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Lotic dragonfly (*Anisoptera: Odonata*) nymphs of the Southeastern United States: identification, distribution and historical biogeography

Jerry A. Louton
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I am submitting herewith a dissertation written by Jerry A. Louton entitled "Lotic dragonfly (*Anisoptera: Odonata*) nymphs of the Southeastern United States: identification, distribution and historical biogeography." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

David A. Etnier, Major Professor

We have read this dissertation and recommend its acceptance:

Dewey Bunting, Charles Pless, Paul Parmalee, Arthur Echternacht

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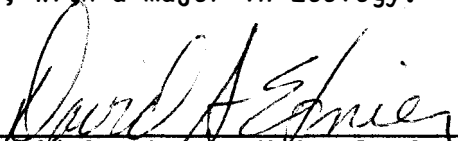
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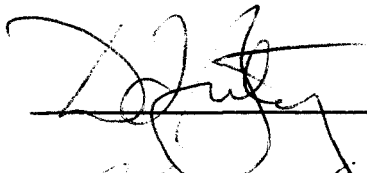
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David A. Etnier, Major Professor

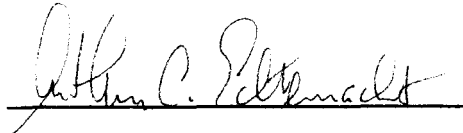
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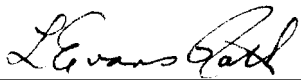


Arthur C. Edmond



Arthur C. Edmond

Accepted for the Council:



Vice Chancellor
Graduate Studies and Research

LOTIC DRAGONFLY (ANISOPTERA:ODONATA) NYMPHS OF THE
SOUTHEASTERN UNITED STATES: IDENTIFICATION,
DISTRIBUTION AND HISTORICAL BIOGEOGRAPHY

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Jerry A. Louton

March 1982

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ABSTRACT

An identification guide to the southeastern United States lotic dragonfly nymphs is constructed. Descriptions, figures, keys, verification tables, and distribution maps are provided to facilitate identification of families, genera, and species. Information developed in the study of nymphs is utilized to evaluate arrangements of taxa that have been traditionally based solely on adult characters. Traditional arrangements are supported except (1) subgenera of the genus *Gomphus* s.l. are highly distinctive in the nymphal stage and should be elevated to generic rank and (2) two species, *Gomphurus consanguis* and *G. rogersi* are improperly placed and as a group deserve generic rank.

A study of ranges of North American species led to an analysis of the historical biogeography of the genera. An analysis of the worldwide distribution of genera of the North American fauna led to the following conclusions: (1) the Nearctic fauna is composed of relicts of a once continuous Holarctic Tertiary fauna, a few Jurassic relicts, and minor lineages derived from the Neotropical realm, (2) species of the modern fauna are considered to have differentiated by late Tertiary or early Pleistocene times and (3) certain other nominal species or yet unrecognized taxa are considered of subspecific rank and of late Pleistocene age.

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CHAPTER I

INTRODUCTION

The systematic study of nymphal anisopterous Odonata has lagged conspicuously behind that of adults. Comprehensive treatments of the North American fauna have given little or no consideration to immature forms (Needham and Heywood, 1929; Needham and Westfall, 1955). The works by Walker (1958) and Walker and Corbet (1975) on the Canadian and Alaskan faunas are exceptional, both providing good nymphal descriptions, keys and figures. The austral portion of the North American fauna remains poorly understood. For that reason, the emphasis of the present work will be on the description or redescription of the many southeastern species that have received inadequate attention in the nymphal stage. This work is intended to (1) provide for the identification of species important in stream survey work, (2) provide information for the verification of the arrangement of species based mainly on adult characters (see Emden, 1957, for a statement of the importance of immature forms in the study of insect classification) and (3) provide an analysis of the historical biogeography of the groups based on inferred phylogenetic relationships and distributional data.

There are approximately seventy species of anisopterous Odonata treated herein. Nymphs of most of the species have been reared, positively associated with adult forms and described in detail sufficient for their identification. In addition to

descriptive material, illustrations, keys, verification tables and range maps are provided as aids to accurate species determination.

This work evolved out of an original intention to study nymphs of the species occurring in Tennessee. This faunal delimitation proved to be unnatural and therefore unsatisfactory. The scope was expanded to include the southeastern United States, itself an unnatural faunal delimitation but one less confining than the previous. To avoid socio-political boundaries the "southeastern United States" is considered to include the area that extends from the boundaries of the prairie region eastward, and the area south of the maximum Pleistocene glacial front (Fig. 151, Appendix A).

It is at once natural and unnatural to divide the anisopterous Odonata into lotic and lentic components. It is ecologically natural. There are fundamental differences between the survival strategies of the two functional groups. Lentic species are relatively r selected. Occurrence of r selected species in lentic habitat is due to the successional (temporal) nature of the breeding places of their immature stages. Two outstanding aspects of their strategies are high tendencies for dispersal and shortened life cycles (see summary of life cycles and dispersal capabilities of different groups of Anisoptera in Corbet, 1963). Lotic habitats are more stable. Although rivers may meander and shoals may shift their position the habitat does not abruptly disappear as may be the case with lentic waters. Lotic species

tend to be relatively K selected, with longer life cycles and lower dispersal tendencies than among lentic groups.

Phylogenetically, the separation into lentic and lotic groups is more ambiguous. Some families are exclusively lotic (Cordulegastriidae), some overwhelmingly lotic (Gomphidae), some mostly lotic (Macromiidae), some with a few lotic genera (Aeshnidae, Corduliidae) and one group (Libellulidae) almost devoid of lotic forms. At the generic level, groups sort out into lentic versus lotic with good consistency. Exceptions include *Gomphus* s.s., *Aeshna*, and *Somatochlora*. Some individual species possess a wide latitude of habitat tolerance but no one species is habitually found in both torrential and stagnant waters.

An advantage of treating an ecologically cohesive group is that historical biogeographical analysis of distribution is simplified. Range limiting factors are assumed to operate in a uniform fashion among these ecologically similar groups.

The delimitation of the scope of this work is such that collections from Surber samples taken within the geographic range of this study may be confidently sorted if care and good judgement are exercised. Using the keys presented herein species taken in "kick-net" samples from all manner of lotic habitats may likewise be identified if they do not include backwater areas that contain rooted emergent or floating vegetation. Some coastal plain streams include a mixture of lentic and lotic habitat and as such all material obtained in sampling them cannot be keyed to species and sometimes even to genus. Provisions for these kinds of

samples are made in the key by including couplets that take most lentic groups out at the generic level. The entire family Libellulidae s.s. is "keyed out" at the family level.

Several major gaps exist in the published knowledge of Odonata that have implications concerning limitations for the present study. The last worldwide catalogue of the Odonata was that of Kirby (1890) and the last catalogue of North American species was that of Muttkowski (1910a). Although relationships have been worked out at the family and subfamily level (Tillyard and Fraser, 1938-1940; Fraser, 1957) the relationships of genera within the subfamilies have not been treated except on a regional basis. The relationships between North American species have been treated only in incidental ways. Some generic subgroups have been suggested based mainly on adult characters. These subgroups are evaluated in this study on the basis of nymphal characters. Affinities between closely related species are often indicated in descriptive treatments when the nearest relative is identified and compared to descriptions of newly discovered species. This lack of information concerning phylogenetic relationships is especially crippling to any attempt at historical biogeographical analysis. The analysis therefore stresses the biogeography of closely related species rather than the evolution of entire species-groups.

CHAPTER II

METHODS

Field work included spring and summer collections (March-September) for five years. The field work was greatly facilitated by four annual University of Tennessee Regional Faunas class field trips to various parts of the southeast during the height of the collecting season (May). Live final instar nymphs were collected in all physiographical areas of the southeastern United States. Field collections were obtained by the "kick-net" method of disturbing substrate upstream of a one-eighth inch wire mesh D-net. Collections were made from all microhabitat types present at a given location. Additional collections were made during fish-seining operations conducted by Dr. David Etnier and his graduate students in ichthyology at the University of Tennessee, Knoxville. Specimens were kept alive and transported in plastic bags containing wet leaves or other vegetable debris and a small amount of water. During hot weather or for extended field trips the bags of specimens were kept on ice.

Laboratory procedures were simplified due to the hardness of dragonfly nymphs. Specimens (one each) were placed in twelve by four inch aluminum window screen "pillow cages" with an identifying label stapled at the top closure. Twenty-four such cages fit in a ten gallon aquarium. Untreated tap water was added to a depth of two inches and aerated by a small aquarium pump with two airstones per aquarium. At emergence, nymphs crawled up the

sides of the cages and adults emerged and clung to the upper portion of the cages. Emerged adults were removed to a dark cabinet for five days to allow hardening of the exoskeleton prior to preservation. The adults were then killed with ethyl acetate and series were preserved part in 65 percent isopropyl alcohol and part dry in glassine envelopes. Adults and exuviae were preserved together.

Illustrations were made with the aid of a camera lucida mounted on a binocular microscope. Fine measurements of head width, abdominal width, and length of hind femur were made with an ocular micrometer and rounded to the nearest hundredth millimeter. Gross measurements of total length and abdominal length were made with vernier calipers accurate to one-tenth millimeter. All ratios of body parts or sclerites were developed from measurements using the ocular micrometer.

A list of materials examined appears in Appendix B. All measurements, description and figures were derived from specimens listed in the appendix. Unpublished locality records from museums are not listed.

CHAPTER III

SYSTEMATIC TREATMENT

The following works on morphology should be at hand before attempting any systematic work on anisopteros Odonata. Adult morphology has been standardized in the excellent work by Chao (1953) and repeated in Matsuda (1965, 1970, 1976) with minor changes. Larval morphology in the present work follows the nomenclature established by Snodgrass (1954). The latter work is the basis for Figures 4, 42, and 77 (Appendix A), which explain the morphological terminology used herein.

The following key is in part an adaptation of earlier works. Needham and Westfall (1955), Walker (1958) and Walker and Corbet (1975) are generally followed at family level and often at generic level. Many new characters are used for the separation of species. Table 1 (Appendix A) describes methods for determining states of characters used in the key and descriptions. The descriptions reiterate characters used in the key couplets and provide additional characters for verification. Additional quantitative data are provided in tabular form. Generic descriptions are given and this information is not repeated under each species in order to conserve space. Range descriptions and maps are another avenue of verification. They must be used with caution because the ranges of some species are incompletely known. Finally, a good stereo dissecting microscope fitted with an ocular micrometer is essential to the use of the following key, descriptions and tables.

Key to the final instar lotic dragonfly (Anisoptera) nymphs of
the southeastern United States.

- 1a. Nymph with two submedian rows of tufts of setae on dorsum of
abdomen (Fig. 1, Appendix A), prementum with strong accessory
spine at base of movable hook (Fig. 32, Appendix A), semi-
terrestrial nymphs found under leaves in seepage areas . . .
. Petaluridae, *Tachopteryx thoreyi*
- 1b. Nymph without submedian rows of tufts of setae on abdomen,
prementum without accessory spine at base of movable hook . . .
. 2
- 2a. Prementum more or less parallel-sided, flat; palpal lobes
parallel-sided and without palpal setae (Figs. 42, 74,
Appendix A), folded labium lies flat beneath head 3
- 2b. Prementum greatly expanded distally, scoop-like; palpal lobes
triangular and with palpal setae (Figs. 77-80, Appendix A);
labium forms cup-like mask over mouth parts when folded
closed (Figs. 30, 31, Appendix A) 55
- 3a. Antennae four-segmented, two subequal basal segments, third
about twice length of basal two, fourth reduced (Figs. 4-14,
Appendix A); pro- and mesotarsi with two segments
. Gomphidae, 4
- 3b. Antennae slender, with six or seven segments (Figs. 2, 3, 15-
19, Appendix A), pro- and mesotarsi with three segments . . .
. Aeshnidae, 51

- 4a. Abdomen flat and broad, about one-fifth longer than wide; dorsum of head and prothoracic sternum with prominent tubercles (Fig. 5, Appendix A) *Hagenius brevistylus*
- 4b. Abdomen narrower, about twice as long as wide or longer, no tubercles on head or prosternum 5
- 5a. Mesocoxae approximate, closer together than pro- and meta-coxae; fourth antennal segment one-half as long as segment three (Fig. 4, Appendix A) *Progomphus obscurus* (*Progomphus alachuensis*, closely related species restricted to Florida, distinguished by abdominal color pattern, see text; *P. bellei*, nymph unknown, also from Florida)
- 5b. Mesocoxae not approximate, fourth antennal segment rudimentary 6
- 6a. Abdominal segment ten longer than nine 7
- 6b. Abdominal segment ten shorter than nine 8
- 7a. Abdominal segment ten tubular, as long as preceding five segments together; burrower in mud or clay substrates of sluggish coastal rivers and ponds *Aphylla williamsoni* (Also *A. protracta*, W. Texas, intermittent streams.)
- 7b. Abdominal segment ten slightly longer than segment nine, western *Phyllogomphoides* (2 species, *P. albrighti* and *P. stigmatus* restricted to streams in western Texas.)
- 8a. Wing pads divergent (Figs. 8, 9, Appendix A), middorsal lengths of abdominal segments eight and nine subequal . . . 9

- 8b. Wing pads parallel (Figs. 6, 7, 10-14, Appendix A), middorsal length of abdominal segment nine longer than segment eight (rarely equal) 14
- 9a. Cerci, epiproct, and paraprocts all subequal in length (Fig. 81, Appendix A) *Erpetogomphus designatus*
- 9b. Cerci distinctly shorter, four-fifths or less length of epiproct or paraprocts (Figs. 82-85, Appendix A)
. *Ophiogomphus*, 10
- 10a. Third antennal segment obovate, length less than twice width at widest point (Figs. 22, 23, Appendix A) 11
- 10b. Third antennal segment elongate, length greater than twice width at widest point (Figs. 20, 21, Appendix A) 12
- 11a. Dorsal abdominal hooks absent (Fig. 135, Appendix A); lateral spines vestigial or absent on abdominal segment seven (Fig. 82, Appendix A); smaller species, less than 23 mm. in length *Ophiogomphus howei*
- 11b. Dorsal abdominal hooks present (Fig. 132, Appendix A); lateral spines present on abdominal segment seven (Fig. 83, Appendix A); larger species, greater than 23 mm. in length *Ophiogomphus mainensis*
- 12a. Third antennal segment less than three times longer than wide 13
- 12b. Third antennal segment about three times longer than wide, northeastern species not known to occur south of Kentucky *Ophiogomphus aspersus*

- 13a. Ligula narrowly convex (Fig. 41, Appendix A), with 19-23
teeth on anterior margin; palpal lobes bearing 9-11 teeth . .
. *Ophiogomphus* sp. A
- 13b. Ligula broadly convex (Fig. 40, Appendix A), with 28-32
teeth on anterior margin; palpal lobes bearing 13-15 teeth
. *Ophiogomphus rupinsulensis*
- 14a. Small lateral spines on abdominal segments eight and nine;
third antennal segment flattened, suboval (Figs. 6, 7,
Appendix A) 15
- 14b. Lateral spines on abdominal segments six or seven to nine
(Figs. 10-14, Appendix A); third antennal segment at least
four times longer than wide 17
- 15a. Third antennal segment about 1.3 times longer than wide,
adjacent inner margins straight and parallel (Fig. 7,
Appendix A); ligula with three (rarely four) median teeth
(Fig. 35, Appendix A) *Stylogomphus albistylus*
- 15b. Third antennal segment suboval, about 1.6 times longer than
wide (Fig. 6, Appendix A); ligula with four (rarely three
or five) median teeth (Fig. 36, Appendix A) 16
- 16a. Teeth of labial palpus in curved row (Fig. 36, Appendix A);
third antennal segment with dorsal papilliform setae dense,
forming a smooth surface *Lanthus vernalis*
- 16b. Teeth of labial palpus in straight row; third antennal seg-
ment with papilliform setae sparse, not forming a smooth
surface *Lanthus parvulus*
(Couplet 16 after Carle, 1980.)

- 17a. Longitudinal ridge present on abdominal segments seven to nine, ridge on each segment terminates posteriorly as spine-like dorsal hook (Figs. 86-88, Appendix A)
 *Dromogomphus* ,18
- 17b. Longitudinal ridges usually absent from dorsum of terminal abdominal segments; if ridges present, dorsal hooks absent or mere triangular projections (Figs. 89-117, Appendix A) 20
- 18a. Lateral spines on abdominal segments seven to nine, dorsal hook on abdominal segment nine about one-half dorsal length of segment ten (Fig. 86, Appendix A); ligula convex (Fig. 42), total length about 40 mm. *Dromogomphus armatus*
- 18b. Lateral spines on abdominal segments six to nine, dorsal hook on abdominal segment nine about one-third dorsal length of segment ten (Figs. 87, 88, Appendix A); ligula straight or slightly convex (Figs. 43, 44, Appendix A); total length less than 37 mm. 19
- 19a. End hook of palpal lobe projected (Fig. 43, Appendix A), dorsal hooks on abdominal segments six to nine (Fig. 87, Appendix A) *Dromogomphus spinosus*
- 19b. End hook of palpal lobe shorter than adjacent tooth (Fig. 44, Appendix A), dorsal hooks on abdominal segments seven to nine (Fig. 88, Appendix A) *Dromogomphus spoliatus*

- 20a. Pro- and mesotibial burrowing hooks present, about equal in length to diameter of adjacent tarsal segment (Figs. 11-13, Appendix A); lateral margins abdominal segments eight and nine serrate 28
- 20b. Pro- and mesotibial burrowing hooks absent or vestigial (Fig. 14, Appendix A); lateral margins abdominal segments eight and nine not serrate *Stylurus*, 21
- 21a. Dorsal length of abdominal segment nine 1.8 to 2.0 times length of segment eight (Fig. 117, Appendix A)
. *Stylurus spiniceps*
- 21b. Dorsal length of abdominal segment nine 1.6 or less length of segment eight (Figs. 110-116, Appendix A) 22
- 22a. Outer margin of labial palpus truncate, end hook short (Fig. 67, Appendix A); dorsal length of abdominal segments eight and nine subequal (Fig. 110, Appendix A)
. *Stylurus intricatus*
- 22b. Outer margin of labial palpus curved to tip, end hook strongly projected (Figs. 66, 68-73, Appendix A); dorsal length of abdominal segment nine about 1.2 or more times length of segment eight 23
- 23a. Dorsal hooks present on abdominal segments eight and nine (Fig. 113, Appendix A), long dark hairs on ventral surface of abdomen *Stylurus ivae*
- 23b. Dorsal hook present on abdominal segment nine only, no long dark hairs on ventral surface of abdomen 24

- 24a. Dorsal length of abdominal segment nine greater than 1.5 times length of abdominal segment eight (Fig. 116, Appendix A), ligula straight (Fig. 70, Appendix A). *Stylurus notatus*
- 24b. Dorsal length of abdominal segment nine less than 1.5 times length of abdominal segment eight (Figs. 111, 112, 114, 115, Appendix A), ligula slightly to strongly convex (Figs. 66, 69, 71, 72, Appendix A) 25
- 25a. Ligula strongly convex (Fig. 66, Appendix A); lateral spines very short, about one-half dorsal length of abdominal segment ten (Fig. 111, Appendix A); small species, mature nymphs about 30 mm. *Stylurus amnicola*
- 25b. Ligula weakly or moderately convex (Figs. 69, 71, 72, Appendix A); lateral spines about three-fifths or greater of dorsal length of abdominal segment ten (Figs. 112, 114, 115, Appendix A); mature nymphs greater than 33 mm. 26
- 26a. Ventral width of abdominal segment nine greater than length (Figs. 112, 114, Appendix A) 27
- 26b. Ventral width of abdominal segment nine equal to or less than length (Fig. 115, Appendix A) *Stylurus plagiatus*
- 27a. Dorsal length of abdominal segment nine greater than 1.3 times dorsal length of segment eight (Fig. 114, Appendix A); smaller species, 33-37 mm. *Stylurus laurae*
- 27b. Dorsal length of abdominal segment nine about 1.3 times dorsal length of segment eight (Fig. 112, Appendix A); larger species, 37-44 mm. *Stylurus scudderi*

- 28a. Dorsal length of abdominal segment ten greater than width; elevated dorsal ridge on all abdominal segments. . *Arigomphus* (Eastern North American; seven lentic species.)
- 28b. Dorsal length of abdominal segment ten less than width; dorsal ridge absent or restricted to posterior segments . . 29
- 29a. Abdominal segment nine one-half or greater than one-half as long as wide; dorsal length of abdominal segment ten two-thirds to three-fourths its width (Figs. 89-91, Appendix A) *Gomphus*, 30
- 29b. Abdominal segment nine less than one-half as long as wide; dorsal length of abdominal segment ten less than one-half its width (Figs. 92-109, Appendix A) 35
- 30a. Midventral length of ninth abdominal segment approximately equal to ventral width (Fig. 91, Appendix A)
. *Gomphus quadricolor*
- 30b. Midventral length of ninth abdominal segment .9 or less of ventral width 31
- 31a. End hook of palpal lobe about equal in size to adjacent tooth, abdominal segment nine approximately one-half as long as wide 32
- 31b. End hook of palpal lobe projected (Figs. 45-46, Appendix A), abdominal segment nine approximately three-quarters as long as wide (Figs. 89-90, Appendix A) 33
- 32a. Sharp middorsal ridge on abdominal segment nine, ligula slightly convex *Gomphus graslinellus*

- 32b. Dorsum of abdominal segment nine rounded, ligula strongly convex *Gomphus descriptus*
- 33a. Small dorsal hook on abdominal segments eight and nine (Fig. 89, Appendix A), total length about 25 mm.
. *Gomphus exilis*
- 33b. Dorsal hook on abdominal segments four to nine (Fig. 90, Appendix A), larger species, 29 mm. or more 34
- 34a. Ligula distinctly convex, total length about 30 mm.
. *Gomphus minutus*
- 34b. Ligula straight or slightly convex (Fig. 46), total length greater than 30 mm. *Gomphus lividus*
- 35a. Dorsal hooks present on abdominal segments eight and nine, lateral spines abdominal segment eight much smaller than those of nine (Figs. 92-101, Appendix A), body covered with coarse cuticular granules *Gomphurus*, 43
- 35b. Dorsal hooks absent on abdominal segment eight (except in *H. abbreviatus* and gomphid Genus A *consanguis*), usually present on segment nine; lateral spines of abdominal segment eight almost as long as those of nine (Figs. 102-109, Appendix A); body usually not covered with coarse cuticular granules (present in Genus A) 36
- 36a. Tips of lateral spines of abdominal segment nine project to or beyond posterolateral margins of segment ten when inter-segmental membranes extended (Figs. 102-107, Appendix A), ligula without a median tooth (Figs. 60-65, Appendix A) . . .
. *Hylogomphus*, 37

- 36b. Tips of lateral spines of abdominal segment nine do not project to postero-lateral margins of segment ten when intersegmental membranes extended (Figs. 108, 109, Appendix A), ligula with a median tooth (Figs. 58, 59, Appendix A) Genus A, 42
- 37a. End hook of palpal lobe well developed, more than twice size of adjacent tooth (Figs. 60-62, 65, Appendix A) 39
- 37b. End hook of palpal lobe less developed, about twice size of adjacent tooth or less (Figs. 63, 64, Appendix A) 38
- 38a. Smaller species, total length about 23-24 mm., palpal lobe end hook approximately equal to adjacent tooth (Fig. 63, Appendix A); small dorsal hook on abdominal segments eight and nine (Fig. 102, Appendix A) . . . *Hylogomphus abbreviatus*
- 38b. Larger species, total length 26.5-27.5 mm.; palpal lobe end hook about twice size of adjacent tooth (Fig. 64, Appendix A); small dorsal hook on segment nine only (Fig. 103, Appendix A) *Hylogomphus brevis*
- 39a. Lateral spines of abdominal segment eight parallel to longitudinal axis of body, dorsal hook absent from abdominal segment nine (Fig. 104, Appendix A), lateral margins of prementum parallel (Fig. 65, Appendix A) *Hylogomphus viridifrons*
- 39b. Lateral spines of abdominal segment eight divergent from longitudinal axis of body, dorsal hook present on abdominal segment nine (Figs. 105-107, Appendix A), lateral margins of prementum convergent anteriorly (Figs. 60-62, Appendix A) 40

- 40a. Lateral spines of abdominal segment six absent or reduced
(Fig. 105, Appendix A) *Hylogomphus carolinus*
- 40b. Lateral spines of abdominal segment six well developed
(Figs. 106-107, Appendix A) 41
- 41a. Palpal lobes armed with 4-5 teeth (Fig. 61, Appendix A) . .
. *Hylogomphus geminatus*
- 41b. Palpal lobes armed with 6-8 teeth (Fig. 62, Appendix A) . .
. *Hylogomphus parvidens*
- 42a. Lateral spines present on abdominal segments six to nine,
small dorsal hooks on abdominal segments eight and nine
(Fig. 109, Appendix A) Genus A *rogersi*
- 42b. Lateral spines present on abdominal segments seven to nine
(rarely six to nine), dorsal hooks absent or vestigial on
abdominal segments eight and nine (Fig. 108, Appendix A) . .
. Genus A *consanguis*
- 43a. Ligula deeply concave (Fig. 50, Appendix A)
. *Gomphurus lineatifrons*
- 43b. Ligula straight or convex (Figs. 48, 49, 51-57, Appendix
A) 44
- 44a. Palpal lobes with 6-9 teeth extending toward apex in a
straight line or shallow curve (Figs. 54, 57, Appendix A) . .
. 45
- 44b. Palpal lobes with 3-5 teeth curving sharply toward a hooked
apex (Figs. 48, 49, 51-53, Appendix A) 48
- 45a. Lateral spines of abdominal segment nine long, 1.5 times
dorsal length of segment ten (Figs. 95, 97, Appendix A) . .
. 46

- 45b. Lateral spines of abdominal segment nine shorter, approximately 1.25 times dorsal length of segment ten (Figs. 96, 98, Appendix A) 47
- 46a. Smaller species, total length 25-30 mm., ligula slightly convex and with minute but distinct median tooth (Fig. 54, Appendix A) *Gomphurus hybridus*
- 46b. Larger species, total length 30-33 mm., ligula convex and without median tooth (Fig. 56, Appendix A)
. *Gomphurus externus*
- 47a. Lateral spines of abdominal segments six and seven divergent from lateral margins of segments (Fig. 96, Appendix A), ligula straight (Fig. 57, Appendix A). . *Gomphurus ventricosus*
- 47b. Lateral spines of abdominal segments six and seven less divergent (Fig. 98, Appendix A), ligula slightly convex (Fig. 55, Appendix A) *Gomphurus fraternus*
- 48a. Lateral spines of abdominal segment nine approximately equal to dorsal length of segment ten (Figs. 93, 94, Appendix A) *Gomphurus crassus* and *ozarkensis*
- 48b. Lateral spines of abdominal segment nine 1.3-2 times dorsal length of segment ten (Fig. 92, 99, 100, Appendix A) . . . 49
- 49a. Smaller species, total length 29-32 mm., lateral spines of segment nine do not reach posterior margin of segment ten (Fig. 92, Appendix A), ligula straight (Fig. 51, Appendix A) *Gomphurus vastus*

- 49b. Larger species, total length 34-40 mm., lateral spines of segment nine reach beyond end of segment ten (Figs. 99, 100, Appendix A), ligula slightly convex (Figs. 48, 49, Appendix A) 50
- 50a. Lateral spines of abdominal segment nine more than 1.5 times dorsal length of segment ten (Fig. 100, Appendix A), coastal plain rivers from central Alabama to Texas
. *Gomphurus modestus*
- 50b. Lateral spines of abdominal segment nine about 1.5 times dorsal length of segment ten (Fig. 99, Appendix A), coastal plain from Alabama to South Carolina . . *Gomphurus dilatatus*
- 51a. Postero-lateral angles of head rounded, lateral spines on abdominal segments six to nine *Aeshna umbrosa*
- 51b. Postero-lateral angles of head angulate, lateral spines on abdominal segments five to nine (Figs. 2, 3, Appendix A) 52
- 52a. Dorsal hooks present on abdominal segments eight and nine, pair of tubercles on dorsum of head . . *Nasiaeshna pentacantha*
(On logs and floating vegetation in sluggish coastal plain rivers, not treated further.)
- 52b. Dorsal hooks absent from all abdominal segments, paired tubercles absent from dorsum of head 53
- 53a. Blade of palpal lobe of prementum approximately parallel-sided, truncate on outer margin (Figs. 75, 76, Appendix A); epiproct subequal in length to paraprocts (Fig. 2a, b, Appendix A); pale median spot on dorsum of segment eight *Boyeria*, 54

- 53b. Blade of palpal lobe of prementum tapers to pointed apex (Fig. 74, Appendix A), epiproct about two-thirds length of paraprocts (Fig. 3, Appendix A), no pale median spot on dorsum of segment eight *Basiaeshma janata*
- 54a. Prementum more than twice as long as broad, posterior margin of folded labium reaches to or beyond posterior margin of mesocoxae (Fig. 75, Appendix A), cerci less than one-fourth length of paraproct in female nymphs, lateral spine of segment four minute or rudimentary *Boyeria grafiana*
- 54b. Prementum less than twice as long as broad, posterior margin of folded labium not reaching posterior margin of mesocoxae (Fig. 76, Appendix A), cerci greater than one-fourth length of paraproct in female nymphs, lateral spine of segment four absent *Boyeria vinosa*
- 55a. Palpal lobes armed with huge irregular teeth (Fig. 77, Appendix A), wing pads divergent (Fig. 15, Appendix A) Cordulegastridae, *Cordulegaster*, 56
- 55b. Palpal lobes armed with even crenations (Figs. 78-80, Appendix A), wing pads parallel (Figs. 16-19, Appendix A) 61
- 56a. Palpal setae four, usually five large and five small premental setae, setae on anterior of frontal shelf spatulate (Fig. 24a, Appendix A) . . . *Cordulegaster erronea*
- 56b. Palpal setae five to seven, five to nine large and three to five small premental setae, setae on anterior of frontal shelf slender (Figs. 24b-f, Appendix A) 57

- 57a. Palpal setae six to seven, usually eight or nine large and four or five small premental setae 58
- 57b. Palpal setae five, usually five or six large and three or four small premental setae 59
- 58a. Anterior margin of frontal shelf convex (Fig. 24c, Appendix A), dorsum of femur with subapical dark spot
. *Cordulegaster obliqua obliqua*
- 58b. Anterior margin of frontal shelf relatively straight (Fig. 24f, Appendix A), dorsum of femur without subapical dark spot
. *Cordulegaster obliqua fasciata*
- 59a. Anterior margin of frontal shelf with median patch of long dark hair setae among shorter marginal setae, anterior margin of frontal shelf very slightly convex (Fig. 24d, Appendix A), total length of mature nymph 31-35 mm.
. *Cordulegaster diastatops*
- 59b. Anterior margin of frontal shelf without median patch of long dark hair setae, anterior margin of frontal shelf convex (Fig. 24e, Appendix B), total length of mature nymph greater than 35 mm. 60
- 60a. Raised dots of frontal shelf crowded anteriorly (Fig. 24b, Appendix B), lateral prothoracic process evenly rounded, restricted to coastal plain of North Carolina, Florida, and Georgia
. *Cordulegaster sayi*
- 60b. Raised dots of frontal shelf spread over wider area (Fig. 24e, Appendix B); lateral prothoracic process asymmetrical, bent posteriorly; widespread eastern species
. *Cordulegaster maculata*

- 61a. Head with frontal shelf projected as a prominent, erect horn; eyes projected dorsally (Figs. 25, 26, 31, Appendix A); legs very long, hind femur reaches beyond eighth abdominal segment (Figs. 16, 17, Appendix A) *Macromiidae* , 62
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A. PETALURIDAE NEEDHAM 1901

This is an ancient family with Jurassic fossils and a wide but discontinuous present-day distribution. The group includes three species in Australia, one in Chile, one in Japan, one in western North America and one in eastern North America (Svihla, 1958). *Tanypteryx* occurs in Asia and North America. All other genera are restricted to a single continental area.

The nymphs are characterized by three-segmented tarsi, non-setose palpal lobes, quadrate and somewhat scoop-shaped prementum, and flattened antennae with six or seven short thick segments (Tillyard, 1917).

Tachopteryx thoreyi (Hagen)

Hagen, 1857 (in *Uropetala*); Selys Longchamps, 1859; Hagen, 1861 (in *Petalura*); Provancher, 1877 (in *Petalura*); Selys Longchamps, 1878a; Calvert, 1893; Williamson, 1900a; Needham, 1901 (desc. nymph); Williamson, 1901a (desc. nymph); Kennedy, 1917a; Garman, 1927; Needham and Heywood, 1929 (figs. nymph); Byers, 1930 (desc. nymph corrected); Needham and Westfall, 1955.

Description. Nymph, Fig. 1; prementum, Fig. 32 (Appendix A). Nymph blackish and unpatterned, total length a little less than 40 mm.

Head rectangular and with prominent eyes; antennae flattened, with seven short thick antennal segments. Prementum massive, wider than long, shallowly scoop-shaped and with lateral hair fringe and paired field of about eight stout setae at postero-lateral

angles. Ligula bifid and secondarily bifid into two unequal parts, anterior margin with fine crenations. Palpal lobes broad, parallel-sided, slightly scoop-like, with hairs on extensor margin, fine crenations on apical and flexor margin, no mental setae; short stout socketed spine at base of curved movable hook. Wing pads long, reaching to apex of sixth segment in preserved specimens, beyond in live ones. Legs not adapted for burrowing; instead of burrowing hooks, tibia armed with three claw-like apical extensions. Abdomen tapers evenly, segments with paired hair tufts; blunt lateral spines on segments two to nine, those on nine about one-half dorsal length of segment ten; dorsal hooks absent. Terminal appendages short and blunt, apex of epiproct and paraprocts with hydrofuge hairs guarding respiratory opening.

Comments. The above description was based on five last instar nymphs. The original nymphal description and illustration (Williamson, 1901a) are inaccurate in several respects. The ligula is not concave, the wing pads are longer and more tapering than shown, and the epiproct is not bifid at the tip. Byers (1930) has pointed out other inaccuracies, most notably omission of the stout spine at the base of the movable hook of the prementum.

Habitat. This semi-terrestrial species lives under leaves and debris at the margin of permanent seepage areas. Of the five final and many middle instar nymphs collected, none have been found in water or mud as stated by Byers (1930) and Needham (1901). Several late and final instar nymphs were kept alive in a tilted

aquarium with a soil substrate, a pool at one end and the dry portion covered with sphagnum moss. The nymphs always preferred to remain under the moss. When placed in the water they floated around aimlessly and struggled out of the water as soon as possible. When moving overland, the nymphs were seen to walk on the ends of their tibia in beetle-like fashion, explaining the utility of the apical tibial claws.

Range. Widespread and locally common east of the prairie provinces (Fig. 152, Appendix A).

B. AESHNIDAE RAMBUR 1842

This is a large family of worldwide distribution with eleven Nearctic genera. Two of these, *Basiaeshna* and *Boyeria*, are important constituents of stream communities in the southeastern United States. An additional species, *Aeshna umbrosa*, is infrequently encountered in woodland streams but the genus is otherwise restricted to lentic habitats (Walker, 1958; Westfall, 1978). *Nasiaeshna pentacantha* is considered to be lotic by Westfall (1978). I have encountered this species in water hyacinth mats in sluggish rivers and canals. Walker (1958) dredged nymphs of this species from "rushes" in backwater areas. *Aeshna* and *Nasiaeshna* are not treated further.

Nymphs of this family are elongate-cylindrical, 30-60 mm. in length when full grown. Antennae are slender and seven-segmented, eyes large and prominent. The prementum is long and flat, palpal lobes are more or less parallel-sided and devoid of setae. The

ligula is not greatly projected and usually with a closed median cleft. There are paired lateral processes on the prothorax, legs are straight, without burrowing hooks, tarsi three-segmented and wing pads parallel. The abdomen is subcylindrical, tapering evenly from middle segments to long terminal appendages, dorsal hooks usually absent and lateral spines are present on segments five or six to nine. The epiproct is usually cleft and subequal in length to the paraprocts.

Boyeria McLachlan 1896

This is a small genus of two old world and two new world species (Walker, 1958). The two new world species are restricted to eastern North America.

Description. Nymphs of this genus are brownish or blackish with banded legs and tarsi, light median blotch on dorsum of eighth abdominal segment and about 35-40 mm. when full grown. Head wide anteriorly at bulging eyes, sides convergent anteriorly to postero-lateral angulation. Palpal lobes of prementum truncate apically, flexor margin bearing about 20-25 low rounded teeth and a slightly projected end hook; ligula with paired submedian teeth and a closed cleft. Abdomen without dorsal hooks, lateral spines present on segments four or five to nine, epiproct and paraprocts long, cerci short (about one-third length epiproct and paraprocts).

Habitat. In the southeastern United States, nymphs of *Boyeria* cling to tangles of debris and root masses at streamside.

Boyeria grafiana Williamson

Williamson, 1907b; Muttkowski, 1908; Martin, 1908-1910; Walker, 1913 (desc. nymph); Garman, 1927; Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Nymph, Fig. 2a; prementum, Fig. 75 (Appendix A). Total length of mature nymph 37-40 mm. Prementum very elongate, posterior of hinge reaching past posterior margin of mesocoxae; movable hook slightly longer than palpal lobe. Lateral spines present on segments four to nine, those on four minute. Epiproct always sharp-tipped; cerci of male about one-third length of epiproct, cerci of female about one-fourth length of epiproct.

Comments. The above description is based on four last instar nymphs. When the comparison is made between the length of prementum in relation to the position of the mesocoxae the prementum and coxae must be in a life-like position (legs extended laterally and labium folded flat). The relative lengths of the prementa are the most constant and usable characters for the separation of these two species.

Habitat. In the southeastern United States *Boyeria grafiana* is confined to cool upland streams where it is infrequently collected.

Range. Great Lakes and Appalachian (Fig. 153, Appendix A).

Boyeria vinosa (Say)

Say, 1839 (in *Aeshna*); Burmeister, 1839 (as *Aeshna quadriguttata* sp.n.); Cabot, 1881 (desc. nymph in *Neuraeschna*); Calvert, 1893 (in *Fonscolumbia*); Calvert, 1898 (as *Aeshna quadriguttata*); Kellicott, 1899 (in *Aeshna*); Williamson, 1900b; Needham, 1901 (desc. nymph); Needham and Hart, 1901 (desc. nymph); Muttkowski, 1908; Martin, 1908-1910; Walker, 1913 (desc. nymph); Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Prementum, Fig. 76 (Appendix A). Total length of mature nymphs 34-37 mm. Prementum less elongate than *B. grafiana*, posterior of hinge reaching about to midline of mesocoxae; movable hook about as long as palpal lobe. Lateral spines present on segments five to nine, epiproct bifid at tip or sharp-tipped; cerci of male and female about one-third length of paraproct.

Comments. This description is based on exuviae of five reared specimens. See comments under *B. grafiana*.

Habitat. This species occurs in a very wide range of lotic habitats from small woodland streams to large rivers. It is apparently tolerant of elevated temperature and turbidity.

Range. Widespread and common east of the prairie provinces (Fig. 154, Appendix A).

Basiaeshna Selys Longchamps 1883

Basiaeshna is a monotypic genus occurring in eastern North America. Both adult and nymphal stages suggest an intermediate morphology between *Boyeria* and *Aeshna* (Walker, 1958).

Basiaeshna janata (Say)

Say, 1839 (in *Aeschna*); Rambur, 1842 (as *Aeschna minor* sp.n.); Hagen, 1861 (in *Aeschna*); Kellicott, 1899; Williamson, 1900b; Needham, 1901 (desc. nymph); Needham and Hart, 1901 (desc. nymph); Needham, 1903a; Muttkowski, 1908; Martin, 1908-1910; Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Nymph, Fig. 3; prementum, Fig. 74 (Appendix A). General form and coloration similar to *Boyeria vinosa*, dark body with banded legs but lacking median light spot on dorsum of abdominal segment eight. Total length about 30 mm. when full grown. Head shape similar to *Boyeria*, eyes bulging antero-laterally, angulate postero-laterally. Prementum very short, scarcely longer than wide; ligula slightly projected and with a slight median cleft, no submedian teeth; palpal lobes tapering to curved point, about fifteen rounded teeth on flexor margin, movable hook about four-fifths length of palpal lobes. Abdomen somewhat spindle-shaped, narrowed anteriorly and tapering posteriorly to pointed appendages. Dorsal hooks absent, lateral

spines on segments five to nine. Epiproct broadly bifid at tip, about two-thirds length of paraprocts; cerci long, about one-half length of paraprocts.

Comments. This description is based on exuviae of two reared specimens and five final instar nymphs. Walker (1958) indicates that nymphs are much larger (up to 40 mm.) in the northern part of their range.

Range. Common and abundant in the eastern United States (Fig. 155, Appendix A). The distribution pattern is similar to that of *Boyeria vinosa* except that *Basiaeshna janata* is less widely distributed on the Gulf Coastal Plain.

C. GOMPHIDAE RAMBUR 1842

This is a large family of worldwide distribution with about 67 species in 13 genera occurring in eastern North America. The genera in North America are lotic or predominately lotic except for *Aphylla* and *Ariogomphus*. Nymphs of *Aphylla williamsoni* burrow in the substrates of coastal plain swamps and sluggish rivers. *Ariogomphus* nymphs occur in lakes and ponds with muddy bottoms and often with emergent vegetation. Nymphs of *Gomphus* s.s. are lotic or lentic.

Nymphs of Gomphidae are easily recognized by two unique characters: four-segmented antennae and two-segmented pro- and mesotarsi. The antennae possess two short basal segments, a flattened third segment that is about twice the length of the basal

two together, and a vestigial or much reduced fourth segment. The prementum is aeshnid-like, somewhat parallel-sided, flattened, and bearing neither premental nor palpal setae. The thorax is usually flattened with the coxae wide apart (except *Progomphus*). Abdominal shape (viewed dorsally) may be ovoid, obovate, or elongate with various degrees of posterior taper. Lateral spines are usually present on segments six to nine (sometimes five to nine, seven to nine, or eight to nine). Dorsal hooks are low and usually not well developed, with a tendency to restriction to posterior segments.

Progomphus Selys Longchamps 1854

This Neotropical genus contains about 25 species, four of which occur in the United States. *Progomphus obscurus* is eastern, *P. borealis* western and *P. alachuensis* and *P. bellei* occur in Florida. The genus is characterized by the long fourth antennal segment and approximate mesocoxae (see below).

Progomphus alachuensis Byers

Byers, 1939; Needham, 1941 (desc. nymph); Needham and Westfall, 1955; Belle, 1973.

Progomphus alachuensis is very similar to *P. obscurus* in both adult and nymphal stages. Nymphs are differentiated from *P. obscurus* by "Abdomen with black markings mostly submedian." Nymphs burrow in "clear sandy-bottomed lakes of northern Florida" (Needham and Westfall, 1955).

Range. Florida (Fig. 156, Appendix A).

Progomphus bellei Knoph and Tennesen

Knoph and Tennesen, 1980.

This species is unknown in the nymphal stage. Adults are considered closely related to *P. obscurus*.

Range. Florida.

Progomphus obscurus (Rambur)

Rambur, 1842 (in *Diastatomma*); Selys Longchamps, 1850 (in *Gomphoides*); Selys Longchamps, 1854, Selys, Longchamps, 1857; Hagen, 1861; Hagen, 1874a (as *borealis*); Selys Longchamps, 1878; Hagen, 1885 (desc. nymph); Williamson, 1900b; Needham and Hart, 1901 (desc. nymph); Needham, 1903a; Calvert, 1901-1908; Needham and Heywood, 1929; Byers, 1930 (desc. nymph); Needham and Westfall, 1955; Belle, 1973.

Description. Numerical data, Table 2; nymph, Fig. 4; prementum, Fig. 33 (Appendix A). Brownish nymphs patterned in black; bodies hairy; short setae mixed in with long hair setae on antennae, anterior of head, and pro- and mesotibia. Body fusiform, not compressed, total length about 28-29 mm. Third antennal segment elongate-cylindrical, fourth segment half as long as third. Prementum widest anteriorly and very long, about 1.6 times longer than wide; palpal lobes rounded distally and without teeth; ligula strongly convex, piliform setae on anterior margin very long. Legs short, body length about nine times length

of hind femur. Burrowing hooks absent, pro- and mesothoracic femur and tibia bent, tibia armed with a dense patch of burrowing seta on extensor surface. Mesocoxae approximate, closer together than pro- and metacoxae. Fore femora with prominent "shoulder" at coxal attachment. Abdomen tapers evenly to apex, strong lateral blotches on dorsum. Sharp lateral spines present on segments five to nine, small sharp dorsal spines on segments one to nine, line of hair setae across anterior of ninth sternite. Segment ten tapering posteriorly, epiproct about 1.6 times dorsal length of segment ten and about 2.3 times length of cerci.

Comments. Measurements for the above description were taken from three exuviae and four final instar nymphs.

Habitat. Nymphs of this species burrow in clean shifting sand in streams and rivers. The morphology of this species reflects its adaptation to rapid burrowing in loose substrates.

Range. Common south of Canada and westward to Colorado (Fig. 157, Appendix A).

Hagenius Selys Longchamps 1854

Hagenius is a monotypic genus restricted to eastern North America.

