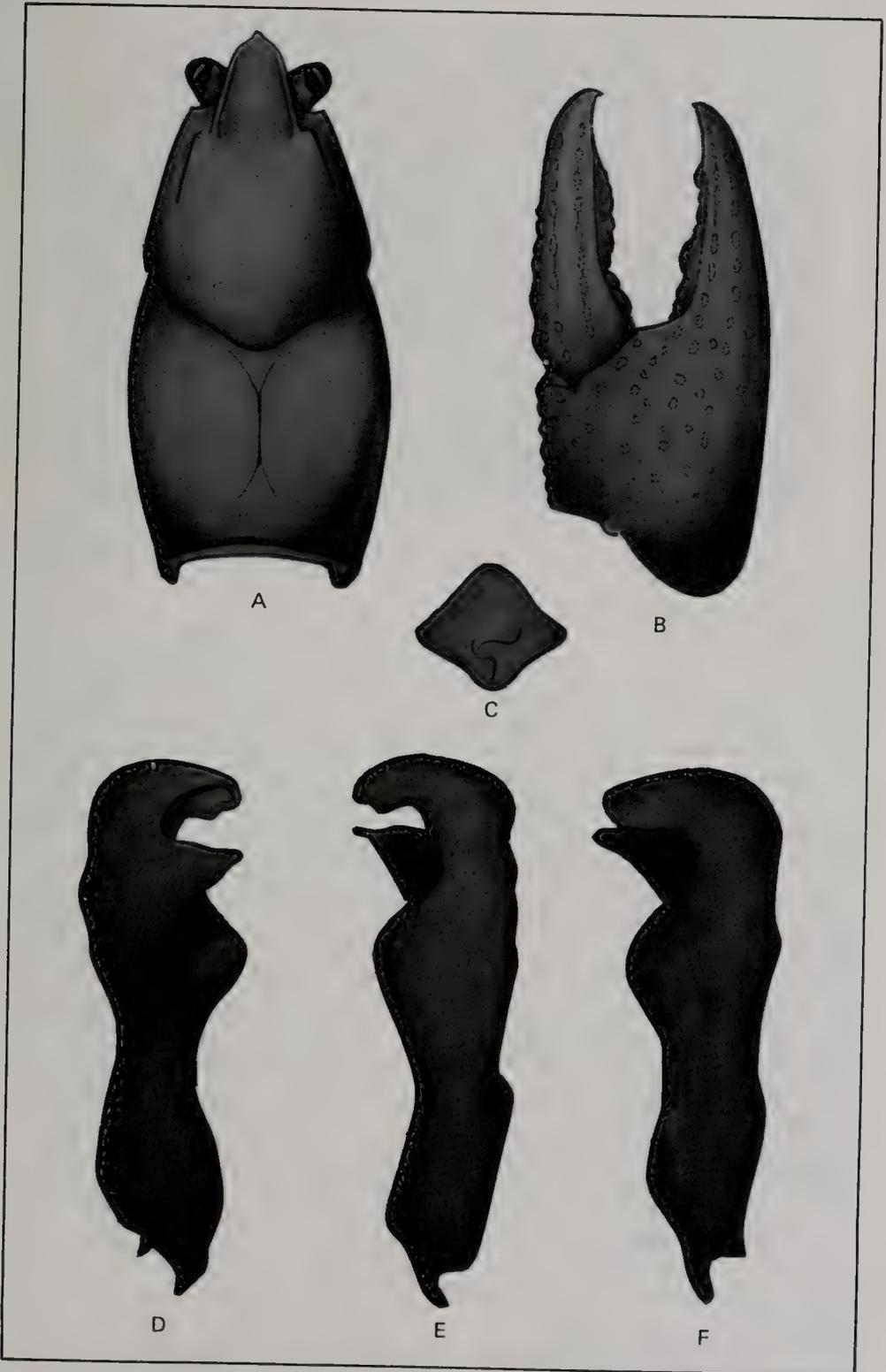


Fig. 167.—*Cambarus diogenes*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.



Fig. 168.—Total distribution of *Cambarus diogenes*.

The Ohio River site is about 67 river km (42 miles) below the mouth of the Cumberland River. The two specimens may represent one of the westernmost natural populations of the species, they may have been waifs captured during a downstream dispersal, or they may have been transplanted as the result of human activities. *C. rusticiformis* has been introduced into the Paint Rock River (Tennessee River drainage), Alabama (Bouchard 1976). Collected in the Ohio River with *C. rusticiformis* were 12 *Orconectes placidus*, a species with a similar overall distribution.

Elsewhere, *C. rusticiformis* lives in rocky runs and adjacent pools and riffles of fast-flowing creeks and small rivers. Other ecological characteristics are unknown.

Cambarus diogenes Girard
(Fig. 167)

Astacus fossor Rafinesque 1817. (Name suppressed by International Commission on Zoological Nomenclature, Opinion 522, 1958.)

Cambarus diogenes Girard 1852
Cambarus nebrascensis Girard 1852
Cambarus obesus Hagen 1870
Cambarus Diogenes var. *Ludoviciana*
Faxon 1885

Description.—Rostrum broad, excavated, with short acumen, lacking marginal spines or tubercles, lacking median carina. Carapace compressed, lacking cervical spines; suborbital margin angular. Areola obliterated. Chela large, heavily punctate; palm with two or three rows of tubercles on mesial surface; dactyl with broad shallow concavity on basal half of opposable margin. Form I gonopod terminates in two elements, both directed caudally at an angle slightly more than 90° to the principal axis of the gonopod: a distally rounded, sclerotized central projection and a slender mesial process. Dorsal color varies from uniformly

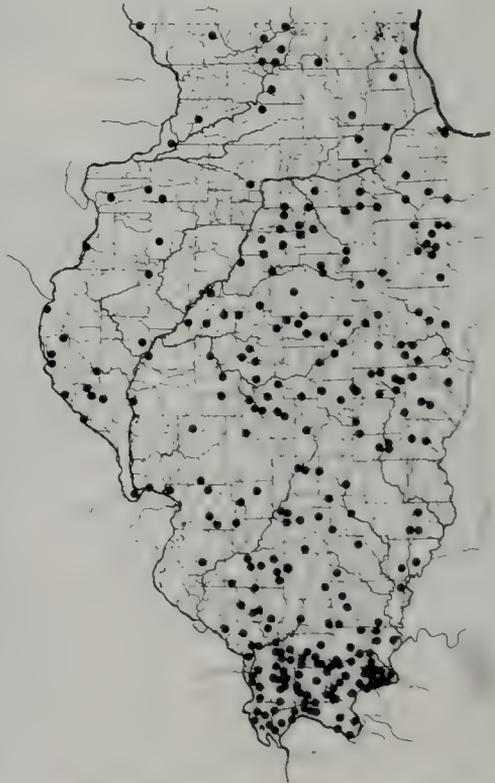


Fig. 169.—Distribution of *Cambarus diogenes* in Illinois; black dots = 1972-1982 collections.

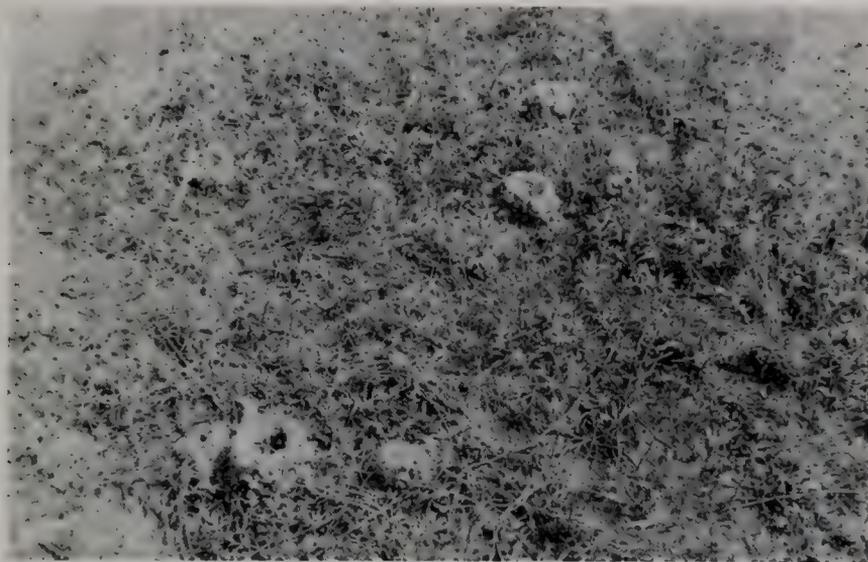


Fig. 170.—Chimney-topped burrows of *Cambarus diogenes* on the floodplain of a slough, 2 mi N Pleasant Grove, Johnson County, Illinois (9 July 1972).

red brown (with thorax lighter red) to green with red outlining abdominal segments, tips of chelae, and margins of rostrum.