Hagenius brevistylus Selys

Selys Longchamps, 1854; Selys Longchamps, 1857; Hagen, 1861; Cabot, 1872 (desc. nymph); Hagen, 1885 (desc. nymph); Calvert, 1893;

Needham, 1897 (desc. nymph); Kellicott, 1899; Williamson, 1899; Needham, 1901 (desc. nymph); Needham and Hart, 1901 (desc. nymph); Needham, 1903a; Williamson, 1907a; Muttkowski, 1908; Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Byers, 1930 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 2; nymph, Fig. 5; prementum, Fig. 34 (Appendix A). Exuviae and nymphs dark reddish-brown to blackish and unpatterned, body only slightly hairy or granulated; large species, about 41 mm. when full grown. Head with paired dorsal horns and acute posterolateral prominences. Additional prominences lateral to antennal bases and frontal shelf. Third antennal segment suboval, about one-tenth longer than wide. Prementum subquadrate, little wider than long; palpal lobes rounded apically, about 20 low crenations extend around end; ligula moderately convex, about 12 teeth and a short fringe of piliform setae on anterior margin. Prominent tubercles lateral to folded labium on prothoracic sternum, mesosternum with blunt lateral tubercles, metasternum with low ridges extending toward coxal bases. Pro- and mesocoxae with ventral longitudinal ridges. Pro- and mesotibia without burrowing hooks; legs very long, total body length only three times length of hind femur. Abdomen broadly oval, segments very close fitting even in preserved specimens, fine fringe of hair setae on lateral margins of all segments. Broad lateral expansions replace usual lateral spines. Middorsal erect prominences on abdominal segments two to six

grade into dorsal ridges on segments seven to nine, segment ten with low elongate prominence. Length of paraprocts longer than epiproct, length of epiproct about twice dorsal length of segment ten and about 2.3 times length of cerci.

Comments. The above description is based on exuviae of two reared specimens and six final instar nymphs.

Habitat. Lack of tibial burrowing hooks and the long thin pro- and mesotibia attest to the non-burrowing habits of this species. This is the only North American non-burrowing gomphid. It is usually found in heaps of leaves and twigs in the quieter parts of lotic waters.

Range. Common and abundant east of the prairie provinces (Fig. 158, Appendix A).

Lanthus Needham 1897

Lanthus includes two species in eastern North America and one in Asia. No generic characterization is attempted. Most published generic accounts are composites of *Lanthus* and *Stylogomphus*.

Lanthus parvulus (Selys Longchamps)

Selys Longchamps, 1854 (in *Gomphus*); Selys Longchamps, 1857 (in *Gomphus*); Selys Longchamps, 1878 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Hagen, 1885 (desc. nymph as *Uropetalia thoreyi*); Needham, 1897 (desc. of nymph and adult composites of *L. parvulus*)

and *L. vernalis*); Garman, 1927; Needham and Westfall, 1955 (composite desc.); Walker, 1958 (desc. nymph); Carle, 1980 (desc. nymph).

Comments. *Lanthus parvulus* was not encountered during field work for this study. Consult Carle (1980) for a description of nymphs.

Habitat. "Small spring-fed streams" (Walker, 1958).

Range. Middle to northern Appalachians (Fig. 159, Appendix A). Most published locality records of *L. parvulus* are actually composite records of *L. parvulus* and *L. vernalis*. Aside from the locations given by Carle (1980) only those of Walker (1958) were considered non-composite (Carle, 1980) and plotted on Fig. 159. Extensive collecting in Tennessee has failed to produce a single typical *L. parvulus* adult leading me to believe that the Virginia records (Fig. 159) may approximate the southern limits of this form.

Lanthus vernalis Carle

Needham and Heywood, 1929 (as *L. parvulus*); Needham and Westfall, 1955 (composite desc. of *L. parvulus* and *L. vernalis*); Carle, 1980 (desc. nymph).

Description. Numerical data, Table 2; nymph Fig. 6; prementum, Fig. 36 (Appendix A). Exuviae dark brownish, unpatterned, total length about 19 mm. Third antennal segment obovate, about 1.6 times

longer than wide and width equal to or slightly greater than width of frontal shelf. Prementum slightly longer than wide; palpal lobes rounded distally, flexor margin slightly convex and bearing nine to ten teeth; ligula moderately convex, with four median teeth. Legs relatively short, total body length over five times length of hind femur. Short lateral spines on abdominal segments seven to nine, dorsal hooks absent. Length of epiproct about twice length of segment ten and about 1.75 times length of cerci.

Comments. The above description is based on exuviae of five reared specimens. Many unassociated nymphs probably referable to this species were not used because of the possibility of *L. parvulus* nymphs among them. See additional comments under *L. parvulus*.

Habitat. ". . . small spring brooks . . . occasionally small rivers of high water quality", (Carle, 1980).

Range. Appalachians from northern Georgia to Maine (Fig. 160, Appendix A).

Stylogomphus Fraser 1922

This is a small Asian-North American genus. The single North American species is widespread in the eastern United States above the fall line. No generic characterization is attempted.

Stylogomphus albistylus (Hagen)

Hagen, 1878 (in *Gomphus*); Hagen, 1878 (as *Gomphus naevius* sp. n.); Calvert, 1893 (in *Gomphus*); Harvey, 1898 (in *Gomphus*);

Needham, 1091 (in *Lanthus*); Garman, 1927 (in *Lanthus*); Needham and Heywood, 1929 (in *Lanthus*); Chao, 1954; Needham and Westfall, 1955 (in *Lanthus*); Walker, 1958 (desc. nymph in *Lanthus*).

Description. Numerical data, Table 2; nymph, Fig. 7, prementum, Fig. 35 (Appendix A). Exuviae dark brownish, unpatterned, total length about 19 mm. Third antennal segment about 1.3 times longer than wide, widest proximally and narrowing distally; adjacent inner margins parallel. Prementum a little longer than wide; palpal lobes rounded distally and bearing six or seven teeth; ligula moderately convex, with three (rarely four) median teeth. Legs short, total body length over six times length of hind femur. Short lateral spines on abdominal segments eight and nine, dorsal hooks absent. Length of epiproct about 1.5 times length of segment ten and 1.5 times length of cerci.

Comments. This description is based on exuviae of nine reared specimens. This species is similar to but easily separable from *Lanthus vernalis* and *L. parvulus*.

Habitat. Shallow rapids of clear streams (Walker, 1958). In Tennessee, nymphs of this species occur in small streams and riffles of moderate-sized rivers.

Range. Eastern North America above the fall line and east of the prairie provinces (Fig. 161, Appendix A).

Ophiogomphus Selys Longchamps 1854

This is a Holarctic genus with the greatest concentration of species in North America (Walker, 1958).

Description. Light brown nymphs with coarse cuticular granules (usually pigmented), usual lateral hair setae, total length 22-28 mm. Third antennal segment flattened, variously broadened. Prementum about a tenth longer than wide; palpal lobes straight, rounded apically, with about fifteen low crenations extending around distal end; middle lobe projected, with 20-30 subquadrate teeth and about 70 piliform setae on anterior margin. Legs somewhat short; pro- and mesotibial burrowing hooks present, about as long as diameter of adjacent tarsal segment. Wing pads divergent. Abdomen blunt and broad; small lateral denticles on all segments; dorsal hooks on abdominal segments two to nine (reduced to low prominences in one species); lateral spines on segments six to nine in western species, seven or eight to nine in eastern species. Abdominal segment eight as long or slightly longer than nine, abdominal segment ten with strong taper posteriorly. Epiproct and paraprocts subequal in length, cerci about three-fourths or less length of epiproct.

Comments. This genus is very similar to *Erpetogomphus*. It may be differentiated on the basis of relative lengths of cerci and epiproct. *Erpetogomphus* also has stronger lateral spines, and spines are present on abdominal segments six to nine. Range

maps are provided for *O. anomalous* (Fig. 162, Appendix A), *O. carolus* (Fig. 164, Appendix A) and *O. colubrinus* (Fig. 165, Appendix A) for purposes of biogeographical analysis of the eastern fauna. These northeastern species are not treated descriptively.

Ophiogomphus aspersus Morse

Morse, 1895; Needham, 1899; Needham, 1901 (desc. nymph); Howe, 1917-1921; Garman, 1927; Needham and Heywood, 1929; Walker, 1933 (desc. nymph); Davis, 1939; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Cuticular granules fine and lightly pigmented, body hairy and more or less uniform brown, total length 25-28 mm. Third antennal segment about three times as long as wide. Prementum slightly convergent anteriorly. Lateral spines on segments seven to nine, those on seven and eight largest; dorsal hooks erect anteriorly, progressively lower and more aslant posteriorly. Cerci three-fourths length of epiproct and 2.5 times median length of segment ten.

Comments. Above description paraphrased from Walker, 1958.

Habitat. Clear cold rapid streams (Walker, 1958).

Range. The Kentucky locality shown on Fig. 163 (Appendix A) and the collection from an unspecified location on the New River in Virginia or North Carolina, mentioned by Kennedy and White (1979), probably approximate the southern boundary of the range of this northeastern species.

Ophiogomphus carolinus Hagen

Hagen, 1885 (desc. nymph?, adults not desc.); Needham, 1899 (desc. types designated by Hagen); Needham and Heywood, 1929; Needham and Westfall, 1955.

NYMPH UNKNOWN?

Comments. Hagen (1885) applied the nomen *O. carolinus* to unassociated nymphs from Kentucky. The designated but undescribed types of this species were one male and two females from North Carolina (Needham, 1899; Needham and Westfall, 1955). Needham published a description based on Hagen's types in 1899. The nymph of *O. rupinsulensis* was unknown at the time and its distribution was thought not to extend south of New York state (Hagen, 1885), hence the supposition that the Kentucky nymphs were referable to the more austral *O. carolinus*. The subsequent accumulation of distributional records as well as morphological indications lead me to believe that Hagen's Kentucky nymphs were probably *O. rupinsulensis* (see Fig. 168, Appendix A and account of *O. rupinsulensis*). The nymphs of Hagen's 1885 description are lost. There are no published records of collections of *O. carolinus* subsequent to the original. It is my opinion that *O. carolinus* should be considered a junior synonym of *O. rupinsulensis* and that the types at the Philadelphia Academy of Sciences remain unnamed.

Ophiogomphus edmodo Needham

Needham, 1951a; Needham and Westfall, 1955.

NYMPH UNKNOWN

Comments. There are no published records of collections of this species subsequent to the original description.

Range. Holotype male labeled "N.C.", no further data. Allotype female from Inglenook, Pa., June 3, 1892. Both specimens are in the collection of the Academy of Natural Sciences of Philadelphia (Needham, 1951a).

Ophiogomphus howei Bromley

Bromley, 1924; Calvert, 1924; Garman, 1927; Needham and Heywood, 1929; Needham and Westfall, 1955; Kennedy and White, 1979 (desc. nymph).

Description. Numerical data, Table 3; antenna, Fig. 23; prementum, Fig. 38; terminal abdominal segments and appendages, Fig. 82; profile of dorsal abdominal hooks, Fig. 135 (Appendix A). Exuviae light tan with coarse lightly pigmented cuticular granules; total length about 21 mm. Third antennal segment less than twice as long as wide. Prementum slightly convergent anteriorly, ligula with 30 teeth. Lateral spines present on abdominal segments eight and nine, absent or vestigial on segment seven. Dorsal hooks of abdomen reduced to low prominences that do not project back over intersegmental membranes. Length of epiproct greater than 2.5 times dorsal length segment ten, cerci about 1.5 times length of epiproct.

Comments. Above description based on a single exuviae. Small size of final instar and lack of dorsal abdominal hooks are sufficient characters to separate this species from others of the genus.

Habitat. Sand and gravel in swiftly flowing rivers (Kennedy and White, 1979).

Range. The collection from Monroe Co., Tennessee (Fig. 166, Appendix A) may represent the southern limits of the distribution of *O. howei*. Unfortunately, this location is now under the waters of Tellico Reservoir.

Ophiogomphus mainensis Packard

Packard, 1863; Selys Longchamps, 1869; Selys Longchamps, 1873 (as *rupinsulensis*); Hagen, 1874b; Selys Longchamps, 1878; Needham, 1897 (as *johannus* sp.n.); Needham, 1899 (as *johannus* and *mainensis*); Calvert, 1901; Harvey, 1901 (as *johannus* and *mainensis*); Needham, 1901 (as *johannus*); Woodruff, 1914 (desc. nymph); Howe, 1917-1921; Garman, 1927 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 3; antenna, Fig. 22; prementum, Fig. 39; terminal abdominal segments and appendages, Fig. 83; profile of dorsal abdominal hooks, Fig. 132 (Appendix A). Exuviae and nymphs light brown with coarse pigmented cuticular granules; total length about 25 mm. Third antennal segment less than twice as long as wide. Prementum widest anteriorly, ligula with about 25 teeth. Lateral spines present on abdominal segments seven to nine; dorsal hooks well developed on segments two to nine, those on posterior segments project over intersegmental membranes. Length of epiproct about 2.5 times dorsal length of segment ten and about 1.5 times length of cerci.

Comments. Above description drawn from exuviae of two reared adults and four final instar nymphs.

Habitat. Clear running streams (Walker, 1958). In Tennessee this species occurs in sand and gravel substrates in larger streams and clear cool rivers.

Range. This is an Appalachian-centered species (Fig. 167, Appendix A). The population reported from eastern Louisiana (Bick, 1957) is doubtful.

Ophiogomphus rupinsulensis (Walsh)

Walsh, 1862 (in *Erpetogomphus*); Selys Longchamps, 1869; Hagen, 1874b; Hagen, 1878; Calvert, 1893; Needham, 1897 (as *Herpetogomphus pictus*); Kellicott, 1899; Needham, 1899; Williamson, 1900b; Needham, 1901; Needham and Hart, 1901 (desc. nymph as *Diastatomma* sp.); Muttkowski, 1908; Garman, 1927; Needham and Heywood, 1929; Walker, 1933 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 3; nymph, Fig. 8; antenna, Fig. 20; prementum, Fig. 40; terminal abdominal segments and appendages, Fig. 84; profile of dorsal abdominal hooks, Fig. 133 (Appendix A). Exuviae and nymphs light brown with coarse pigmented cuticular granules; total length about 26 mm. Third antennal segment about 2.5 times longer than wide. Prementum more or less parallel-sided, ligula with about 30 teeth. Lateral spines present on abdominal segments seven to nine; dorsal hooks well developed

on segments two to nine, those on posterior segments projected over intersegmental membranes. Length of epiproct usually less than 2.5 times length of segment ten, cerci less than 1.5 times length of epiproct.

Comments. Above description based on exuviae of ten reared adults.

Habitat. "Streams . . . tolerant of silt" (Walker, 1958). This species is much more widely distributed and common in Tennessee than any other species of *Ophiogomphus*. This probably indicates a wide latitude of habitat tolerance.

Range. This species is widespread and relatively common above the fall line (Fig. 168, Appendix A).

Ophiogomphus sp. A

Description. Numerical data, Table 3; antenna, Fig. 21; prementum, Fig. 41; terminal abdominal segments and appendages, Fig. 85; profile of dorsal abdominal hooks, Fig. 134 (Appendix A). Exuviae light brown with coarse cuticular granules, total length about 27 mm.; living nymphs orange-brown. Antennae broad and flat, third segment 2.2 to 2.4 times longer than wide. Prementum narrowed anteriorly; palpal lobes short, ligula narrow, strongly convex and bearing about twenty teeth. Lateral spines present on abdominal segments seven to nine, dorsal hooks well developed on segments two to nine. Length of epiproct about 2.2 times dorsal length of segment ten and about 1.3 times length of cerci.

Comments. This very distinctive nymph is easily recognized by the form of the prementum and third antennal segment. The above description is based on exuviae of 16 reared specimens. *Ophiogomphus* sp. A is to be described and named in a paper in the Proceedings of the Biological Society of Washington (Louton, 1981).

Habitat. Nymphs of this species occur in pockets of cherty gravel in bedrock-bottomed headwater streams of the Western Highland Rim in Tennessee.

Range. Frank Carle (personal communication) suggests that the records of *O. mainensis* reported from Louisiana (Fig. 167, Appendix A) appear to be the species. The only other localities are in Tennessee (Fig. 169, Appendix A).

Expetogomphus Selys Longchamps 1858

This is a genus of about 20 species including one widespread southeastern United States species, five western U.S. species and the remainder in Mexico and Central America.

Description. Very similar to *Ophiogomphus*. Nymphs uniform brown with coarse cuticular granules, total length about 25 mm. Spatulate scale-like setae absent from antennae, third antennal segment flattened but narrowly elongate. Prementum similar to *Ophiogomphus*. Legs short, pro- and mesotibial burrowing hooks about as long as diameter of adjacent tarsal segment. Wing pads divergent. Abdomen blunt and broad; small lateral denticles on all segments; dorsal hooks on segments two to nine, hooks low and

not projecting far over intersegmental membranes; strong lateral spines on segments six to nine. Abdominal segment ten with strong taper posteriorly. Epiproct, paraprocts and cerci all subequal in length.

Erpetogomphus designatus Hagen

Hagen, 1857; Selys Longchamps, 1859; Hagen, 1861; Hagen, 1885 (desc. nymph); Calvert, 1901-1908; Kennedy, 1917; Needham and Heywood, 1929; Byers, 1930; Needham and Westfall, 1955.

Description. Numerical data, Table 2; nymph, Fig. 9; prementum, Fig. 37; profile of dorsal abdominal hooks, Fig. 131 (Appendix A). Preserved nymphs light to dark brown, unpatterned; cuticular granules lightly pigmented; total length about 25 mm. Third antennal segment about 3.5 times as long as wide. Prementum about as long as wide, parallel-sided; lateral lobes with about ten low rounded or triangular teeth; anterior margin of ligula with about twenty teeth. Strong lateral spines present on abdominal segments six to nine; dorsal hooks erect on segments two to four, thereafter represented by low midapical projections. Epiproct, paraprocts and cerci all subequal.

Comments. Above description taken from five final instar nymphs.

Habitat. Nymphs were taken from medium-sized rivers with moderate to slow current. This species appears to be able to tolerate turbid water, elevated temperatures and silty substrate.

Range. United States from Maryland to Kansas southward and into northern Mexico (Fig. 170, Appendix A).

Dromogomphus Selys Longchamps 1854

This is a Nearctic genus of three species distributed in eastern North America.

Description. Brownish elongate nymph, total length about 30-40 mm. Flattened third antennal segment elongate, parallel-sided, more than three times longer than wide and about twice length proximal two combined; fourth segment rudimentary. Prementum parallel-sided, about a tenth longer than wide, anterior margin variable but median tooth always present, movable hook about as long as palpal lobe. Legs of moderate length, hind femur one-fourth to one-fifth total length of nymph; tibial burrowing hooks about as long as diameter of adjacent tarsal segment; wing pads reach base of fourth abdominal segment. Abdomen evenly tapering and elongate, sharp lateral spines on segments six or seven to nine, dorsal hooks on segments four or seven to nine, dorsum of segment nine with a median ridge terminating in a sharp spine that is at least one-fourth as long as dorsal length of segment ten, lateral margins of segments eight and nine serrate.

Comments. Nymphs of *Dromogomphus* are superficially similar to nymphs of the lotic species of *Gomphus* s.s. but are separable by presence of the spine-like dorsal hooks of *Dromogomphus*.

Dromogomphus armatus Selys

Selys Longchamps, 1854; Selys Longchamps, 1857 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Selys Longchamps, 1873; Selys Longchamps, 1878a; Needham and Heywood, 1929; Needham and Westfall, 1955; Westfall and Tennessen, 1979 (figs. nymph).

Description. Numerical data, Table 4; prementum, Fig. 42; terminal abdominal segments and appendages, Fig. 86 (Appendix A). Nymph uniform brown, darker posteriorly, total length about 40 mm. Prementum with anterior margin convex, end hooks strongly projected, palpal lobes usually with nine to ten teeth. Abdomen with lateral spines on segments seven to nine, dorsal hooks on segments seven to nine, dorsal hook on segment nine about one-half dorsal length of segment ten.

Comments. The above description is based on one exuviae and one last instar nymph. Of three characters used by Westfall and Tennessen (1979) to separate *D. armatus* from the other members of this genus (1. number of abdominal segments bearing lateral spines, 2. length of dorsal hook on segment nine and 3. shape of anterior margin of prementum) I have seen only the second character break down. Some *D. spinosus* nymphs from the western portion of its range have dorsal hooks up to one-half the dorsal length of segment ten.

Habitat. Nymphs were taken from a brown-stained, muck-bottomed, vegetated, sluggish, coastal plain stream.

Range. Coastal plain from Louisiana to North Carolina (Fig. 171 (Appendix A)).

Dromogomphus spinosus Selys

Selys Longchamps, 1854; Selys Longchamps, 1857 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Calvert, 1893; Needham, 1897 (desc. nymph); Kellicott, 1899; Williamson, 1900b (desc. nymph); Needham and Hart, 1901 (desc. nymph); Garman, 1927; Needham and Heywood, 1929; Byers, 1930 (desc. nymph); Wright, 1946 (desc. nymph); Needham and Westfall, 1955; Westfall and Tennessen, 1979 (figs. nymph).

Description. Numerical data, Table 4; nymph, Fig. 10; prementum, Fig. 43; terminal abdominal segments and appendages, Fig. 87 (Appendix A). Exuviae and nymphs uniform brown, darker posteriorly, total length about 34 mm. Prementum with ligula straight or slightly concave, end hook projected, palpal lobes usually with seven to eight teeth. Abdomen with lateral spines on segments six to nine, dorsal hooks on segments three or four to nine, dorsal hook on segment nine one-half or less dorsal length of segment ten.

Comments. Above description based on six unreaired exuviae.

Habitat. Streams, rivers, or glacial lakes (Walker, 1958). Nymphs were collected from a wide variety of lotic habitat types from large turbid rivers to small clear streams and from muddy to sandy bottoms.

Range. Common and abundant east of the prairie provinces (Fig. 172, Appendix A).

Dromogomphus spoliatus (Hagen)

Hagen, 1857 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Kellicott, 1899; Williamson, 1900b; Needham, 1904 (desc. nymph); Muttkowski, 1908; Garman, 1927; Needham and Heywood, 1929; Wright, 1946 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph); Westfall and Tennesen, 1979 (figs. nymph).

Description. Numerical data, Table 4; prementum, Fig. 44; terminal abdominal segments and appendages, Fig. 88 (Appendix A). Exuviae light brown, often lighter on tenth segment and lateral abdominal spines, total length about 32 mm. Prementum with anterior margin straight or slightly convex, end hook smaller than adjacent tooth, palpal lobes usually with seven to eight teeth. Abdomen with lateral spines on segments six to nine, dorsal hooks on segments seven to nine, dorsal hook on segment nine about one-third dorsal length of segment ten.

Comments. Above description based on three exuviae (two reared) and one final instar nymph. The very distinctive form of the labium will easily separate *D. spoliatus* nymphs from other species of the genus.

Habitat. Nymphs were collected from sandy areas of small rivers with moderate to swift current and from a small, clear, spring-fed, sand-bottomed impoundment.

Range. The distribution of this species is prairie-centered and apparently encroaching eastward as the result of deforestation. *Dromogomphus spoliatus* is most commonly encountered in the western portion of its range (Fig. 171, Appendix A).

Gomphus Leach 1815

This is a Holarctic genus of about 100 species. Centers of diversity are in North America and eastern Asia.

Description. Brownish elongate nymphs, total lengths about 25-34 mm. Third antennal segment elongate, parallel-sided, more than three times longer than wide and about twice length of proximal two; fourth segment rudimentary. Prementum parallel-sided, a little longer than wide; ligula variable and middle tooth present or absent; palpal lobes with variable end hook and about seven to eleven quadrate or obliquely truncate teeth, movable hook about as long as palpal lobe. Legs of moderate length, hind femur about one-fifth total length of nymph; tibial burrowing hooks about as long as diameter of adjacent tarsal segment. Parallel wing pads reach base of fourth abdominal segment. Abdomen long and tapering; lateral spines on segments six to nine; dorsal hooks on segments four to nine, seven to nine, eight and nine or nine only; lateral margins of segments eight and nine sparsely denticulate. Segment ten about two-thirds as long as wide.

Comments. The above description applies only to southeastern United States lotic nymphs of *Gomphus* s.s. as delimited by Needham

and Westfall (1955). The relationship between the European type species *G. vulgatissimus* and North American and Asian species of *Gomphus* s.s. is uncertain (Walker, 1957, 1958; Needham, 1947). An examination of the published account of *G. vulgatissimus* nymphs (Hagen, 1885) indicates that the nomen *Gomphus* s.s. is misapplied with regard to the North American fauna. North American nymphs of *Hylogomphus* fit the description of *G. vulgatissimus* closely. It is possible that Nearctic species of *Hylogomphus* are actually *Gomphus* s.s. and species usually called *Gomphus* s.s. in North America are without a name.

The entire subfamily Gomphinae is in need of revision at the generic level. For present purposes traditional arrangements (e.g. Needham and Westfall, 1955) are followed except that subgeneric names are used at the generic level.

Table 5 lists all species of *Gomphus* s.s. with habitat preference and distribution.

Gomphus descriptus Banks

Banks, 1896; Needham, 1897; Needham, 1901 (desc. nymph); Needham and Hart, 1901 (desc. nymph); Needham, 1903 (corrected desc. nymph); Garman, 1927; Needham and Heywood, 1929; Needham, 1943 (as *mortimer* sp.n. and as *argus* sp.n.); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 6. Similar to *G. lividus*. Prementum parallel-sided, anterior margin almost straight and with a median tooth, palpal lobe with end hook weakly projected and ten

to eleven obliquely truncate teeth. Abdomen evenly tapered, low dorsal hooks on segments seven to nine, lateral spines on segments six to nine.

Comments. Above description paraphrased from Walker (1958). This midwestern and northeastern species probably has its southern limits in North Carolina. In many years of collecting in Tennessee I have not yet encountered this species.

Habitat. Rapid streams (Walker, 1958).

Range. Great Lakes-Appalachian distribution south to Kentucky and North Carolina (Fig. 173, Appendix A).

Gomphus exilis Selys

Selys Longchamps, 1854; Hagen, 1885 (desc. nymph); Calvert, 1893; Kellicott, 1899; Williamson, 1900b; Needham, 1901 (desc. nymph); Needham and Hart, 1901 (desc. nymph); Muttkowski, 1908; Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 6; prementum, Fig. 45; terminal abdominal segments and appendages, Fig. 89 (Appendix A). Exuviae uniform brown, total length about 25 mm. Prementum parallel-sided, anterior margin convex and with minute median tooth, and hook strongly projected, teeth obliquely truncate and about as high as wide. Abdomen with moderate taper, minute dorsal hooks on segments eight and nine, lateral spines on segments six to nine.

Comments. The above description is based on the exuviae of a single reared specimen. The nymph of this species is similar to *G. lividus* except for shape of the ligula and total length of the mature nymph.

Habitat. Quiet streams, shallow marsh-boarded lakes (Walker, 1958). This species is apparently associated with soft substrates.

Range. Eastern North America (east of Mississippi River), sparse on the Gulf Coastal Plain (Fig. 174, Appendix A).

Gomphus flavocaudatus Walker

Walker, 1940; Needham and Westfall, 1955; Westfall, 1974.

NYMPH UNKNOWN

Comments. Westfall (1974) suggests that *G. flavocaudatus* may represent the southern end of a cline continuous with *G. exilis*.

Range. Gulf Coastal Plain of Mississippi and Louisiana (Fig. 174, Appendix A).

Gomphus graslinellus Walsh

Walsh, 1862; Walsh, 1863; Selys Longchamps, 1869; Hagen, 1885 (desc. nymph); Kellicott, 1899; Williamson, 1900b; Needham and Hart, 1901 (desc. nymph); Williamson, 1903b; Garman, 1927; Needham and Heywood, 1929, Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 6 (Appendix A). Total length about 30 mm. Prementum one-eighth longer than wide, sides parallel;

anterior margin weakly convex, without a median tooth; palpal lobes with 6-7 teeth, end hook as small as adjacent tooth. Abdominal shape similar to *G. lividus*, dorsal hooks on segments two to nine, dorsum of segment nine longitudinally ridged, lateral spines on segments six to nine.

Comments. Above description paraphrased from Walker (1958). A significant difference exists between Walker's description and the key to nymphs in the same work. The description states lateral spines on segments seven to nine; the key, spines on segments six to nine. Other descriptions cited above indicate spines on segments six to nine.

Habitat. Ponds, lakes, slow streams (Walker, 1958).

Range. This species follows the margin of the prairies and encroaches eastward to Ohio (Fig. 175, Appendix A). This distribution is similar to that of *Dromogomphus spoliatus* (Fig. 171, Appendix A).

Gomphus lividus Selys

Selys Longchamps, 1854; Hagen, 1854 (as *sordidus* sp.n.); Selys Longchamps, 1857; Hagen, 1861; Calvert, 1893 (as *minutus*); Needham, 1897 (as *umbratus* sp.n.); Kellicott, 1899; Williamson, 1900b; Needham, 1901 (desc. nymph as *sordidus*); Williamson, 1903b; Muttkowski, 1908; Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Byers, 1930 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 6, prementum, Fig. 46; terminal abdominal segments and appendages, Fig. 90 (Appendix A). Exuviae brownish, total length about 33 mm. Prementum parallel-sided, ligula almost straight; end hook of palpal lobe projected, teeth obliquely truncate and about as high as wide. Abdomen with moderate taper, dorsal hooks on segments four to nine, lateral spines on segments six to nine.

Comments. The above description is based on the exuviae of five reared males. This species appears to be quite variable in both adult and nymphal characters (see above synonymies). The end hook of the palpal lobes of the labium and the dorsal hooks of the abdomen are both often reduced. The number of teeth on the lateral lobe can be reduced by apparent fusion of adjacent teeth.

Habitat. Gently-flowing streams and wave-beaten shores of lakes (Walker, 1958). Nymphs have been taken from a wide variety of lotic habitats from small streams to medium-sized rivers. They prefer silty areas overlain by a little plant debris.

Range. Widespread and common east of the prairie provinces (Fig. 176, Appendix A).

Gomphus minutus Rambur

Rambur, 1842; Selys Longchamps, 1854; Selys Longchamps, 1857; Hagen, 1861; Calvert, 1893; Needham, 1904 (desc. nymph in

error); Needham and Heywood, 1929; Byers, 1930 (desc. nymph); Westfall, 1950 (desc. nymph); Needham and Westfall, 1955.

Description. Numerical data, Table 6. Dark brownish elongate nymph, total length about 30 mm. Prementum about one-fifth longer than wide; sides subparallel, slightly convergent anteriorly; ligula convex, a minute tooth in middle; palpal lobes armed with six to seven teeth, end hook projected. Abdomen with lateral spines on segments six to nine, dorsal hooks on segments seven to nine.

Comments. Above description and tabular data paraphrased from Byers (1930) and Westfall (1950) and checked against the exuviae of a single reared female. Specimen and descriptions coincide except for the following: (1) Westfall (1950), uses the term emargination to describe the shape of the posterior margin of abdominal segments seven to nine (this is not the case in the specimen before me nor in Byer's description) and (2) the exuviae before me possesses a longitudinally ridged dorsum of the ninth abdominal segment. This latter character state is used by Needham and Westfall (1955) in their key to diagnose this species. All descriptions prior to Byers (1930) are of nymphs of other species (Westfall, 1950).

Habitat. Lakes and streams (Byers, 1930).

Range. Coastal Plain from Florida to South Carolina (Fig. 177, Appendix A).

Gomphus quadricolor Walsh

Walsh, 1862; Walsh, 1863; Kellicott, 1899; Williamson, 1900b; Muttkowski, 1908; Howe, 1922 (as *alleni*); Needham and Heywood, 1929; Walker, 1932 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Numerical data, Table 6; nymph, Fig. 11; terminal abdominal segments, Fig. 91 (Appendix A). Exuviae uniform dark brown, total length about 26 mm. Prementum parallel-sided, ligula convex, median tooth minute or absent; end hook of palpal lobe projected, five to seven low-rectangular or irregular teeth. Abdomen long and tapering, segment nine about as long as wide, small dorsal hooks on segments eight and nine.

Comments. The above description is based on exuviae of five reared specimens.

Habitat. Rapid streams (Walker, 1958). Nymphs of this species were collected in Tennessee from sand-silt pockets in medium-sized rivers with good (Duck River) or excellent (Little River) water quality.

Range. Widespread in the eastern United States east of the prairie provinces and above the fall line (Fig. 178, Appendix A).

Gomphurus Needham 1901

This species grouping is that used by Needham (1901) at subgeneric rank. Westfall (1978) lists this group at generic

rank. Relationships between North American species and certain Holarctic species of *Gomphus* s.l. are uncertain.

Description. Nymphs brownish, unpatterned, with granular surface, and broad flat abdomen; total length 25-40 mm. Third antennal segment elongate, parallel-sided, twice or more total length of proximal two; fourth segment rudimentary. Prementum parallel-sided, up to one-fifth longer than wide; ligula variable, median tooth always absent; three to nine subquadrate teeth on palpal lobe, end hook variously projected, movable hook about as long as palpus. Legs of moderate length, hind femur one-fifth to one-sixth total length of nymph; tibial hooks about as long as diameter of adjacent tarsal segment. Parallel wing pads reach about to base of fourth abdominal segment. Abdomen broad and tapering abruptly at segments eight and nine, lateral spines on segments six to nine (rarely seven to nine), dorsal hooks on segments eight and nine (rarely on segments seven to nine). Lateral margins of segments eight and nine denticulate. Segment ten about half as long as wide.

Comments. Nymphs of *Gomphurus* may be split into two groups, i.e. *G. vastus*, *G. crassus*, *G. dilatatus*, *G. modestus*, *G. lineatifrons* and another group consisting of *G. fraternus*, *G. hybridus*, *G. externus* and *G. ventricosus*. The first group (*vastus*-group) is characterized by palpal lobes that bear three or four low subquadrate teeth, a greatly projected end hook, and larger size when mature (30-40 mm.). The second group (*fraternus*-group)

is characterized by palpal lobes that bear five or more small triangular teeth in a more or less straight line, a small end hook that does not project beyond the adjacent tooth, and smaller size when mature (25-33 mm.).

Gomphurus adelphus (Selys Longchamps)

Selys Longchamps, 1857; Hagen, 1861; Selys Longchamps, 1878a; Hagen, 1885 (desc. nymph?); Needham, 1901; Muttkowski, 1908; Howe, 1917-1921; Needham and Heywood, 1929; Needham and Westfall, 1955.

NYMPH UNKNOWN (Needham and Westfall, 1955)

Comments. Although listed as unknown above, Hagen (1885) described the nymph of this species by "supposition". The only useful characters included in the description were:

1. Middle lobe of labium "slightly rounded but not produced".
2. End hook of labial palpus not longer than teeth.
3. Lateral spines on segment nine twice length of segment ten.

Range. New England (New York and Massachusetts), Needham and Westfall, 1955.

Gomphurus crassus (Hagen)

Hagen, 1878; Kellicott, 1895 (as *fraternus walshii* ssp.n.); Kellicott, 1899 (as *externus*); Williamson, 1900b; Calvert, 1901; Muttkowski, 1908; Williamson, 1919; Garman, 1927; Broughton, 1928 (desc. nymph in error); Needham and Heywood, 1929; Needham and Westfall, 1955 (nymphal characters in error); Westfall, 1975.

Description. Numerical data, Table 7; prementum, Fig. 52; terminal abdominal segments and appendages, Fig. 93 (Appendix A). Exuviae unpatterned, granular surface, total length 31-32 mm. Prementum about one-fifth longer than wide, convergent anteriorly; ligula straight. Labial palpus with strong end hook and four to five subquadrate teeth. Abdomen with short lateral spines on segments six to nine, those of segment nine about as long as middorsal length of segment ten and not surpassing posterolateral margins of segment ten; small dorsal hooks on segments eight and nine.

Comments. This description is based on exuviae of four reared nymphs. Broughton (1928) described the nymph of *G. crassus* on the basis of unreared material. Several characters, especially the form of the lateral lobes, differ so radically from the reared material before me that I am assuming her suppositional association in error.

Gomphus crassus is one of the easier nymphs to identify in this genus. It is the only nymph with strongly hooked lateral lobes and lateral spines of abdominal segment nine subequal to the middorsal length of segment ten. This combination of characters is highly unusual since the other species possessing the hooked palpal lobes usually have lateral spines on the ninth segment that are 1.5 times as long as the middorsal length of segment ten.

Habitat. Nymphs have been taken in the Duck River in the Nashville Basin of central Tennessee in pockets of sand, silt and organic debris. The microhabitat appeared to be shared most closely with *G. quadricolor*.

Range. Interior Lowlands and Low Plateaus (Fig. 179, Appendix A).

Gomphurus dilatatus (Rambur)

Rambur, 1842; Selys Longchamps, 1854; Selys Longchamps, 1857; Hagen, 1861; Kellicott, 1899; Williamson, 1900b; Needham, 1903a; Needham, 1903b (desc. nymph *lineatifrons* as *dilatatus*); Calvert, 1921; Calvert, 1923; Needham and Heywood, 1929; Byers, 1930; Needham and Westfall, 1955; Westfall, 1974 (figs. nymph).

Description. Numerical data, Table 7; prementum, Fig. 48; terminal abdominal segments and appendages, Fig. 99 (Appendix A). Large species, total length about 40 mm. Prementum about one-fifth longer than wide, convergent anteriorly; ligula slightly convex and without median tooth. Labial palpus with end hook strongly projected and bearing three to five low rectangular teeth. Abdomen with lateral spines moderately long, those of segment nine about one and one-half times middorsal length of segment ten, their tips surpassing posterolateral margin of segment ten. Small dorsal hooks on segments eight and nine.

Comments. This description is based on two reared and four unreared exuviae from Florida. *Gomphurus dilatatus* closely

resembles *G. modestus* in both nymphal and adult stages. Westfall (1975) suggests three characters for separation of the two species, (1) relative length of premental scales (longer in *modestus*), (2) number and size of lateral serrations on abdominal segment nine (20-24 in *G. modestus* and 24-31 in *G. dilatatus*) and (3) larger dorsal abdominal hooks in *G. dilatatus*. Of the three characters only the second is not relative, not requiring both species at hand for comparison. Additional quantitative characters are presented in the above description and Table 5 (Appendix A).

Habitat. Sandy-bottomed streams and rivers.

Range. Coastal Plain and Piedmont provinces, Alabama to South Carolina (Fig. 180, Appendix A).

Gomphurus externus (Hagen)

Hagen, 1857; Selys Longchamps, 1859; Hagen, 1861; Walsh, 1862 (as *fraternus*); Walsh, 1863 (as *consobrinus*); Selys Longchamps, 1869 (as *consobrinus*); Needham, 1897 (desc. nymph as *fraternus*); Williamson, 1900b; Calvert, 1901; Needham, 1901 (adult as *externus*, nymph as *fraternus*); Needham and Hart, 1901 (desc. nymph); Muttkowski, 1908; Kennedy, 1917b; Garman, 1927; Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph); Westfall, 1974.

Description. Numerical data, Table 7, prementum, Fig. 56; terminal abdominal segments and appendages, Fig. 95 (Appendix A). Total length about 31 mm. Prementum about one-fifth longer than

wide, parallel-sided; ligula wide, convex, and without median tooth. Labial palpus with end hook same size as adjacent tooth; eight to nine teeth on flexor margin (proximal teeth sub-quadrated, distal teeth pointed). Abdomen with well developed lateral spines on segments six to nine, those on segment nine more than one and one-half times middorsal length of segment ten, their tips surpassing posterior margin of segment ten. Blunt dorsal hooks on segments eight and nine.

Comments. Description based on six unrealed exuviae from the Wabash River in Illinois. These specimens conform well to Walker's (1958) description and figures except for lack of dorsal hooks on abdominal segments eight and nine in Walker's figure. Needham and Hart (1901) indicates dorsal hooks on those segments based on Illinois material. Presence of dorsal hooks on abdominal segments eight and nine may be a variable feature in this species.

Gomphurus externus, *G. fraternus*, *G. hybridus* and *G. ventricosus* comprise the most difficult group of species to separate within this genus. All are similar in general form of the labium and lateral spines of the abdominal segments. Use the key and table for the genus with great care in separating species of this group.

Habitat. This species was collected from the Wabash River in Illinois from a point where the river is turbid, with a silt, sand and gravel bottom and moderate current. Walker (1958)

describes the nymphal habitat as more or less turbid rivers with muddy bottoms.

Range. Prairie region eastward into Indiana and Kentucky (Fig. 181, Appendix A).

Gomphurus fraternus (Say)

Say, 1839 (in *Aeschna*); Selys Longchamps, 1854 (in *Gomphus*); Selys Longchamps, 1857 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Walsh, 1863 (in *Gomphus*); Needham, 1897 (in *Gomphus*); Kellicott, 1899 (in *Gomphus*); Williamson, 1900b (in *Gomphus*); Calvert, 1901 (in *Gomphus*); Needham, 1901 (desc. nymph in *Gomphus*); Needham, 1903b (desc. nymph in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Whedon, 1914 (in *Gomphus*); Howe, 1917-1921 (in *Gomphus*); Garman, 1927 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Westfall, 1956 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 7; prementum, Fig. 55; terminal abdominal segments and appendages, Fig. 98 (Appendix A). Total length about 28 mm. Prementum about one-tenth longer than wide, convergent anteriorly; ligula slightly convex, often with a vestigial median tooth. End hook of labial palpus slightly larger than or equal to adjacent tooth; seven or eight teeth on flexor margin (proximal teeth subquadrate, distal teeth pointed). Abdomen with moderately developed lateral spines on segments six to nine; those on segment nine about one and one-third times middorsal length of segment ten, their tips just reaching to

posterolateral margin of segment ten. Small blunt dorsal hooks on segments eight and nine.

Comments. This description is based on the exuviae of one reared female and an unreared nymph collected syntopically. The nymph of this species was briefly described by Needham (1901). Walker (1958) redescribed nymphs from Canada as both the nominal subspecies and as a new subspecies, *G. fraternus manitobanus* that differed only in size. There may be great variation with regard to number of teeth on the lateral lobes for this species. Walker (1958) gives a low count of six while Needham (1901) gives a high count of eleven. Walker (1958) also states that the vestigial median tooth of the prementum may be present or absent.

Habitat. Nymphs were taken in a silty backwater of a moderate-sized river in eastern Tennessee. Walker (1958) describes the habitat as rapid streams or shallows of large lakes (in Canada).

Range. Distribution centered in the Interior Lowlands and Low Plateaus (Fig. 182, Appendix A).

Gomphurus hybridus (Williamson)

Williamson, 1902 (in *Gomphus*); Broughton, 1928 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Westfall, 1956 (in *Gomphus*).

Description. Numerical data, Table 7; prementum, Fig. 54; terminal abdominal segments and appendages, Fig. 97 (Appendix A).

Total length about 27 mm. Prementum about one-fifth longer than wide, ligula slightly convex and bearing a small median tooth. Palpal lobes armed with eight to nine subquadrate teeth, end hook not projected. Abdomen tapers more abruptly than other members of genus. Well developed lateral spines on segments six to nine, those of segment nine about one and three-fourths times middorsal length of segment ten, their tips reaching far beyond posterior margin of segment ten. Blunt dorsal hooks present on segments eight and nine.

Comments. This description is based on six final instar nymphs. Although I have not reared *G. hybridus*, these nymphs conform well to the description by Broughton (1928) of exuviae of specimens reared by E.B. Williamson, 1902).

Habitat. Nymphs were collected from large turbid sandy-margined rivers with moderate current and from silt pockets in medium-sized riffle-pool rivers.

Range. Coastal Plain and Interior Low Plateaus (Fig. 183, Appendix A).

Gomphurus lineatifrons (Calvert)

Needham, 1903b (desc. nymph as *Gomphus dilutatus*); Calvert, 1921 (in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Westfall, 1974 (in *Gomphus*).

Description. Numerical data, Table 7, prementum, Fig. 50; terminal abdominal segments and appendages, Fig. 101 (Appendix A).

Large species, total length about 38 mm. Prementum less than one-fifth longer than wide, ligula strongly concave and without a median tooth. Palpal lobes armed with six to eight small quadrate teeth and a strongly projected end hook. Abdomen with long lateral spines, those of segment nine almost twice middorsal length of segment ten and their tips far surpass posterior margin of segment ten. Large blunt dorsal hooks on segments seven to nine.

Comments. This description is based on the exuvium of one reared female and three final instar nymphs.

Habitat. Nymphs were collected in backwaters of large streams and small rivers where debris has accumulated but some current remains.

Range. Interior Low Plateau and Appalachian province south of New York state (Fig. 184, Appendix A).

Gomphurus modestus (Needham)

Williamson, 1914 (as *Gomphus consanguis?*); Needham, 1942 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Westfall, 1974 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 7; prementum, Fig. 49; terminal abdominal segments and appendages, Fig. 100 (Appendix A). Large species, total length about 36 mm. Prementum one-tenth to one-fifth longer than wide, ligula slightly convex and without median tooth. Palpal lobes armed with three to four low rectangular

teeth and strongly projected end hook. Abdomen with long lateral spines; those of segment nine about one and three-fourths times middorsal length of segment nine about one and three-fourths times middorsal length of segment ten, their tips surpassing posterior margin of segment ten. Large blunt dorsal hooks on segments eight and nine.

Comments. This description is based on eighteen exuvia only one of which was reared. *Gomphurus modestus* and *G. dilatatus* are very similar in both nymphal and adult characters. The seventeen unreared exuviae fit Westfall's (1974) description well and their determinations are further supported by the apparently allopatric distributions of the two species (see Map 30).

Habitat. Medium-sized streams to large sandy or muddy rivers on the Coastal Plain.

Range. Gulf Coastal Plain, Alabama to Texas (Fig. 180, Appendix A).