Marlow (1960) examined geographic variation in *C. diogenes* and concluded that only two subspecies could be recognized: *C. d. ludovicianus* in the Lake Ponchartrain drainage and southern Louisiana and *C. d. diogenes* throughout the rest of the range of the species. However, according to Hobbs (1969, 1974b), *C. diogenes* is a complex of forms, and *C. d. ludovicianus* probably is more widespread than Marlow thought. Illinois specimens show tremendous variation in the shape of the carapace and rostrum and in coloration. If several taxa presently are included in "*C. diogenes*," more than one may be found in Illinois. The only other described species in the subgenus *Lacunibambarus* are *C. acanthura*, restricted to the Tennessee and Alabama drainages of Tennessee, Alabama, and Georgia (Hobbs 1981) and *C. miltus* from Baldwin County, Alabama (Fitzpatrick 1978b).

Distribution and Habitat.—*C. diogenes* ranges along the Atlantic Pied-

mont and Coastal Plain from New Jersey and Pennsylvania south to central Georgia, in Gulf drainages from Georgia to eastern Texas, and north in the Mississippi and Great Lakes basins to western New York and Pennsylvania, Michigan, Wisconsin, Minnesota, and North Dakota. The westernmost populations occur in the Platte River drainage of Colorado and Wyoming (Fig. 168).

C. diogenes occurs statewide in Illinois (Fig. 169) and is generally common. It is abundant in the Shawnee Hills and on the Coastal Plain of southern Illinois, less common in northern and western Illinois. Its burrowing habits preclude easy collecting, and consequently, the number of collections (Fig. 169) does not adequately reflect its abundance in Illinois.

C. diogenes first was recorded from Illinois by Hagen (1870), who described the specimens collected at Lawn Ridge (Marshall County), Belleville, and Evanston as a new species, *Cambarus obesus*. Forbes' (1876) only comments on "*C. obesus*" were: "Very common. The largest in the state."

The burrowing behavior of *C. diog-*

Table 19.—Frequency of occurrence of form I males, females carrying eggs (ovigerous), and females carrying young, in Illinois collections of *Cambarus diogenes*.

Month	Number of Collections	Number and Percent of Collections with					
		Form I Males		Ovigerous Females		Females with Young	
January	7	0	0	1	14	0	0
February	7	4	57	0	0	0	0
March	14	8	57	1	7	0	0
April	22	4	18	3	14	0	0
May	34	0	0	3	9	1	3
June	46	1	2	0	0	2	4
July	60	1	2	0	0	0	0
August	45	0	0	0	0	0	0
September	34	0	0	0	0	0	0
October	55	3	5	0	0	0	0
November	15	4	27	0	0	0	0
December	3	0	0	0	0	0	0

enes is described by Grow (1981). In contrast to other Illinois burrowing crayfishes, *P. gracilis*, *P. viaevividis*, and *F. fodiens*, which burrow in prairie marshes, swamps, and on wooded floodplains, respectively, *C. diogenes* lives primarily along streams. Populations also are found away from streams in lowland areas (Fig. 170) having clay soil, especially on the Coastal Plain. Such colonies often are marked by hundreds of chimneys.

Burrows characteristically are relatively shallow (10–30 cm) in Illinois but vary in depth in relation to the size of the crayfish and may extend down a meter. Hobbs (1981:226–227) observed burrow openings in banks 5 m above water level of the Apalachicola River in Georgia. Usually a chimney-topped hole in a stream bank leads to an underwater chamber and a second, nearly horizontal, tunnel leading into the stream. Large individuals may have more elaborate dwellings with several tunnels and several openings with or without chimneys. Burrows may be found along any stream in Illinois but are most common in rocky areas.

Retrieving a *C. diogenes* from a burrow seldom requires excavating the entire burrow but does require patience. If the water at the entrance of the burrow is disturbed, the curious crayfish

eventually will investigate the disturbance and can be grabbed as it surfaces. The wait is usually only a few minutes.

Life History.—*C. diogenes* leaves its burrows in late winter–early spring and in fall to mate in open water (Hargitt 1890; Hay 1896; Williams & Leonard 1952). Presumably they then return to their burrows, although ovigerous females and females with young are found both in burrows and in open water (Williamson 1907). When young leave the mother, they seek cover in rocky parts of streams or marginal vegetation of standing water bodies until large enough to burrow. When they reach about 20 mm total length, they have begun burrowing.

Nothing of the food habits, growth, or longevity of *C. diogenes* is known, presumably because of the difficulty in obtaining adequate series of specimens. Presumably it leaves the burrow at night to forage on vegetation (Crocker & Barr 1968). The largest specimens in the Illinois Natural History Survey collection are a 61.3-mm CL ovigerous female and a 61.0-mm form I male in a jar labelled “Morris & Marseilles, Grundy & LaSalle counties, Illinois” (no date). The right chela of the male measures 57.5 mm in length; that of the female measures 46.9 mm.

In the present survey, form I males

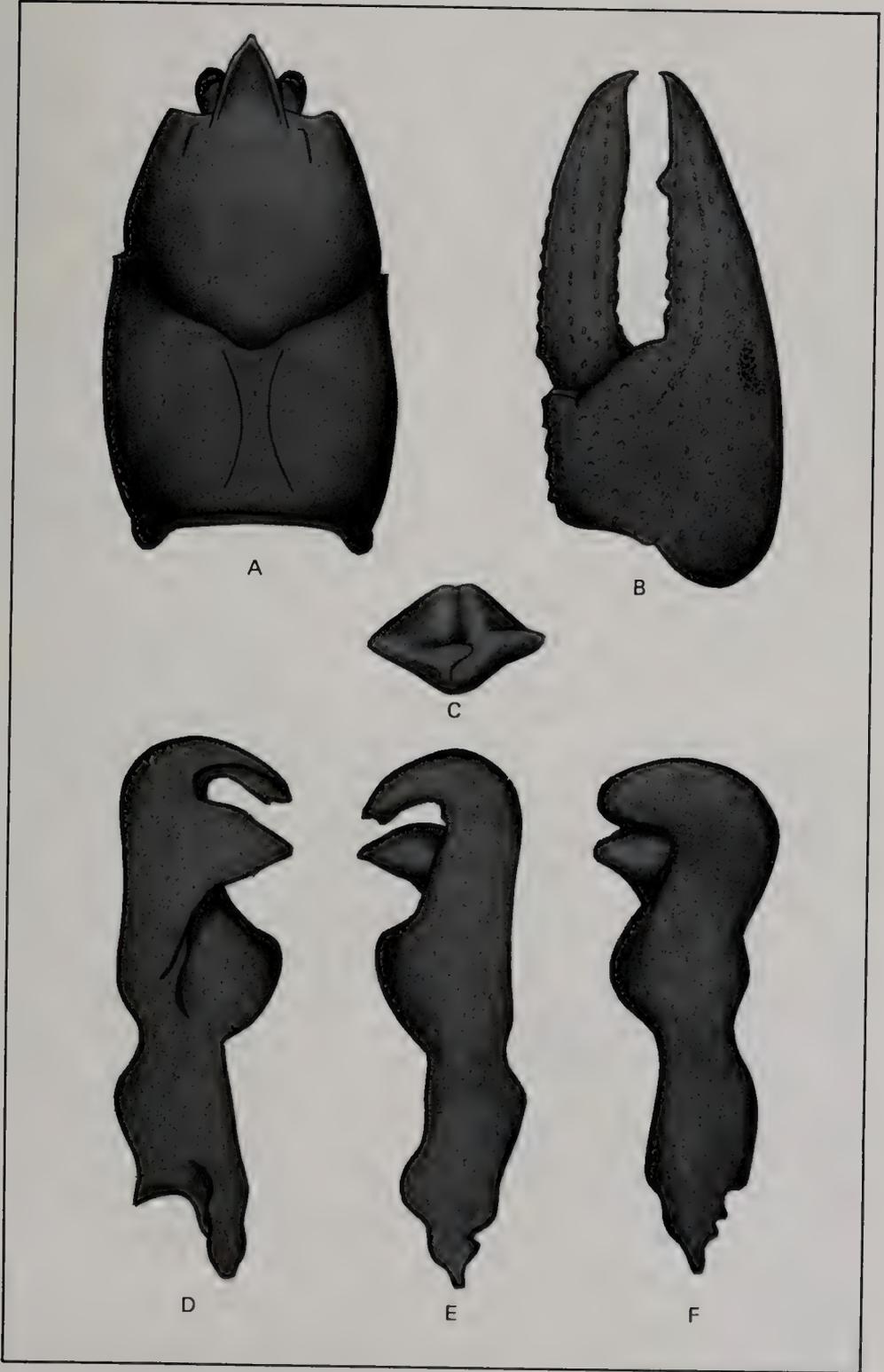


Fig. 171.—*Cambarus robustus*. A, dorsal view of carapace; B, dorsal view of right chela; C, annulus ventralis; D, mesial view of gonopod of form I male; E, lateral view of gonopod of form I male; F, lateral view of gonopod of form II male.

were collected from February through July (except in May), and in October and November (Table 19); Brown (1955) found form I males in Illinois from March through September, except in July. The primary peak of occurrence is in February and March, and a secondary peak occurs in November (Table 19). Elsewhere, matings have been observed in March, April, May (Hargitt 1890; Hay 1896; Evermann & Clark 1920), and October (Williams & Leonard 1952). In Louisiana, form I males were found in March, April, and October (Penn & Marlow 1959) and in Georgia in January, April, and October (Hobbs 1981). Ortmann (1906) recorded form I males in Pennsylvania from March through November. Among the *C. diogenes* examined by Marlow (1960), form I males were present in every month except January, but were most prevalent in April and September. Although the occurrence of form I males suggests that mating in *C. diogenes* may occur in almost any month, activity probably peaks in late winter-early spring (Feb-