Gomphurus ozarkensis (Westfall)

Westfall, 1975 (in *Gomphus*).

Description. Numerical data, Table 7; prementum, Fig. 53; terminal abdominal segments and appendages, Fig. 94 (Appendix A). Prementum about one-fifth longer than wide, convergent anteriorly; ligula straight and without median tooth. Labial palpus with strong end hook and four to five (rarely six) subquadrate teeth.

Abdomen with lateral spines longer than *G. crassus*, those of segment nine about one-third longer than dorsal length of segment ten and surpassing posterolateral margins of segment ten.

Comments. This description is based on exuviae of nine specimens reared by Dr. George Harp. A description by Dr. Harp is in press.

Range. Interior Highlands (Fig. 179, Appendix A).

Gomphurus septima (Westfall)

Westfall, 1956 (in *Gomphus*).

NYMPH UNKNOWN

Comments. The type series is from the Warrior River, Tuscaloosa Co., Alabama (Westfall, 1956). It also occurs on the Piedmont of North Carolina (Fig. 185, Appendix A).

Gomphurus vastus (Walsh)

Walsh, 1862 (in *Gomphus*); Selys Longchamps, 1869 (in *Gomphus*); Cabot, 1872 (figs. nymph? in *Gomphus*); Hagen, 1885 (desc. nymph in *Gomphus*); Calvert, 1893 (in *Gomphus*); Kellicott, 1899 (in *Gomphus*); Williamson, 1900b (in *Gomphus*); Needham, 1901 (in *Gomphus*); Needham and Hart, 1901 (in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Walker, 1908 (in *Gomphus*); Wilson, 1917 (in *Gomphus*); Howe, 1917-1921 (in *Gomphus*); Calvert, 1921 (in *Gomphus*); Garman, 1927 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*); Westfall, 1974 (figs. nymph in *Gomphus*).

Description. Numerical data, Table 7; nymph, Fig. 12; prementum Fig. 51; terminal abdominal segments and appendages, Fig. 92 (Appendix A). Total length about 30 mm. Prementum about one-fifth longer than wide, ligula straight and without median tooth. Palpal lobes armed with three to five subquadrate teeth and a strongly projected end hook. Abdomen with well developed lateral spines, those of segment nine about one and one-third times middorsal length of segment ten, their tips not reaching posterior margin of segment ten.

Comments. This description based on exuviae of seven reared specimens. Walker's (1958) description of the nymph is the best for this species though not adequate to distinguish it from all others.

Habitat. Nymphs were collected in medium to large rivers. Walker (1958) describes the nymphal habitat in Canada as large lakes and rivers.

Range. Widespread in the United States and Canada east of the prairie provinces, rare on the Coastal Plain (Fig. 186, Appendix A).

Gomphurus ventricosus (Walsh)

Walsh, 1863 (in *Gomphus*); Williamson, 1900b (in *Gomphus*); Needham, 1901 (in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Howe, 1917-1921 (in *Gomphus*); Garman, 1927 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (in *Gomphus*).

Description. Numerical data, Table 7; prementum Fig. 57; terminal abdominal segments and appendages, Fig. 96 (Appendix A). Total length about 28 mm. Prementum about one-third longer than wide, ligula straight and without a median tooth. Palpal lobes armed with seven to nine small teeth, end hook not projected. Abdomen tapering to narrow-elongate segment nine; lateral spines of moderate length, those of segments eight and nine thin and divergent, spines of segment nine about one and one-third times middorsal length of segment ten and their tips do not reach to posterolateral margin of segment ten. Small dorsal hooks on segments eight and nine.

Comments. This description is based on exuviae of two reared specimens. *Gomphurus ventricosus* nymphs have not been previously associated nor described.

Habitat. Nymphs were collected from a moderate sized turbid river with a bottom of silt, cobble and bedrock. Nymphs were at the margin of steep soil banks stabilized by roots of terrestrial plants.

Range. Great Lakes-Appalachian and Interior Low Plateaus distribution (Fig. 187, Appendix A).

Hylogomphus Needham 1951b

This species grouping is after Needham (1951b) and Needham and Westfall (1955) at subgeneric rank. Nymphs are similar to those of *Gomphurus*. Their surface is less granular, bodies flatter and

and spines of segments seven and eight tend to be stronger than in *Gomphurus*.

Description. Nymphs brownish, unpatterned, surfaces less granular than *Gomphurus*, abdomen very flattened; total length 22-27 mm. Third antennal segment elongate, narrow, parallel-sided, more than twice total length of proximal two; fourth segment rudimentary. Prementum parallel-sided, slightly longer than wide; ligula slightly convex, median tooth absent; four to nine obliquely truncate teeth on palpal lobes, end hook variable, movable hook about as long as palpus. Legs longer than *Gomphurus*, hind femur greater than one-fifth total length of nymph; tibial hooks about as long as diameter of adjacent tarsal segment. Parallel wing pads reach about to base of fourth abdominal segment. Abdomen tapers abruptly at segments eight and nine, lateral spines on segments six to nine (rarely on seven to nine), dorsal hook on segment nine (may be vestigial or absent). Lateral margins of segments eight and nine denticulate. Segment ten about half as long as wide.

Comments. The known nymphs are conveniently divided into two groups. The first group (*H. abbreviatus*, *H. brevis*, and *H. viridifrons*) contains species with seven or eight teeth, a short palpal end hook and relatively short, subparallel abdominal spines. The second group (*H. carolinus*, *H. geminatus* and *H. parvidens*) contains species with four to six teeth, a well-developed palpal end hook and strong lateral abdominal spines that diverge from the longitudinal axis of the body.

Habitat. Nymphs of this genus occupy clear cool rivers of the Appalachian highlands and sandy creeks on the Coastal Plain.

Hylogomphus abbreviatus (Hagen)

Hagen, 1878 (in *Gomphus*); Calvert, 1893 (in *Gomphus*); Needham, 1901 (desc. nymph in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Currie, 1917 (in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*).

Description. Numerical data, Table 8; prementum, Fig. 63; terminal abdominal segments and appendages, Fig. 102 (Appendix A). Exuviae light brown, unpatterned, somewhat darker posteriorly, abdominal hair setae lighter than ground color of body, total length about 23 mm. Prementum parallel-sided, ligula wide; palpal lobe bearing seven to nine teeth, end hook about as small as adjacent tooth. Abdomen broad and flat, lateral spines not strongly divergent, small dorsal hooks on segments eight and nine.

Comments. The above description based on ten exuviae collected and determined by K.J. Tennessen. If the small end hook is a reliable character, that alone will separate it from other nominal species.

Habitat. In the southern part of its range this species occurs in Piedmont rivers.

Range. Appalachian and Piedmont rivers from Main to South Carolina (Fig. 188, Appendix A).

Hylogomphus brevis (Hagen)

Hagen, 1878 (in *Gomphus*); Hine, 1901 (in *Gomphus*); Needham, 1901 (desc. nymph in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Currie, 1917 (in *Gomphus*); Howe, 1917-1921 (in *Gomphus*); Garman, 1927 (in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*).

Description. Numerical data, Table 8; prementum, Fig. 64; terminal abdominal segments and appendages, Fig. 103 (Appendix A). Exuviae dark brown, unpatterned, darkened posteriorly, abdominal hair setae lighter than ground color of body, total length about 27 mm. Prementum parallel-sided, ligula wide; palpal lobes bearing seven to eight teeth, end hook about twice size of adjacent tooth. Abdomen broad and flat, lateral spines not strongly divergent, small dorsal hook on segment nine.

Comments. This description is based on exuviae of five reared specimens. Needham (1901) briefly characterized *H. brevis* by comparing it to *H. abbreviatus*. The description does not contain sufficient information to separate it from other species of the genus.

Habitat. Nymphs of this species were collected in sand-silt pockets from clear swift rivers of high water quality.

Range. Great Lakes-Appalachian (Fig. 189, Appendix A).

Hylogomphus carolinus (Carle)

Carle, 1979 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 8; prementum, Fig. 60; terminal abdominal segments and appendages, Fig. 105 (Appendix A). Exuviae light brown, unpatterned, abdominal hair setae darker than ground color of nymph, total length about 23 mm. Prementum convergent anteriorly, ligula narrow; palpal lobes with five to six teeth, end hook projected. Abdomen narrower, lateral spines divergent, small dorsal hook on segment nine.

Comments. This description is based on exuviae of two reared specimens and three nymphs collected syntopically. Nymphs of this species were previously described by Carle (1979) from three unassociated exuviae. Absence of the lateral abdominal spine of segment six was given as a character for separation of *H. carolinus* from related species. Reduced spines are present in three of five (including both reared) specimens before me.

Range. Piedmont-Coastal Plain interface of North and South Carolina (Fig. 190, Appendix A).

Hylogomphus geminatus (Carle)

Carle, 1979 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 8; prementum, Fig. 61; terminal abdominal segments and appendages, Fig. 106 (Appendix A). Exuviae light brown, unpatterned, abdominal hair setae darker than ground color of body, total length about 23 mm. Prementum convergent anteriorly, ligula narrow; palpal lobes with four to five teeth, end hook projected. Abdomen narrow, lateral spines strong and divergent, small dorsal hook on segment nine.

Comments. Above description is based on exuviae of six reared specimens. Nymphs of this species are very close to *H. carolinus* and best separated by distributional data.

Habitat. Clear Coastal Plain streams.

Range. Panhandle of Florida (Fig. 190, Appendix A).

Hylomorphus parvidens (Currie)

Currie, 1917 (in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Carle, 1979 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 8; prementum, Fig. 62; terminal abdominal segments, Fig. 107 (Appendix A). Exuviae light brown, unpatterned, abdominal hair setae darker than ground color, total length about 26 mm. Prementum slightly convergent anteriorly, ligula narrow; palpal lobes armed with six teeth, end hook strongly projected. Abdomen narrow, lateral spines strong and divergent, dorsal hook on segment nine.

Comments. This description is based on the exuviae of a single reared specimen. Nymphs of this species were previously described by Carle (1979) from reared specimens but the description contains relatively few specific characters. Nymphs and adults of this species are very similar to those of *H. carolinus* and *H. geminatus*.

Habitat. The nymph of this species was collected in a large, cool, sand and gravel bottomed stream containing a high diversity of other aquatic insects and of apparently high water quality.

Range. Piedmont and eastern slope of Blue Ridge from Georgia to Maryland (Fig. 190, Appendix A).

Hylogomphus viridifrons (Hine)

Williamson, 1900b (as *Gomphus* sp.); Hine, 1901 (in *Gomphus*); Currie, 1917 (in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*).

Description. Numerical data, Table 8; nymph, Fig. 13; prementum, Fig. 65; terminal abdominal segments and appendages, Fig. 104 (Appendix A). Exuviae dark brown, unpatterned, darkened posteriorly, abdominal hair setae lighter than ground color, total length about 27 mm. Prementum parallel-sided or slightly wider anteriorly, ligula wide; palpal lobes armed with six to eight teeth; end hook strongly projected. Abdomen broad and flat, lateral spines not divergent, dorsal hook absent from ninth segment.

Comments. This description is based on exuviae of nine reared specimens. No useful description of this species exists in the literature. One may easily confuse nymphs of *H. viridifrons* with those of *H. brevis*. Although "typical" specimens may be easily separated, intermediate forms of both species exist that

must be carefully considered before assigning a name to them. The degree of development of the labial end hook and the presence or absence of the dorsal abdominal hook of the ninth segment are sometimes unreliable.

Habitat. Nymphs of this species were collected from clear swift rivers of high water quality.

Range. Great Lakes-Appalachian and Interior Low Plateaus (Fig. 191, Appendix A).

Genus A

Two species formerly called *Gomphus* (*Gomphurus*) *consanguis* and *G. (G.) rogersi* have been misplaced within the genus *Gomphus* s.s. Adults of these two species differ from typical *Gomphurus* species in the (1) form of the anterior and posterior hamules, (2) form of the vulvar laminae of females, (3) "unclubbed" condition of the abdomen, (4) color pattern and (5) habit of perching on foliage versus horizontal surfaces as typical of true *Gomphurus* species. Nymphs differ from typical *Gomphurus* species by possessing short and sharp lateral spines on abdominal segment nine and by the shape of the palpal lobe.

In most respects the two species of this complex are more similar to *Hylogomphus* than *Gomphurus*. When Genus A *rogersi* was originally described it was compared to *Hylogomphus parvidens* (Gloyd, 1936).

Genus A *consanguis* (Selys Longchamps)

Selys Longchamps, 1879 (in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Westfall and Trogdon, 1962 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 9; prementum, Fig. 58; terminal abdominal segments and appendages, Fig. 108 (Appendix A). Brownish unpatterned nymphs with granular surface, total length about 28 mm. Prementum about as wide as long, slightly convergent anteriorly; ligula convex and bearing a median tooth. Labial palpus with end hook projected, armed with a curved row of five to seven subquadrate teeth. Abdomen with sharp-tipped lateral spines on segments six or seven to nine, those of segment nine shorter than middorsal length of segment ten and their tips do not reach to posterolateral margins of segment ten. Dorsal abdominal hooks absent from all segments although a median patch of spinules may be evident on segment nine.

Comments. This description is based on exuviae of six reared specimens and six syntopically collected nymphs. Westfall and Trogdon's (1962) description relies heavily on the absence of the lateral spines of the sixth abdominal segment to differentiate Genus A *consanguis* from Genus A *rogersi*. However, six of twelve specimens before me possess small lateral spines on the sixth segment.

Habitat. Nymphs were collected in two types of habitat. The Sullivan Co., Tennessee location is near the locality of Westfall

and Trogon (1962). This is a small (2 m. wide), turbid, warm (15°C in early April), spring-fed stream with few tributaries and no shade. Nymphs were also taken and reared at Copper Creek in Scott Co., Virginia. Copper Creek is a major tributary to the Clinch River, with a substrate of *Justicia*-anchored gravel shoals, sand, cobble and long pools. The temperature at this location was 15°C. Nymphs of Genus *A rogersi* were found at the same time of year in cool upland streams with temperatures around 11°C. If these two species are as closely related as they seem this difference in temperature preference may represent the major niche partitioning mechanism.

Range. Appalachian Province from western Virginia to northern Alabama (Fig. 192, Appendix A).

Genus *A rogersi* (Gloyd)

Gloyd, 1936 (in *Gomphus*); Needham, 1943 (desc. nymph as *Gomphus consanguis*); Klots, 1944 (in *Gomphus*); Needham and Westfall, 1955 (as *Gomphus consanguis*); Westfall and Trogon, 1962 (in *Gomphus*).

Description. Numerical data, Table 9; prementum, Fig. 59; terminal abdominal segments and appendages, Fig. 109 (Appendix A). Total length about 28 mm. Prementum about one-fifth longer than wide, ligula convex and with a small median tooth. Palpal lobes armed with a curved row of eight to nine subquadrate teeth, end hook about equal to adjacent tooth. Abdomen with relatively short lateral spines, those of segment nine about equal to middorsal

length of segment ten and not reaching to posterior margin of segment ten. Small blunt dorsal hooks on segment eight and nine.

Comments. This description is based on exuviae of six reared specimens. The original nymphal description by Needham (1943) as *Gomphus consanguis* contains but a single specific character, "lateral spines of the ninth abdominal segment about as long as segment ten".

Habitat. Nymphs were collected from silt-pockets in upland streams. This species was found in association with *Lanthus vernalis*, *Cordulegaster maculatus*, and *C. diastatops* and was usually the only *Gomphus* s.l. present.

Range. Appalachians from Pennsylvania to northern Georgia (Fig. 193, Appendix A).

Stylurus Needham 1897

This species grouping is that used by Needham (1947) and Needham and Westfall (1955) at the subgeneric level and Williamson (1932a) and Westfall (1978) at the generic level. The following treatment considers only North American species. Relationships between Nearctic and certain European species remain uncertain (Walker, 1958).

Description. Nymphs light brown, abdomen variously patterned with darker brown, surface smooth, abdomen moderately to extremely elongate, total length 27-44 mm. Third antennal segment elongate,

parallel-sided, about twice length of proximal two; fourth segment rudimentary. Prementum parallel-sided, one-third to one-half longer than wide; ligula variable, median tooth absent; one to four quadrate teeth on palpal lobes, end hook usually long and thin, movable hook about as long as palpus. Legs short, hind femur about one-seventh to one-ninth total length of nymph; tibial hooks absent or vestigial. Abdomen with moderate to extreme taper; lateral spines on segments six to nine; dorsal hooks on segments eight and nine, nine only, or absent; lateral margins of posterior abdominal segments not denticulate. Abdominal segment ten variable, from about as long as wide to slightly more than one-half as long as wide.

Comments. The unusual form of the prementum and palpi, lack of lateral abdominal denticles, lack of burrowing hooks, and presence of a distinct color pattern make these nymphs easy to separate from other genera of *Gomphus* s.l. (*Gomphus*, *Gomphurus*, *Hylgomphus*, *Ari gomphus* and Genus A). Needham and Westfall (1955) rely on the relative width of the abdomen and head for separation of this genus from other *Gomphus* s.l. The narrow abdomen alluded to is a striking feature in the more elongate species but is not evident in the more robust forms.

Habitat. Nymphs of this genus occur in small woodland streams, large cold upland streams, and large turbid rivers.

Stylurus amnicola (Walsh)

Walsh, 1862 (in *Gomphus*); Williamson, 1900b (in *Gomphus*); Needham and Hart, 1901 (desc. nymph in *Gomphus*); Williamson, 1901b (in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Butler, 1914 (as *Gomphus abditus*); Kennedy, 1917b (as *Gomphus*); Garman, 1927 (as *Gomphus*, key and figs. nymph in error); Walker, 1928 (desc. nymph in *Gomphus*); Needham and Heywood; 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 66; terminal abdominal segments and appendages, Fig. 111 (Appendix A). Exuviae thin, fragile and weakly patterned in brown, total length about 30 mm. Prementum elongate, somewhat parallel-sided, ligula strongly convex; palpal lobe armed with two or three low subquadrate teeth, end hook extremely projected. Abdomen with moderate taper for genus, dorsal length of abdominal segment nine about 1.2 times segment eight, lateral spines and dorsal hook of segment nine weakly developed, segment ten much wider than long.

Comments. Description based on two unreared exuviae from the Wabash River in Illinois. Original nymphal description by Needham and Hart (1901) was from material of suppositional association and is brief. Description of reared material by Walker (1928, 1958) conforms well to specimens described herein.

Habitat. Rivers (Walker, 1958). The two specimens described above were collected from a large turbid river (Wabash) in Illinois.

Range. Widely distributed but infrequently collected from large rivers east of the 100th meridian (Fig. 194, Appendix A).

Stylurus intricatus (Hagen)

Hagen, 1857 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Kennedy, 1917b (in *Gomphus*); Walker, 1928 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 67; terminal abdominal segments and appendages, Fig. 110 (Appendix A). Nymphs weakly patterned with pale brownish blotches, on abdomen four rows of blotches may be variously coalesced; total length less than 30 mm. Prementum wide anteriorly; ligula strongly convex; outer margin of palpal lobe truncate, end hook weakly projected, one to four low teeth. Broad abdomen with abrupt taper, segments eight and nine subequal in length, lateral spines very short, dorsal hook of segment nine absent, segment ten much wider than long.

Comments. Description based on two last instar nymphs. Earlier descriptions are brief but adequate to distinguish this highly distinctive form.

Habitat. Muddy-bottomed rivers (Kennedy, 1917b).

Range. Prairie provinces from Missouri to Utah (Fig. 195, Appendix A).

Stylurus ivae Williamson

Williamson, 1932a; Needham and Westfall, 1955 (in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 68; terminal abdominal segments and appendages, Fig. 113 (Appendix A). Nymphs hairy and strongly patterned, paired submedian blotches coalesced on posterior segments, terminal appendages and dorsum of tenth segment yellow, total length about 35 mm. Prementum elongate, slightly wider anteriorly, ligula slightly convex, end hook of lateral lobe moderately projected, teeth strongly incised. Abdomen tapering evenly posteriorly, ventrally clothed with long blackish hairs, lateral spines very short, dorsal hooks on segments eight and nine, segment ten somewhat wider than long, terminal abdominal appendages long.

Comments. Description based on three final instar nymphs and exuviae of two reared specimens. The nymph of this species has not been previously described although characters for the separation of this species were given in key and tabular form in Needham and Westfall (1955).

Habitat. Brown-stained, sand-bottomed coastal plain rivers with moderate current.

Range. Coastal Plain from Florida to North Carolina (Fig. 195, Appendix A).

Stylurus laurae Williamson

Williamson, 1932a, Needham, 1943 (in *Gomphus* desc. nymph in error); Needham and Westfall, 1955 (in *Gomphus*, key in error).

Description. Numerical data, Table 10; nymph, Fig. 14; prementum, Fig. 69; terminal abdominal segments and appendages, Fig. 114 (Appendix A). Nymph strongly patterned in brown, paired submedian blotches, median blotches on posterior segments, segment ten and terminal abdominal appendages dark brown, total length about 35 mm. Prementum elongate, wider anteriorly, ligula slightly convex, end hook of lateral lobe moderately projected, teeth subquadrate. Prementum elongate, wider anteriorly, ligula slightly convex, end hook of palpal lobe moderately projected, two or three subquadrate teeth. Abdomen tapering evenly posteriorly, segment nine about 1.3 times dorsal length of segment eight, lateral spines moderately long, dorsal tubercle on segment nine, segment ten somewhat wider than long.

Comments. Above description based on exuviae of ten reared specimens from throughout the range of this species. The nymph has not been previously described. The nymphal description in Needham (1943) of unassociated material was apparently of *S. scudderi*.

Habitat. Nymphs were taken in sandy areas of Appalachian and Piedmont Province streams and in sandy, often brown-stained, Coastal Plain streams. Water quality always appeared high and diversity of aquatic organisms good whenever this species was encountered.

Range. Widespread in the southeastern United States, westward to Texas, northward to Michigan and Maryland (Fig. 196, Appendix A).

Stylurus notatus (Rambur)

Rambur, 1842 (in *Gomphus*); Hagen, 1861 (in *Gomphus*); Walsh, 1862 (as *fluviialis* n.sp.); Hagen, 1885 (desc. nymph in error); Williamson, 1900b (in *Gomphus*); Williamson, 1901b (in *Gomphus*); Needham, 1903b (desc. nymph in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Garman, 1927 (in *Gomphus*); Walker, 1928 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 70; terminal abdominal segments and appendages, Fig. 116 (Appendix A). Elongate nymph patterned in brown intensifying posteriorly to ninth segment, tenth segment light tan, terminal appendages brownish, total length about 40 mm. Prementum wide anteriorly, ligula straight, end hook moderately projected, three oblique teeth about as high as wide. Abdomen long and tapering, segment nine longer than wide and about 1.5 times length of segment eight, lateral spines moderately developed, dorsal hook on segment nine strong, segment ten a little wider than long.

Comments. Description based on a single last instar exuviae. The nymph was adequately described by Walker (1928, 1958). This species is similar to *S. plagiatus* in the nymphal stage. The rather long ninth segment and straight anterior margin of the prementum of *S. notatus* are sufficient characters to distinguish the species.

Habitat. Large rivers and lakes (Walker, 1958).

Range. Interior Low Plateau centered species (Fig. 197, Appendix A).

Stylurus plagiatus (Selys Longchamps)

Selys Longchamps, 1854 (as *plagiatus* and as *elongatus* sp.n. in *Gomphus*); Hagen 1861 (in *Gomphus*); Hagen, 1885 (desc. nymph as *plagiatus* and *notatus*); Kellicott, 1899 (in *Gomphus*); Williamson, 1900b (in *Gomphus*); Needham, 1901 (desc. nymph in *Gomphus*); Needham and Hart, 1901 (desc. nymph in *Gomphus*); Williamson, 1901b (in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Walker, 1928 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Byers, 1930 (desc. nymph in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 71; terminal abdominal segments and appendages, Fig. 115 (Appendix A). Elongate nymph patterned similar to *S. notatus* except with additional dark lateral bands on abdominal segments (dorsal and/or ventral), total length about 35 mm. Prementum a little longer than in *S. notatus*, ligula distinctly convex, two or three low wide teeth on palpal lobes, end hook moderately projected. Abdomen long and tapering, segment nine longer than wide and about 1.4 times length of segment eight, lateral spines a little stouter than in *S. notatus*, dorsal hook of segment nine well developed (see comments), segment ten a little wider than long.

Comments. This description is based on exuviae of two reared specimens. Walker's (1958) description of the nymph of this

species is the best of those listed above. Coastal plain nymphs of this species may possess a hugely exaggerated hook on the ninth abdominal segment.

Habitat. Rivers and large lakes (Walker, 1958). Nymphs of this species were collected from shallow, clear, sandy-bottomed coastal plain rivers and lakes and from turbid sandy-bottomed rivers of the interior.

Range. Common and widespread in the eastern United States (Fig. 198, Appendix A).

Stylurus potulentus (Needham)

Needham, 1942 (in *Gomphus*).

NYMPH UNKNOWN

Comments. Although nymphs of *S. potulentus* and *S. townesi* have been reared and positively associated with the adult stage (M.J. Westfall, personal communication), the description of the immature forms of these species remains unpublished.

Range. Central Gulf Coast from Mississippi to the Florida panhandle (Fig. 199, Appendix A).

Stylurus scudderi (Selys Longchamps)

Selys Longchamps, 1873 (in *Gomphus*); Harvey, 1898 (in *Gomphus*); Needham, 1901 (desc. nymph in *Gomphus*); Williamson, 1901b (in *Gomphus*); Muttkowski, 1908 (in *Gomphus*); Garman, 1927 (in *Gomphus*);

Walker, 1928 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 72; terminal abdominal segments and appendages, Fig. 112 (Appendix A). Large robust nymph with paired median blotches on segments two to ten, terminal abdominal appendages dark, total length about 37-41 mm. Prementum wider anteriorly, ligula slightly convex, one to four low wide teeth on palpal lobes, end hook moderately projected. Abdomen broad, segment nine wider than long and about 1.2 times longer than segment eight, lateral spines well-developed, small dorsal hook on segment nine, segment ten wider than long.

Comments. The above description is based on exuviae of ten reared specimens from Tennessee and North Carolina. This species was adequately described by Needham (1901) and Walker (1928). The key to nymphs in Needham and Westfall (1955) indicates absence of the dorsal hook on segment nine. Needham (1901) indicates hook present, Walker (1928) present or absent.

Habitat. Rivers and lakes in Canada (Walker, 1928), creeks in New York state (Needham, 1901).

Range. Great Lakes-Appalachian (Fig. 200, Appendix A).

Stylurus spiniceps (Walsh)

Walsh, 1962 (in *Macrogomphus*); Cabot, 1872 (desc. nymph in *Gomphus*); Hagen, 1885 (desc. nymph in *Gomphus*); Needham, 1897 (as

Gomphus segregans sp.n.); Kellicott, 1899 (in *Gomphus*); Williamson, 1900b (in *Gomphus*); Garman, 1927 (in *Gomphus*); Walker, 1928 (desc. nymph in *Gomphus*); Needham and Heywood, 1929 (in *Gomphus*); Needham and Westfall, 1955 (in *Gomphus*); Walker, 1958 (desc. nymph in *Gomphus*).

Description. Numerical data, Table 10; prementum, Fig. 73; terminal abdominal segments and appendages, Fig. 117 (Appendix A). Elongate nymph with paired submedian elongate blotches on dorsum of abdomen, light area between giving impression of continuous light stripe down the abdomen, total length over 40 mm. Prementum short, wide anteriorly, ligula straight, palpal lobe armed with two teeth that are higher than wide, end hook strongly projected. Abdomen narrow and drawn out posteriorly, segment nine twice longer than wide and more than 1.8 times length of segment eight, lateral spines slender, small dorsal hook on segment nine, segment ten as long as wide.

Comments. The above description is based on five final instar nymphs. The very elongate ninth abdominal segment is sufficient to separate this from all members of the genus.

Habitat. Rivers and lakes in Canada (Walker, 1958). Nymphs in the southeastern United States taken from clean moderate-sized rivers with sand and gravel substrates.

Range. Eastern North America, uncommon below the fall line (Fig. 201, Appendix A).

Stylurus townesi Gloyd

Gloyd, 1936.

NYMPH UNKNOWN

Comments. See comments under *S. potulentus*.

Range. Coastal Plain and Piedmont from Alabama to South Carolina (Fig. 199, Appendix A).

D. CORDULEGASTRIDAE CALVERT 1892

The Cordulegastridae are a small, ancient but widespread group of about 35 species distributed among four genera (*Allogaster*, *Anotogaster*, *Chlorogomphus* and *Cordulegaster*). Only the genus *Cordulegaster* has North American representatives. The remainder of the family is Oriental or Palearctic (Fraser, 1929).

Tillyard (1917) characterized nymphs of Cordulegastridae as possessing antennae of 7 slender joints, divergent wing pads, spoon-shaped mask with palpal lobes of "complicated" dentition. Fraser's (1929) monograph of the family does not treat the nymphal stages.

Cordulegaster Leach 1815

This Holarctic genus consists of about fourteen species, many of which possess nominal subspecies. North America is the center of distribution with nine species (one extending southward into Central America). Six species occur in eastern North America. Nymphs of this genus bury themselves shallowly in pockets of sand in seepages and streams.

Description. Nymphs large, 30-45 mm. when full grown, head and thorax broad, abdomen tapering very evenly to long posterior appendages, body very hairy. Antennae seven segmented, two thick and five slender-elongate segments, broad frontal shelf between antennal bases margined with row of scale-like setae and array of brown dots on dorsal surface. Eyes prominently placed on antero-lateral angles of broad head, posterolateral angles rounded. Prementum mask-like, covering primary mouthparts; palpal lobes triangular and armed with huge irregular teeth; premental and palpal setae as well as movable hook present; ligula narrow, bifid; fringe of short hair setae on anterior margin lateral to ligula. Prothorax with hair-fringed dorso-lateral processes often termed "epaulettes". Wing pads strongly divergent. Legs relatively unmodified, burrowing hooks absent. Abdomen subcylindrical and evenly tapering; dorsal hooks absent; lateral spines absent in western North American forms; present on segments eight and nine in eastern forms. Epiproct and paraprocts long, slender, sharp-tipped and subequal in length; cerci very short, about one-fourth or less length of epiproct.

Comments. The setation of the prementum and palpal lobes is very important and frequently used in identifying nymphs of this genus to species. While the numbers of setae (used for separation in the key and descriptions) is usually constant in the final instar nymphs, there is a tendency in earlier instars for the counts to be reduced on one or both of the palpal lobes. Therefore

reliability of determination will fall off sharply when working with middle and early instar nymphs unless all characters are carefully considered.

Cordulegaster diastatops (Selys Longchamps)

Selys Longchamps, 1854 (in *Thecaphora*); Selys Longchamps, 1857; Scudder, 1866 (as *lateralis*); Cabot, 1872 (desc. nymph as *sayi*); Selys Longchamps, 1878a; Hagen, 1885 (desc. nymph); Needham, 1901 (desc. nymph); Garman, 1927; Fraser, 1929; Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Frontal shelf, Fig. 24d (Appendix A). Total length about 31-35 mm. Frontal shelf slightly convex, raised dots crowded anteriorly on dorsum, scale-like setae on anterior margin parallel-sided and blunt-tipped, median tuft of long blackish hairs among scales. Palpal setae five, prementum usually with five large and three or four small setae. Dorso-lateral projection of prothorax straight and blunt. Length of lateral spines of segment nine about .4 length of lateral margin of its segment.

Comments. This description is based on two final instar nymphs. Nymphs of this species are similar to *C. maculatus* nymphs but may be distinguished on the basis of several slight but reliable characters, (see key) as well as the smaller size of *C. diastatops*.

Habitat. Nymphs have been taken in seeps and spring-fed bogs in upland (Blue Ridge Province) situations.

Range. Upland areas east of the prairie, uncommon on the Coastal Plain (Fig. 202, Appendix A).

Cordulegaster erronea Hagen

Hagen, 1878; Calvert, 1893; Kellicott, 1899; Williamson, 1900b; Garman, 1927; Fraser, 1929 (*erronea* desc. in error); Needham and Heywood, 1929; Needham and Westfall, 1955.

Description. Nymph, Fig. 15; frontal shelf, Fig. 24a (Appendix A). Total length about 40 mm. or less. Frontal shelf broadly convex; raised dots on dorsum large and evenly spaced; scale-like setae on its anterior margin spatulate, widest at their apices. Palpal setae four, prementum with 5-6 large and about 5 small setae. Dorso-lateral projection of prothorax very wide and rounded distally. Length of lateral spines of abdominal segment nine about one-fourth length of lateral margin of its segment.

Comments. This description is based on exuviae of five reared specimens and seven final instar nymphs. This is the most distinctive and easy to identify nymph of *Cordulegaster*.

Habitat. Nymphs are found in spring seepages in the Appalachian Highlands and less frequently encountered in larger streams or at low elevations.

Range. Appalachian and Interior Low Plateaus with an outpost population in Louisiana (Fig. 203, Appendix A).

Cordulegaster maculata Selys Longchamps

Selys Longchamps, 1854; Hagen, 1861; Selys Longchamps, 1878a; Calvert, 1893; Needham, 1901 (desc. nymph); Garman, 1927; Fraser, 1929; Needham and Heywood, 1929; Byers, 1930 (desc. nymph); Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Frontal shelf, Fig. 24e (Appendix A). Total length about 40 mm. or more. Frontal shelf broadly convex, raised dots spread over entire dorsum, scale-like setae on its anterior margin parallel-sided and blunt-tipped. Palpal setae five, prementum usually with six large and four or five small setae. Dorso-lateral projections of prothorax bent slightly rearward. Length of lateral spines of segment nine less than one fourth length of lateral margin of its segment.

Comments. The above description is based on exuviae of seven reared specimens and five final instar nymphs.

Habitat. Nymphs of this species were taken in a wide variety of habitats from seepage areas to small rivers.

Range. Eastern North America above the fall line and eastern Gulf Coastal Plain (Fig. 204, Appendix A).

Cordulegaster maculata ssp. A.

Adults of *C. maculata* from the western Gulf Coastal Plain show several distinctive and constant features that differ with specimens from the rest of the range. In a separate paper I am

describing this form as a new subspecies. Nymphs are similar to the nominal species but smaller. See additional comments under zoogeographic treatment of the genus.

Habitat. Headwater springs and small cool streams of the western Coastal Plain.

Range. Records from Louisiana and possibly Texas and Arkansas are referable to this subspecies (Fig. 204, Appendix A).

Cordulegaster obliqua obliqua (Say)

Say, 1839 (in *Aeschna*); Walsh, 1862; Selys Longchamps, 1878a; Kellicott, 1899; Williamson, 1900b; Harvey, 1901; Needham, 1905 (desc. nymph); Muttkowski, 1908; Garman, 1927; Fraser, 1929; Needham and Heywood, 1929; Needham and Westfall, 1955; Walker, 1958 (desc. nymph).

Description. Frontal shelf, Fig. 24c (Appendix A). Total length about 40 mm. Frontal shelf strongly convex, raised dots spread evenly over dorsum; row of scale-like setae on anterior margin long, evenly tapered and sharp-tipped, a single row of long blackish hairs just behind these scale-like setae. Palpal setae six or seven, prementum with about eight large and four or five small setae. Dorso-lateral projections of prothorax broadly rounded. Length of lateral spines of segment nine very short, about one-fifth length of lateral margin of its segment.

Comments. This description is based on four final instar nymphs. This form is very similar to the following subspecies

(*C. obliqua fasciata*) and these forms have been lumped together and raised to species by various authors. Here I follow the interpretation of Fraser (1929). Nymphs show slight but apparently consistent differences.

Habitat. Nymphs were taken in a spring-fed seep and a small sandy stream in upland areas.

Range. Upland areas of eastern North America (Fig. 205, Appendix A).

Cordulegaster obliqua fasciata Rambur

Rambur, 1842 (as *fasciata*); Selys Longchamps, 1854 (as *Taeniogaster obliquus*); Hagen, 1861 (as *obliquus*); Selys Longchamps, 1878a (as *fasciata*); Needham, 1901 (faulty desc.); Muttkowski, 1908 (faulty desc.); Fraser, 1929; Needham and Heywood, 1929 (faulty desc.); Byers, 1930 (nymphal desc., catalogue, as *fasciatus*); Needham and Westfall, 1955 (nymphal key and table, as *fasciatus*).

Description. Frontal shelf, Fig. 24f (Appendix A). Total length about 45 mm. Frontal shelf weakly convex, raised dots crowded anteriorly on dorsum; blackish scale-like setae on anterior margin long, evenly tapered and sharp-tipped, not arranged in a single row, blackish hairs intermixed with scale-like setae. Palpal setae six or seven, prementum with about eight large and four or five small setae. Dorso-lateral projections of prothorax broadly rounded. Length of lateral spines of segment nine short, about one-fifth length of lateral margin of its segment.

Comments. The above description is based on two late instar nymphs. This form is very similar to *C. obliqua obliqua*. See comments under that subspecies.

Habitat. Nymphs of this species inhabit cool, spring-fed, sandy-bottomed, coastal plain streams.

Range. Coastal Plain from Florida to North Carolina. Isolated record from Louisiana (Fig. 205, Appendix A).

Cordulegaster sayi Selys

Say, 1839 (as *obliqua*, var. A); Selys Longchamps, 1854; Selys Longchamps, 1857; Hagen, 1861; Needham, 1903b (desc. nymph?); Muttkowski, 1908; Fraser, 1929; Needham and Heywood, 1929; Needham and Westfall, 1955.

Description. Frontal shelf, Fig. 24b (Appendix A). Frontal shelf broad and slightly convex, raised dots few, tiny, and crowded anteriorly on dorsum; row of setae on anterior slender, sharp-tipped and long. Palpal setae five, prementum with about six large and four or five small setae. Dorso-lateral projection of prothorax straight and blunt. Length of lateral spines of segment nine about one-fourth length of lateral margin of its segment.

Comments. This description was based on a single middle instar nymph identified and supplied by K.J. Tennessen. The original nymphal description by Needham (1903b) recounts the generic characters. The only specific references are to the

number of palpal setae (five) and the condition of the ligula (secondarily bifid into two equal parts). The condition of the ligula is said to separate *C. sayi* from *C. maculatus* and *C. diastatops*, all three of which possess five palpal setae. However, the specimen before me does not have the ligula divided as mentioned above.

Habitat. Spring-fed seepages on the Coastal Plain.

Range. Coastal Plain from Florida to North Carolina (Fig. 206, Appendix A).

E. MACROMIIDAE GLOYD 1959

The modern arrangement of families (Macromiidae, Corduliidae, Libellulidae s.s., as in Westfall, 1978) follows the past arrangement of subfamilies (as in Needham and Westfall, 1955). The categorical level at which these group names should be applied remains controversial (Gloyd, 1959; Lieftink, 1971). Nymphs of these three "families" are of several types but they uniformly possess slender seven-jointed antennae. The prementum is widened anteriorly, scoop-shaped, with premental setae in two series, and the ligula is absent. Palpal lobes are widened apically, with crenations and palpal setae. Legs are unmodified and wing pads are parallel. The abdomen is obovate, the hind end usually blunt. Lateral abdominal spines are usually present on segments eight and nine and the dorsal hooks are variable.

Macromiidae is a small family of five genera distributed in the Nearctic, Ethiopian, Oriental and Australian regions (Fraser, 1957). Two genera occur in North America, *Didymops* which is endemic and *Macromia* which occurs in all four faunal provinces. Nymphs have very long legs (apex of hind femur reaches to base of ninth abdominal segment), eyes that project upward, a prominent pyramidal horn on the front of the head, deeply incised palpal crenations, and dorsal hooks on abdominal segments two to nine or ten.

Didymops Rambur 1842

This is a genus of two species, one widespread in eastern North America, the other limited to Florida. *Didymops* nymphs are very similar to those of *Macromia* from which they may be separated by the more bulging sides of the head, longer lateral spines of the ninth abdominal segment, lower and broader dorsal abdominal hooks and dorsal hook on the tenth abdominal segment absent in *Didymops*.

Didymops floridensis Davis

Davis, 1921; Needham and Heywood, 1929; Byers, 1930; Needham and Westfall, 1955.

Nymphs very similar to *D. transversa* except total length about 35 mm., crenations of palpal lobes sharp and without spinules, and three lateral setae. These characters are drawn from the key to nymphs of *Didymops* in Needham and Westfall (1955). The nymph of *D. floridensis* has never been described in detail.

Range. Florida (Fig. 207, Appendix A).

Didymops transversa (Say)

Say, 1829 (in *Libellula*); Burmeister, 1829 (as *Epophthalmia cinnomonea*); Rambur, 1842 (as *servillei*); Hagen, 1861; Selys, 1871; Cabot, 1890 (desc. nymph); Calvert, 1893; Kellicott, 1899; Williamson, 1900b; Needham, 1901 (desc. nymph); Martin, 1907; Muttkowski, 1908; Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Needham and Westfall, 1955; Walker and Corbet, 1975 (desc. nymph).

Description. Nymph, Fig. 16; head, Fig. 25; prementum, Fig. 80; terminal abdominal segments and appendages, Fig. 118; profile of abdominal hooks, Fig. 136 (Appendix A). Nymph light-colored with flattened body and long banded legs, total length about 25-30 mm. Head about twice as wide as long, sides bulging; eyes projected dorsally; prominent frontal horn between antennae. Prementum wide anteriorly, scoop-shaped, five premental setae, row of five spinules on anterior margin. Palpal lobes with high crenations, each with a cluster of spinules at apex; five large palpal setae plus a smaller basal seta; row of spinules on flexor margin; movable hook about half as long as palpal lobe. Lateral hooks of abdominal segments eight and nine strong and divergent from longitudinal axis of body, spines of segment nine long, reaching almost to tips of anal appendages in inflated specimens (beyond in live or formalin-preserved specimens). Dorsal hook absent from segment ten.

Comments. This description is based on exuviae of two reared adults and nine final instar nymphs. *Didymops transversa* nymphs are very similar to the preceding species and quite similar to species of *Macromia*.

Habitat. Nymphs of this species occur commonly in streams and rivers throughout the southeast where they sprawl on the bottom in backwater areas and cover themselves with a thin layer of silt.

Range. Common and abundant in eastern North America (Fig. 208, Appendix A).

Macromia Rambur 1842

In eastern North America the genus *Macromia* is represented by a small complex of structurally similar species differentiated mainly by color pattern. Four well known and distinctive species occur in the southeastern United States and are treated below. In addition, *Macromia margarita* was described from North Carolina by Westfall (1947). A single additional collection has been reported from South Carolina (White, et al. 1980). The nymph is unknown. *Macromia pacifica*, a prairie species (see Fig. 212 Appendix A) is unknown in the nymphal stage. *Macromia wabashensis* was described from Indiana by Williamson (1909) but additional collections have not been reported. Nymphs of southeastern species sprawl along stream and river margins wherever current is reduced enough for some debris to accumulate.

Description. Nymphs similar to *Didymops*, flattened body, broad abdomen, legs very long, total body length about 28-35 mm. Head about twice as wide as long, widest across eyes; prominent upturned pyramidal horn between antennae, a pair of postero-lateral tubercles on dorsum. Prementum almost identical to *Didymops*. Lateral spines of abdominal segments eight and nine less divergent and projected than *Didymops*, those of segment nine not reaching beyond posterior margin of segment ten. Dorsal hooks higher and generally not as broad as on *Didymops*, small dorsal hook present on segment ten.

Macromia alleghaniensis Williamson

Williamson, 1909; Needham and Heywood, 1929; Needham and Westfall, 1955.

Description. Terminal abdominal segments and appendages, Fig. 120; profile of abdominal hooks, Fig. 139 (Appendix A). Total length about 28 mm. Dorsal hooks of abdominal segments high and falcate, similar to *M. georgina* but hooks narrower in profile; dorsal hook of nine does not greatly overhang segment ten. Lateral spines of abdominal segment nine less projected than in *M. georgina*, their apices not reaching posterior margin of segment ten in preserved specimens.

Comments. The above description is based on the exuviae of a single reared male. The nymph of *M. alleghaniensis* is very similar to the nymph of *M. georgina*. A great deal of care should be

exercised in attempting to distinguish between these two species and all characters should be considered.

Habitat. In the southern portion of its range this species occurs in marginal debris in cool upland streams.

Range. Southern Appalachians and Interior Low Plateau (Fig. 209, Appendix A).

Macromia georgina (Selys)

Selys, 1878b (*Epopthalmia georgina*); Martin, 1907; Williamson, 1909 (as *M. georgina* and *M. australensis* sp. n.); Needham and Heywood, 1929; Needham and Westfall, 1955.

Description. Profile of head, Fig. 31; terminal abdominal segments and appendages, Fig. 121; profile of abdominal hooks, Fig. 140 (Appendix A). Total length about 28 mm. Very similar to *M. alleghaniensis* but posterolateral tubercles on rear of head much higher, about as high as width at base (see Fig. 31, Appendix A). Dorsal hooks of abdominal segments falcate, slightly wider in profile than *M. alleghaniensis*; dorsal hook of segment nine reaching almost to posterior margin of segment ten (beyond in live specimens). Lateral spines of segment nine more projected than *M. alleghaniensis*, reaching beyond posterolateral margin of segment ten.

Comments. The above description is based on the exuviae of three reared males. See comments under *M. alleghaniensis*.

Habitat. Nymphs of *M. georgina* occur in streams and small rivers mostly below the fall line in the southeastern United States. This species apparently tolerates higher turbidity and temperatures than does *M. alleghaniensis*.

Range. Widespread and common on the Coastal Plain, less common above the fall line (Fig. 210, Appendix A).