ruary-April) and in fall (September-November).

Ovigerous females have been found in January (Bundy 1877), April (Hay 1896; Evermann & Clark 1920; Creaser 1932), and May in Indiana (Williamson 1907); in April and May in Pennsylvania (Ortmann 1906) and Iowa (Phillips 1980); in April (Williams & Leonard 1952) and May in Kansas (Harris 1900); from late March to May in Wisconsin (Graenicher 1913); and in September in Georgia (Hobbs 1981). Marlow (1960) examined ovigerous females from March (1 female), April (19), May (17), and October (1). Females carry young in May and June in Pennsylvania (Ortmann 1906) and in Indiana (Williamson 1907; Evermann & Clark 1920), and in June in Michigan (Creaser 1932). In Illinois, females were found to carry eggs from January through May, except



Fig. 172.—Total distribution of *Cambarus robustus*.



Fig. 173.—Distribution of *Cambarus robustus* in Illinois. The two records (Adams and Macon counties) are from Faxon (1885) and Rietz (1912).

in February, and young in May and June (Table 19).

Because of the difficulty in obtaining adult *C. diogenes*, few females with eggs or young attached were collected in the present survey. Five females (43.7–56.4 mm CL) collected in April and May were carrying 183–518 (mean, 295.2) eggs. The highest number of eggs was on the smallest female. Eggs varied in diameter from 2.1 to 3.0 mm, and unlike other crayfishes examined during the present survey, in *C. diogenes* egg diameter has a significant correlation ($r = 0.97$) with length of the female: egg diameter = $-1.280 + 0.077$ CL.

A 48.5-mm CL female collected in Johnson County on 19 May 1973 had 606 early-instar young attached; a 47.2-mm CL female collected in Christian County on 8 June 1979 had 45 late-instar young attached. Two females collected in Indiana in 1906 were carrying 87 and 215 young (Williamson 1907).

***Cambarus robustus* Girard**
(Fig. 171)

Cambarus robustus Girard 1852

Description.—Rostrum moderately broad, shallowly excavated, lacking median carina; margins converge anteriorly, lack terminal tubercles or spines; acumen moderately large. Carapace dorsoventrally flattened, with large cervical spines; suborbital margin angular. Areola moderately wide, narrowest part about 12–17 percent of length. Chela large, heavily punctate; palm with two rows of tubercles on mesial surface; base of fixed dactyl with deep dorsal and ventral impressions. Form I gonopod terminates in two elements: a distally rounded, sclerotized central projection curved at an angle of more than 90° to the principal axis of the gonopod, and a large gently tapering mesial process curved at about 90° to principal axis. Dorsally green brown.