Macromia illinoiensis Walsh

Walsh, 1862; Selys Longchamps, 1871; Cabot, 1890 (desc. nymph ?); Calvert, 1893; Kellicott, 1899; Williamson, 1900b; Martin, 1907; Walker, 1908; Muttkowski, 1908; Williamson, 1909; Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Walker, 1937 (fig. nymph); Westfall, 1947; Needham and Westfall, 1955; Walker and Corbet, 1978 (desc. nymph).

Description. Nymph, Fig. 17; head, Fig. 26; terminal abdominal segments and appendages, Fig. 119; profile of abdominal hooks, Fig. 137 (Appendix A). Total length about 30 mm., nymph similar to *M. taeniolata* but smaller. Dorsal hooks of abdominal segments six to eight broad and flattened dorsally, almost obliquely truncate in profile; hook on segment nine much lower than in *M. taeniolata*. Lateral spines of abdominal segments projected about as *M. taeniolata*, those of segment nine reaching to posterolateral margins of segment ten in preserved specimens.

Comments. This description is based on exuviae of 18 reared specimens. See comments under *M. taeniolata*.

Habitat. In the southeastern United States, nymphs of this species are usually collected in areas of reduced current where debris accumulates along the stream margin. This species prefers cool upland streams and rivers and is uncommon or absent from the Coastal Plain.

Range. Widespread and common above the fall line (except for the Piedmont Province) in eastern North America (Fig. 211, Appendix A).

Macromia taeniolata Rambur

Rambur, 1842; Hagen, 1861; Selys, 1874; Cabot, 1890 (desc. nymph?); Calvert, 1893; Kellicott, 1899; Williamson, 1900b; Martin, 1907 (*Epophthalmia taeniolata*); Muttkowski, 1908; Williamson, 1909; Needham and Heywood, 1929; Needham and Westfall, 1955.

Description. Terminal abdominal segments and appendages, Fig. 122; profile of abdominal hooks, Fig. 138 (Appendix A). Total length about 34 mm.; nymph very similar to *M. illinoiensis* but much larger. Dorsal hooks of abdominal segments six to eight broad, obliquely truncate in profile; hook on segment nine much higher than *M. illinoiensis*. Lateral spines of abdominal segments projected about as *M. illinoiensis*, those of segment nine reaching to posterolateral margin of segment ten in preserved specimens.

Comments. The above description is based on the exuviae of a single reared specimen. This species differs from *M. illinoiensis*

by being larger and having higher dorsal abdominal hooks. In the table of species presented in Needham and Heywood (1929) the frontal horn of *M. taeniolata* was said to be blunter than that of *M. illinoiensis*. This is not the case in the specimen before me and this character was not used in the key to nymphs in Needham and Westfall (1955).

Habitat. Nymphs of this species occur in large rivers and streams in lowland and upland habitats and apparently tolerates higher temperature and turbidity levels than does *M. illinoiensis*.

Range. Common and widespread in the southeastern United States (Fig. 213, Appendix A).

F. CORDULIIDAE SELYS LONGCHAMPS 1871

This group of genera represents the old subfamily Cordulinae of Selys Longchamps (1871). This group has been elevated to family status in recent works (Walker and Corbet, 1975, Westfall, 1978). A good but brief discussion of the reasons for and against elevation to family status is contained in Walker and Corbet (1975).

The Corduliidae are worldwide in distribution, containing about thirty genera. Seven genera occur in North America. Two of these, *Neurocordulia* and *Helocordulia* are often encountered in lotic habitats and are treated below. Nymphs of the genus *Somatochlora* are rarely encountered except in seepage bogs. Two genera, *Epicordulia* and *Tetragoneuria* (sometimes lumped as *Epitheca*,

Walker, 1966), include lentic species that may be encountered in very sluggish lotic situations.

Nymphs of Corduliidae possess deep emarginations between crenations of the labial palpi and each crenation bears a cluster of spinous setae; ten or fewer palpal setae and small spinules of the flexor margin of the labial palpi. Legs are shorter than in Macromiidae, apex of the hind femur reaches about to posterior of abdominal segment six. Cerci are usually greater than one-half the length of the paraprocts.

Neurocordulia Selys Longchamps 1871

This is a small genus of six species restricted to North America. In the southeastern United States nymph of *Neurocordulia* are most often encountered in large turbulent rivers. *Neurocordulia yamaskanensis* nymphs are found both in turbulent rivers and wave-beaten areas of large reservoirs. One species (*N. alabamensis*) occurs in spring-fed streams on the Coastal Plain.

Description. Head not quite twice as wide as long and possessing wide frontal shelf of horn and pair of small dorsal tubercles. Prementum with five to seven palpal setae and seven to nine prementals, crenations of the palpi deeply emarginate. Strong blunt dorsal hooks on segments two to seven, those of eight and nine usually lower and slanting rearward; lateral spines of abdominal segments eight and nine strong, those of segment eight usually divergent from longitudinal axis of body.

Neurocordulia alabamensis Hodges

Needham and Westfall, 1955 (attributed to Hodges, nymphal desc.).

Description. Terminal abdominal segments and appendages, Fig. 123; profile of dorsal abdominal hooks, Fig. 146 (Appendix A). Nymphs dark brown, unpatterned, small, total length about 18 mm. Frontal shelf broadly convex. Four or five large and three or four small premental setae, six palpal setae. Abdomen narrower than other species of genus, lateral spines of segment eight moderately divergent, those of segment nine subparallel, not reaching beyond tips of abdominal appendages; dorsal hooks high, falcate, and acute-tipped.

Comments. This description is based on the exuviae of a single reared male and five final instar nymphs. The first description of this species (adults) appeared in Needham and Westfall (1955) who excerpted the description from a manuscript by Robert S. Hodges that, as far as can be ascertained, did not subsequently appear in print.

Habitat. Nymphs have been collected in sand-bottomed spring-fed streams with gentle current and frequently brown-stained water. Nymphs cling to tangles of debris where the current is strong.

Range. Coastal Plain from Louisiana to North Carolina (Fig. 214, Appendix A).

Neurocordulia molesta Walsh

Walsh, 1863; Muttkowski, 1910b (as *elara*); Davis, 1929 (as *elara*); Byers, 1937 (adult as *elara*, nymph as *xanthosoma*); Needham and Westfall, 1955.

Description. Head, Figs. 27 and 30; terminal abdominal segments and appendages, Fig. 124; profile of dorsal abdominal hooks, Fig. 141 (Appendix A). Nymphs dark brown or blackish and unpatterned, total length about 21 mm. Frontal shelf projected into pyramidal horn; labium with five or six large and three or four premental setae, six palpal setae. Abdomen broad and blunt; lateral spines of segment eight strongly divergent, those of segment nine divergent and very long, reaching beyond tips of abdominal appendages; dorsal hooks high, erect and blunt-tipped.

Comments. This description is based on the exuviae of a single reared female, 3 exuviae, and 8 final instar nymphs. The projection of the frontal shelf make this nymph the easiest to identify of the genus.

Habitat. Nymphs are usually encountered on logs or boulders in large or medium-sized rivers with moderate to strong current. The presence of this species in the Mississippi River near Memphis, TN, and on the Coastal Plain indicate a tolerance to turbidity and elevated temperature. This species also occurs in cool, clear upland rivers.

Range. Widespread in the southeastern United States (Fig. 215, Appendix A).

Neurocordulia obsoleta (Say)

Say, 1839 (in *Libellula*); Burmeister, 1839 (as *Libellula polysticta* sp. n.); Hagen, 1861 (in *Didymops*); Selys Longchamps, 1871 (in *Epitheca*); Hagen, 1890; Calvert, 1893; Calvert, 1898 (as *polysticta*); Williamson, 1900b; Needham, 1901 (desc. nymph); Martin, 1907; Walker, 1913 (nymph contrasted to *yamaskanensis*); Garman, 1927 (desc. nymph); Davis, 1929; Needham and Heywood, 1929; Byers, 1937; Needham and Westfall, 1955.

Description. Terminal abdominal segments and appendages, Fig. 125; profile of dorsal abdominal hooks, Fig. 143 (Appendix A). Nymphs brownish, unpatterned, total length about 21 mm. Frontal shelf broadly convex, labium with five large and two or three premental setae, six palpal setae. Abdomen broad and blunt; lateral spines of segment eight strongly divergent and very long, reaching far beyond the tips of abdominal appendages; dorsal hooks blunt-tipped and angled posteriorly.

Comments. This description is drawn from the exuviae of a single specimen reared by K.J. Tennesen. All published figures of this species show the distinctive lateral spines on segment eight (long and divergent) that are highly diagnostic for this species.

Habitat. Collections of this species have been reported from a lake in Pennsylvania (Walker, 1913), the Potomac River (Byers, 1937), ". . . streams, lakes . . ." (Howe, 1917-1921),

Cumberland River in Kentucky (H. Garman, 1924), and a lake in New York (Needham, 1925). The exuviae collected by K.J. Tennesen (above) was taken from cypress in a Florida lake.

Range. Widespread in the eastern United States (Fig. 216, Appendix A).

Neurocordulia virginensis Davis

Davis, 1927; Davis, 1929; Needham and Heywood, 1929; Byers, 1937 (desc. nymph); Needham and Westfall, 1955.

Description. Terminal abdominal segments and appendages, Fig. 126; profile of dorsal abdominal hooks, Fig. 144 (Appendix A). Nymph similar to *N. yamaskanensis* in general form and coloration ground color yellowish brown, variegated with dark brown, dorsal hooks blackish, legs banded, twice on femur and tibia; total length about 21 mm. Frontal shelf broadly convex. Six or seven large and three or four small premental setae, six palpal setae. Lateral spines of abdominal segments eight and nine subparallel, those of segment nine not reaching beyond tips of abdominal appendages; dorsal hooks blunt-tipped and strongly angled posteriorly.

Comments. This description is based on five final instar nymphs that conform well to Byers' (1937) description and appear distinct from *N. yamaskanensis* nymphs. However, it should be kept in mind that Byers' (1937) description was of unassociated material and no subsequent reports of associations have been

published. The identity of the above nymphs are subject to question. If this determination is correct, *N. virginiensis* appears very similar to and difficult to distinguish from *N. yamaskanensis* in the nymphal stage. The only useful differences seem to be lower dorsal abdominal hooks and slightly less divergent abdominal spines in *N. virginiensis*.

Habitat. Nymphs of this species were taken in the Conasauga River in extreme southeastern Tennessee. At that locality the river is clear, cool, with many gravel riffles and beds of water willow (*Justicia*). The Conasauga River apparently serves as a northern dispersal route since many coastal plain species seem to reach the most "upland" portion of their range there.

Range. Coastal Plain with intrusion into marginal highlands (Fig. 217, Appendix A).

Neurocordulia xanthosoma (Williamson)

Williamson, 1908 (in *Platycordulia* n. gen.); Kennedy, 1917b; Needham and Heywood, 1929; Bird, 1932; Byers, 1937 (desc. nymph in error); Needham and Westfall, 1955; Williams, 1976; Williams and Dunkle, 1976 (desc. nymph).

Description. Terminal abdominal segments and appendages, Fig. 127; profile of dorsal abdominal hooks, Fig. 142 (Appendix A). Nymphal exuviae brownish, legs obscurely banded, total length about 23 mm. Frontal shelf broadly convex. Six or seven large and three or four premental setae, seven palpal setae. Lateral

spines of abdominal segment eight moderately divergent, those of segment nine slightly divergent and strongly projected, reaching past apex of terminal appendages. Dorsal hooks of abdomen bent posteriorly on segments three and four, very low and angled rearward on segments six to nine.

Comments. The above description is based on six final instar exuviae. This species is quite distinctive in both number of palpal setae (seven) and form of the fourth and fifth abdominal hooks (bent).

Habitat. Nymphs have been found clinging to logs in an impoundment (Williams and Dunkle, 1976) and from somewhat turbid medium-sized rivers.

Range. Prairie centered with slight eastward intrusion into forested areas (Fig. 218, Appendix A).

Neurocordulia yamaskanensis (Provancher)

Provancher, 1875 (in *Aeschna*); Provancher, 1877 (in *Epitheca*); Selys Longchamps, 1878b (*yamaskanensis*); Hagen, 1890; Martin, 1907; Walker, 1908; Williamson, 1908; Walker, 1913 (desc. nymph); Garman, 1927; Davis, 1929; Byers, 1937; Needham and Westfall, 1955; Walker and Corbet, 1978 (desc. nymph).

Description. Nymph, Fig. 28; head, Fig. 28; terminal abdominal segments and appendages, Fig. 128; profile of dorsal abdominal hooks, Fig. 145 (Appendix A). Nymph similar to *N. virginiensis*, ground color

yellowish brown, variegated with dark brown, dorsal hooks blackish, legs banded, twice on femur and tibia; total length about 22 mm. Frontal shelf broadly convex, dorsal tubercles of head reduced. Six or seven large and three or four small premental setae, six palpal setae. Lateral spines on abdominal segment eight divergent, slightly divergent on segment nine, spines of segment nine not reaching beyond tips of abdominal appendages; dorsal hooks blunt-tipped and strongly angled posteriorly, very low on segment nine.

Comments. The above description was based on three exuviae (one reared) and three final instar nymphs. Nymphs of this species are very similar to *N. virginiensis*.

Habitat. This species has great habitat latitude. In the southeastern United States nymphs have been collected from logs in reservoirs (Tennessee, 1979) and from cool upland rivers of high water quality. Walker and Corbet (1975) record this species from streams and lakes in Canada.

Range. Great Lakes-Appalachian centered distribution (Fig. 219, Appendix A).

Helocordulia Needham 1901

Helocordulia is a small genus of two very similar species restricted to eastern North America.

Description. Head about twice as wide as long as possessing a broad frontal shelf between the antennae similar to *Neurocordulia*

except that in *Helocordulia* the shelf is covered with a dense pubescence; dorsal tubercles absent. The labium is typical for the family and similar to *Neurocordulia* except that the crenations of the palpal lobes are less deeply emarginate. Abdomen widest at segments six and seven, tapering gradually anteriorly and more abruptly posteriorly giving it a distinctive form. Well-developed lateral abdominal spines of segments eight and nine subparallel, those of nine reaching about to the tips of the abdominal appendages. Dorsal abdominal hooks are falcate and acute-tipped on segments seven to nine, vestigial on six.

Helocordulia selysii (Hagen)

Hagen, 1878 (*Cordulia selysii*); Needham, 1901; Martin, 1907; Kennedy, 1924 (desc. nymph); Needham and Heywood, 1929 (nymphal table); Needham and Westfall, 1955 (nymphal key); McMahan and Gray, 1957 (*H. uhleri* var. *selysii*).

Description. Terminal abdominal segments and appendages, Fig. 129; profile of dorsal abdominal hooks, Fig. 148 (Appendix A). Nymph very similar to *H. uhleri*, bands of femora less distinct, total length about 18 mm. Prementum with about nine long and two or three short setae on each side, palpal setae seven. Lateral spines of abdominal segments eight and nine subparallel, a little longer than *H. uhleri*. Dorsal abdominal hooks on segments seven to nine falcate, higher than *H. uhleri*, hook on segment nine projects beyond apical margin of segment ten; hook on segment six vestigial but more distinct than for *H. uhleri*.

Comments. This description is based on a single final instar nymph from South Carolina. Kennedy's (1924) original description of nymphs of this species is very similar to the specimen above except that, unlike Kennedy's nymph, this one possesses a vestigial abdominal hook on segment six. Kennedy's description was based on a single unrealed last instar exuviae.

Habitat. Kennedy (1924) collected his single exuviae from the side of a boathouse on an artificial pond. The South Carolina specimens were collected from a brown-stained coastal plain stream of high water quality. Adults were collected from Louisiana where they flew along a clear, spring-fed coastal plain stream of high water quality.

Range. Coastal Plain and Piedmont (Fig. 220, Appendix A).

Helocordulia uhleri (Selys)

Selys Longchamps, 1871; Needham, 1901 (desc. nymph); Martin, 1907; Muttkowski, 1908; Kennedy, 1924 (figs. nymph); Garman, 1927 (desc. nymph); Needham and Heywood, 1929; Needham and Westfall, 1955; Walker and Corbet, 1978 (desc. nymph).

Description. Nymph, Fig. 19; head, Fig. 29; prementum, Fig. 78; terminal abdominal segments and appendages, Fig. 130; profile of dorsal abdominal hooks, Fig. 147 (Appendix A). Nymph dark brownish, femora with apical and subapical bands, total length about 20 mm. Prementum with about eight long and four short setae on each side, palpal setae seven. Lateral spines on abdominal segments

eight and nine short and subparallel. Dorsal abdominal hooks on segments seven to nine low and falcate, hook of segment nine does not project beyond posterior margin of segment ten; hook on segment six vestigial.

Comments. The above description is based on the exuviae of a single reared male and six final instar nymphs. Nymphs of this species are very similar to *N. selysii*, differing only by larger size and lower dorsal abdominal hooks in *H. uhleri*. All Tennessee specimens had seven palpal setae although Needham (1901) described "seven or six" in New York specimens. "Lateral setae usually six" appeared in the couplet separating *H. uhleri* from *H. selysii* in Needham and Westfall (1955).

Habitat. Nymphs of this species are found in small woodland streams associated with sandy substrates and a little plant debris and also in clear moderate-sized rivers.

Range. Eastern North America above the fall line from Arkansas to Nova Scotia and Quebec (Fig. 220, Appendix A).

CHAPTER IV

DISTRIBUTION AND BIOGEOGRAPHY

This section is concerned with descriptive and phylogenetic approaches to dragonfly biogeography in eastern North America. The descriptive aspect of this biogeographic study consists of attempts to delimit the distributional ranges of species (Figs. 152-220, Appendix A) to aid in identification, shed light on the ecology (range limiting factors) of the species or species groups, and to supply the basic data (ranges) for the phylogenetic portion (historical biogeography) of this section.

Distributional Data

Sources of distributional data for the range maps are of three types: (1) literature records from taxonomic or faunistic works, (2) unpublished records from museums and university collections and (3) records of my own field collections. A summary of the sources of distributional data is contained in Table 11. Collection records were obtained from the following museums: Louisiana State University Collection of Insects, University of Georgia Collection of Insects, Philadelphia Academy of Natural Science, and the University of Michigan Museum of Zoology.

Maps

The base maps (see Fig. 151, Appendix A) are modified from the University of Michigan Museum of Zoology county outline map by drawing in portions of Canada, outlining the physiographic

province boundaries (after Fenneman, 1938), outlining the Pleistocene maximum glacial front (after Fenneman, 1938), and showing the eastern extent of the prairie provinces including the "prairie peninsula" (after Transeau, 1935). Locality records were plotted by county. Counties in the eastern United States form an irregular grid of convenient size. Canadian counties are too large and records are therefore plotted approximately from municipal locations.

Patterns of Endemism

In describing the range of the species treated in the systematics section it was soon seen that traditional biotic provinces (see summary of systems in Pielou, 1979) were of little use. A system was therefore developed utilizing patterns of endemism rather than regions based on percent of faunal similarity. Although there is validity to biotic provinces they rarely correspond to the range of any particular organism. The following categories of endemism were developed for lotic odonates as a convenient method for quickly designating the type of distribution pattern. The distributions of species of eastern lotic forms fall into seven basic patterns.

1. Eastern ubiquitous. The range of *Dromogomphus spinosus* (Fig. 172, Appendix A) is typical of the most generalized pattern. The northern limits as shown are apparently temperature controlled. A line from middle Manitoba, across Ontario just north of the Great Lakes and across Quebec just north of and parallel to the

St. Lawrence River, follows a band of steep temperature gradient that is especially defined north of the St. Lawrence River where cold Arctic air is abruptly "warmed" by Atlantic waters. This line is the northern limit of almost all lotic species. The clear wedge to the west corresponds to the "prairie peninsula" which is an area of reduced and sporadic winter precipitation (Transeau, 1935). There are two probable consequences of this: (1) a reduced habitat (or quality of habitat) for nymphs and (2) an atypical habitat for adults of species that forage in woodlands. To the south, distributional records occur widely over the Coastal Plain but in irregular fashion. This is due in part to lack of thorough state surveys in any of the coastal states from New Jersey to Texas, with the exception of South Carolina and Louisiana. It should also be expected that lotic habitats on the Coastal Plain are reduced in quality and quantity and when fully surveyed the Coastal Plain will show a patchy distribution for the species that do occur there. The Piedmont physiographic province lies mostly within the aforementioned poorly surveyed states so that the paucity of records there may be due to lack of collections rather than any real faunal differences. However, real differences may exist because the middle Piedmont is an area of heavy residual soils (especially red clays) with the poorest ground water supply in eastern North America (Geraghty et al., 1973, Fenneman, 1938).

2. Prairie. Fig. 181 (Appendix A) shows the distribution of *Gomphurus externus*. The eastern limits correspond well with

the prairie boundary and the scattered records east of the boundary correspond with major prairie outliers within the eastern deciduous forests (see maps of prairie outliers in Transeau, 1935).

3. Eastern uplands. The range of *Ophiogomphus rupinsulensis* (Fig. 168, Appendix A) exemplifies this pattern and is similar to the "ubiquitous" distribution pattern above except that the Coastal Plain and Piedmont provinces are essentially eliminated. This distribution is typical of a great many species.

4. Great Lakes - Appalachian. *Hylogomphus brevis* (Fig. 189, Appendix A) typifies this distribution. In looking at the southern portion of this pattern it appeared that the distribution of this species was tightly controlled by physiography. In the northern portion of its range this species appears to undergo a "physiographical release." This is probably because temperature is the primary limiting factor rather than substrate type (as a function of physiography). At warmer latitudes cool lotic habitat is available only in the Appalachian highlands. Some species that occupy a limited portion of this area are designated simply Appalachian or Great Lakes in distribution.

5. Interior Low Plateaus. The range of *Gomphurus crassus* (Fig. 179, Appendix A) is an irregular triangle that roughly corresponds to the Interior Lowlands and Low Plateaus. This area slopes northward and the boundary between the two physiographic provinces is indistinct (Fenneman, 1938). The Appalachian highlands form a highly effective eastern boundary and the Mississippi embayment and prairies the western boundary.

6. Interior Highlands. The triangles of Fig. 179 (Appendix A) represent the known distribution of *Gomphurus ozarkensis*, probably the only lotic dragonfly endemic to the Interior Highlands. This subdivision is notable more for what does not occur there than for what does.

7. Coastal Plain. The two species, *Gomphurus dilatatus* and *G. modestus* (Fig. 180, Appendix A), are closely related. Their distributions taken together represent a "full Coastal Plain" distribution, typically including the transgression into the Piedmont Province. The Piedmont-Coastal Plain faunal similarity is reasonable physiographically. Hammond's (1964) land form system of descriptive surface geology essentially denies the existence of the Piedmont as a distinctive surface feature, since it is part of a more or less continuous relief gradient from the base of the Blue Ridge Province to the Atlantic.

Fig. 221 (Appendix A) shows the complete system of endemic regions, proposed for lotic dragonflies. The categories and subcategories are listed below the map together with the number of species in each. If we look at endemism in terms of Coastal Plain versus upland areas we see twenty coastal plain species versus forty upland species. This high number of Coastal plain endemics is surprising considering the relatively young age and physical homogeneity of the Coastal Plain. Most of the Coastal Plain was submerged or existed as a swampy lowland until Pliocene times (Schuchert, 1955). The high degree of coastal plain endemism is discussed below.

Generic Distribution

The following discussion is developed from the range maps (Figs. 152-220, Appendix A), from treatments of higher systematic categories (Tillyard, 1917, Fraser, 1957, Belle, 1979), and information contained in the Zoological Record.

Tachopteryx. *Tachopteryx thoreyi* is the only petalurid in eastern North America and the only species of the genus. *Tanyp-teryx hageni* found in western North America is placed in a different subfamily. These species are scattered relicts of a worldwide Jurassic fauna. Fossil records indicate that petalurids were the dominant odonates (Fraser, 1957). *Tachopteryx thoreyi* adults have the peculiar habit of foraging from vertical perches on tree trunks. This habit certainly restricts their distribution to east of the prairie region (Fig. 152, Appendix A).

Basiaeshna. *Basiaeshna* is a monotypic genus occurring in eastern North America (Fig. 155, Appendix A). Fraser (1957) placed this genus in the subfamily Gomphaeshinae which is of worldwide distribution. Relationships within this group are uncertain.

Boyeria. *Boyeria* is a Holarctic genus (Tillyard, 1917) with two species occurring in North America. Fraser (1957) placed this genus in the subfamily Gomphaeshinae with six other genera, including *Basiaeshna* (above). The two North American species have highly sympatric (almost nested) distributions. *Boyeria*

grafiana has an upland distribution pattern (Fig. 153, Appendix A). *B. vinosa* is ubiquitous in the eastern United States (Fig. 154, Appendix A).

Progomphus. *Progomphus* is a large western hemisphere genus of 53 nominal species. The group is primarily South American but a small group of four closely allied species ("*obscurus*-group" of Belle, 1973) occurs in the United States. The "*obscurus*-group" is part of a larger group of 10 species possessing a unique adult character (a slender midventral process on abdominal segment one) and occurring from Central America and the Greater Antilles northward to Oregon and New England (Belle, 1973). The "*obscurus*-group" consists of *P. alachuensis* (Fig. 156, Appendix A), *P. borealis*, *P. obscurus* (Fig. 157, Appendix A) and *P. bellei*. *Progomphus borealis* occurs from Oregon and California eastward to Colorado and western Texas and southward to northwestern Mexico. This species is set apart morphologically from the two eastern species (see figures in Byers, 1939). *Progomphus obscurus* is a widespread eastern United States species occupying sandy-bottomed streams and rivers. It is close morphologically in all stages to *P. alachuensis* (see Byers, 1939) which is restricted to Florida.

I believe that all three of these *Progomphus* species were derived from an *obscurus*-like ancestor by two successive divisions of the ancestral range. The first division was an east-west division that split off the ancestral *P. borealis* population.

This could have been accomplished via a split in a boreal corridor during an unfavorable glacial period. However, because of the austral distribution of the genus, I suspect that the split occurred in a southern corridor due to increased aridity following a wet cool glacial period. The *P. alachuensis* ancestral population probably split off from the *P. obscurus* main population by isolation as a relict population during a dry interglacial period. Subsequent cooling may have allowed sympatry with *P. obscurus*. *Progomphus bellei* possibly has a similar origin.

Hagenius. This genus is monotypic with *H. brevistylus* occurring in eastern North America (Fig. 158, Appendix A). Its nearest relatives are in the genus *Sieboldius* of the eastern Palearctic and Oriental regions (Walker, 1958). The two genera comprise the subfamily Hageniinae. Since the disjunction is at the generic level it may indicate an early (late Tertiary) isolation.

Lanthus. *Lanthus* is a small genus of one Asian and two Nearctic species (Carle, 1980). The two North American species, *L. parvulus* and *L. vernalis*, are similar morphologically and have overlapping ranges generally restricted to the Appalachian Highlands (Figs. 159, 160, Appendix A). The highly sympatric range of these two species is surprising considering their morphological similarity.

Stylogomphus. *Stylogomphus* is a small amphipacific genus with one species in North America (Tillyard and Fraser, 1957, Carle, 1980). *Stylogomphus albistylus* has an interior-upland range extending from the Ozarks and southern Appalachians to Nova Scotia with scattered Great Lakes records (Fig. 161, Appendix A).

Ophiogomphus. *Ophiogomphus* is a Holarctic genus (Tillyard, 1917) with a strong center of diversity in eastern North America (Figs. 162-169, 222 Appendix A). The phylogeny of the genus has not been elaborated.

North American species of *Ophiogomphus* apparently form two phylogenetic complexes, one eastern and one western. Both nymphal morphology (e.g. relative lengths of epiproct and paraprocts) and adult morphology (e.g. shape of male anterior and posterior hamules) support this contention. The eastern complex consists of seven distinct species. The western complex forms a rather tight cluster of closely related species. Their distributions are far less sympatric than the eastern species. This indicates that the western lineage is a relatively recent development in the evolution of the genus. Relationships within the eastern group are very difficult to ascertain and pairs of closely related species seen in other genera (below) are not evident. This group shows a high degree in overlap of species ranges with most species confined to the Great Lakes-Appalachian region (Fig. 222, Appendix A). *Ophiogomphus* is an example of a group whose zoogeography offers little insight into its phylogeny and vice versa. Ranges

are apparently controlled by rather uniform limiting factors. Species of *Ophiogomphus* have an early synchronous emergence that is possibly triggered by a narrow range of temperature. A narrow range of temperature tolerance would explain the early synchronous emergence as well as the rigidly controlled distribution patterns of most species.

Erpetogomphus. *Erpetogomphus* is a mostly Neotropical genus of a dozen species whose center of diversity is in Central America (Needham and Westfall, 1955). Four species occur in the United States, three in the southwestern United States and one, *E. designatus*, is southeastern (Fig. 170, Appendix A). The phylogeny of this genus has not been previously discussed. Based on morphological and geographical evidence affinities appear to lie with Holarctic groups. It is suspected that this genus represents an old lineage split off from *Ophiogomphus*-like precursors by a middle or late Tertiary event.

Dromogomphus. The genus *Dromogomphus* consists of three species restricted to eastern North America. *Dromogomphus spinosus* has the most generalized distribution and is sympatric over part of its range with the other two species (Figs. 172, 223, Appendix A). *Dromogomphus armatus* is restricted to the Coastal Plain from North Carolina to Louisiana and *D. spoliatus* occurs from Ohio to Texas (Fig. 171, Appendix A).

Relationships among these three species have not been previously discussed. Evidence indicating relationships seems

somewhat conflicting. While *D. armatus* and *D. spoliatus* are most similar in general adult coloration, *D. spinosus* is intermediate between them in the form of the female vulvar lamina and male genitalia (second hamules). Nymphal morphology is likewise conflicting in that the form of the ligula of *D. spoliatus* and *D. spinosus* are similar while the form of the palpal end hooks are similar in *D. spinosus* and *D. armatus* (see Westfall and Tennessen, 1979). I therefore suggest that these three species are related through extinct intermediate forms. The vicariance events that led to speciation were probably north-south disjunctions of the sort described for *Cordulegaster* (below). There is no indication of the degree of close relationships between species that is seen in the morphology and zoogeography of some members of *Gomphurus* or *Hylogomphus* (below).

Gomphus s.l. This generic complex is Holarctic, with the center of diversity in North America (Needham, 1947). Relationships between groups within this complex have not been evaluated. In North America the genus *Gomphus* s.l. includes the following groups (sometimes treated as subgenera): *Arigomphus*, *Gomphus* s.s., *Gomphurus*, *Hylogomphus*, *Stylurus* and Genus A.

Gomphus s.s. The genus *Gomphus* s.s. is a rather heterogeneous group of Holarctic and Oriental species of unclear relationships (Needham, 1951b). Since only a small percentage of the species of *Gomphus* s.s. were treated herein a general interpretation of zoogeographic and phylogenetic trends is not

feasible. Some trends seen in allied groups (e.g. *Gomphurus*) are evident in regional complexes of this genus. One pair of nominal species that are closely related and may even be conspecific (Westfall, 1974) are an example. *Gomphus exilis* is a widely distributed upland interior species of sluggish lotic habitats while the nearly identical *G. flavocaudatus* occupies an apparently disjunct coastal plain range from central Mississippi to southeastern Louisiana (Fig. 174, Appendix A). This may be another example of a Pleistocene-induced vicariance.

Gomphurus. The genus *Gomphurus* was first delimited by Needham (1901) as a subgenus containing a complex of mostly eastern North American species. An additional species was described by Needham (1944) from Szechuan, China.

If the ranges of North American species of *Gomphurus* (Figs. 179-187, Appendix A) are overlain (Fig. 224, Appendix A), a rather meaningless tangle is seen. By separating the subgroups that exist within the genus and redrawing the maps patterns emerge (Figs. 225, 226, Appendix A). There are two recognizable subgroups within *Gomphurus*. The two groups are delimited by the form of the palpal lobes of the nymphal stage. In one of these groups (*vastus*-group, Fig. 225, Appendix A) the palpal lobes terminate as a hook-like projection. This group consists of *G. crassus*, *G. dilatatus*, *G. lineatifrons*, *G. modestus*, *G. ozarkensis*, and *G. vastus*. Of these species *G. crassus*, *G. lineatifrons* and *G. vastus* occupy upland areas. *Gomphurus ozarkensis* is similar to *G. vastus* and *G. lineatifrons* through extinct intermediate forms.

The *fraternus*-group is diagnosed by absence of the projected palpal end hook. This group consists of *G. externus*, *G. fraternus*, *G. hybridus*, *G. septima*, and *G. ventricosus*. Two species, *G. ventricosus* and *G. fraternus* are highly sympatric upland species (Fig. 226, Appendix A). The remaining three species are seen as coastal plain (or lowland) vicariads derived from ancestors of one or both upland species. *Gomphurus hybridus* and *G. septima* occupy turbid sandy lowland streams and are similar to each other and to the upland *G. fraternus*. *Gomphurus externus* lives in sluggish muddy streams in the West and Midwest and stands apart from the remainder of the group. Its unusual prairie distributional pattern may be controlled by the "open country" foraging habits of the adults. Records of *G. externus* from "barrens" areas of the Midwest may represent Hypsithermal relict populations.

Hylogomphus. The Nearctic genus *Hylogomphus* (Figs. 188-191, Appendix A) may be divided into two groups on the basis of form of the lateral abdominal spines. One group occupies a collective range within the Great Lakes-Appalachian region. The second group consists of one upland species and three closely related coastal plain forms. The first group (*parvidens*-group) is delimited by long abdominal spines that diverge from the longitudinal axis of the body and includes *H. apomyius*, *H. carolinus*, *H. geminatus*, and *H. parvidens*. Although the nymph of *H. apomyius* has not been described, the adult was compared to *H. parvidens* when described (Donnelley, 1966). Nymphs of *Hylogomphus* sp. within the range of *H. apomyius* are

parvidens-like and will probably prove to be the immature stage of *H. apomyius*.

Hylogomphus parvidens is considered to represent the upland portion of upland-coastal plain vicariance (Fig. 227, Appendix A). In this case there are three nominal species, *H. apomyius*, *H. carolinus* and *H. geminatus* on the Coastal Plain or Piedmont. Carle (1979) described adults and nymphs of *H. carolinus* and *H. geminatus* and compared them to *H. parvidens*. Both species are morphologically close to *H. parvidens*. This similarity as well as the restricted range of these species suggests the possibility of a three-way vicariance event. *Hylogomphus apomyius* is morphologically distinct from the other three species and probably represents an earlier, possibly pre-Pleistocene, speciation event.

Hylogomphus abbreviatus, *H. brevis*, and *H. viridifrons* (Fig. 227, Appendix A) comprise the other subgroup (*abbreviatus*-group) within the genus. They are characterized by relatively shorter and parallel lateral abdominal spines. These species are homogeneous in form but less so than those of the *parvidens*-group. The degree of morphological divergence within this lineage suggests the possibility that these species are not as recently derived as species in the *parvidens*-group. Vestiges of the original adaptive shifts as speciation may be seen in the ecology and distribution of these species. *Hylogomphus viridifrons* and *H. brevis* may be collected syntopically in pristine streams in the southern Appalachians. *Hylogomphus brevis* has a Great Lakes-Appalachian distribution and tolerates only cold pristine streams

in the southern part of its range. *Hylogomphus viridifrons* tolerates warmer and more turbid streams and its range extends into the Interior Low Plateaus. The coexistence of these two species suggests that their range divergence is due to adaptive shifts associated with speciation events rather than competitive exclusion. *Hylogomphus abbreviatus* has a range comparable to that of *H. brevis* but it is shifted southward (Figs. 188, 189, Appendix A). This species presumably tolerates elevated temperature and turbidity.

Genus A. This group consists of the two species previously called *Gomphurus consanguis* and *G. rogersi*. These species do not fit into any North American genus. Both species are restricted to the Appalachians south of the maximum glacial front. Field collection data indicates a consistent 4°C difference in water temperature at collection sites. Genus A. *rogersi* occurs in the cooler streams. This difference in thermal preference is indicated in the ranges of the two species (Figs. 192, 193, Appendix A). The two species were not collected syntopically.

Stylurus. *Stylurus* is a Nearctic complex of about a dozen species (Figs. 194-201, Appendix A). Schmidt (1961) moved the European *Gomphus lineatus* to *Stylurus* making the genus nominally Holarctic in distribution. Williamson (1932a) and Needham and Westfall (1955) subdivided this genus into two groups, the *intricatus*-group and the *plagiatus*-group on the basis of the structure of the male and female genitalia. Figure 228 (Appendix A) shows the relative distribution of all species of the genus.

When the genus is subdivided along the two groups mentioned above (Figs. 229, 230, Appendix A) a pattern of staggered distributions from north to south emerges. The *intricatus* and *plagiatus* groupings are further indicated in the immature stage by the relative elongation of the terminal abdominal segments (see systematic section).

The *intricatus*-group (Fig. 229, Appendix A) is a larger complex of less obvious relationships including *S. amnicola*, *S. intricatus*, *S. ivae*, *S. laurae*, *S. potulentus*, *S. scudderi* and *S. townesi*. Additional study of male genitalia within this group may be useful in clarifying relationships. The posterior hamules appear to be slight variations on a general theme in *S. amnicola*, *S. ivae*, *S. laurae*, *S. scudderi* and *S. townesi*. *Stylurus intricatus* is a small western species of uncertain relationships while *S. potulentus*, a coastal plain species, seems intermediate or entirely misplaced in this group. Needham and Westfall (1955) perhaps placed too much emphasis on the angle of placement rather than on shape of the posterior hamule in separating these groups.

Stylurus amnicola and *S. scudderi* are two upland species. Ancestors similar to these two northern forms may have given rise to at least three of the coastal plain forms in this group (i.e. *S. ivae*, *S. laurae*, and *S. townesi*). I do not think that the apparent center of diversity at the bottom of Figure 229 (Appendix A) indicates a secondary center of adaptive radiation. This does not appear to be a complex of closely related species and as mentioned above, one of these species is probably presently placed within the wrong subgroup (*S. potulentus*).

In the *plagiatus* group (Fig. 230, Appendix A), two species, *S. notatus* and *S. spiniceps* are upland species that are probably temperature limited to upland habitats in the southern parts of their ranges. *Stylurus plagiatus*, the third member of the group, has the widest and most austral range of the three species and is morphologically most similar to *S. notatus*. These two species are probably sympatric derivatives of once allopatric populations.

Cordulegaster. *Cordulegaster* is a Holarctic genus centered in eastern North America with diversity attenuating across Asia toward Europe (see Fraser, 1957). There appears to be two distinct lines of evolution among North American species of *Cordulegaster*. Four allopatric western species share a distinctive venational character as well as nymphal characters. Eastern North America contains four highly sympatric species centered in the Appalachian Highlands. In addition, there are two nominal species restricted to the Coastal Plain and several outpost populations of the "upland" species (Fig. 231, Appendix A).

The Appalachian-centered fauna consists of *C. diastatops*, *C. erronea*, *C. maculata*, and *C. obliqua*. *Cordulegaster erronea* has the most restricted range of the four species but also has a Coastal Plain outpost population in the Tunica Hills region north of Baton Rouge, Louisiana. This population is 400 miles from the nearest published *C. erronea* record (Fig. 203, Appendix A). *Cordulegaster maculata* and *C. obliqua* have similar upland distributions (Figs. 204, 205, Appendix A). Both species also

have apparent coastal plain vicariads. I have collected *C. maculata*-like adults from Louisiana that are distinct at least at the subspecific level and I suspect that most if not all of the western Gulf Coastal Plain records are referable to this form. *Cordulegaster obliqua* has a closely related coastal plain vicariad originally described as *C. obliqua fasciata* and subsequently elevated to species rank (see systematic section). Populations of this form range from North Carolina to northern Florida. *Cordulegaster fasciata* has also been reported from Louisiana (Bick, 1957) near the locality records of *C. obliqua* in Arkansas reported by Harp and Rickett (1977). I suspect that most if not all of these coastal plain isolates of *C. obliqua* are conspecific and best regarded as *C. obliqua fasciata* until these specimens are brought together and critically examined. *Cordulegaster diastatops* has a similar distribution to that of *C. maculata* and *C. obliqua*. Bick (1950) reported that an apparent outpost population of *C. diastatops* from southern Mississippi in an area unlike the usual upland habitat of this species. *Cordulegaster sayi* is set apart from its upland counterpart. It is a distinctive but *maculatus*-like species restricted to the Coastal Plain from northern Florida to coastal North Carolina. The closely related species or subspecies of *Cordulegaster* thus consist of upland-coastal plain vicariance pairs (Fig. 232, Appendix A).

Didymops. *Didymops* is a Nearctic genus of two species placed in the subfamily Epophthalminae of the Corduliidae by Fraser (1957).

This subfamily (Family Macromiidae of Gloyd, 1959) is of Arctogaeon (Megagaeon of Darlington, 1957) distribution and contains four genera including *Didymops* and *Macromia* that are set apart from the others by virtue of the "macromine form" of the nymph (Fraser, 1957). Both species of *Didymops* are restricted to eastern North America (Figs. 207, 208, Appendix A). *Didymops transversa* is of "eastern-ubiquitous" distribution while *D. floridensis* is restricted to Florida. These species show a distribution pattern almost identical to that of *Progomphus obscurus* and *P. alachuensis*.

Macromia. *Macromia* is an almost cosmopolitan genus. It is excluded only from the Neotropical and Antarctic realms (Fraser, 1957). Subfamilial placement and allied genera are discussed briefly under *Didymops* above. The relationships among eastern North American species of *Macromia* have never been meaningfully discussed. It is my opinion that these are a complex of closely related and poorly understood species. There is indication of great variability within species (Williamson, 1909).

There are four well known species in the southeastern United States, *M. alleghaniensis*, *M. georgina*, *M. illinoensis*, and *M. taeniolata* and one common and widespread midwestern and western species, *M. pacifica*, known only in the adult stage. Two eastern species are known from their type series and little else, *M. margarita* from North Carolina and *M. wabashensis* from Illinois. Both are unknown in the nymphal stage.

Of the four southeastern species known in the nymphal stage *M. illinoensis* has the most northern range and is generally

distributed above the fall line. In the nymphal stage *M. illinoiensis* resembles *M. taeniolata* especially in the form of the broad dorsal abdominal hooks. These two species have overlapping ranges with *M. illinoiensis* shifted to the north and *M. taeniolata* shifted to the south (Figs. 211, 213, 233, Appendix A). *Macromia taeniolata* nymphs occur in a wider range of habitat types and are found in cool upland streams as well as turbid coastal plain streams.

Macromia alleghaniensis and *M. georgina* are morphologically similar in the nymphal stage, both having relatively thin falcate dorsal abdominal hooks. Their ranges are generally allopatric and exhibit the upland-coastal plain vicariance pattern (Figs. 209, 210, 233, Appendix A). Both species occur in similar habitat types with one species above and one below the fall line.

Neurocordulia. *Neurocordulia* is a Nearctic genus of six species, most of which occur in the southeastern United States (Figs. 214-219, Appendix A). The relationships among species of this group have never been discussed. Needham and Westfall (1955) mention that *N. xanthasoma* and *N. molesta* differ from the other species of the genus and from each other by possessing unique adult and nymphal characters. *Neurocordulia alabamensis* stands apart from other species of the genus on the basis of general nymphal form and especially form of the dorsal abdominal hooks. *Neurocordulia obsoleta* has a highly distinctive nymphal stage possessing unusually long and divergent eighth abdominal spines. All of these species are morphologically divergent and a

reconstruction of their exact relationships is probably impossible. Two species remain, *N. yamaskanensis* and *N. virginiensis* that appear to show a close similarity and relationship. Adult differences are mostly colorational and nymphal differences are also slight. The distribution of these two species (Fig. 235, Appendix A) are shown separately from the map of the entire genus (Fig. 234, Appendix A). Again the pattern of upland-lowland vicariance is seen when the ranges of closely related species are isolated from the remainder of the genus.

Neurocordulia has the most austral center of diversity of eastern North American lotic genera. This may be due to a southern (Neotropical or Ethiopian) origin for the genus. Williamson (1908) suggests *Aeschnosoma* (Neotropical) and *Libellulosoma* (Ethiopian) as genera most closely allied to *Neurocordulia*.

Helocordulia. *Helocordulia* is a small genus of two nominal species restricted to eastern North America. Needham (1901) suggests *Tetragoneuria* (*Epitheca* of Walker, 1966) of Holarctic distribution as its nearest relative. *Helocordulia uhleri* is distributed in interior-upland habitats from Nova Scotia to the Ozarks. *Helocordulia selysii* is a closely related coastal plain form possibly isolated from *H. uhleri* during Quaternary climatic fluctuations (Figs. 220, 236, Appendix A). In these taxa morphology and range data suggest a subspecific ranking. They have, however, been reported as sympatric in part of their ranges (McMahon and Gray, 1957).

Evolution and Historical Biogeography

Modern techniques of historical biogeography generally include a search for causal relationships in congruence of patterns of phylogeny, distribution and geological sequences (Ball, 1975). The controversy over the vicariance model of historical biogeography as presented by Croizat et al. (1974), Rosen (1975, 1978), and Nelson (1973), involves strong claims by the above authors of the hypotheticalo-deductive superiority of vicariance techniques and resistance in some quarters to these claims (for a criticism typical of degree and kind, see McDowell, 1978). I am accepting the basic tenets of vicariance methods (vicariance versus dispersal, ambiguity of centers of origin concepts, and the general validity of tracks as reflections of the distributions of ancestral biotas) while recognizing alternative explanations as regards highly vagile organisms and/or truly insular biotas. By accepting the subdivision of ancestral odonate faunas (rather than chance dispersal) useful hypotheses may be put forward. (1) There is congruence between phylogenetic and geological sequences (phylogeny as the dependent variable). From this, inferences may be made concerning the age of various branches (categories of taxa) of cladograms. (2) There is congruence in the locations of various relict elements of the ancestral biota.

Odonate phylogenetics. There are no useful phylogenies (cladograms) for the higher categories of odonates. The

systematic literature of the order remains unconsolidated and Kirby's (1890) synoptic catalogue is too out of date to be useful. Fraser's (1957) reclassification of the order with the update of the Gomphidae by Belle (1979) are the most useful sources of general information on classification and distribution to the subfamily level. Figure 149 shows a tentative cladistic arrangement of the families with the major synapomorphies unifying the "clades." This scheme differs from Fraser's (1957) arrangement mainly because his groupings were based on "persistent archaic characters," a practice long fallen into disrepute (Hennig, 1965). Figure 150 (Appendix A) presents the tentative cladogram for subfamilies of Gomphidae. The outstanding biogeographic aspect of this arrangement is that the three "primitive" subfamilies (Ictinogomphinae, Gomphoidinae, Epigomphinae) are pantropical except for minor Nearctic lineages of late Tertiary or Quaternary origin (discussed below).

Some information is available concerning relationships among lower taxa and these are discussed below. General geological sequences follow the summary of Dott and Batten (1976). Regional physiography of the southeastern United States follows Fenneman (1938). Excellent summaries exist for Tertiary and Quaternary histories of the southeastern United States biota and include Graham (1964), the symposia edited by Holt (1969, 1970, 1971), Wright and Frey (1965), and Graham (1972).

Composition of the Nearctic Lotic Fauna

The North American fauna of lotic Anisoptera is composed of endemic elements (8 genera), Holarctic elements (8 genera),

elements shared with Neotropica (1 genus), near cosmopolitan elements (1 genus) and two Jurassic relicts.

Endemic elements. Eastern endemic elements include species of the gomphid genera *Erpetogomphus*, *Dromogomphus*, and *Hyllogomphus*, the aeshnid genus *Basiaeschna*, the macromiid genus *Didymops*, and the corduliid genera *Neurocordulia* and *Helocordulia*. There is an additional monotypic western endemic genus, *Octogomphus*. Most of these genera were probably derived from the Tertiary Holarctic fauna. *Neurocordulia* and *Helocordulia* are of uncertain relationships but possibly of austral derivation. Two additional endemic genera deserve special treatment as Jurassic relicts (below).

Elements shared with Neotropica. *Progomphus* is a Neotropical-centered genus. The center of diversity for *Progomphus* is in South America. *Progomphus* is part of a complex of genera placed in the exclusively Neotropical subfamily Gomphoidinae. The distribution of *Progomphus* species suggests that closure of the Isthmus of Panama during the mid-Pliocene allowed the formation of a minor secondary center of diversity in North America. The western lotic genus *Neogomphoides* and the lentic genus *Aphylla* are also recent arrivals from Neotropica. *Erpetogomphus* is frequently and properly cited as a Neotropical genus but it is related to Holarctic groups and has not invaded South America.

Holarctic elements. The faunal connections between eastern North America and southeastern Asia are considered to be vestiges of the biota of the middle to late Miocene that was continuous

across boreal North America, Asia, and Europe via Beringia (Graham, 1964). The species of the cordulegastrid genus *Cordulegaster*, gomphid genera *Ophiogomphus*, *Gomphus* s.s., *Gomphurus*, *Stylurus*, and the aeshnid genus *Boyeria* are widespread Holarctic genera. Two additional gomphid genera, *Lanthus* and *Stylogomphus*, have more restricted distributions, being limited to upland or montane habitats in southeast Asia and eastern North America. This sort of continental disjunction parallels that of other groups of aquatic insects (Ross, 1967), diplopods (Hoffman, 1969), mammals (Handley, 1971), and various plant groups (Graham, 1964; Wood, 1970; Little, 1970). The four phytogeographically important Tertiary relict areas are (1) southeast Asia, (2) southwestern Europe and Asia minor, (3) southeastern North America including Mexican disjuncts and (4) northwestern North America (Wood, 1970). These relict areas correspond well with generic disjunctions of lotic odonates. There is no odonate faunal sharing at the species level indicating little likelihood of late Pliocene-Pleistocene exchange. The non-boreal nature of these groups further indicates range extension across a temperate (Tertiary) Beringia. Distributional patterns of lotic Odonata do not indicate Tertiary faunal connections between North America and Europe.

Cosmopolitan elements. Species of the macromiid genus *Macromia* are excluded only from Neotropical and Antarctic realms. These species are very mobile (vagile) ecological generalists whose distribution apparently reflects their ecology more than their history.

Relict elements. The two North American petalurid genera, *Tachopteryx* and *Tanypteryx* are relicts of ancient and once widespread Jurassic faunas. The genus *Tanypteryx* is represented by one Asian and one western North American species and is placed in a monotypic subfamily. *Tachopteryx* is monotypic. Belyshev (1974) considers the relict distributions of the Petaluridae to represent the circumference of Pangea.

Range Limiting Factors

T.T. MaCan (1961) in a comprehensive survey discussed the factors that limit microhabitat preference and entitled his article "Factors that limit the range of freshwater animals." Although this article is extremely useful in many ways it contains little information pertinent to range limitation. Corbet (1963) and Tillyard (1917) discuss many aspects of odonate biology but do not address range limiting factors.

Although every ecological parameter imaginable probably plays a role in the determination of microhabitat preference most of these are probably of little importance at range level. From the preceding discussion of distribution patterns of lotic Anisoptera I would like to suggest a few factors that may act (and interact) on distribution.

Temperature. From the range maps (Figs. 152-220, Appendix A) we can see several trends within generally distributed as well as more restricted species. Ranges are greatly staggered from north to south and much less so from east to west. There is a

boundary across southern Canada and up the St. Lawrence region that represents the maximum northward distribution of almost all species. This line represents the point at which cold Arctic air meets relatively warm Atlantic air along a region of steep temperature gradient (Canadian National Atlas, 1974). Temperature is probably a primary limiting factor for most species at these latitudes. Throughout the remainder of North America temperature probably plays a secondary role in determining range limits by cueing certain life-history events necessary to proper synchrony of those events with temperate climatic sequences. Response to given temperature cues would tie the range of a particular species to a range of temperature (and therefore geography) that could not change until physiological adjustments (evolution) were made. This would explain much of the north-south range staggering.

Humidity. By rather indirect means humidity may play a role in range limitation as well as microhabitat limitation. Certain species of gomphids are restricted to the plains area of the interior lowlands. These are light-colored open country foragers whose coloration and habits would be unsuitable to woodland life. Distributions of such species are controlled by prairie boundaries which in turn are controlled by humidity gradients.

Physiography. Physiography probably operates in several indirect ways. Physiography dictates parent material which in turn dictates substrate characteristics. Nymphal substrate preferences are well documented (Corbet, 1963). Climatic effects

also are associated with physiography. The Appalachian highlands (especially Blue Ridge and Plateau areas) allow southward extension of the ranges of many otherwise boreal and cold temperate species and act as an east-west (cold) barrier to warm temperate species.

Speciation Rates

There are various sources of information concerning rates of insect evolution. Quaternary paleontologists including Coope (1970), Matthews (1980), Morgan and Morgan (1980), and Campbell (1980) contend that there has been no proven examples of Pleistocene evolution in fossil Coleoptera. Species differentiated no later than late Tertiary. Conversely, Ross and Ricker (1971) indicate many waves of speciation among stoneflies (*Allocapnia*) during the Pleistocene based on neontological evidence. Evolution of the entire genus *Allocapnia* is seen to have occurred during the late Pliocene-Pleistocene period. High rates of evolution are attributed to other groups of Plecoptera (Illies, 1965) and to Trichoptera (Ross, 1956).

It is difficult to reconcile these views. While differential rates of evolution among lineages seems reasonable it is difficult to visualize a slower rate among the most speciose group of organisms on earth (Coleoptera). Briggs (1966) suggests the possibility of different rates of evolution within groups based on position of origin relative to evolutionary centers. He considers speciation rates to be slow (and successful) in evolutionary centers and rapid (and unsuccessful or dead end) at

peripheral locations. This line of thinking may be pertinent in light of the boreal locations of the beetle faunas mentioned above. It would be interesting to see if south-temperate fossil beetle faunas are as conservative.

The best information concerning rate of evolution of temperate lotic Anisoptera may be derived from the previous discussion of distribution of the Neotropical genus *Progomphus*. If one accepts the mid-Pliocene as the closing date of the Isthmus of Panama (Pielou, 1979) then six million years is sufficient time for the formation of a complex of the ten related Central American species. The assumption is that this warm-adapted genus would have spread northward immediately upon closure of the isthmus when climatic were favorable (relatively warm).

Four of these ten species form a distinctive subcomplex, the *obscurus*-group, restricted to northern Mexico and the United States (Belle, 1973). These nominal species have vicariated along a familiar east-west, then north-south pattern seen in the distribution of other genera of Anisoptera as well as some vertebrate groups (see Mengel, 1964). These patterns of closely related forms are probably associated with late Pliocene-Pleistocene events. These nominal species are so similar that they could be regarded as regional morphs or subspecies.

Though information is sketchy at best, it appears that the highly distinctive species of lotic Anisoptera speciated during the Tertiary and that their ranges were undoubtedly altered many times during the Plio-Pleistocene. Closely related pairs of

nominal species that are distinguished by minor characters may have arisen as late as the Pleistocene from small isolated populations stranded in favorable lowland habitats. Coope (1970) discusses paleontological evidence concerning a pair of sibling beetle species thought to be of recent origin until they were found as contemporaneous early Pleistocene fossils. Attempts at dating speciation events from neontological data are therefore speculative.

Patterns of Speciation

Temperature, humidity, and physiography are probably three major limiting factors in the distribution of lotic Anisoptera species. Most of the patterns that we have seen of closely related pairs of allopatric species (or subspecies) have consisted of upland-coastal plain vicariant pairs. Whether these pairs represent examples of incipient speciation, dead end events, or mere morphological races is subject to debate (see summary of controversy in Coope, 1970). Even if these geminate pairs do not represent speciation in action, their distributions may nevertheless be taken as analogues of the type of patterns that lead to differentiation. Pleistocene events may have been of too short duration for insect speciation to occur but they at least give some insight into effects of other climatic fluctuations of longer duration (pre-Pleistocene) that must have led to isolation and speciation.

The upland-lowland vicariance pattern explains the high number of apparent coastal plain endemics (20 species). The

Coastal Plain may be viewed as a vast relatively undifferentiated plain upon which are scattered an archipelago of isolated marginal lotic habitats. There are no secondary centers of diversity in the Coastal Plain. The evidence is that each coastal plain endemic was derived from an upland species independently and coastal plain endemics are glacial relicts.

It is remarkable that there is but a single endemic Ozarkian species (*G. ozarkensis*). This species and *G. crassus* which is endemic to the Interior Low Plateaus represent an apparent vicariant event. The relative lack of endemics suggests that the Ozark-Ouchita highlands (Interior Highlands) are functionally a constricted extension of the eastern upland areas. Little (1970) suggests a close relationship between the two areas on the basis of the few tree endemics in the Ozarks.

I have not treated the western fauna except for a few widespread species that intrude into the prairie peninsula and "barren" areas of the Midwest. There is a substantial western lotic fauna that is highly isolated from that of the eastern portion of North America. The western-eastern faunal/floral break dates from the elevation of western mountain ranges during the Pliocene and subsequent development of the xeric "Madro-Tertiary" biota west of the uplift (Graham, 1964). These orogenic events probably date the isolation and speciation of many of the western forms.

CHAPTER V

SUMMARY

1. Lotic Anisoptera are relatively K selected. The lentic forms are relatively r selected. This difference is due to differential stability of habitat. Shallow lentic waters are of a highly successional nature. Lotic Anisoptera are much less vagile than their lentic counterparts and this is reflected in the ecology and biogeography of the groups.

2. The traditional arrangements of taxa based on adult structures are supported by nymphal morphology except in the following: (1) subgenera of *Gomphus* s.l. should be elevated to generic rank and (2) *Gomphurus consanguis* and *G. rogersi* are misplaced and are morphologically unique at the generic level in the North American fauna.

3. The North American lotic Anisoptera fauna is generally descendent from a continuous Holarctic "Arcto-Tertiary" biota that fragmented by the late Tertiary. Additional elements include two Jurassic relict genera and minor lineages derived from the South American fauna after formation of the Isthmus of Panama in the Pliocene.

4. Spatial patterns of closely related species indicate speciation of the pairs or groups may have preceded glacial-induced vicariance. Upland-lowland vicariant pairs explain the high number of Coastal Plain endemic species. Spatial patterns of less closely related species indicate earlier speciation events possibly associated with faunal disjunction of late Tertiary age.

5. Speciation rates are suggested by fossil evidence from other insect groups and from chronologies evident in cladistic-geochronological congruence. Most distinctive species probably originated during the late Tertiary modernization of the continental biotas. Neotropical lineages that spread northward after the formation of the Pliocene land bridge are little differentiated. This is true also for the upland-Coastal Plain vicariads. These recently derived nominal species are highly allopatric and many should be considered as subspecies.

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APPENDICES

APPENDIX A

Table 1. Characters used in the descriptions and tables of species (method of measurement or character state choices in parentheses).

Character	Method of Measurement
1. total length	anterior of head to tip of abdominal appendages (vernier calipers)
2. length abdomen	ventral, anterior segment one to tip of abdominal appendages (vernier calipers)
3. length hind femur	extensor margin (ocular micrometer)
4. width head	widest point across eyes (ocular micrometer)
5. width abdomen	widest point (ocular micrometer)
6. total length/femur	item 1 divided by item 3
7. antennal ratio	length segment three divided by combined lengths segments one and two (ocular micrometer)
8. length/width of prementum	length from hinge line to apex of ligula divided by width at widest point (ocular micrometer)
9. end hook on palpal lobe (of labium)	does projection of end hook exceed that of adjacent tooth (yes-no)
10. number teeth of palpal lobe	number on one lobe (do not count end hook)
11. ligula	shape (convex, concave or straight)
12. median tooth on ligula	(present, absent or vestigial)
13. lateral spine lengths segments 6-9/dorsal length segment 10	spine length from tip to base at junction intersegmental membrane of each segment divided by mid-dorsal length of segment ten (ocular micrometer)

Table 1 (continued)

Character	Method of Measurement
14. lengths abdominal segments 8 and 9/length segment 10	each segment divided by dorsal length of segment ten (ocular micrometer)
15. epiproct/paraprocts	lengths from apex to articulation with segment ten of epiproct divided by length of paraproct (ocular micrometer)
16. length/width of segment 9	width at widest point divided by midventral length (ocular micrometer)
17. length segment 9/ length segment 8	middorsal lengths (ocular micrometer)
18. segments with dorsal hooks	abdominal segments (numbered as Fig. 4, Appendix A) bearing middorsal hooks
19. n	number of specimens measured

Table 2. Character states of *Progomphus*, *Hagenius*, *Lanthus*, *Stylogomphus* and *Erpetogomphus* species. Explanation of characters in Table 1 (Appendix A).

	<i>Progomphus obscurus</i>	<i>Hagenius brevistylus</i>	<i>Lanthus vernalis</i>	<i>Stylogomphus albistylus</i>	<i>Erpetogomphus designatus</i>
total length (mm)	27.4- 29.9 (28.6)	39.0- 43.4 (41.1)	18.2- 18.8 (18.6)	17.3- 19.6 (18.7)	23.1- 26.1 (24.7)
length abdomen (mm)	19.3- 20.6 (20.0)	25.8- 27.9 (26.8)	11.5- 11.9 (11.6)	11.6- 13.0 (12.2)	15.0- 17.5 (16.1)
length hind femur (mm)	3.14- 3.43 (3.25)	13.6- 14.7 (13.9)	3.57- 3.71 (3.64)	2.86- 3.14 (2.96)	4.57- 4.71 (4.60)
width head (mm)	5.14- 5.43 (5.22)	7.9- 8.9 (8.3)	4.86- 5.0 (4.91)	4.14- 4.57 (4.32)	5.21- 5.57 (5.39)
width abdomen (mm)	5.43- 6.43 (5.79)	20.2- 22.6 (21.4)	6.29- 6.71 (6.44)	5.57- 6.43 (5.95)	6.57- 7.71 (7.20)
total length/ femur	8.16- 9.36 (8.83)	2.68- 3.24 (2.95)	5.07- 5.27 (5.17)	6.05- 6.85 (6.31)	5.05- 5.71 (5.36)
antennal ratio	2.0- 2.67 (2.47)	2.29- 3.08 (2.64)	2.32- 2.78 (2.56)	2.30- 3.25 (2.40)	1.77- 2.04 (1.90)
length/width prementum	1.53- 1.67 (1.60)	.81- .90 (.85)	1.0- 1.05 (1.03)	1.0- 1.10 (1.05)	1.0- 1.05 (1.02)
length/width 3d seg. ant.	3.0- 3.20 (3.12)	1.06- 1.19 (1.12)	1.56- 1.70 (1.62)	1.15- 1.45 (1.29)	3.43- 3.83 (3.63)

Table 2 (continued)

	<i>Progomphus obscurus</i>	<i>Hagenius brevistylus</i>	<i>Lanthus vernalis</i>	<i>Stylogomphus albistylus</i>	<i>Erpetogomphus designatus</i>
no. teeth palpal lobe	0	19- 22	9- 10	6- 7	10- 11
ligula	cx	cx	cx	cx	cx
no. teeth ligula	0	10- 12	4	3	19- 22
lat. spine seg. 5/length seg. 10	.24- .30 (.28)				
lat. spine seg. 6/length seg. 10	.31- .38 (.34)				.35- .48 (.41)
lat. spine seg. 7/length seg. 10	.33- .48 (.39)		.13- .29 (.21)		.50- .72 (.60)
lat. spine seg. 8/length seg. 10	.34- .46 (.39)		.27- .57 (.46)	.33- .53 (.46)	.62- .72 (.67)
lat. spine seg. 9/length seg. 10	.23- .36 (.30)	1.09- 1.24 (1.20)	.87- 1.07 (1.00)	.63- .76 (.70)	.71- 1.00 (.82)
dorsal length seg. 8/length seg. 10	.97- 1.21 (1.07)	2.26- 2.61 (2.40)	2.25- 2.43 (2.34)	2.00- 2.29 (2.19)	1.92- 2.04 (1.95)
dorsal length seg. 9/length seg. 10	1.03- 1.25 (1.15)	2.16- 2.50 (2.34)	2.56- 2.86 (2.69)	2.33- 2.53 (2.47)	1.88- 1.92 (1.90)
dorsal length epiproct/ length seg. 10	1.27- 1.92 (1.60)	1.70- 2.27 (1.87)	1.73- 2.00 (1.92)	1.42- 1.72 (1.53)	2.71- 2.80 (2.76)

Table 2 (continued)

	<i>Progomphus obscurus</i>	<i>Hagenius brevistylus</i>	<i>Lanthus vernalis</i>	<i>Stylogomphus albistylus</i>	<i>Erpetogomphus designatus</i>
epiproct/ cerci	2.08- 2.47 (2.27)	2.10- 2.50 (2.34)	1.73- 1.78 (1.76)	1.33- 1.69 (1.59)	.97- 1.03 (1.01)
length/width 9th seg.	.56- .65 (.59)	.30 .32 (.31)	.28- .31 (.30)	.31- .35 (.33)	.33- .35 (.34)
length seg. 9/ seg. 8	1.03- 1.13 (1.07)		1.13- 1.18 (1.15)	1.10- 1.22 (1.15)	.94- 1.00 (.97)
dorsal hooks on segments	1-9	2-10	0	0	2-9
n	7	8	5	9	5

Table 3. Character states for southeastern species of *Ophiogomphus*.
Explanation of characters in Table 1 (Appendix A).

	<i>aspersus*</i>	<i>howei</i>	<i>marinensis</i>	<i>rupinulensis</i>	sp. A
total length (mm)	15-28	22.6	23.6- 25.2 (24.7)	24.8- 27.5 (26.6)	24.5- 28.8 (25.8)
length abdomen (mm)		14.3	14.9- 16.5 (16.0)	15.0- 18.7 (17.3)	16.0- 19.0 (17.6)
length hind femur (mm)		3.17	3.72- 4.0 (3.88)	4.23- 4.83 (4.53)	3.60- 4.20 (3.85)
width head (mm)		4.83	5.51- 5.66 (5.56)	5.38- 6.07 (5.75)	5.40- 6.15 (5.35)
width abdomen (mm)		5.93	7.04- 7.86 (7.44)	7.72- 8.97 (8.26)	7.20- 8.55 (8.08)
tot. length/ femur		7.13	6.11- 6.69 (6.37)	5.65- 6.26 (5.85)	6.81- 7.22 (6.95)
antennal ratio		2.32	2.2- 2.50 (2.20)	2.25- 2.50 (2.37)	1.67- 1.87 (1.81)
length/width prementum		1.13	1.09- 1.15 (1.13)	1.12- 1.19 (1.15)	1.07- 1.15 (1.12)
length/width 3d. seg. ant.	3.0	1.57	1.59- 1.84 (1.72)	2.45- 2.73 (2.61)	2.18- 2.45 (2.34)
no. teeth palpal lobe		14	13- 14	13- 15	9- 11

Table 3 (continued)

	<i>aspersus*</i>	<i>howei</i>	<i>mainensis</i>	<i>rupinsulensis</i>	<i>sp. A</i>
ligula		CX	CX	CX	CX
no. teeth		32	23-	28-	19-
ligula			27	32	23
lat. spine		0	.14-	.25-	.18-
seg. 7/length			.32	.45	.36
seg. 10			(.26)	(.35)	(.29)
lat. spine		.20	.21-	.34-	.25-
seg. 8/length			.40	.50	.43
seg. 10			(.33)	(.43)	(.33)
lat. spine		.25	.31-	.43-	.25-
seg. 9/length			.48	.54	.48
seg. 10			(.38)	(.47)	(.39)
dorsal length		2.0	1.52-	1.83-	1.45-
seg. 8/length			1.84	2.0	1.82
seg. 10			(1.64)	(1.92)	(1.66)
dorsal length		1.75	1.52-	1.67-	1.45-
seg. 9/length			1.76	1.82	1.79
seg. 10			(1.59)	(1.74)	(1.63)
dorsal length		2.85	1.97-	2.13-	1.94-
epiproct/ length seg. 10			2.88	2.59	2.46
			(2.44)	(2.37)	(2.24)
epiproct/ cerci	1.33	1.50	1.29-	1.23-	1.22-
			1.64	1.42	1.33
			(1.51)	(1.32)	(1.27)
length/width		.38	.33	.31-	.3-
9th seg.			.37	.34	.37
			(.35)	(.33)	(.35)
n		1	6	10	16

*Data from Walker, 1958

Table 4. Character states for species of *Dromogomphus*.
Explanation of characters in Table 1 (Appendix A).

	<i>armatus</i>	<i>spoliatus</i>	<i>spinosus</i>
total length (mm)	39.1-40.8	30.2-32.9 (31.7)	32.8-36.5 (34.4)
length abdomen (mm)	26.0-27.6	20.0-22.3 (21.2)	22.5-24.2 (23.5)
length hind femur (mm)	7.86-8.29	7.0-7.86 (7.47)	7.29-8.0 (7.60)
width head (mm)	6.57-7.0	5.57-6.0 (5.82)	5.85-6.43 (6.19)
width abdomen (mm)	8.86-9.29	8.57-9.29 (8.86)	7.86-9.29 (8.43)
tot. length/femur	4.72-5.19	4.02-4.35 (4.25)	4.17-4.71 (4.48)
antennal ratio	1.86-1.95	2.06-2.29 (2.19)	2.0-2.40 (2.21)
length/width prementum	1.07-1.14	1.08-1.11 (1.09)	1.07-1.12 (1.09)
end hook on palpal lobe	yes	no	yes
no. teeth palpal lobe	9-10	6-8	6-8
ligula	cx	s1 cx	st
med. tooth ligula	yes	yes	yes

Table 4 (continued)

	<i>armatus</i>	<i>spoliatus</i>	<i>spinosus</i>
lat. spine seg. 6/dorsal length seg. 10	0	.11- .18 (.14)	.19- .22 (.21)
lat. spine seg. 7/dorsal length seg. 10	.30- .32	.20- .28 (.26)	.30- .41 (.37)
lat. spine seg. 8/dorsal length seg. 10	.50- .54	.30- .41 (.36)	.47- .53 (.49)
lat. spine seg. 9/dorsal length seg. 10	.70- .74	.91- 1.02 (.98)	.80- .87 (.85)
dorsal length seg. 8/length seg. 10	1.80- 1.88	1.55- 1.64 (1.61)	1.59- 1.79 (1.71)
dorsal length seg. 9/length seg. 10	2.56- 2.60	2.04- 2.16 (2.11)	2.18- 2.44 (2.37)
dorsal length epiproct/length seg. 10	1.20- 1.22	1.41- 1.47 (1.43)	1.28- 1.41 (1.33)
epiproct/ cerci	1.13- 1.17	1.13- 1.29 (1.23)	1.14- 1.25 (1.20)
length/width 9th seg.	.68- .70	.73- .77 (.75)	.66- .70 (.68)
length 9th seg./ length 8th seg.	1.38- 1.42	1.29- 1.35 (1.32)	1.35- 1.41 (1.33)
dorsal hooks on segments	7-9	7-9	3/4- 9
n	2	4	6

Table 5. Habitat preference of nymphs and distribution of North American species of *Gomphus*.

Species	Habitat	Distribution
<i>australis</i>	sand bottomed lakes (Westfall, 1950)	Fla.
<i>borealis</i>	lakes, ponds, slow streams (Walker, 1958)	Can., N.H. to N.C.
<i>cavillaris</i>	sand-bottomed lakes (Westfall, 1950)	Fla.
<i>confraternus</i>	rapid streams (Needham and Westfall, 1955)	Cal., Ore., Wash.
* <i>descriptus</i>	streams (Walker, 1958)	MW, NE to N.C.
<i>diminutus</i>	nymph unknown	N.C.
* <i>exilis</i>	streams and ponds (Needham and Westfall, 1955)	EUS
* <i>flavocaudatus</i>	nymph unknown	La., Miss.
* <i>graslinellus</i>	ponds, lakes, slow streams (Walker, 1958)	MW
<i>hodgesi</i>	nymph unknown	Ala. to Miss.
<i>kurilis</i>		Cal., Nev., Ore.
* <i>lividus</i>	streams, rivers, lakes (Walker, 1958)	EUS
<i>militaris</i>	"small muddy ponds and stagnant pools of streams" (Bird, 1934)	N.M. to Tex.
* <i>minutus</i>	lakes and streams (Byers, 1930)	La. to Fla.
<i>oklahomensis</i>		Okla., Tex., W. La.
* <i>quadricolor</i>	streams and rivers (Walker, 1958)	NE to Ala.

Table 5 (continued)

Species	Habitat	Distribution
<i>spicatus</i>	boggy lakes and ponds (Walker, 1958)	NE
<i>williamsoni</i>	nymph unknown	Ind.

*Species considered southeastern, lotic.

Table 6. Character states of *Gomphus* species. Explanation of characters in Table 1 (Appendix A).

	<i>descriptus</i> *	<i>exilis</i>	<i>gracilineellus</i> *	<i>lividus</i>	<i>minutus</i> *	<i>quadricolor</i>
total length (mm)	29.0	25.1	29.0	31.3-33.5 (32.5)	29-30	25.4-26.3 (25.8)
length abdomen (mm)	18.0	16.6	18.0	20.7-22.0 (21.4)	19-21	16.4-17.6 (16.9)
length hind femur (mm)	5.70	5.14	6.00	5.71-6.57 (6.28)	6	5.43-5.57 (5.50)
width head (mm)		5.14	5.50	5.86-6.17 (6.03)	5.5	5.14-5.43 (5.29)
width abdomen (mm)	8.00	6.43	8.00	7.71-8.71 (8.40)	7	6.07-6.57 (6.39)
total length/femur	5.09	4.88	4.83	5.09-5.48 (5.23)	4.92	4.56-4.84 (4.71)
antennal ratio	2.00	2.00	1.75	1.82-2.06 (1.95)		1.77-1.86 (1.82)
length/width prementum	1.00	1.08		1.02-1.08 (1.06)	1.2	1.13-1.20 (1.17)
end hook on palpal lobe	no	yes	no	yes	yes	yes
No. teeth palpal lobe	10	7		6-7	6-10	5-7
ligula	st-cx	cx	cx	st-cx	cx	cx

Table 6 (continued)

	<i>descriptus*</i>	<i>exilis</i>	<i>graslinellus*</i>	<i>lividus</i>	<i>minutus*</i>	<i>quadricolor</i>
med. tooth ligula	no	yes	no	no	yes	yes
lat. spine seg. 6/length seg. 10		.16		.16- .22 (.18)		.10- .15 (.13)
lat. spine seg. 7/length seg. 10		.29		.29- .34 (.33)		.24- .28 (.26)
lat. spine seg. 8/length seg. 10		.36		.31- .42 (.37)		.28- .35 (.31)
lat. spine seg. 9/length seg. 10	.50-	.58	.40	.50- .67 (.60)	.4- .5	.51- .58 (.55)
dorsal length seg. 8/length seg. 10		1.20		1.44- 1.67 (1.54)		1.48- 1.54 (1.50)
dorsal length seg. 9/length seg. 10		1.64		2.00- 2.36 (2.17)		2.30- 2.41 (2.37)
dorsal length epiproct/ length seg. 10	1.40	.82		1.11- 1.22 (1.14)	1	.84 .99 (.93)
dorsal hooks on segments	7- 9	8- 9	2- 9	4- 9	4- 9	9
epiproct/ cerci		1.12		1.14- 1.17 (1.15)		1.03- 1.18 (1.12)

Table 6 (continued)

	<i>descriptus*</i>	<i>exilis</i>	<i>gracilineellus*</i>	<i>lividus</i>	<i>minutus*</i>	<i>quadricolor</i>
length/width 9th seg.	.50	.88	.55	.68- .87 (.76)	.75- .86	.93- 1.04 (.98)
length seg. 9/ seg. 8	1.29	1.37	1.50	1.37- 1.49 (1.43)		1.54- 1.61 (1.58)
n		1		5		5

*Data from Walker, 1958.

Table 7. Character states of *Gomphaurus* species. Explanation of characters in Table 1 (Appendix A).

	<i>ovatus</i>	<i>di-latus</i>	<i>easternus</i>	<i>fraterius</i>	<i>hybridus</i>	<i>lineatiformis</i>	<i>modestus</i>	<i>ovakensis</i>	<i>vatus</i>	<i>ventriosus</i>
total length (mm)	31-32 (31.5)	38.6-40.9 (39.4)	30-33 (30.5)	28.0-28.3	25-31 (26.8)	37-40 (38.3)	34-38 (35.7)	28.0-30.2 (29.3)	28-31 (30)	28-29
length abdomen (mm)	19-19.5 (19.25)	25.6-27.0 (26.3)	20-21 (20.3)	17.5-18.5	15.5-19 (17)	24-29 (26.3)	21-26 (22.8)	18.6-19.8 (19.2)	19-20 (19.6)	18-19.5
length hind femur (mm)	5.14-5.71 (5.43)	6.86-7.14 (7.07)	6.0-6.57 (6.36)	5.86-6.14	5.29-5.71 (5.44)	6.72-7.42 (7.12)	5.86-6.57 (6.33)	5.25-5.85 (5.48)	5.14-5.71 (5.41)	5.43
width head (mm)	5.71-6.0 (5.88)	6.71-7.14 (7.02)	5.86-6.14 (6.02)	5.50-5.71	5.29-5.87 (5.47)	6.86-7.0 (6.93)	6.57-7.0 (6.79)	5.40-5.70 (5.55)	5.71-6.0 (5.77)	5.57-5.71
width abdomen (mm)	7.57-8.29 (8.07)	9.71-11.71 (10.32)	8.0-8.42 (8.21)	7.57	6.57-8.43 (7.82)	12.0-12.86 (12.43)	8.71-9.57 (9.15)	7.50-8.55 (7.83)	7.57-8.0 (7.75)	7.57-7.86
tot. length femur	5.60-6.03 (5.81)	5.39-5.73 (5.59)	4.61-5.02 (4.80)	4.51-4.78	4.38-5.43 (4.93)	5.29-5.66 (5.41)	5.41-5.91 (5.65)	5.16-5.68 (5.36)	5.15-5.86 (5.55)	5.16-5.34
antennal ratio	2.0	2.14-2.33 (2.21)	1.83-2.0 (1.90)	2.57-2.58	1.83-2.30 (2.04)	2.0-2.17 (2.11)	1.92-2.38 (2.15)	1.93-2.14 (2.04)	2.40-2.60 (2.50)	2.60
length/width prementum	1.18-1.23 (1.21)	1.18-1.22 (1.21)	1.17-1.24 (1.19)	1.10-1.14	1.16-1.26 (1.21)	1.13-1.17 (1.16)	1.08-1.25 (1.16)	1.16-1.28 (1.23)	1.13-1.20 (1.23)	1.32-1.35
end hook on palpal lobe	yes	yes	no	no	no	yes	yes	yes	yes	no
no. teeth on palpal lobe	4-5	3-5	8-9	7-8	8-9	6-8	3-4	4-6	3-5	7-9
ligula	str.	sl. conv.	conv.	sl. conv.	sl. conv.	conc.	sl. conv.	str.	str.	str.
med. tooth ligula	yes	no	no	no	vest.	yes	no	no	no	no

Table 7 (continued)

	<i>cruentus</i>	<i>dilatatus</i>	<i>extremus</i>	<i>fratermus</i>	<i>hybridus</i>	<i>lineatiformis</i>	<i>modestus</i>	<i>osarkensis</i>	<i>vastus</i>	<i>ventricosus</i>
denticles seg. 8	10- 12 (11.5)	11- 13 (11.7)	6- 10 (7.3)	9- 12	8- 13 (10.1)	10- 17 (12)	10- 16 (13)	8- 14 (11.4)	13- 15 (13.8)	6- 7
denticles seg. 9	22- 24 (23.5)	23- 29 (25.7)	16- 22 (17.7)	18- 19	16- 24 (19.3)	22- 32 (25)	20- 27 (23.1)	16- 22 (18.9)	20- 24 (22.7)	16- 17
lat. spine seg. 6/dorsal length seg. 10	.13- .17 (.16)	.22- .31 (.26)	.30- .50 (.39)	.40- .43	.35- .58 (.43)	.34- .53 (.43)	.22- .44 (.31)	.19- .27 (.25)	.20- .30 (.27)	.37- .46
lat. spine seg. 7/dorsal length seg. 10	.29- .37 (.33)	.46- .57 (.54)	.45- .63 (.54)	.43- .50	.38- .77 (.55)	.51- .63 (.58)	.57- .81 (.70)	.42- .58 (.45)	.43- .56 (.48)	.66- .69
lat. spine seg. 8/dorsal length seg. 10	.41- .53 (.48)	.71- .95 (.82)	.65- .83 (.71)	.63- .68	.61- 1.08 (.77)	.83- .91 (.88)	.81- 1.12 (.96)	.60- .81 (.70)	.56- .63 (.58)	.74- .77
lat. spine seg. 9/dorsal length seg. 10	1.0- 1.16 (1.09)	1.32- 1.76 (1.57)	1.58- 1.72 (1.63)	1.29- 1.33	1.61- 1.92 (1.70)	1.84- 2.03 (1.91)	1.56- 1.87 (1.72)	1.23- 1.54 (1.36)	1.33- 1.44 (1.38)	1.26- 1.27
dorsal length seg. 8/length seg. 10	2.13 2.33 (2.25)	2.49- 2.82 (2.62)	2.06- 2.27 (2.19)	2.21- 2.27	2.0- 2.31 (2.16)	2.63- 2.76 (2.69)	2.18- 2.70 (2.40)	2.46- 2.68 (2.57)	2.28- 2.59 (2.45)	2.44- 2.62
dorsal length seg. 9/length seg. 10	2.33 2.67 (2.50)	2.70- 3.14 (2.92)	2.19- 2.53 (2.36)	2.33- 2.36	2.15 2.50 (2.31)	2.94- 3.09 (3.0)	2.42- 2.90 (2.63)	2.58- 2.83 (2.71)	2.41- 2.81 (2.64)	2.52- 2.77
dorsal length epiproct/ length seg. 10	1.50- 1.63 (1.57)	1.59- 2.03 (1.75)	1.45 1.73 (1.63)	1.53- 1.64	1.73- 1.93 (1.82)	1.71- 1.86 (1.80)	1.49- 1.81 (1.67)	1.69- 1.92 (1.78)	1.60- 1.81 (1.71)	1.47- 1.52
spine seg. 9 surpass post. marg. seg. 10	no	yes	yes	yes	yes	yes	yes	no	no	no
dorsal hooks on segments	8-9	8-9	8-9	8-9	8-9	7-9	8-9	8-9	8-9	8-9
n	4	6	6	2	5	4	18	9	7	2

Table 8 (continued)

	<i>abbreviatus</i>	<i>brevis</i>	<i>carolinus</i>	<i>geminatus</i>	<i>parvidens</i>	<i>viridifrons</i>
denticles seg. 8	7- 12 (8.6)	11- 12 (11.2)	4- 7 (5.2)	3- 6 (4.8)	7	11- 14 (12.0)
denticles seg. 9	15- 20 (17.5)	17- 20 (18.6)	12- 16 (13.4)	7- 13 (9.2)	13	17- 22 (19.9)
lat. spine seg. 6/length seg. 10	.27- .56 (.43)	.46- .64 (.54)	0- .26 (.13)	.27- .36 (.31)	.40	.40 .63 (.51)
lat. spine seg. 7/length seg. 10	.64- .81 (.73)	.69 .88 (.78)	.57- .77 (.64)	.74- .91 (.86)	.80	.60 .76 (.70)
lat. spine seg. 8/length seg. 10	.86- 1.05 (.96)	.88 1.04 (.95)	.87- 1.04 (.94)	1.19- 1.30 (1.25)	1.20	.76 1.08 (.90)
lat. spine seg. 9/length seg. 10	1.23- 1.40 (1.33)	1.19 1.40 (1.32)	1.45- 1.52 (1.49)	1.74- 1.96 (1.84)	1.68	1.28 1.58 (1.48)
dorsal length seg. 8/length seg. 10	1.92- 2.27 (2.11)	2.15 2.24 (2.18)	2.09- 2.27 (2.18)	2.17- 2.48 (2.26)	2.24	2.16 2.42 (2.31)
dorsal length seg. 9/length seg. 10	2.0- 2.36 (2.19)	2.15 2.24 (2.20)	2.13- 2.27 (2.22)	2.17- 2.57 (2.34)	2.24	2.24 2.45 (2.33)
sup. anal append.	1.46- 1.82 (1.65)	1.80 2.12 (1.98)	2.0- 2.26 (2.10)	1.82- 2.0 (1.93)	1.92	1.68 2.09 (1.95)
dorsal hooks on segments	9	9	9	9	9	9

Table 8 (continued)

	<i>abbreviatus</i>	<i>brevis</i>	<i>carolinus</i>	<i>geminatus</i>	<i>parvidens</i>	<i>viridifrons</i>
lat. spines divergent	no	no	yes	yes	yes	no
n	10	5	5	6	1	9

Table 9. Character states of Genus A species.

	<i>consanguis</i>	<i>rogersi</i>
total length (mm)	26.4- 29.0 (28.0)	28.0- 29.0 (28.6)
length abdomen (mm)	16.8- 19.0 (18.1)	16.0- 17.5 (17.0)
length hind femur (mm)	5.00- 5.57 (5.30)	5.00- 5.71 (5.41)
width head (mm)	5.29- 5.86 (5.68)	5.50- 5.71 (5.60)
width abdomen (mm)	7.29- 8.29 (7.68)	8.14- 8.57 (8.37)
total length/femur	5.12- 5.64 (5.29)	4.99- 5.70 (5.35)
antennal ratio	1.75- 2.20 (1.93)	2.17- 2.45 (2.33)
length/width prementum	.96- 1.04 (1.00)	1.16- 1.19 (1.17)
end hook on palpal lobe	yes	no
no. teeth palpal lobe	5- 7	8- 9
ligula	cx	cx
med. tooth ligula	yes	yes
denticles seg. 8	5.0- 9.0 (7.3)	5.0- 8.0 (6.7)

Table 9 (continued)

	<i>consanguis</i>	<i>rogersi</i>
denticles seg. 9	15.0- 20.0 (17.7)	17.0- 23.0 (19.4)
lat. spine seg. 6/length seg. 10	0- .18 (.06)	.33- .45 (.37)
lat. spine seg. 7/length seg. 10	.24- .47 (.37)	.47- .53 (.49)
lat. spine seg. 8/length seg. 10	.41- .64 (.52)	.63- .67 (.65)
lat. spine seg. 9/length seg. 10	.64- .87 (.76)	.93- 1.00 (.96)
dorsal length seg. 8/length seg. 10	1.76- 2.13 (1.90)	1.88- 2.00 (1.93)
dorsal length seg. 9/length seg. 10	1.94- 2.31 (2.11)	2.00- 2.13 (2.05)
dorsal length epiproct/length seg. 10	1.32- 1.47 (1.41)	1.50- 1.73 (1.59)
spines seg. 9 surpass post. marg. seg. 10	no	no
dorsal hooks on segments	0	8- 9
n	12	6

Table 10. Character states of *Stylurus* species. Explanation of characters in Table 1 (Appendix A).

	<i>amnicola</i>	<i>intricatus</i>	<i>ivae</i>	<i>laurae</i>	<i>notatus</i>	<i>plagiatus</i>	<i>scudderi</i>	<i>sptriceps</i>
total length (mm)	30.0-30.5	27.0-29	32.9-36.8 (34.5)	33.0- (34.6)	39.0 36.9	33.2-41.3	36.8-43.8 (39.1)	41.9- (43.1)
length abdomen (mm)	20.6-21.2	15.4-16.2	22.9-25.6 (23.8)	22.5-25.2 (24.2)	24.9	25.9-26.9	26.0-27.8 (26.7)	30.4-32.6 (31.8)
length hind femur (mm)	4.00	4.00	3.86-4.29 (4.03)	4.00-4.71 (4.23)	4.29	4.86-5.00	4.86-5.57 (5.21)	4.57-5.00 (4.77)
width head (mm)	5.86-6.00	5.21-5.36	6.14-6.57 (6.40)	6.29-6.71 (6.47)	6.00	6.14-6.43	6.71-7.57 (7.27)	6.14-6.57 (6.31)
width abdomen (mm)	6.29-6.36	7.14-7.86	7.71-9.14 (8.28)	7.14-8.29 (7.66)	6.57	7.14-7.71	8.43-9.43 (8.87)	6.43-7.57 (7.03)
total length/femur	7.50-7.62	6.75-7.25	8.02-9.20 (8.56)	7.22-9.10 (8.22)	9.09	6.83-7.38	6.80-8.02 (7.52)	8.76-9.54 (9.02)
antennal ratio	1.67-1.83	1.67-1.80	1.71-1.87 (1.81)	1.60-1.86 (1.77)	1.86	1.83-2.17	1.56-2.00 (1.72)	1.86-2.25 (1.97)
length/width prementum	1.60-1.63	1.28-1.39	1.57-1.70 (1.64)	1.33-1.55 (1.46)	1.28	1.32-1.45	1.30-1.42 (1.36)	1.24-1.38 (1.31)
no. teeth palpal lobe	2 3	1 4	2	2 3	3	2 3	1 4	2
ligula	cx	cx	cx	cx	st	cx	cx	st
lat. spine seg. 6/length seg. 10	.20- .29	.17- .24	.22- .35 (.26)	.26- .40 (.33)	.29	.22- .27	.28- .41 (.34)	.09- .16 (.14)

Table 10 (continued)

	<i>annicola</i>	<i>intricatus</i>	<i>ivae</i>	<i>laurae</i>	<i>notatus</i>	<i>plagiatus</i>	<i>scudderii</i>	<i>spinticeps</i>
lat. spine seg. 7/length seg. 10	.29- .31	.28- .31	.29- .41 (.34)	.34- .48 (.41)	.34	.31- .34	.33- .47 (.39)	.13- .20 (.17)
lat. spine seg. 8/length seg. 10	.29- .31	.41- .31	.36- .45 (.39)	.45- .42 (.49)	.37	.43- .45	.42- .60 (.50)	.16- .30 (.20)
lat. spine seg. 9/length seg. 10	.40- .54	.48- .62	.46- .56 (.49)	.57- .68 (.63)	.61	.80- .82	.56- .73 (.64)	.50- .61 (.56)
dorsal length seg. 8/length seg. 10	1.89- 1.94	1.86- 1.93	1.71- 2.22 (1.91)	1.76- 1.86 (1.81)	2.00	1.92- 2.05	1.83- 2.05 (1.90)	2.21- 2.64 (2.37)
dorsal length seg. 9/length seg. 10	2.17- 2.40	1.86- 2.07-	2.05- 2.56 (2.28)	2.43- 2.56 (2.50)	3.07	2.73- 2.82	2.17- 2.37 (2.26)	4.04- 4.77 (4.37)
dorsal length epiproct/ length seg. 10	1.37- 1.57	1.38-	1.58- 1.76 (1.64)	.91- 1.16 (1.02)	1.07	.93 .94	1.11- 1.40 (1.22)	.84- 1.02 (.90)
dorsal spines on segments	9	0	8- 9	9	9	9	9	9
length/width 9th seg.	.73- .91	.44- .50	.67- .79 (.70)	.75- .92 (.83)	1.18	1.00- 1.20	.63- .79 (.73)	2.00- 2.50- (2.27)
epiproct/ cerci	1.31- 1.41	1.11- 1.18	1.38- 1.54 (1.44)	1.05- 1.18 (1.11)	1.16	1.21- 1.24	1.02- 1.16 (1.07)	1.12- 1.22 (1.15)
seg. 9/ seg. 8	1.15- 1.24	1.00- 1.07	1.15- 1.23 (1.19)	1.33- 1.45 (1.38)	1.54	1.33- 1.47	1.14- 1.23 (1.20)	1.81- 1.94 (1.85)
n	2	2	5	10	1	2	10	5

Table 11. Sources of published distributional data.