Distribution and Habitat.—*C. robustus* ranges from Connecticut and southern Ontario south to northwestern

North Carolina and eastern Kentucky and west to Michigan and central Indiana (Fig. 172). It occupies rocky areas of fast-flowing streams, and sometimes is found in rocky lakes and ponds (Crocker & Barr 1968; Berrill 1978).

The only Illinois records (Fig. 173) are from the late nineteenth and early twentieth centuries. Faxon (1885) reported *C. robustus* from Decatur (Macon County, Sangamon River system), and Rietz (1912) reported four specimens from Quincy (Adams County, Mississippi River drainage). Although the Quincy specimens cannot be located, the Decatur specimens are in the U.S. National Museum (USNM 63291) and unquestionably document the former presence of the species in the state. *C. robustus* is rare even as far west as Indiana (Eberly 1955), and the Illinois collections must have represented relict populations left over from a more widespread distribution in a cooler postglacial climate. Many streams today around Quincy are spring-fed, and considerable effort was expended in unsuccessful attempts to locate surviving populations of *C. robustus* in what appear to be suitable habitats. The Sangamon River, flowing through Decatur, was badly polluted in the early part of this century (Jewell 1920), is now impounded by Lake Decatur, and appears unlikely to support a population of *C. robustus*.

Life History.—Crocker (1957) reported form I males in New York collections made from April through October and observed copulation in October and May (the latter in a lamprey trap). Form I males have been collected in Pennsylvania in May and July–November; the smallest was about 63 mm total length (about 32 mm CL) (Ortmann 1906). In southern Ontario, form I males were 25–55 mm CL (Berrill 1978). Ovigerous females have been found in July in New York (Crocker 1957) and Pennsylvania (Ortmann 1906); the Pennsylvania female, 84 mm total length (about 42 mm CL), carried 228 eggs. Females with young attached

have been observed in April and August in New York (Crocker 1957). Young feed on immature insects; adults feed mainly on aquatic plants (Creaser 1934).

CONSERVATION

Unfortunately, it appears that *Macrobrachium ohione* and *Cambarus robustus* already have disappeared from Illinois. *C. robustus* may have disappeared from Illinois naturally rather than because of man-induced changes in the environment. Our earliest records indicate that it was relict in Illinois, presumably having been reduced from a more widespread distribution to small areas near Quincy and Decatur. Elsewhere it inhabits cool to cold streams and apparently was reduced in warm postglacial Illinois (probably during the Xerothermic period) to small populations that subsequently were unable to perpetuate themselves. *M. ohione* probably disappeared because of the extensive modification and degradation of Illinois' large rivers. Especially harmful to *M. ohione* would have been the loss of aquatic vegetation associated with increased siltation, channelization, and chemical pollution.

Unless protective measures are taken, several more species of native decapods are likely to disappear from Illinois. The following four species have restricted ranges in the state and are threatened with extirpation. They should receive as much protection as possible by our adding them to the Illinois List of Endangered and Threatened Species and protecting their habitats.

The distribution of *Orconectes indianensis* has been reduced dramatically in Illinois as a result of severe pollution and other major modifications of the Saline River system. Remaining populations are restricted to the South Fork of the Saline River in Gallatin, Johnson, Pope, Saline, and Williamson counties, Robinette (Eagle) Creek in Gallatin County, and Honey Creek in Hardin County. Elsewhere the species

occurs only in a small area of Indiana.

Orconectes kentuckiensis occurs only in Big, Hosick, and Peters creeks in Hardin County, and although the distribution of this species in Illinois probably has changed little historically, its persistence is threatened by modifications of the riparian habitats in Hardin County. Trees have been removed from many miles of stream bank, resulting in less shading of the stream and higher water temperatures. Water has been diverted in ever-increasing amounts from its natural drainage for use in agriculture. The lowered water table is reducing the size of Big Creek. Elsewhere, *O. kentuckiensis* occurs only in a small area of northwestern Kentucky.