Region	Source
Alabama	Smith and Hodges, 1938; Wright, 1943b.
Arkansas	Harp and Rickett, 1977.
Connecticut	Garman, 1927.
District of Columbia	Donnelly, 1961.
Florida	Byers, 1930, 1934, 1936; Davis and Fluno, 1938; Westfall, 1953.
Georgia	Root, 1924.
Illinois	Needham and Hart, 1901.
Indiana	Montgomery, 1925-1955; Williamson, 1917.
Iowa	Elrod, 1898; Hummel and Haman, 1975; Miller, 1906; Wells, 1917; Whedon, 1912.
Kansas	Huggins, 1978; Kennedy, 1917.
Kentucky	Resner, 1970; Williamson, 1905.
Louisiana	Bick, 1957.
Maine	Borrer, 1944, 1951.
Maryland	Fisher, 1940; Moorefield, 1941.
Massachusetts	White, 1979; White et al., 1974.
Mississippi	Bick, 1950; Westfall, 1952.
Michigan	Kormondy, 1958, 1962.
Missouri	Williamson, 1932b.
New Hampshire	White and Morse, 1973.
New Jersey	Beatty, 1946.
New York	Hood, 1932; Needham, 1903b, 1928.
North Carolina	Brimley, 1938; Westfall, 1942.

Table 11 (continued)

Region	Source
North and South Dakota	Bick et al., 1977.
Ohio	Alrutz, 1959, 1961; Balcuinas, 1980; Borrer, 1937, 1938; Borrer and Epstein, 1942; Cruden and Currie, 1961; Harwood, 1960.
Oklahoma	Bick and Bick, 1957.
Pennsylvania	Ahrens et al., 1968; Beatty et al., 1969, 1970.
South Carolina	Montgomery, 1940; White et al., 1980.
Tennessee	Trogdon, 1961; Wright, 1938, 1943a.
Texas	Ferguson, 1940; Gloyd, 1958; Harwell, 1951.
Virginia	Gloyd, 1951
West Virginia	Cruden, 1962; Tarter, 1976.
Wisconsin	Hilsenhoff, 1972; Muttkowski, 1908, 1910c; Ries, 1969.
United States	Dunkle, 1975; Kormondy, 1960; Roback and Westfall, 1967; Wilson, 1909.
Northeast	Howe, 1917-1921.
Southeast	Byers, 1931; Cuyler, 1968; Tennessen, 1979; Williamson, 1903a, 1934; Wilson, 1912; Wright, 1937, 1939.
Midwest	Ahrens, 1938.
Southwest	Williamson, 1914.
Canada	Walker, 1958; Walker and Corbet, 1975.

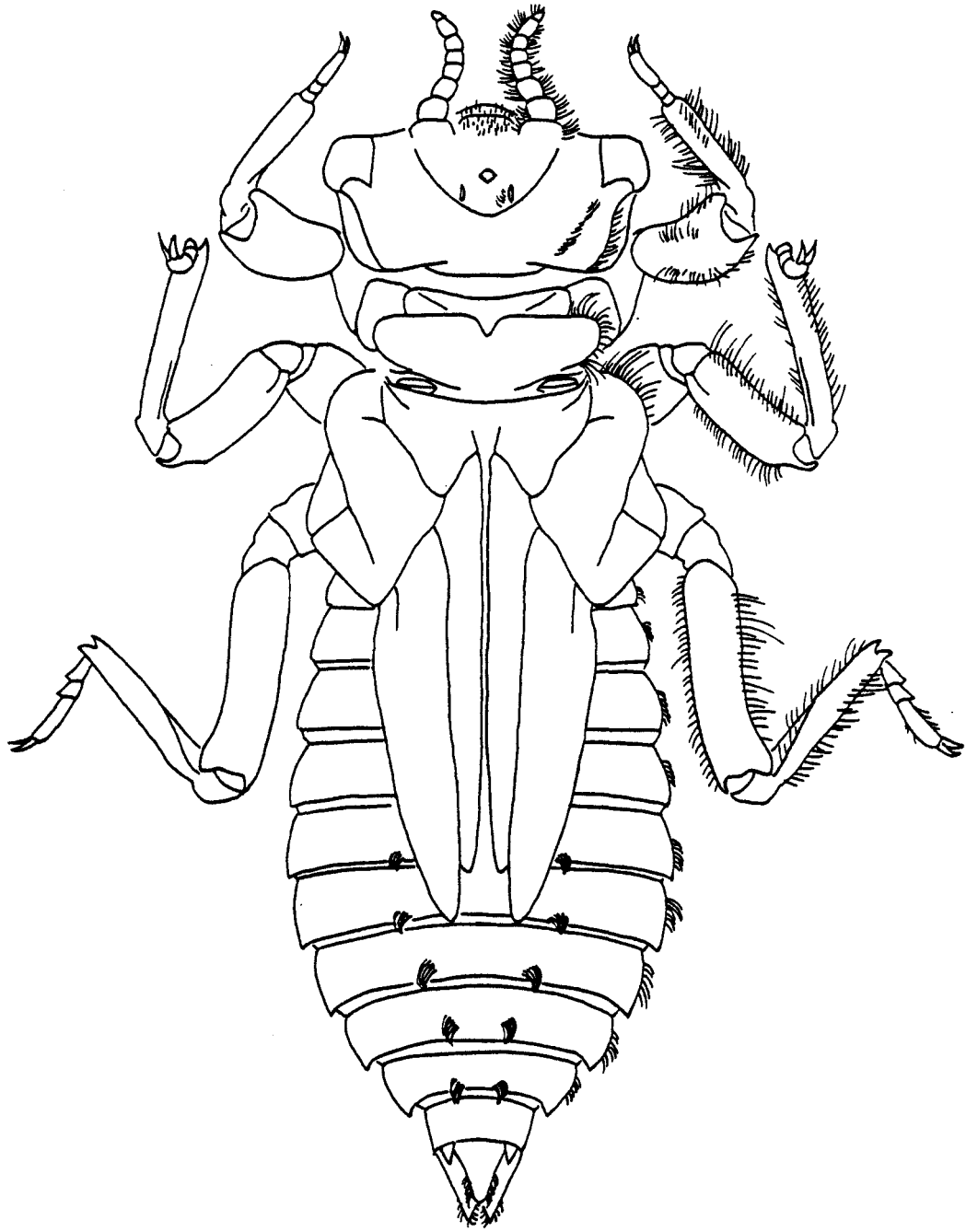


Figure 1. *Tachopteryx thoreyi*.

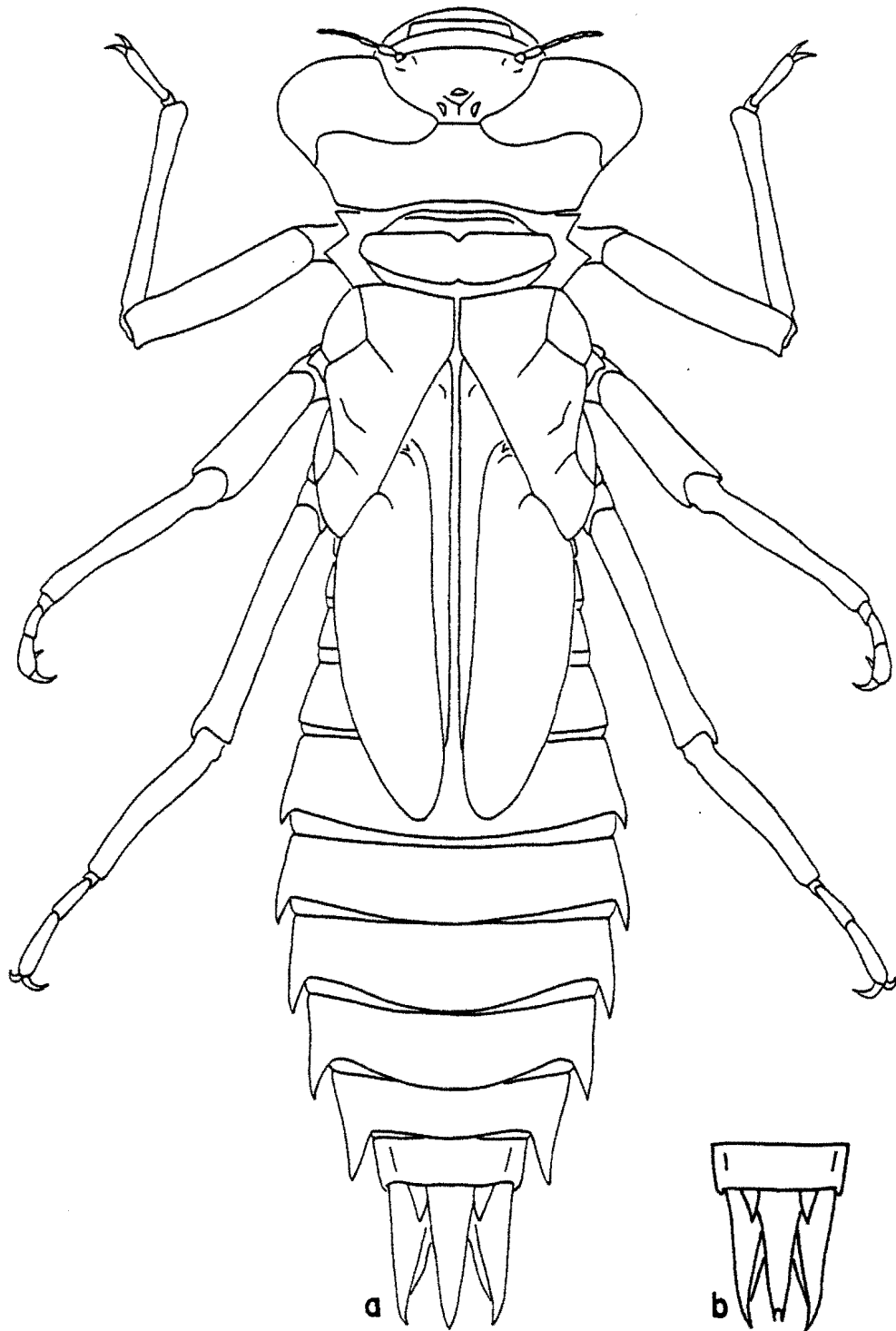


Figure 2. *Boyeria*, a. *Boyeria grafiana*, b. terminal abdominal appendages of *Boyeria vinosa*.

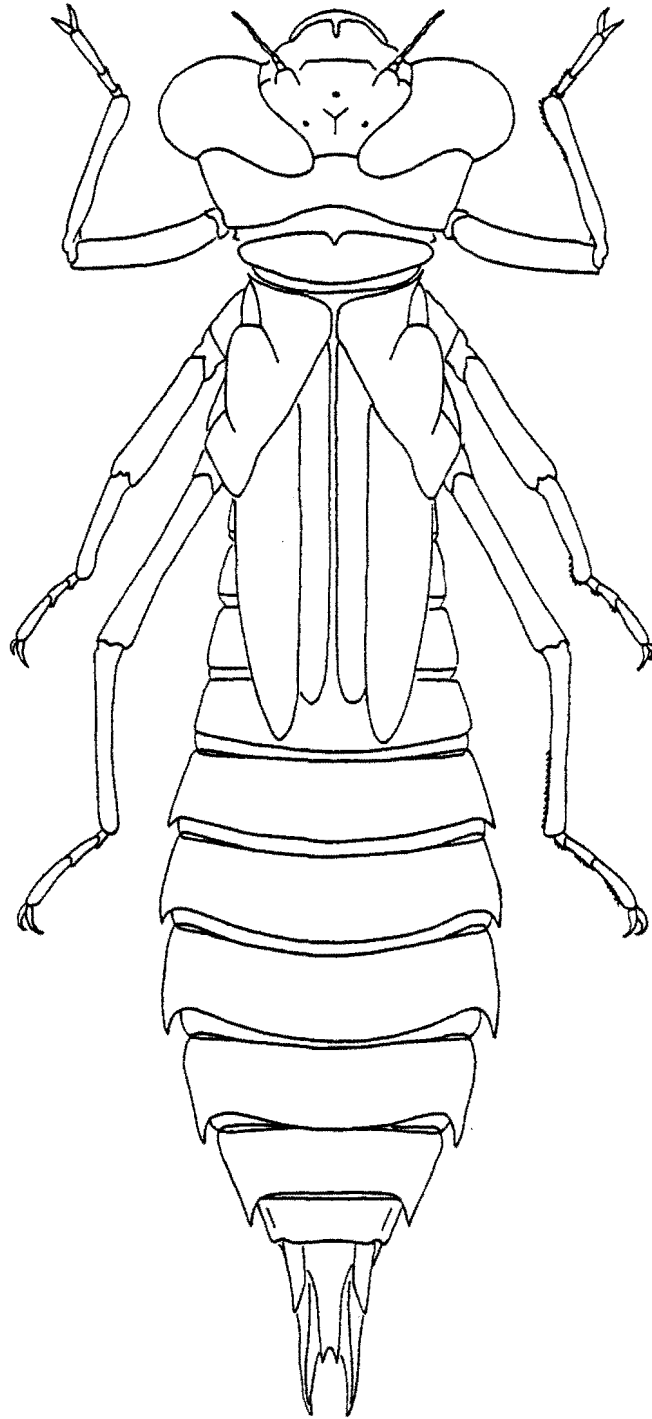


Figure 3. *Basiaeshna janata*.

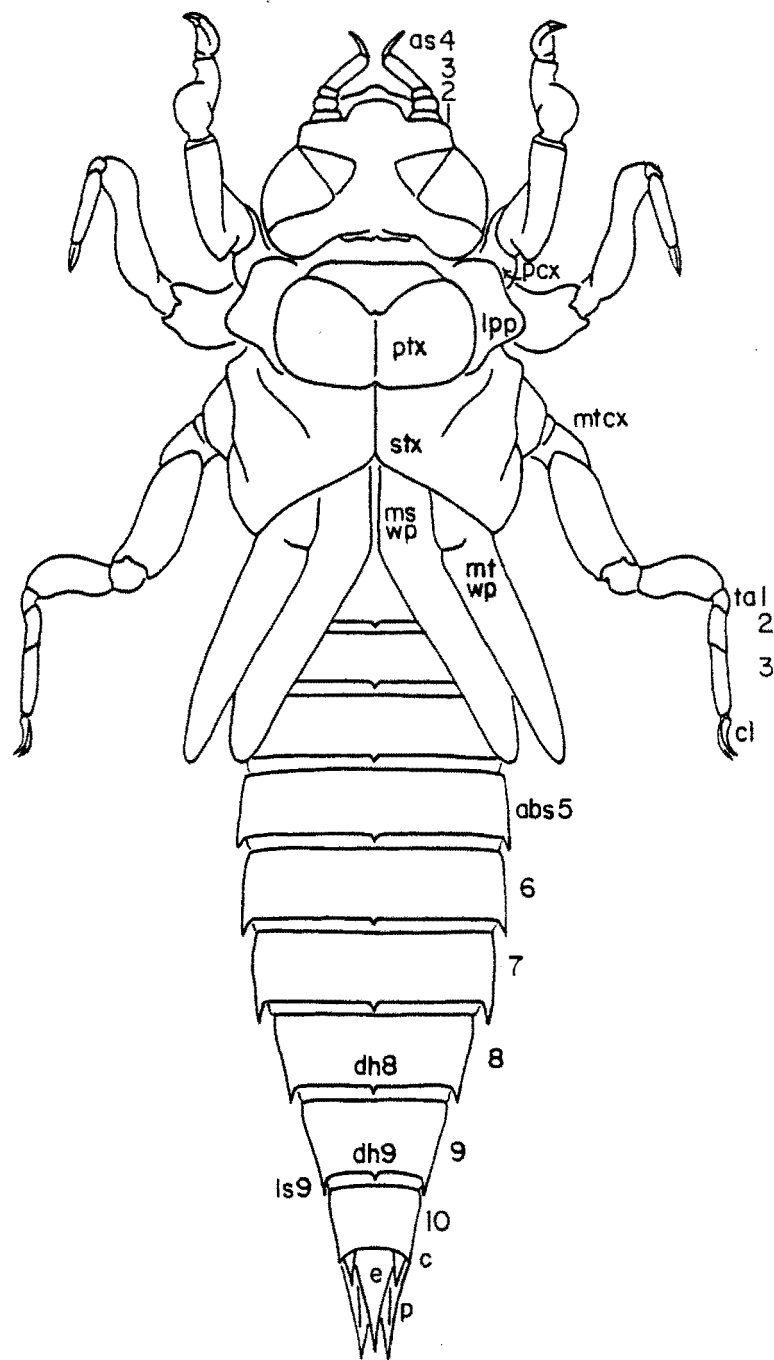


Figure 4. *Progomphus obscurus* (as=antennal segment, ta=tarsus, cl=claw, ti=tibia, f=femur, mtcx=metacoxa, mscx=mesocoxa, pcx=procoxa, ptx=prothorax, lpp=lateral prothoracic process, stx=synthorax, mswp=mesothoracic wing pad, mtwp=metathoracic wing pad, abs=abdominal segment, dh=dorsal hook, ls=lateral spine, c=cerci, e=epiproct, p=paraproct).

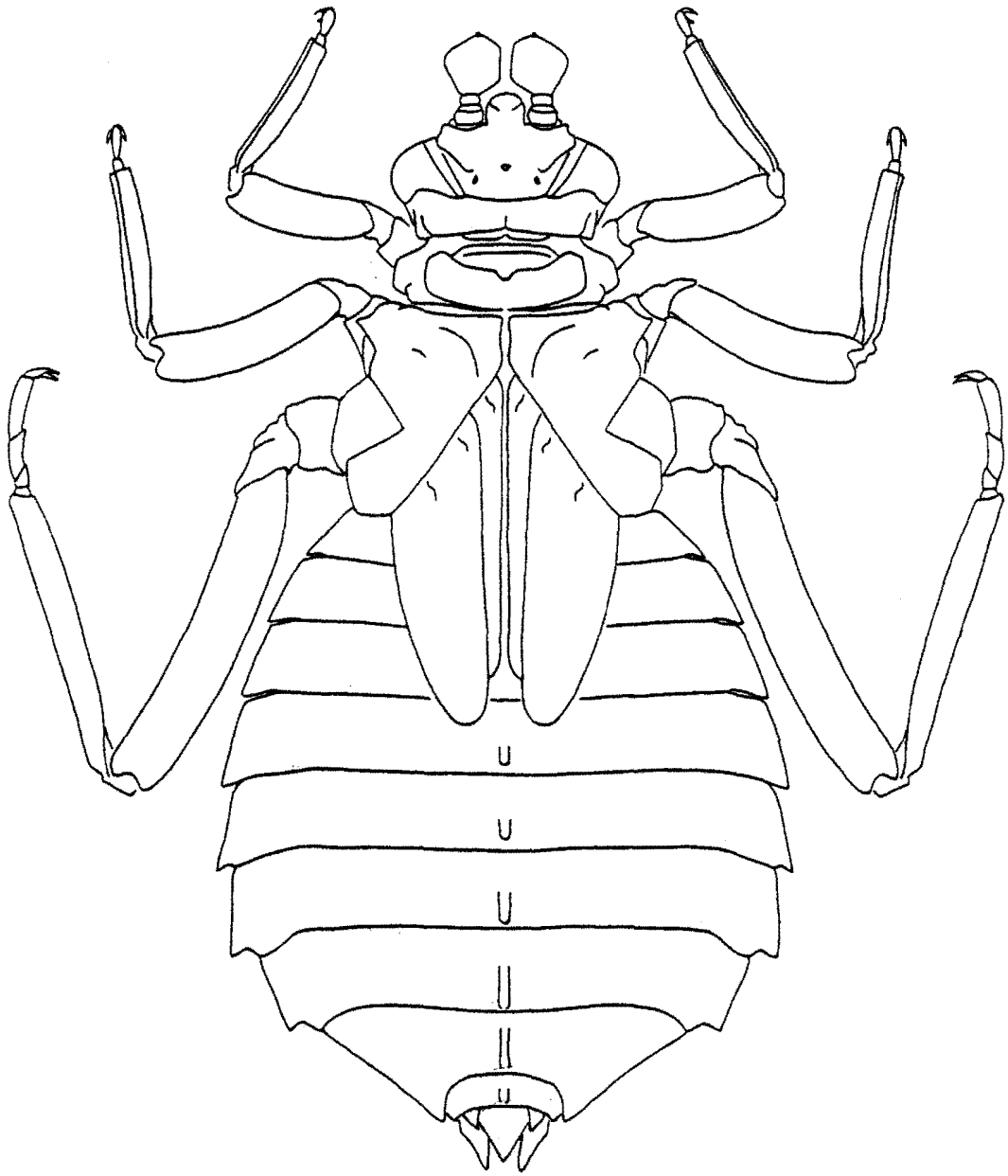


Figure 5. *Hagenius brevistylus*.

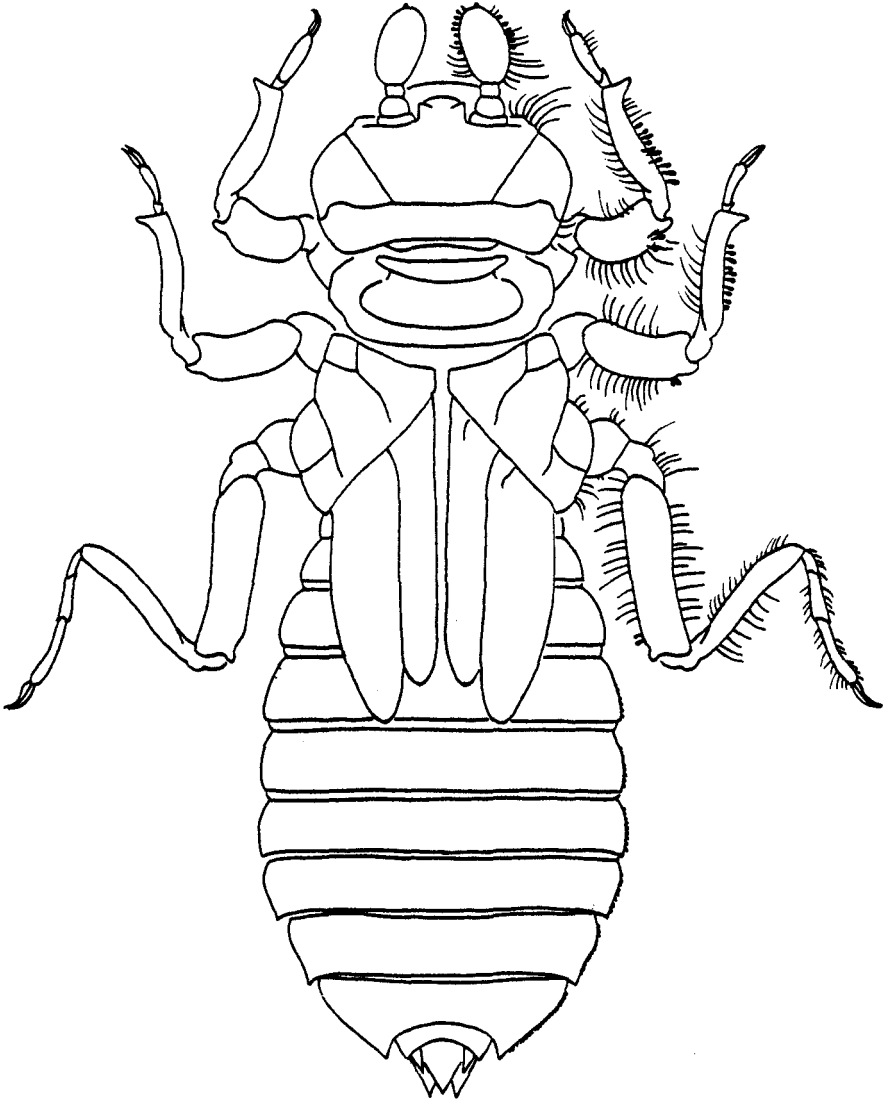


Figure 6. *Lanthus vernalis*.

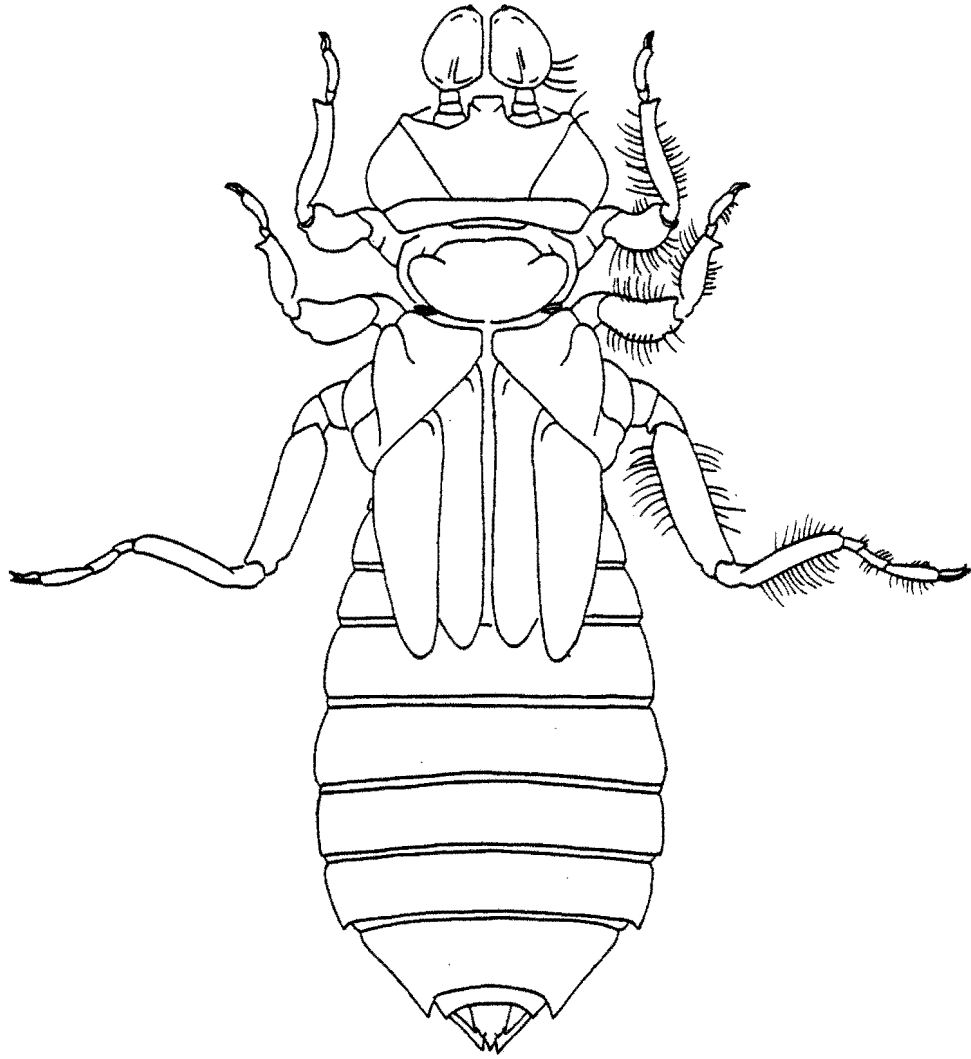


Figure 7. *Stylogomphus albistylus*.

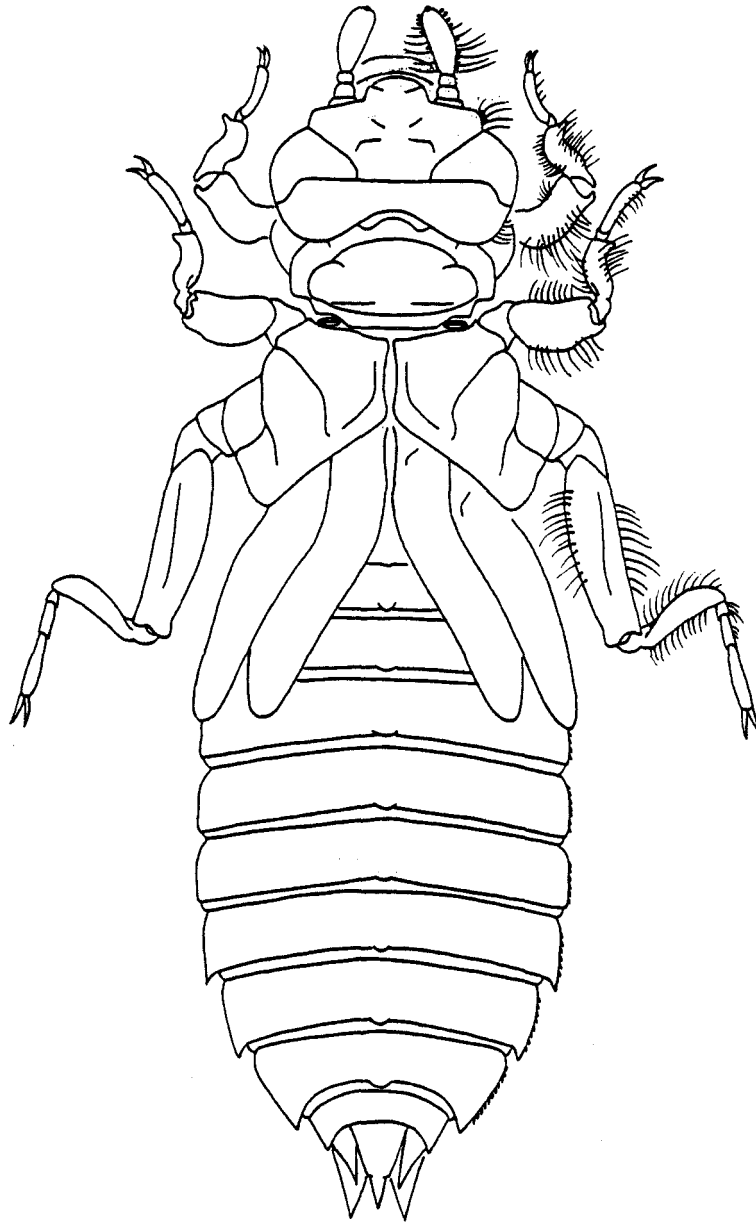


Figure 8. *Ophiogomphus rupinsulensis*.

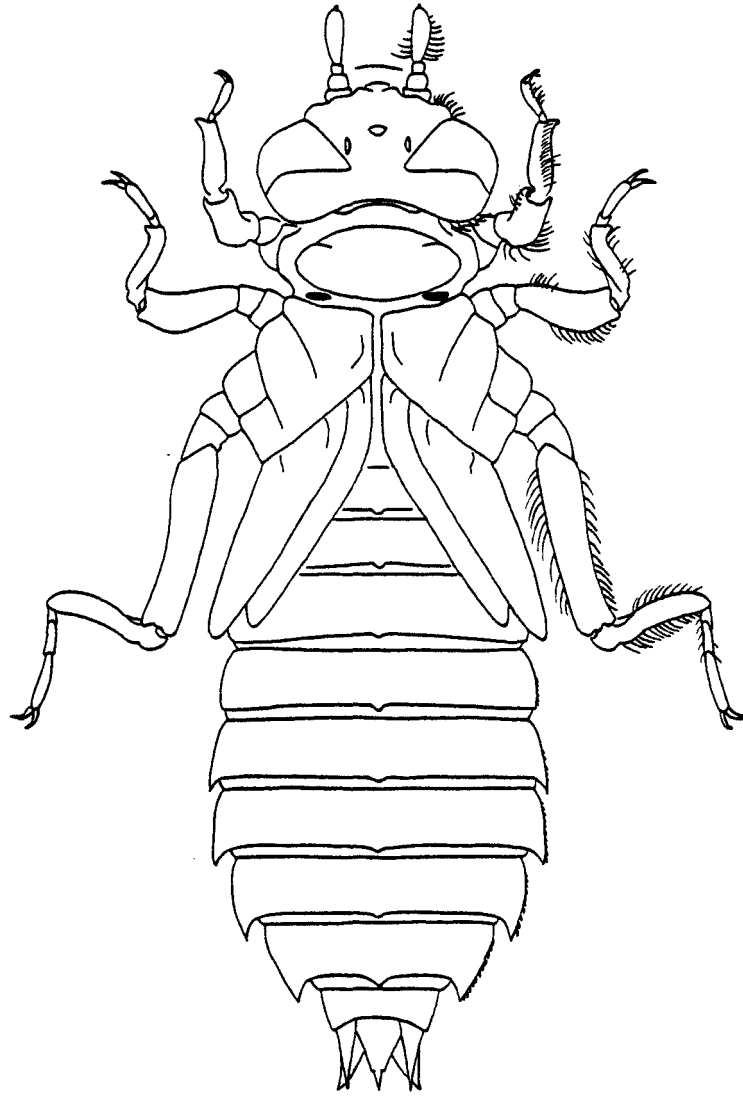


Figure 9. *Erpetogomphus designatus*.

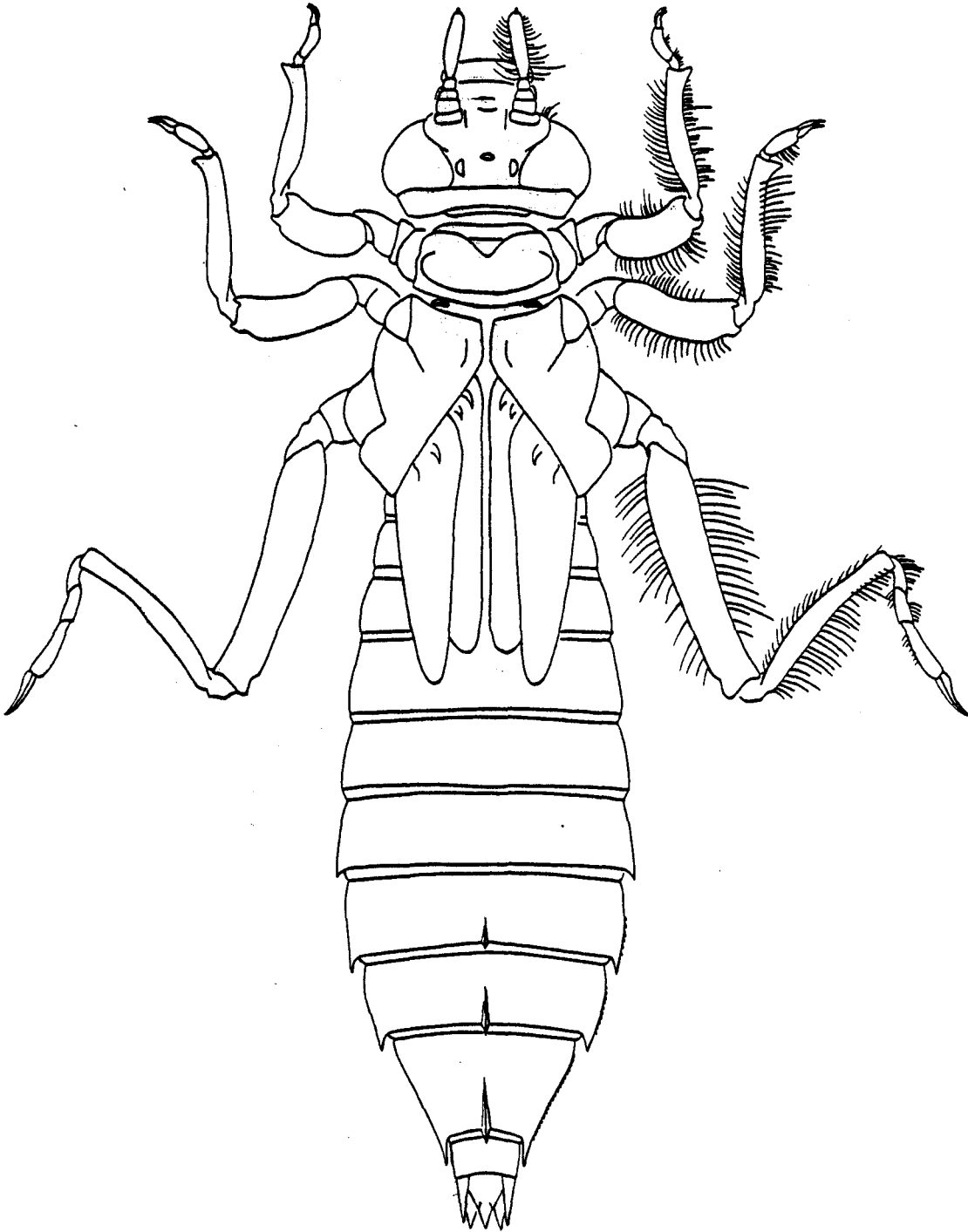


Figure 10. *Dromogomphus spinosus*.

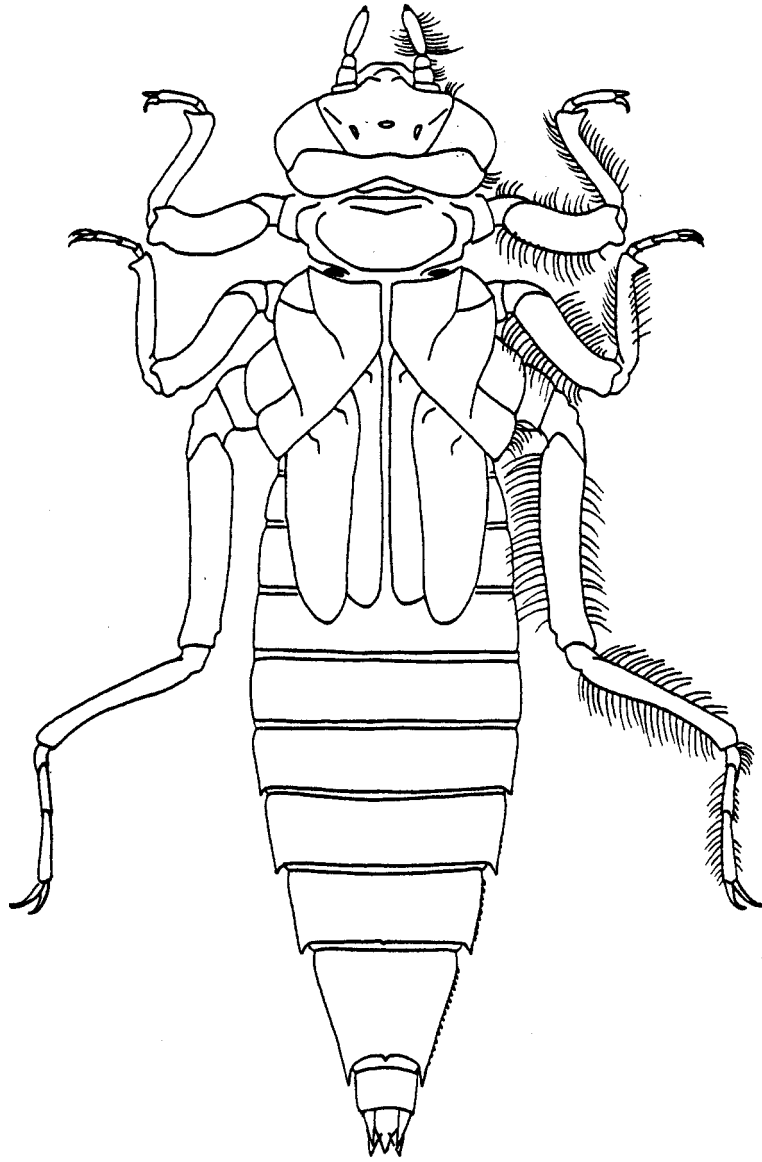


Figure 11. *Gomphus quadricolor*.

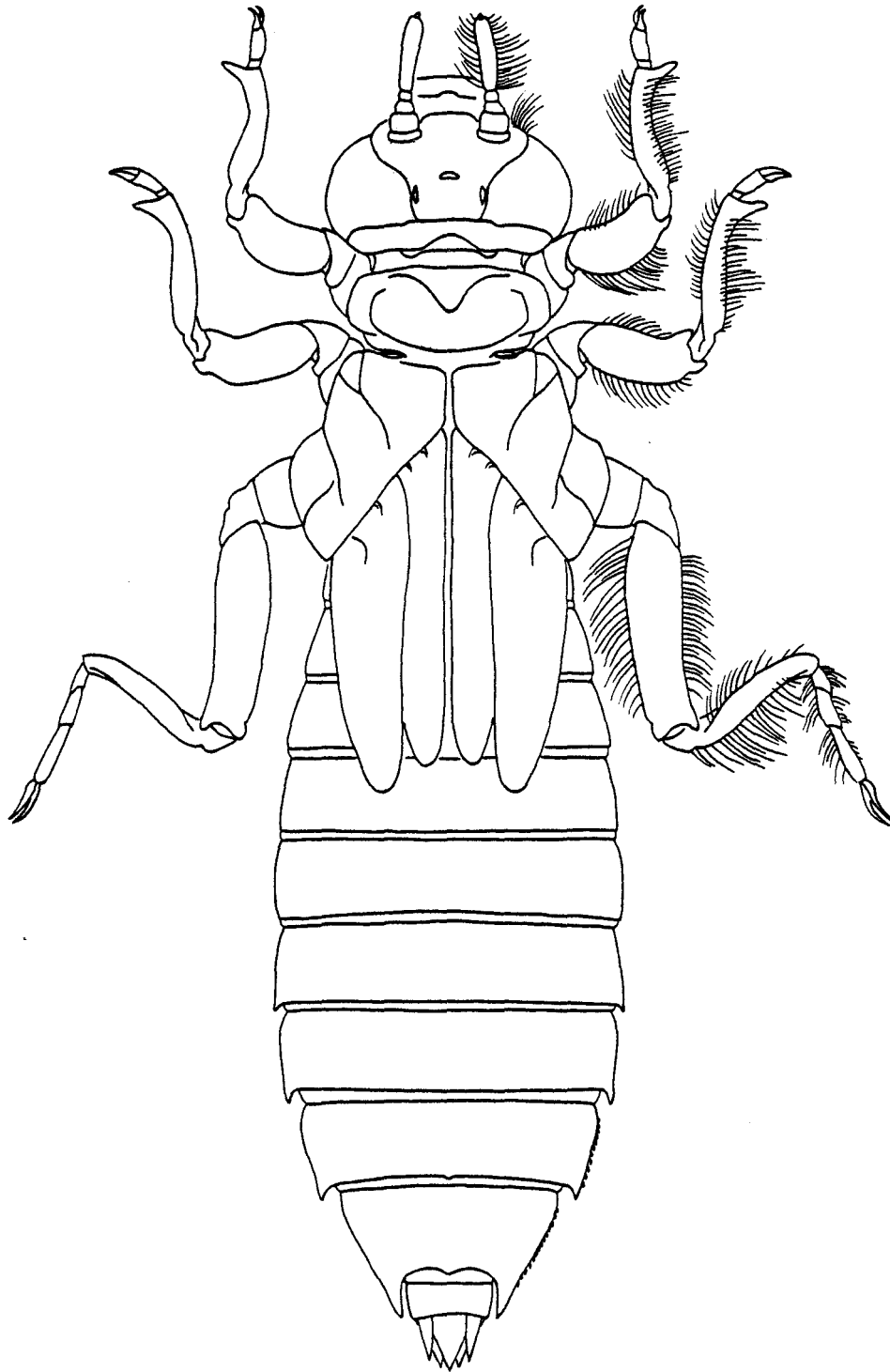


Figure 12. *Gomphurus vastus*.