Orconectes placidus is common throughout much of Kentucky and Tennessee, but in Illinois it maintains a sizeable population only in Big Creek in Hardin County and is threatened by the same stream modifications threatening *O. kentuckiensis*.

Orconectes lancifer is restricted in Illinois to Horseshoe Lake in Alexander County. Although under the supervision of the Illinois Department of Conservation, the lake has been severely modified in recent decades, and much of it now is surrounded by agricultural fields and grasses. If the unusual biota of Horseshoe Lake is to persist, subsequent modifications of the lake should be allowed only after careful consideration of their environmental impact. Elsewhere *O. lancifer* occurs uncommonly throughout the former Mississippi Embayment.

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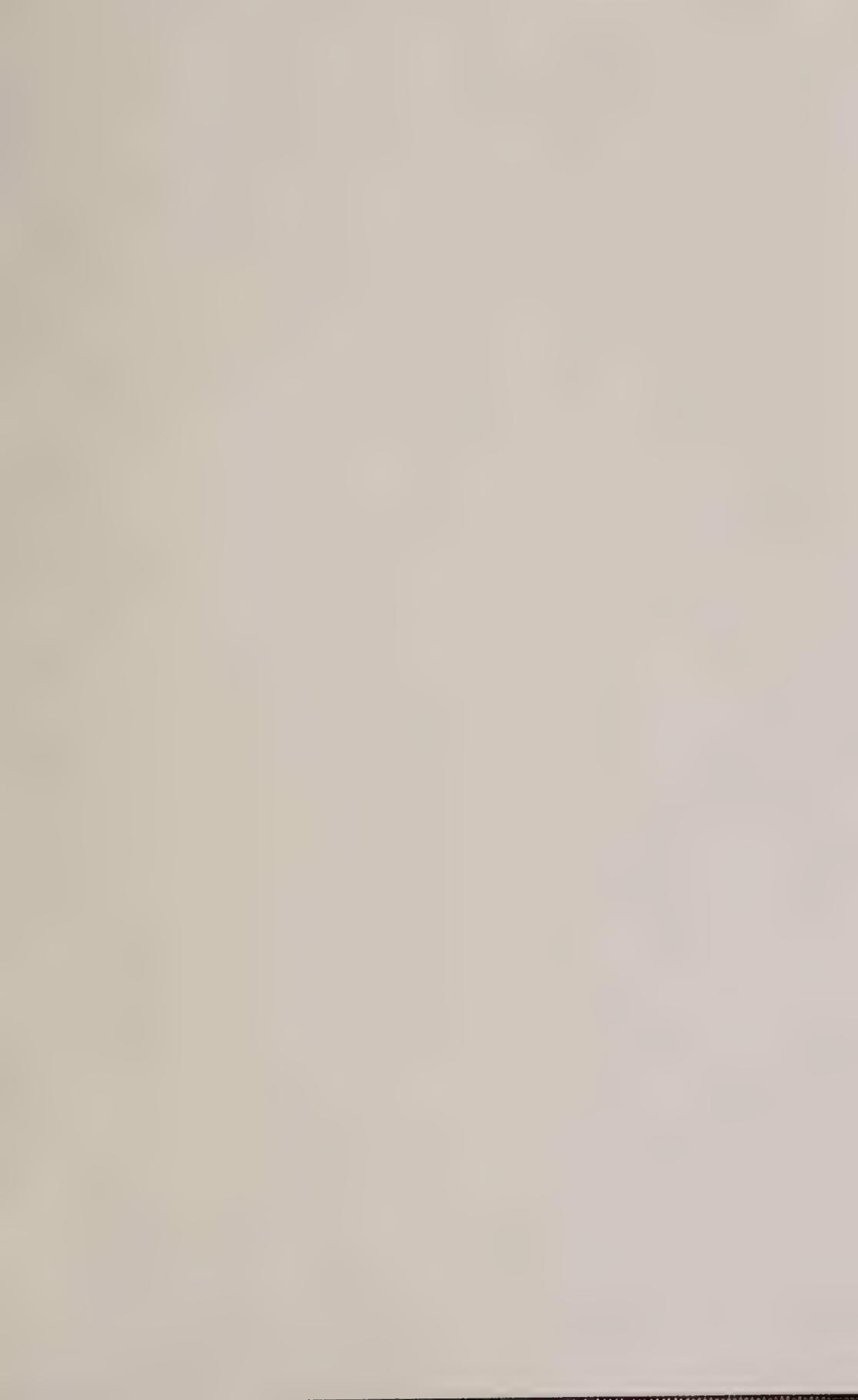
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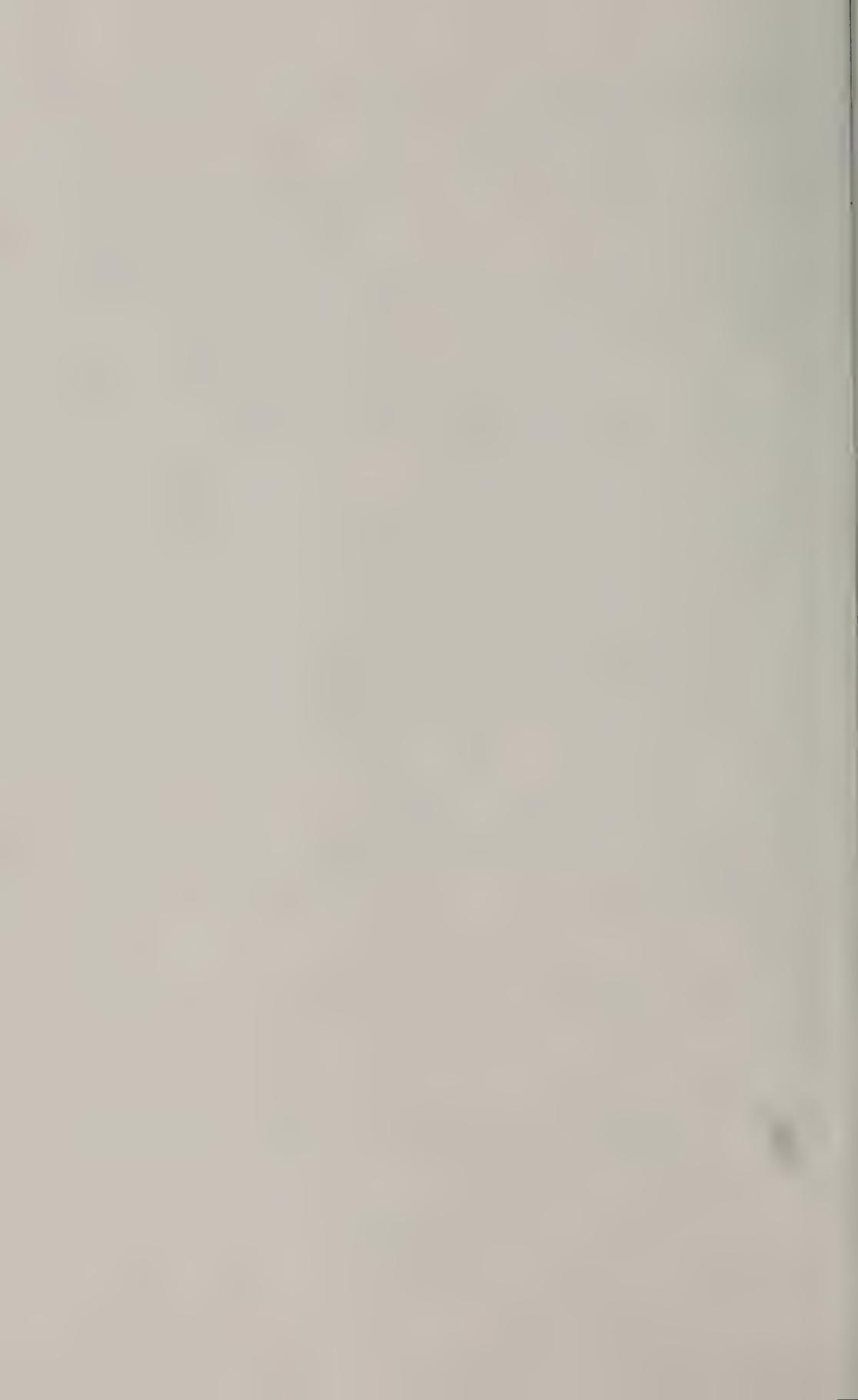
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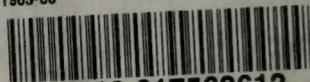
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