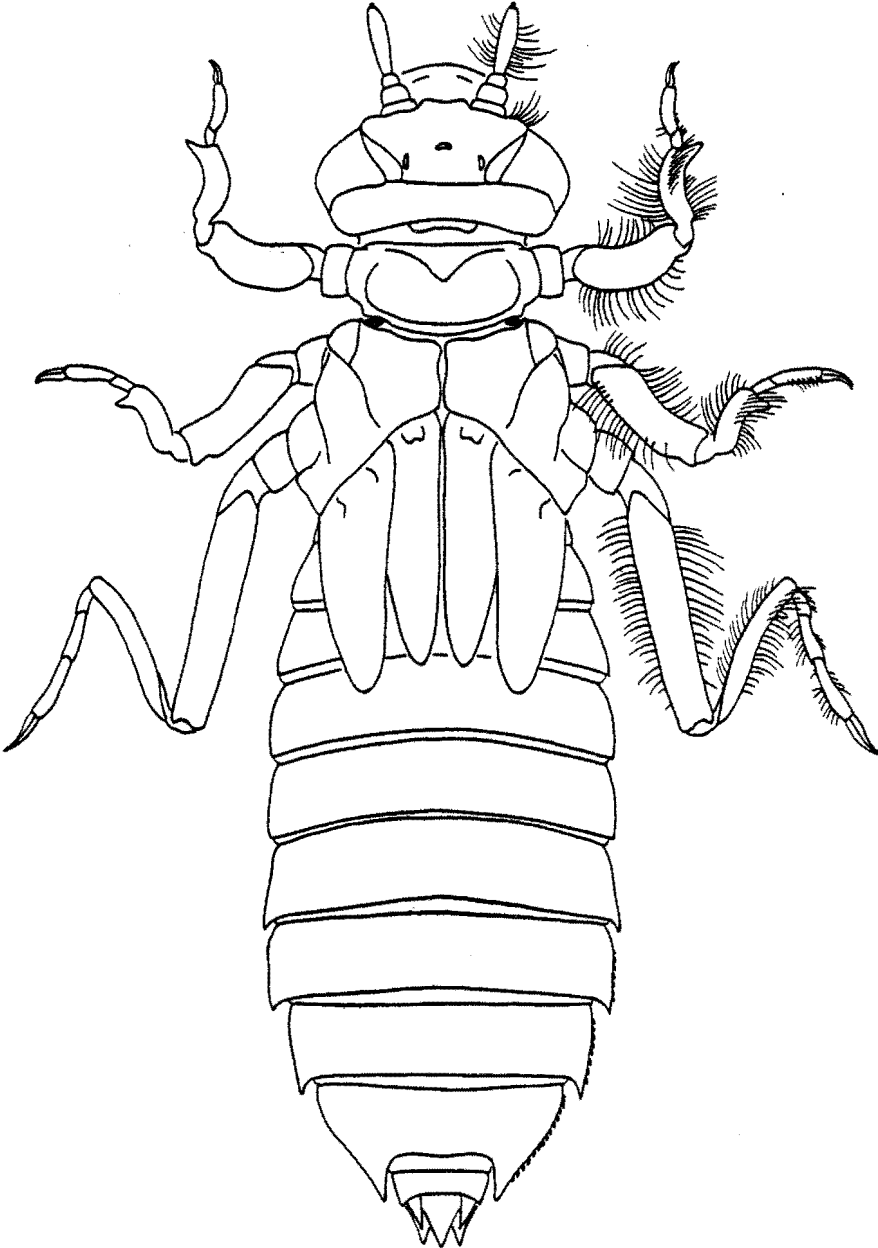


Figure 13. *Hylogomphus viridifrons*.

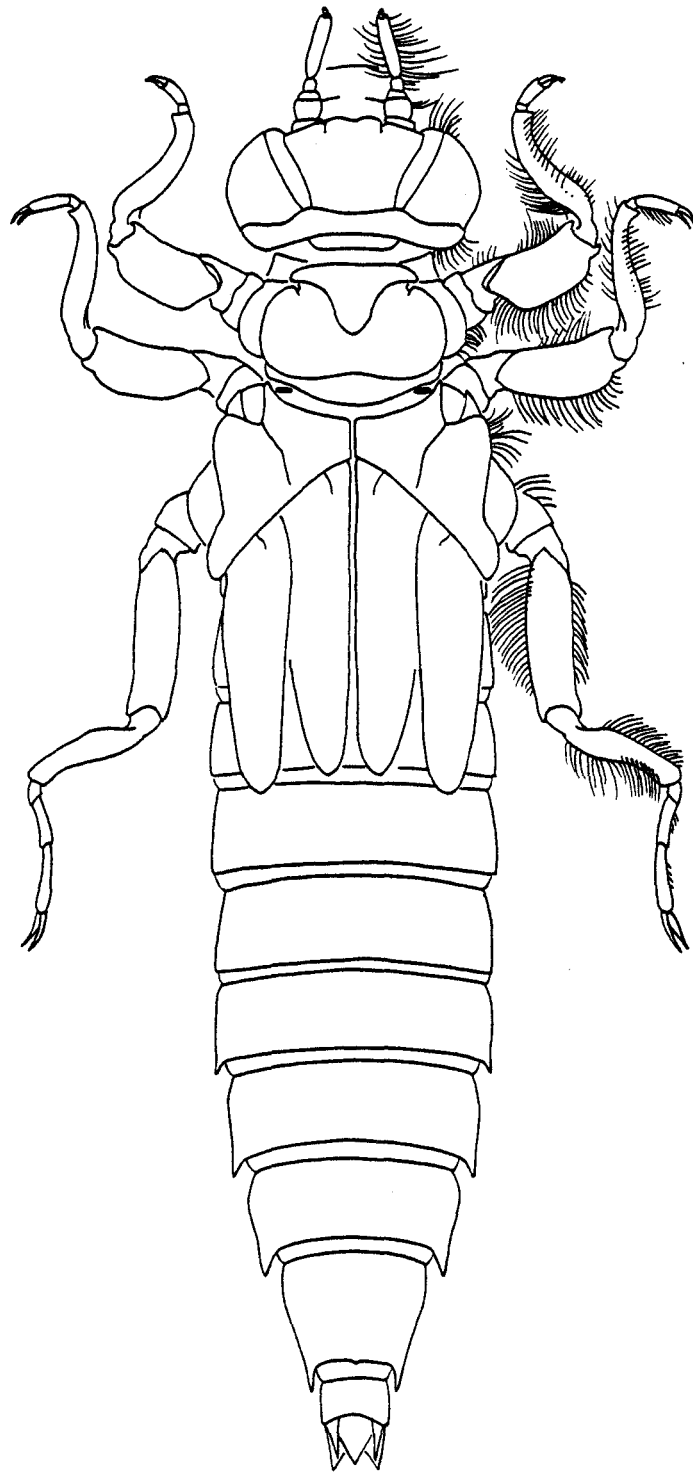


Figure 14. *Stylurus laurae*.

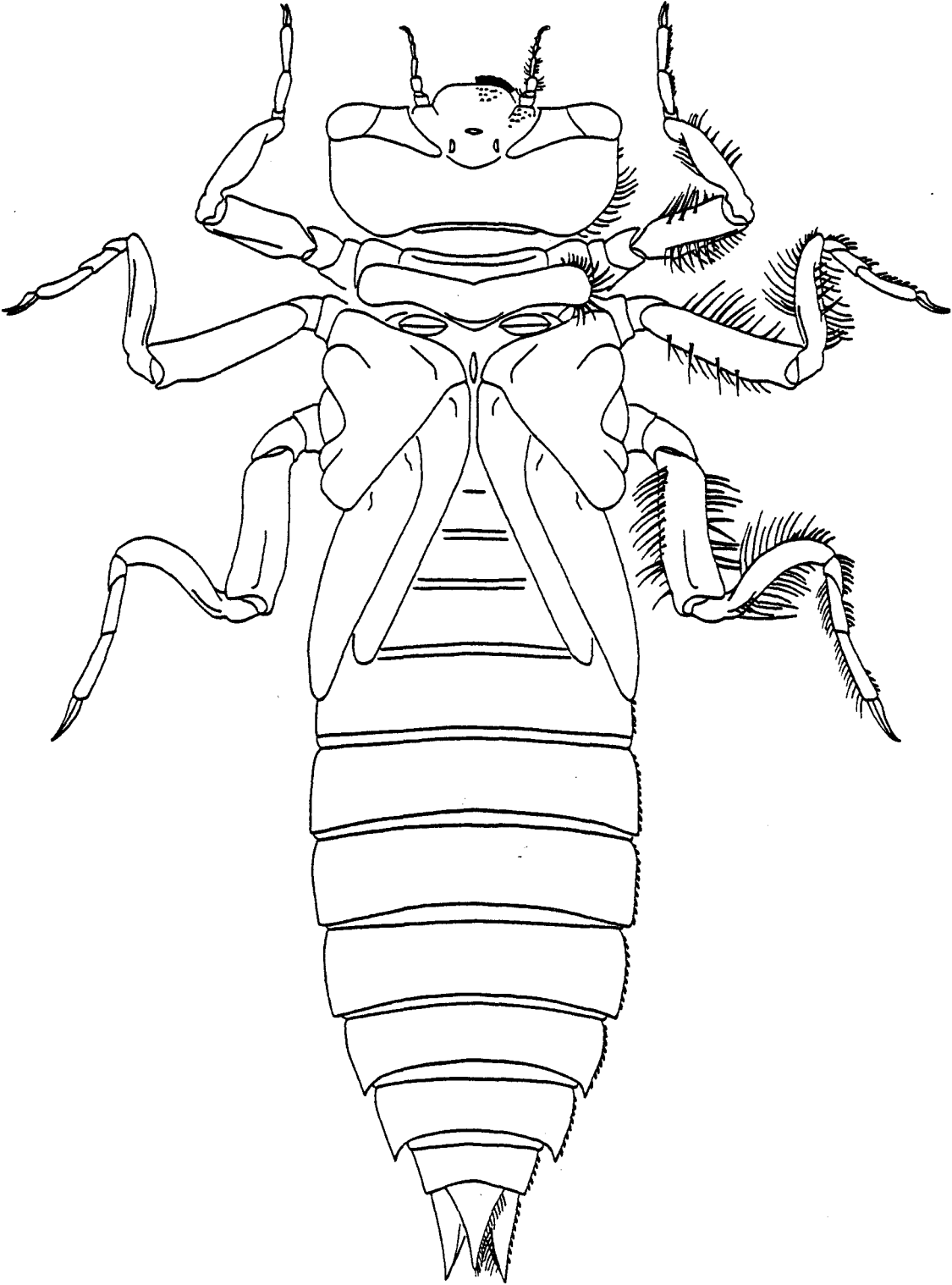


Figure 15. *Cordulegaster erronea*.

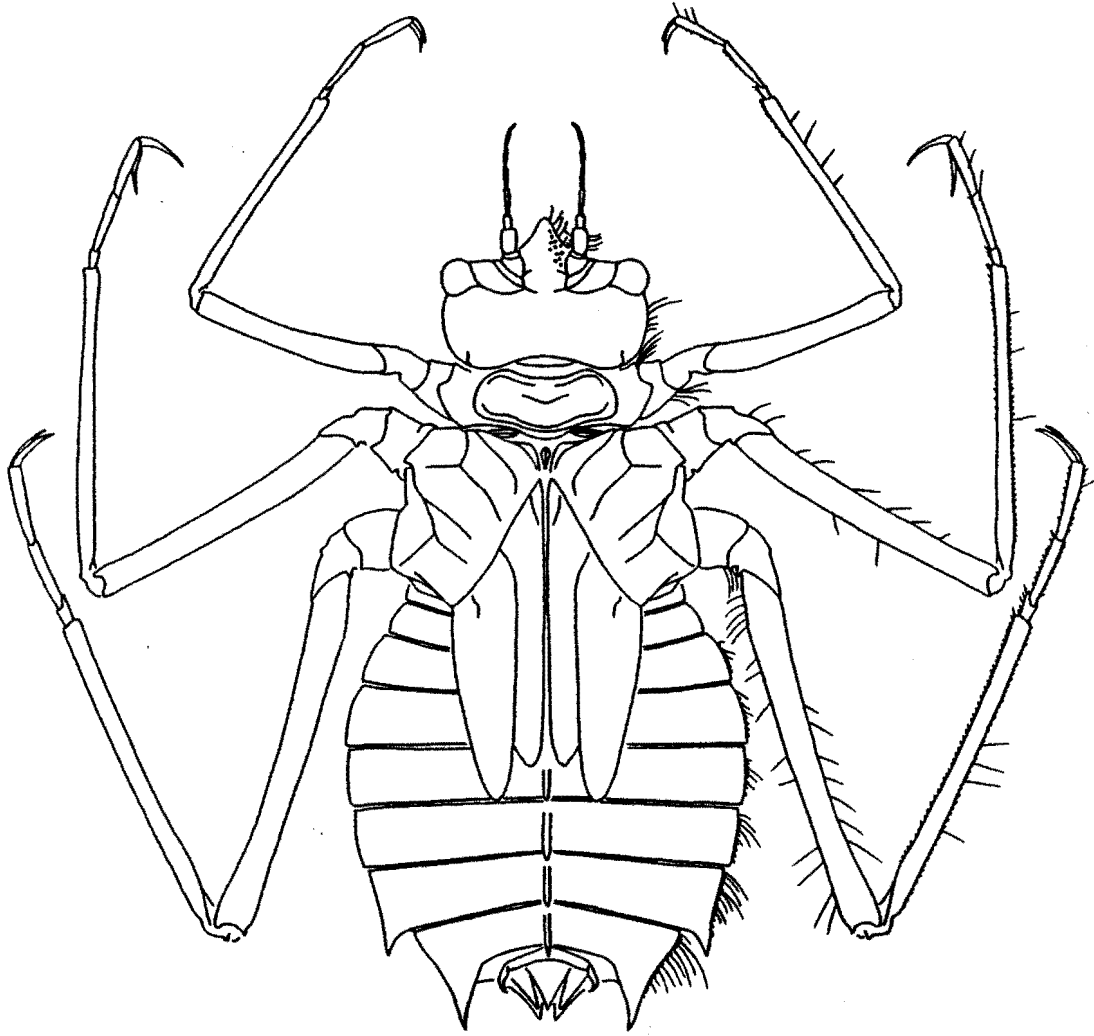


Figure 16. *Didymops transversa*.

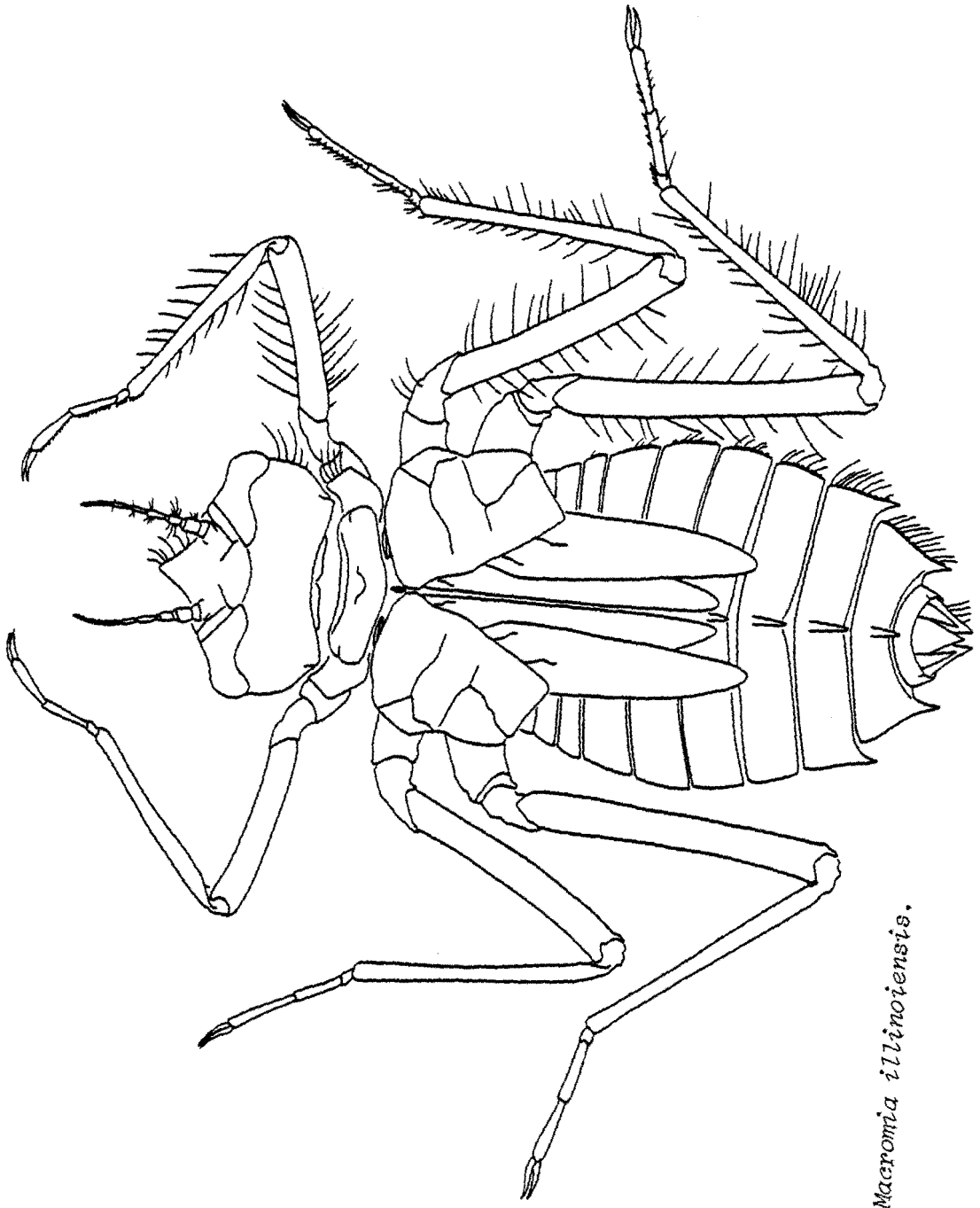


Figure 17. *Macromia illinoensis*.

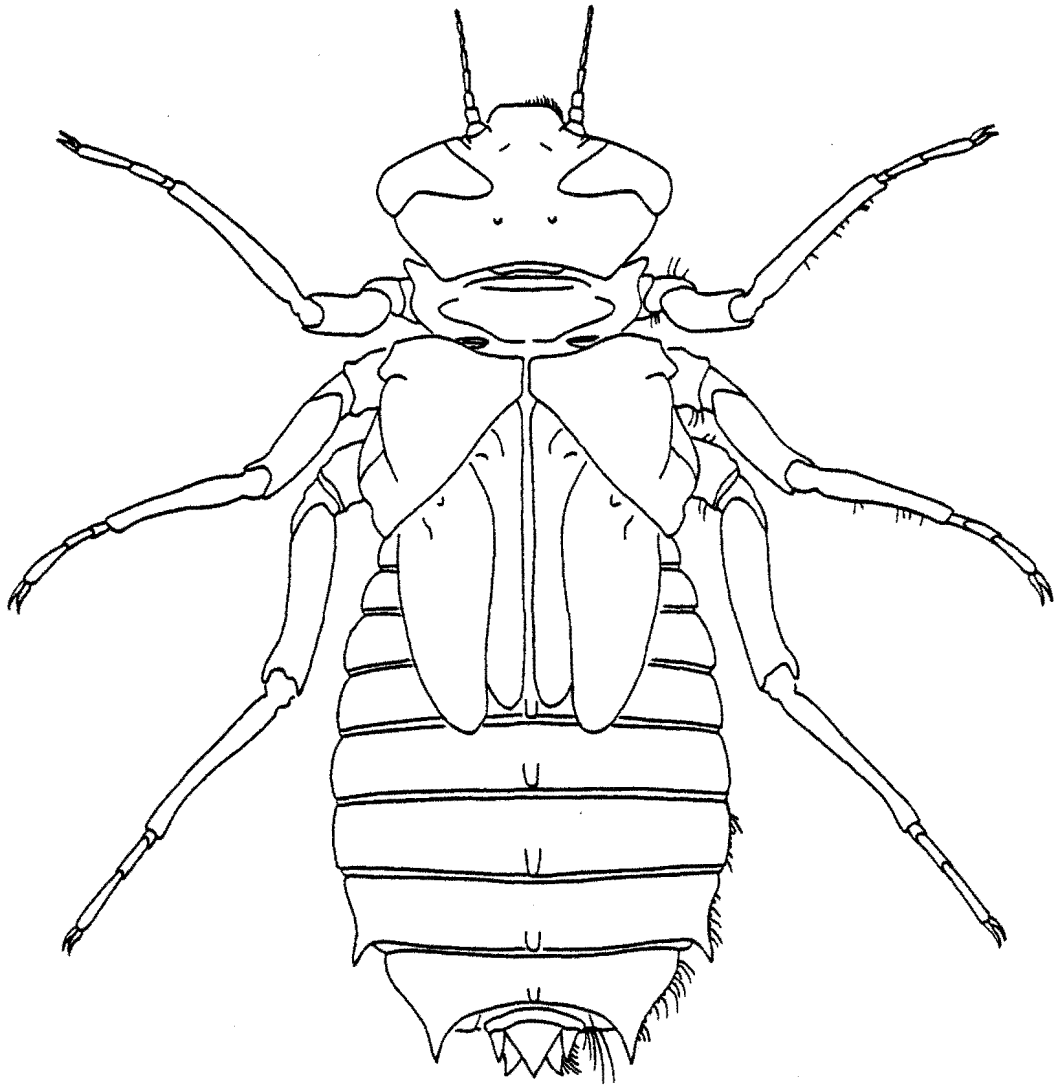


Figure 18. *Neurocordulia yamaskanensis*.

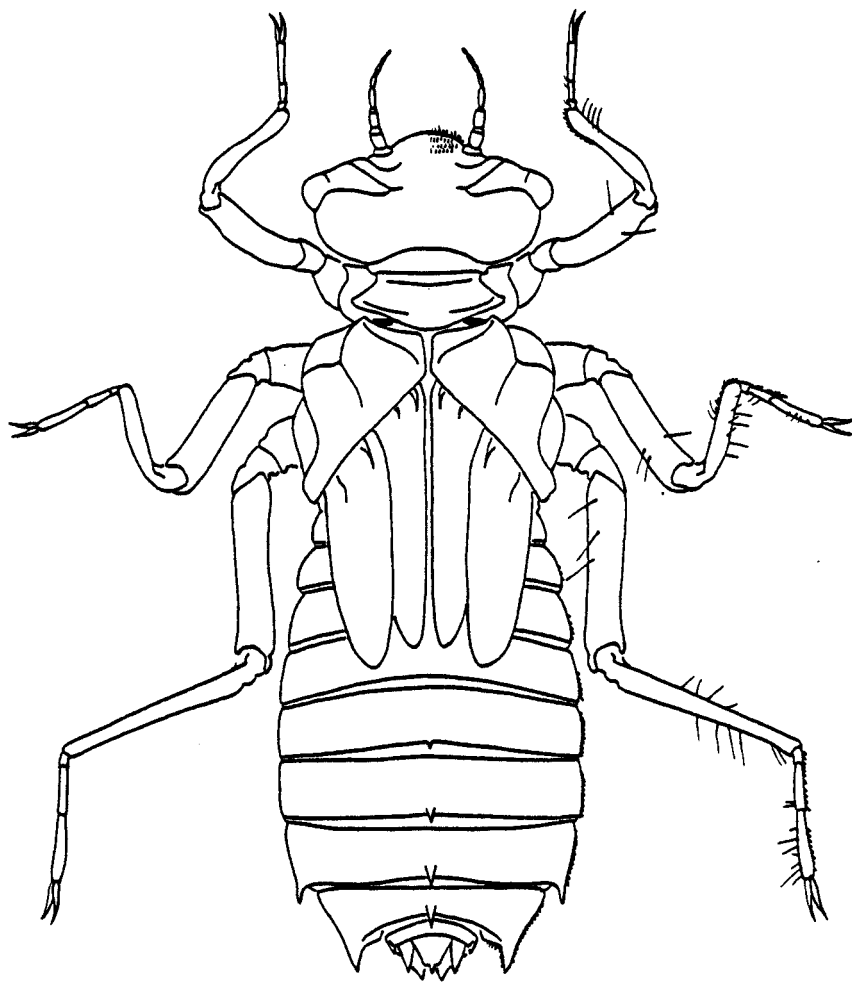


Figure 19. *Helocordulia uhleri*.

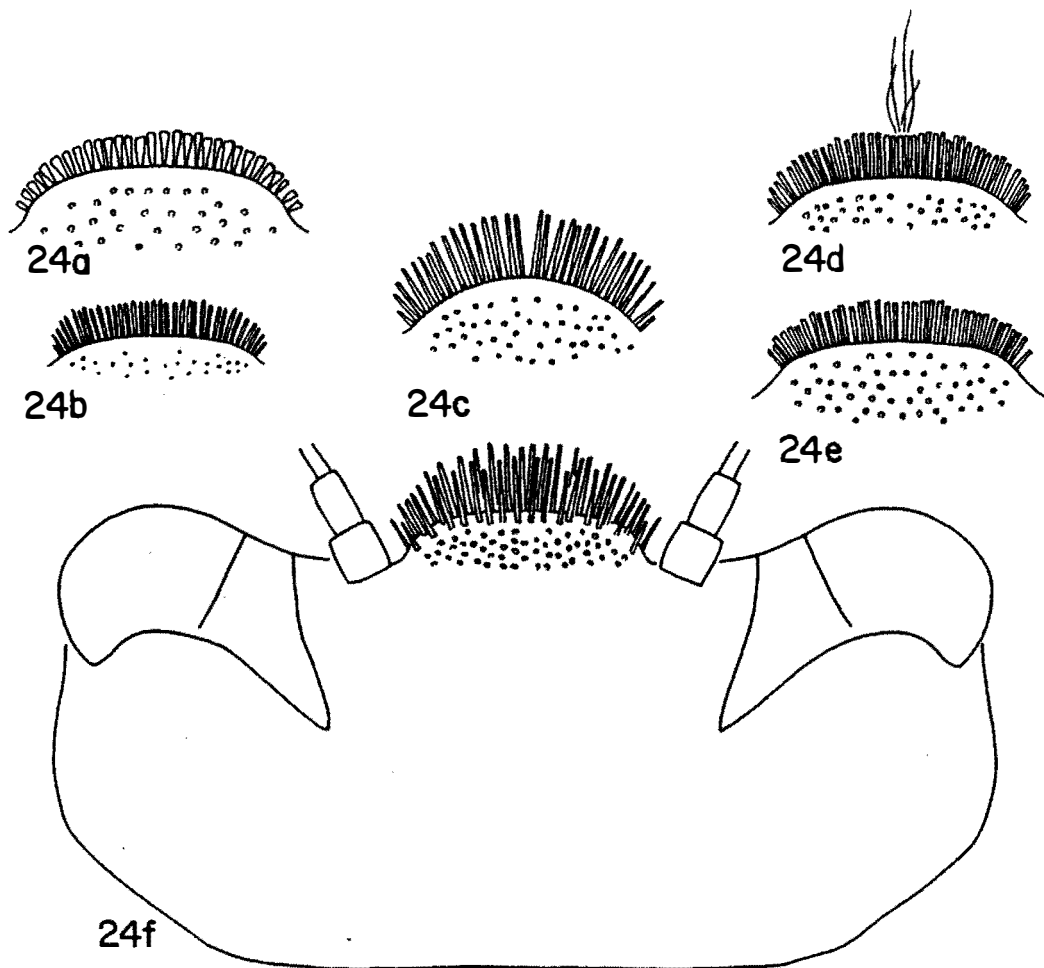
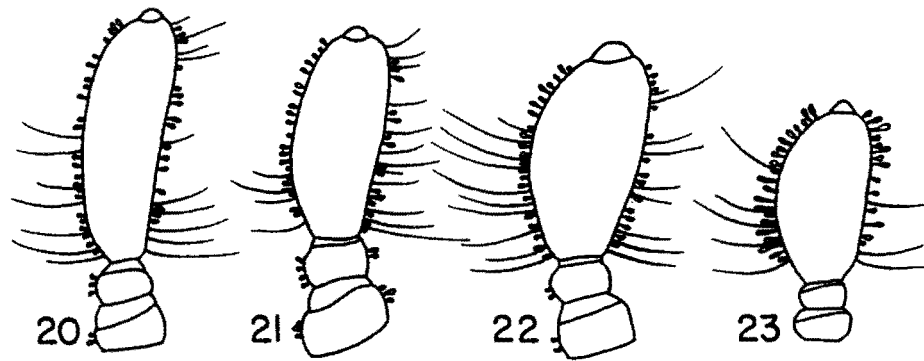


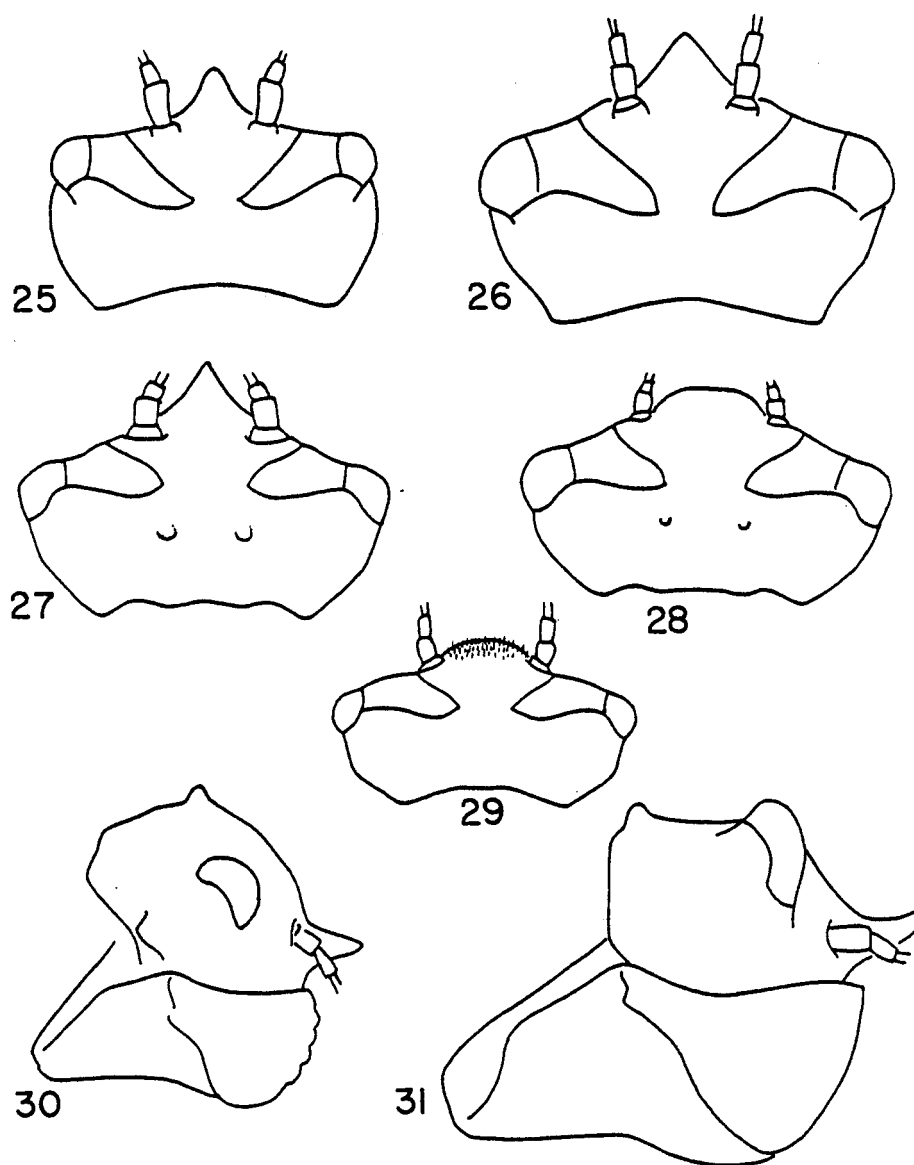
Figure 20. Antenna of *Ophiogomphus rupinsulensis*.

Figure 21. Antenna of *Ophiogomphus* sp. A.

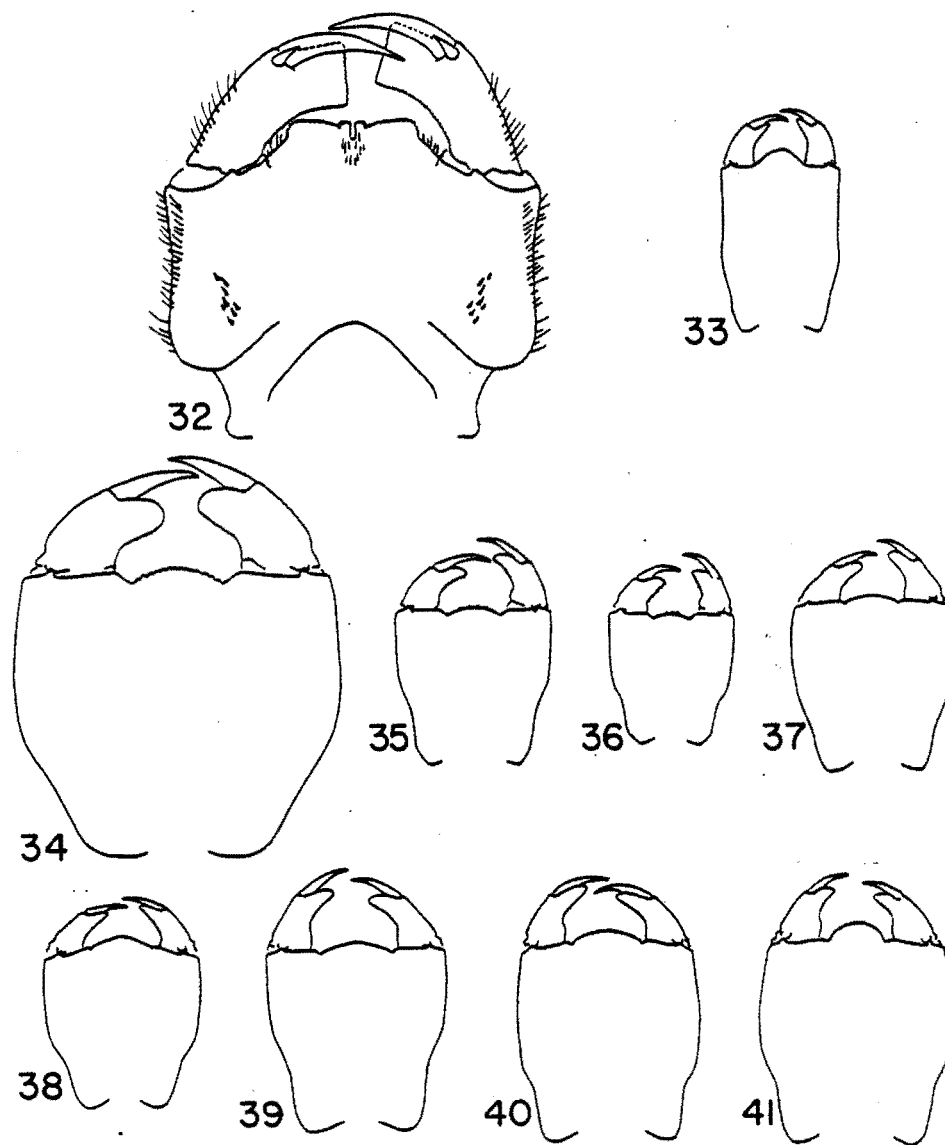
Figure 22. Antenna of *Ophiogomphus mainensis*.

Figure 23. Antenna of *Ophiogomphus howei*.

Figure 24. Setation of frontal shelf of *Cordulegaster*, a. *C. erronea*, b. *C. sayi*, c. *C.o. obliqua*, d. *C. diastatops*, e. *C. maculata*, f. *C.o. fasciata*.



- Figure 25. Dorsum of head of *Didymops transversa*.
 Figure 26. Dorsum of head of *Macromia illinoiensis*.
 Figure 27. Dorsum of head of *Neurocordulia molesta*.
 Figure 28. Dorsum of head of *Neurocordulia yamaskanensis*.
 Figure 29. Dorsum of head of *Helocordulia uhleri*.
 Figure 30. Lateral view of head of *Neurocordulia molesta*.
 Figure 31. Lateral view of head of *Macromia georgina*.



- Figure 32. Prementum of *Tachopteryx thoreyi*.
 Figure 33. Prementum of *Progomphus obscurus*.
 Figure 34. Prementum of *Hagenius brevistylus*.
 Figure 35. Prementum of *Stylogomphus albistylus*.
 Figure 36. Prementum of *Lanthus vernalis*.
 Figure 37. Prementum of *Erpetogomphus designatus*.
 Figure 38. Prementum of *Ophiogomphus howei*.
 Figure 39. Prementum of *Ophiogomphus mainensis*.
 Figure 40. Prementum of *Ophiogomphus rupinsulensis*.
 Figure 41. Prementum of *Ophiogomphus* sp. A.

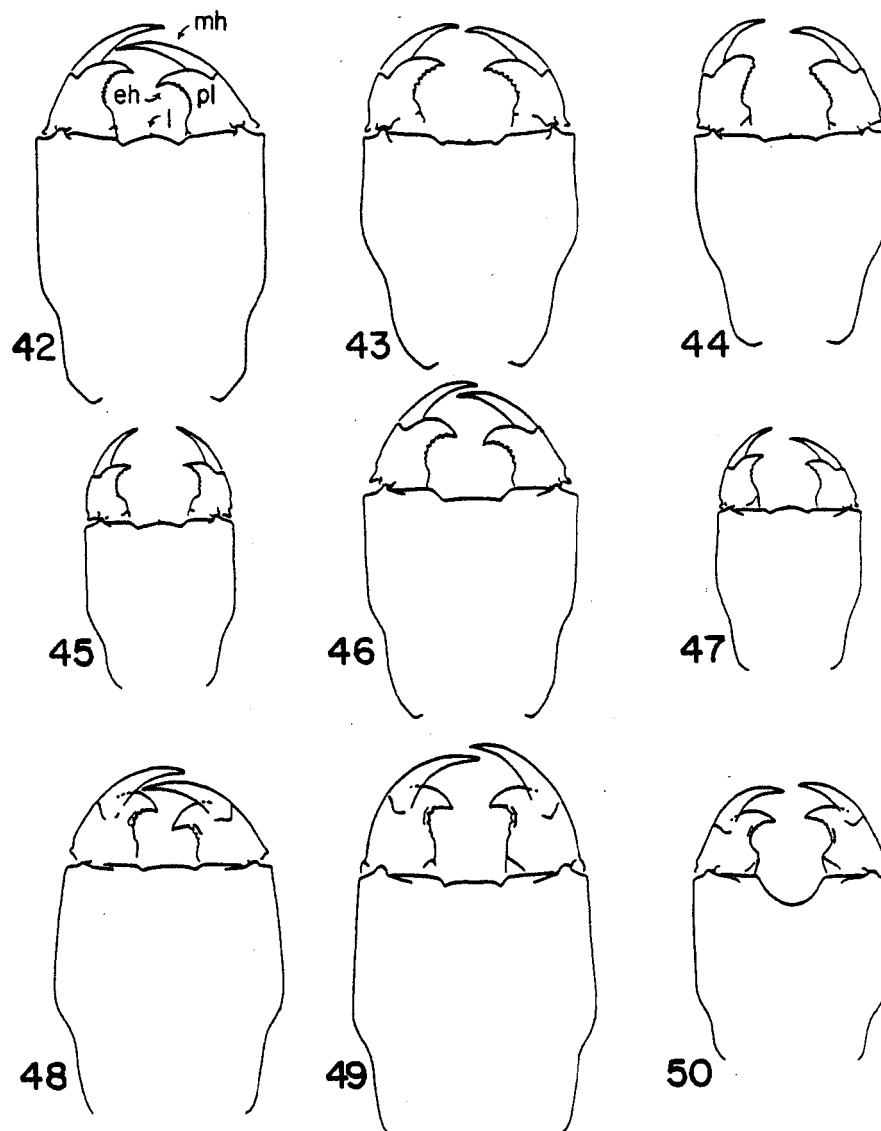


Figure 42. Prementum of *Dromogomphus armatus* (mh=movable hook, eh=end hook, pl=palpal lobe, l=ligula).

Figure 43. Prementum of *Dromogomphus spinosus*.

Figure 44. Prementum of *Dromogomphus spoliatus*.

Figure 45. Prementum of *Gomphus exilis*.

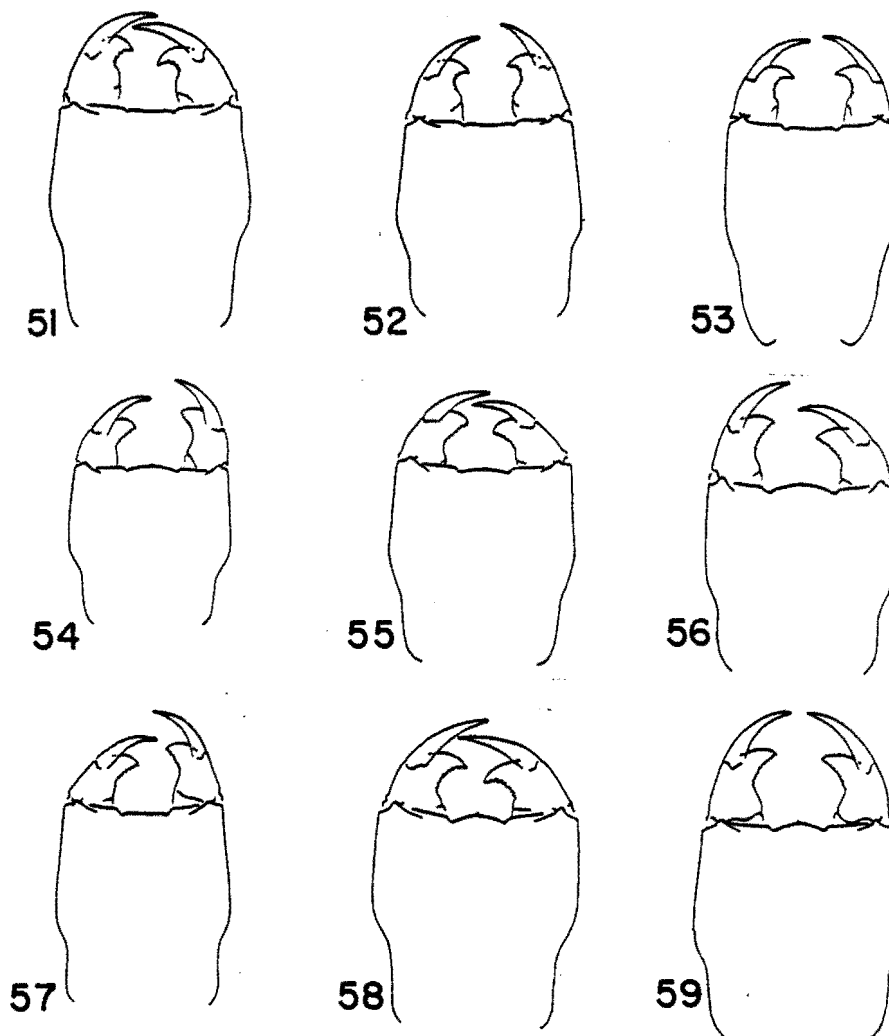
Figure 46. Prementum of *Gomphus lividus*.

Figure 47. Prementum of *Gomphus quadricolor*.

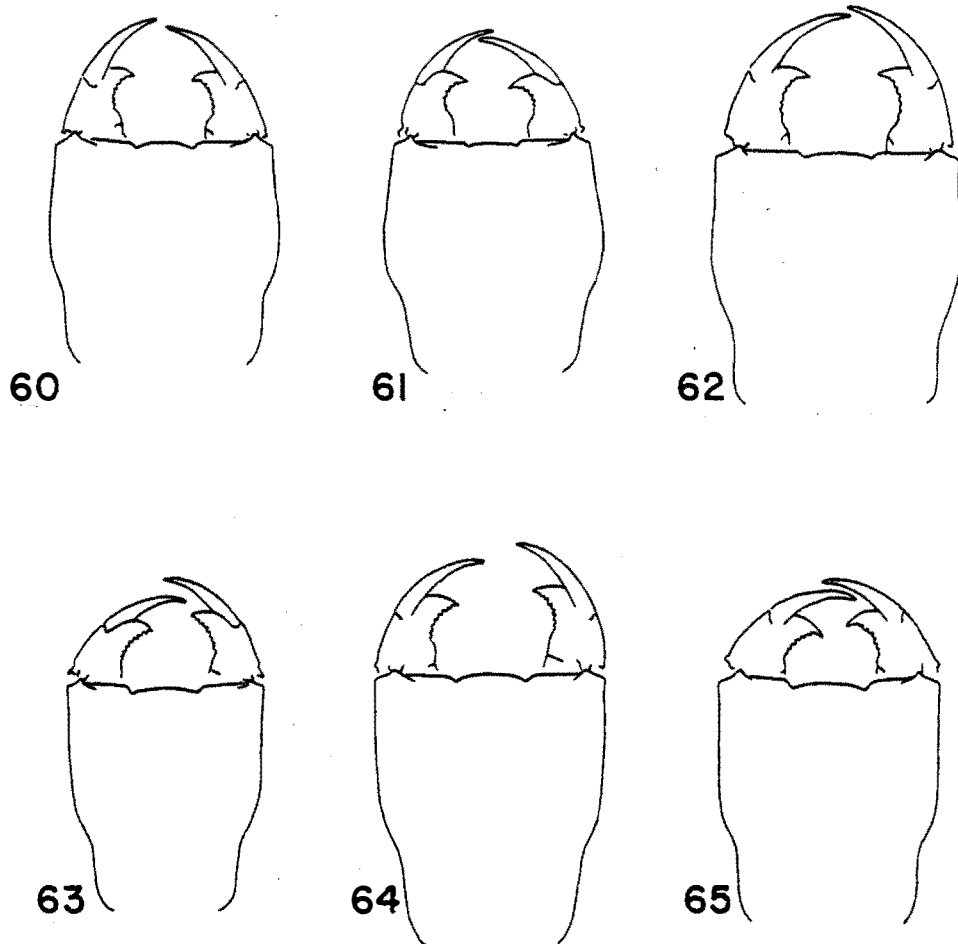
Figure 48. Prementum of *Gomphurus dilatatus*.

Figure 49. Prementum of *Gomphurus modestus*.

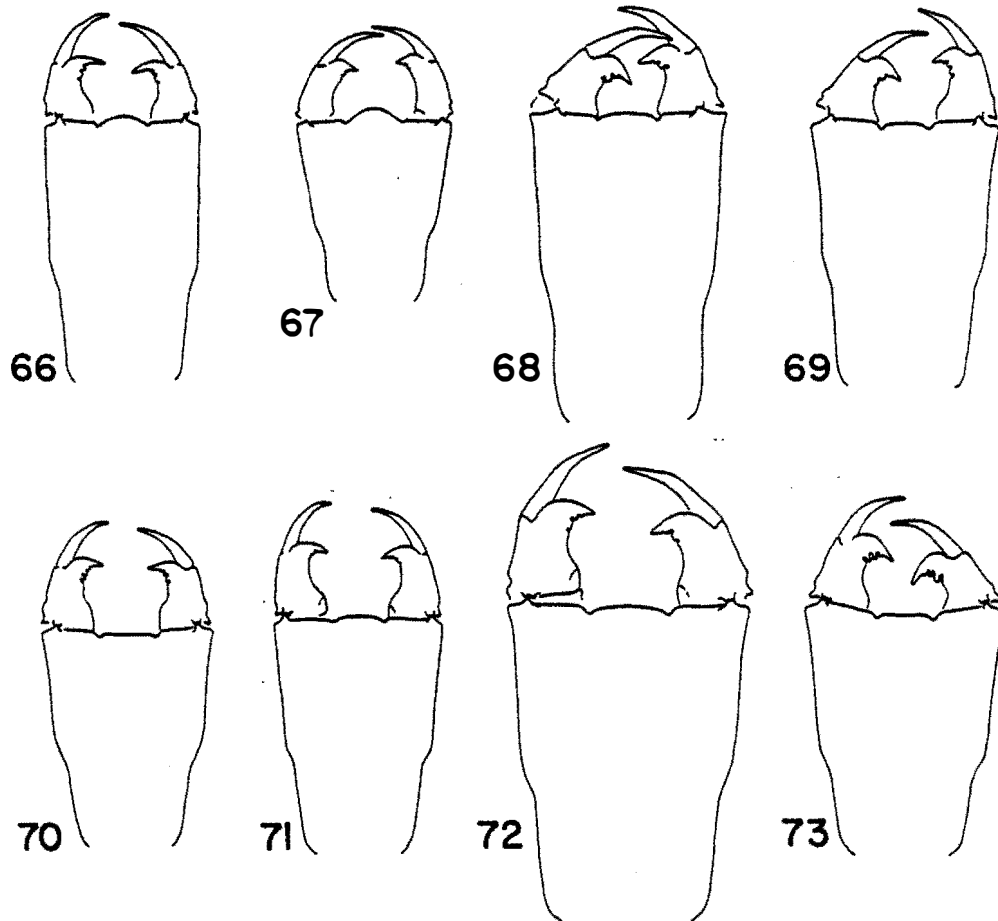
Figure 50. Prementum of *Gomphurus lineatifrons*.



- Figure 51. Prementum of *Gomphurus vastus*.
 Figure 52. Prementum of *Gomphurus crassus*.
 Figure 53. Prementum of *Gomphurus ozarkensis*.
 Figure 54. Prementum of *Gomphurus hybridus*.
 Figure 55. Prementum of *Gomphurus fraternus*.
 Figure 56. Prementum of *Gomphurus externus*.
 Figure 57. Prementum of *Gomphurus ventricosus*.
 Figure 58. Prementum of Genus A *consanguis*.
 Figure 59. Prementum of Genus A *rogersi*.



- Figure 60. Prementum of *Hylogomphus carolinus*.
Figure 61. Prementum of *Hylogomphus geminatus*.
Figure 62. Prementum of *Hylogomphus parvidens*.
Figure 63. Prementum of *Hylogomphus abbreviatus*.
Figure 64. Prementum of *Hylogomphus brevis*.
Figure 65. Prementum of *Hylogomphus viridifrons*.



- Figure 66. Prementum of *Stylurus amnicola*.
 Figure 67. Prementum of *Stylurus intricatus*.
 Figure 68. Prementum of *Stylurus ivae*.
 Figure 69. Prementum of *Stylurus laurae*.
 Figure 70. Prementum of *Stylurus notatus*.
 Figure 71. Prementum of *Stylurus plagiatus*.
 Figure 72. Prementum of *Stylurus scudderi*.
 Figure 73. Prementum of *Stylurus spiniceps*.

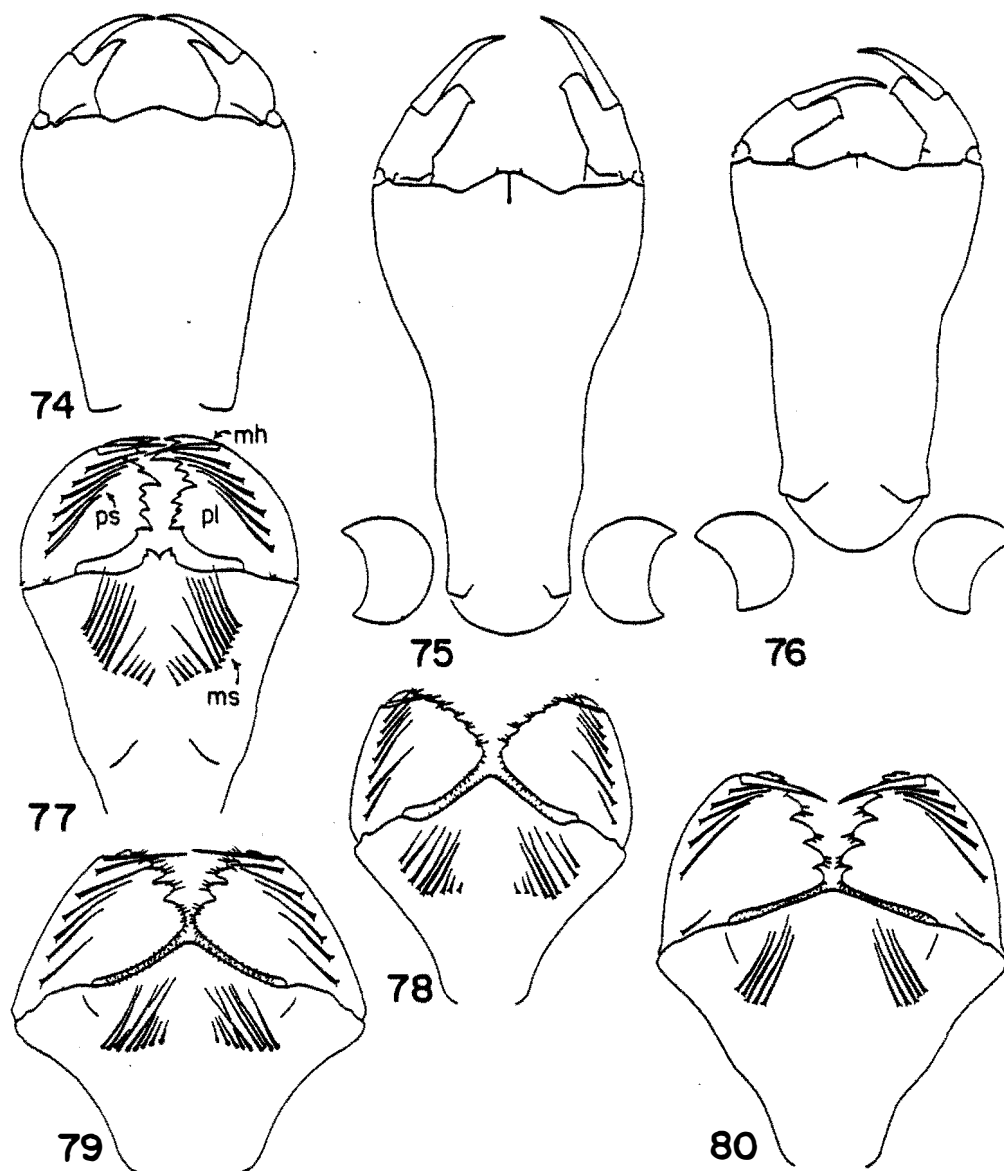


Figure 74. Prementum of *Basiaeshna janata*.

Figure 75. Prementum of *Boyeria grafiana* (showing relative position of mesocoxae).

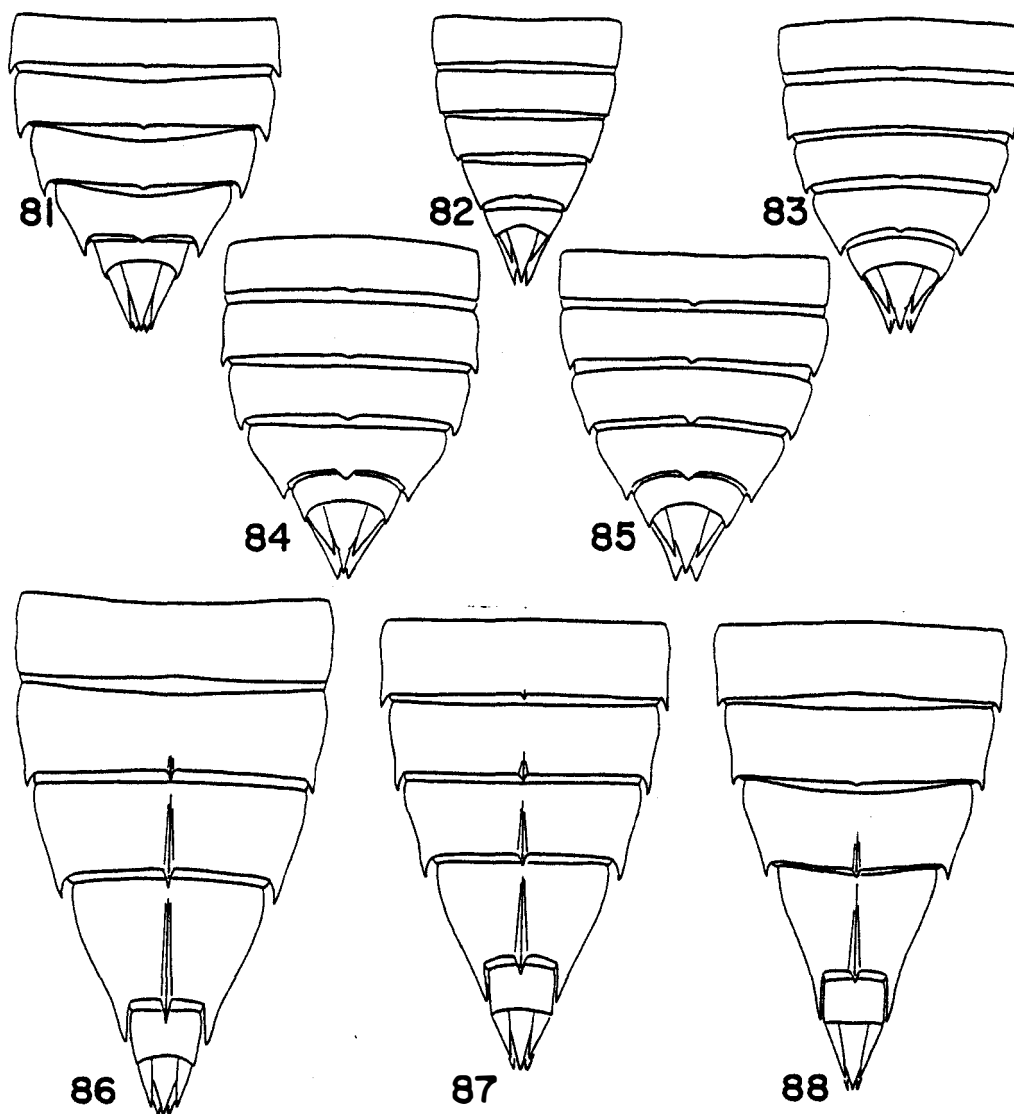
Figure 76. Prementum of *Boyeria vinosa* (showing relative position of mesocoxae).

Figure 77. Prementum of *Cordulegaster obliqua* (mh=movable hook, ps=palpal seta, pl=palpal lobe, l=ligula, ms=mental seta).

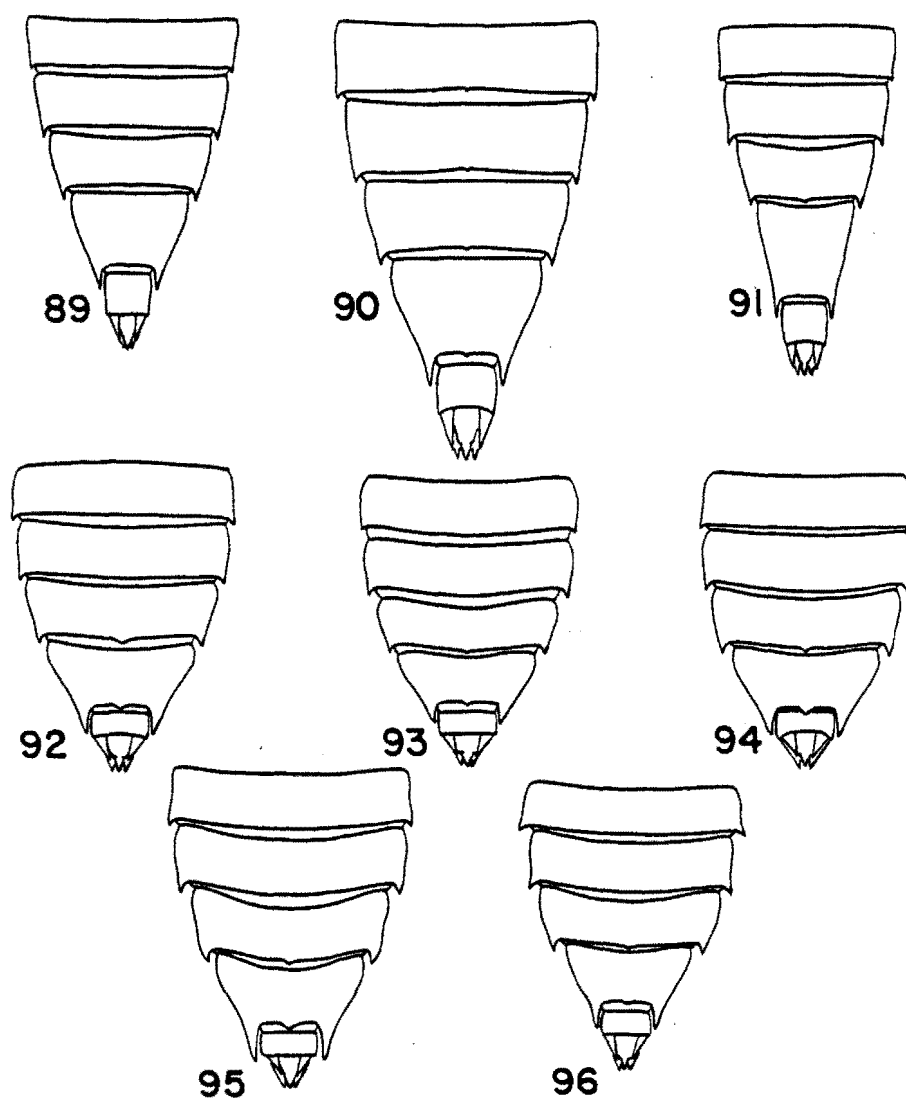
Figure 78. Prementum of *Helocordulia uhleri*.

Figure 79. Prementum of *Neurocordulia molesta*.

Figure 80. Prementum of *Didymops transversa*.



- Figure 81. Terminal abdominal segments of *Erpetogomphus designatus*.
 Figure 82. Terminal abdominal segments of *Ophiogomphus howei*.
 Figure 83. Terminal abdominal segments of *Ophiogomphus mainensis*.
 Figure 84. Terminal abdominal segments of *Ophiogomphus rupinsulensis*.
 Figure 85. Terminal abdominal segments of *Ophiogomphus* sp. A.
 Figure 86. Terminal abdominal segments of *Ophiogomphus armatus*.
 Figure 87. Terminal abdominal segments of *Dromogomphus spinosus*.
 Figure 88. Terminal abdominal segments of *Dromogomphus spoliatus*.



- Figure 89. Terminal abdominal segments of *Gomphus exilis*.
 Figure 90. Terminal abdominal segments of *Gomphus lividus*.
 Figure 91. Terminal abdominal segments of *Gomphus quadricolor*.
 Figure 92. Terminal abdominal segments of *Gomphurus vastus*.
 Figure 93. Terminal abdominal segments of *Gomphurus crassus*.
 Figure 94. Terminal abdominal segments of *Gomphurus ozarkensis*.
 Figure 95. Terminal abdominal segments of *Gomphurus externus*.
 Figure 96. Terminal abdominal segments of *Gomphurus ventricosus*.

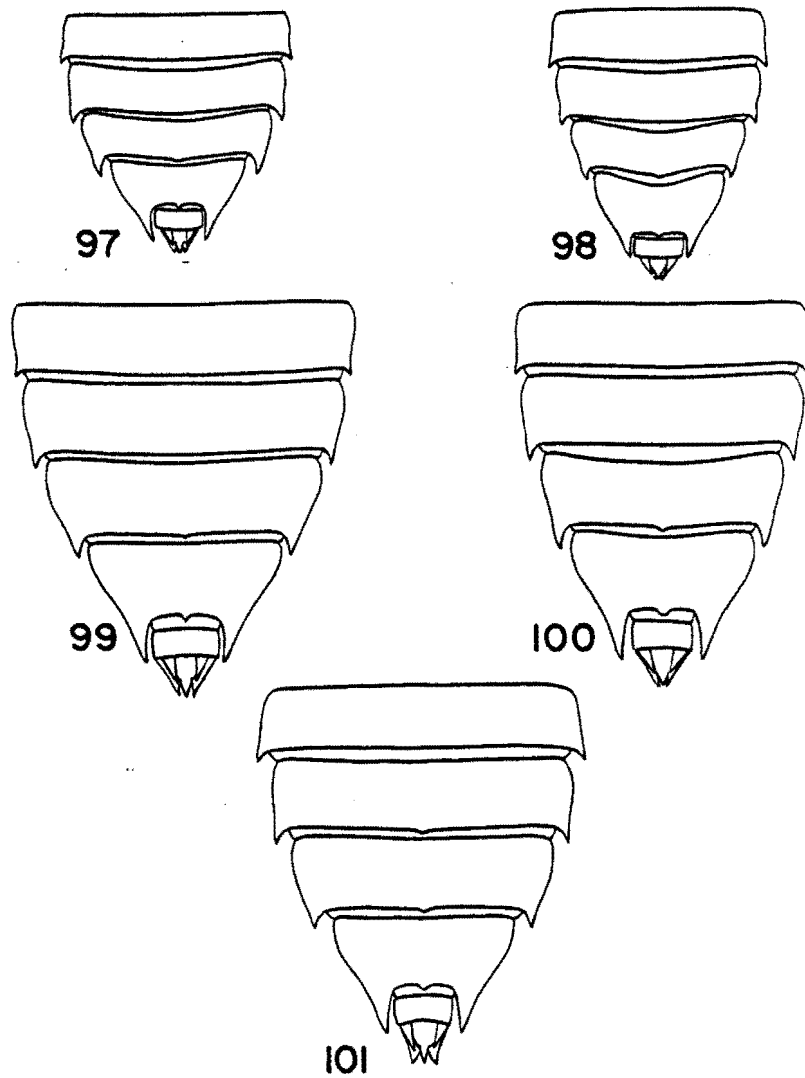
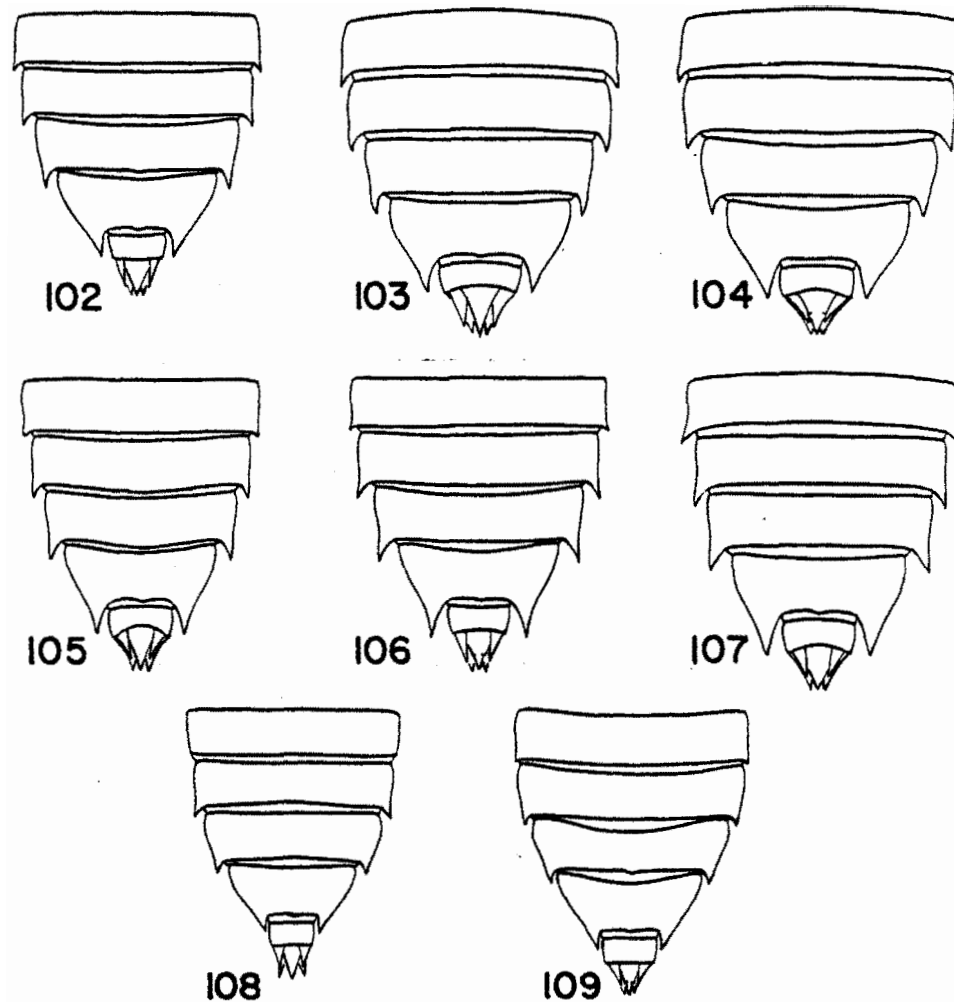


Figure 97. Terminal abdominal segments of *Gomphurus hybridus*.
 Figure 98. Terminal abdominal segments of *Gomphurus fraternus*.
 Figure 99. Terminal abdominal segments of *Gomphurus dilatatus*.
 Figure 100. Terminal abdominal segments of *Gomphurus modestus*.
 Figure 101. Terminal abdominal segments of *Gomphurus lineatifrons*.



- Figure 102. Terminal abdominal segments of *Hylonomphus abbreviatus*.
 Figure 103. Terminal abdominal segments of *Hylonomphus brevis*.
 Figure 104. Terminal abdominal segments of *Hylonomphus viridifrons*.
 Figure 105. Terminal abdominal segments of *Hylonomphus carolinus*.
 Figure 106. Terminal abdominal segments of *Hylonomphus geminatus*.
 Figure 107. Terminal abdominal segments of *Hylonomphus parvidens*.
 Figure 108. Terminal abdominal segments of Genus A *consanguis*.
 Figure 109. Terminal abdominal segments of Genus A *rogersi*.

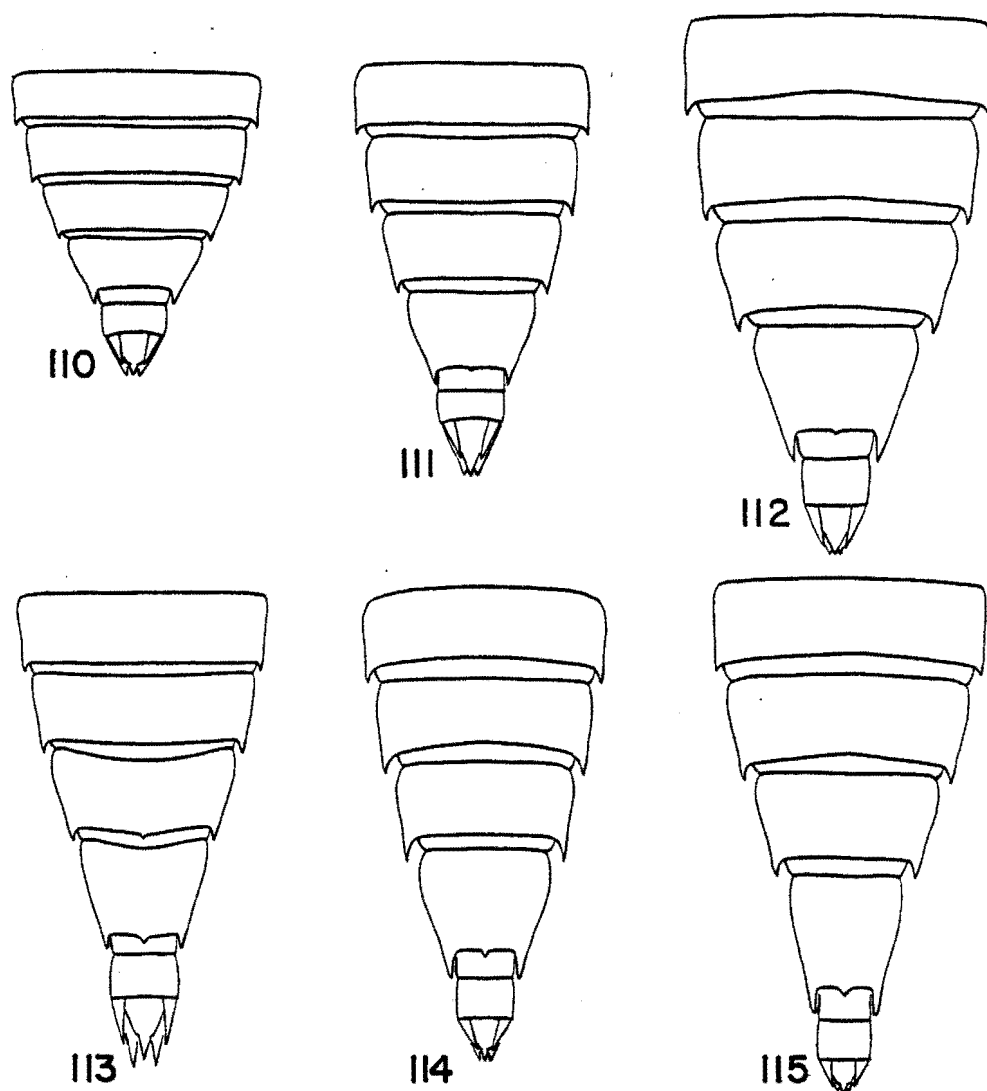
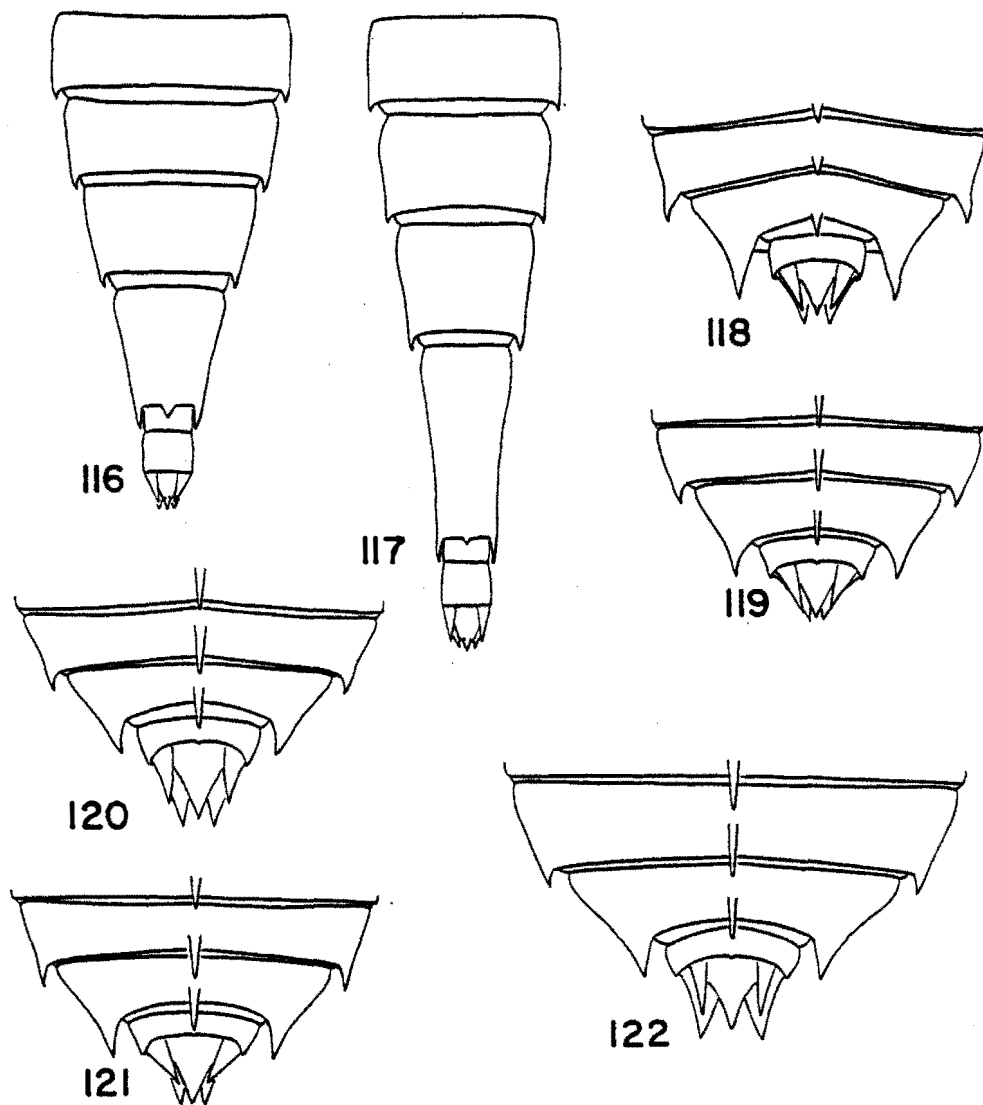


Figure 110. Terminal abdominal segments of *Stylurus intricatus*.
 Figure 111. Terminal abdominal segments of *Stylurus amnicola*.
 Figure 112. Terminal abdominal segments of *Stylurus scudderi*.
 Figure 113. Terminal abdominal segments of *Stylurus ivae*.
 Figure 114. Terminal abdominal segments of *Stylurus laurae*.
 Figure 115. Terminal abdominal segments of *Stylurus plagiatus*.



- Figure 116. Terminal abdominal segments of *Stylurus notatus*.
 Figure 117. Terminal abdominal segments of *Stylurus spiniceps*.
 Figure 118. Terminal abdominal segments of *Didymops transversa*.
 Figure 119. Terminal abdominal segments of *Macromia illinoiensis*.
 Figure 120. Terminal abdominal segments of *Macromia alleghaniensis*.
 Figure 121. Terminal abdominal segments of *Macromia georgina*.
 Figure 122. Terminal abdominal segments of *Macromia taeniolata*.

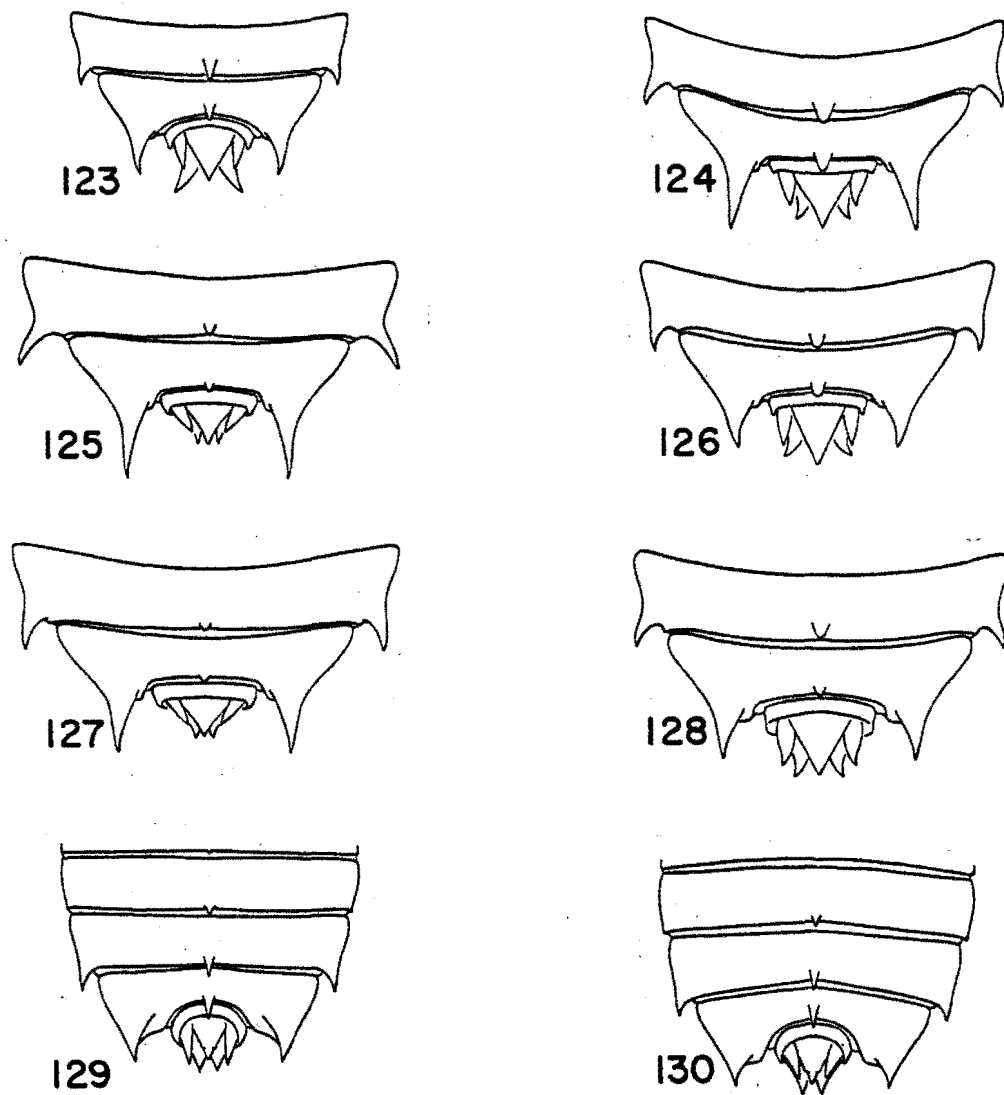


Figure 123. Terminal abdominal segments of *Neurocordulia alabamensis*.

Figure 124. Terminal abdominal segments of *Neurocordulia molesta*.

Figure 125. Terminal abdominal segments of *Neurocordulia obsoleta*.

Figure 126. Terminal abdominal segments of *Neurocordulia virginiensis*.

Figure 127. Terminal abdominal segments of *Neurocordulia xanthosoma*.

Figure 128. Terminal abdominal segments of *Neurocordulia yamaskanensis*.

Figure 129. Terminal abdominal segments of *Helocordulia selysi*.

Figure 130. Terminal abdominal segments of *Helocordulia uhleri*.

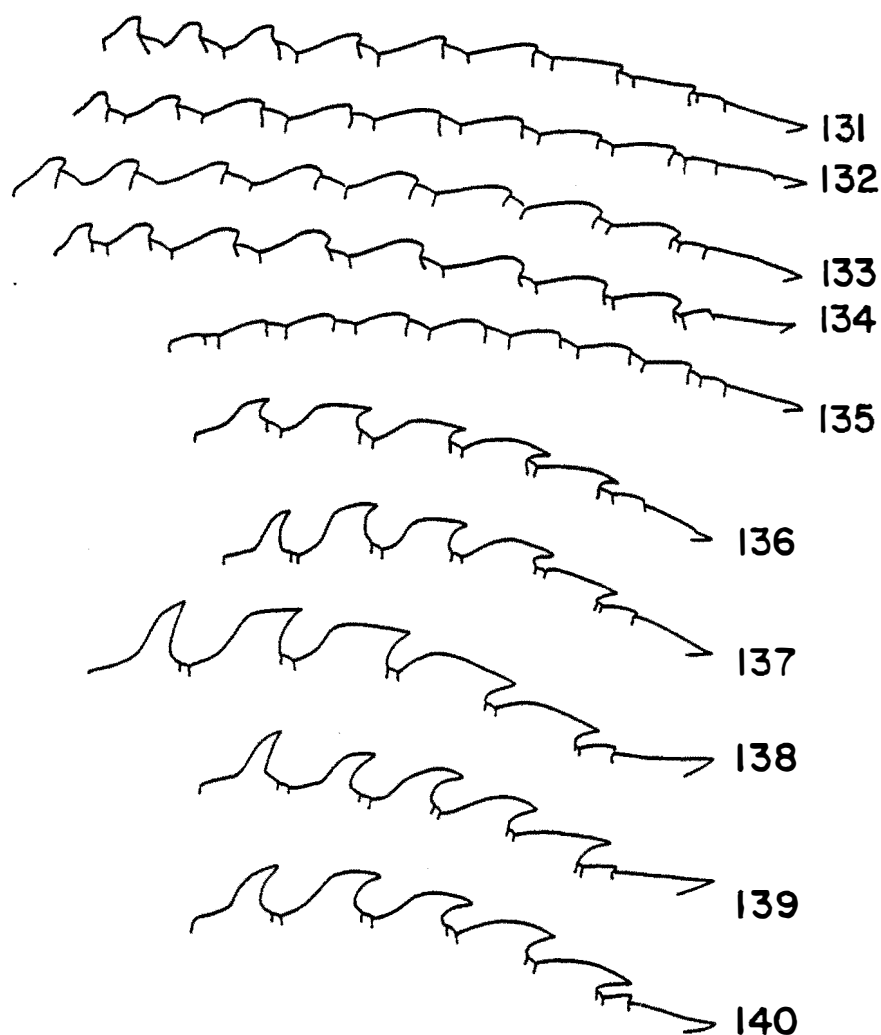


Figure 131. Profile of dorsal abdominal hooks of *Erpetogomphus designatus*.

Figure 132. Profile of dorsal abdominal hooks of *Ophiogomphus mainensis*.

Figure 133. Profile of dorsal abdominal hooks of *Ophiogomphus rupinsulensis*.

Figure 134. Profile of dorsal abdominal hooks of *Ophiogomphus* sp. A.

Figure 135. Profile of dorsal abdominal hooks of *Ophiogomphus howei*.

Figure 136. Profile of dorsal abdominal hooks of *Didymops transversa*.

Figure 137. Profile of dorsal abdominal hooks of *Macromia illinoiensis*.

Figure 138. Profile of dorsal abdominal hooks of *Macromia taeniolata*.

Figure 139. Profile of dorsal abdominal hooks of *Macromia alleghaniensis*.

Figure 140. Profile of dorsal abdominal hooks of *Macromia georgina*.

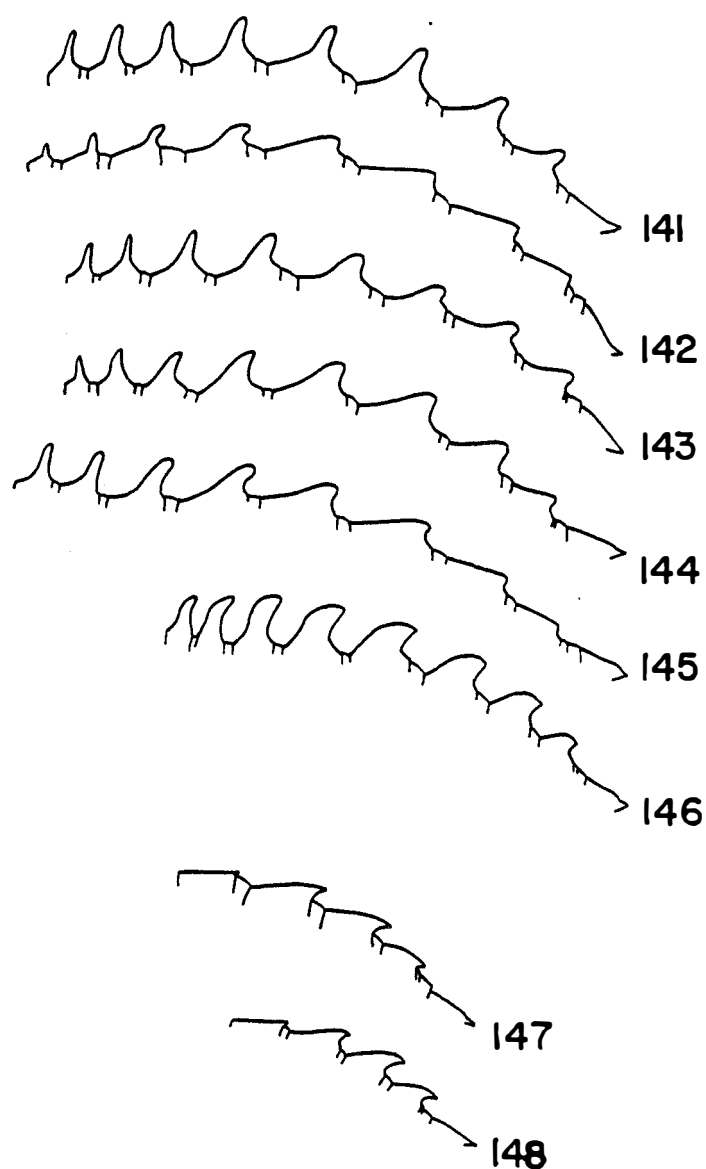


Figure 141. Profile of dorsal abdominal hooks of *Neurocordulia molesta*.

Figure 142. Profile of dorsal abdominal hooks of *Neurocordulia xanthosoma*.

Figure 143. Profile of dorsal abdominal hooks of *Neurocordulia obsoleta*.

Figure 144. Profile of dorsal abdominal hooks of *Neurocordulia virginiensis*.

Figure 145. Profile of dorsal abdominal hooks of *Neurocordulia yamaskanensis*.

Figure 146. Profile of dorsal abdominal hooks of *Neurocordulia alabamensis*.

Figure 147. Profile of dorsal abdominal hooks of *Helocordulia uhleri*.

Figure 148. Profile of dorsal abdominal hooks of *Helocordulia selysii*.

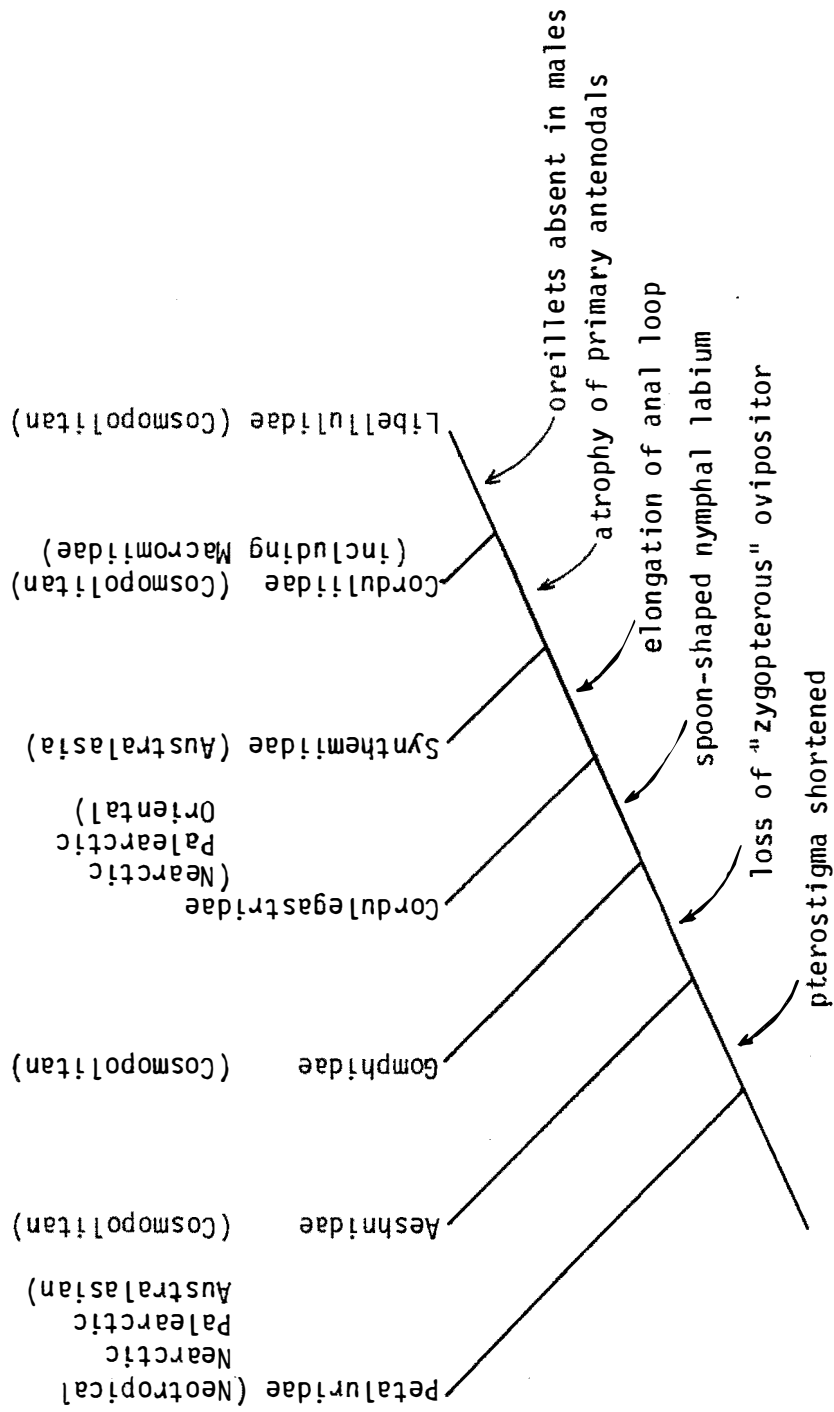


Figure 149. Cladogram of Anisoptera families (modified and rearranged from Fraser, 1957).

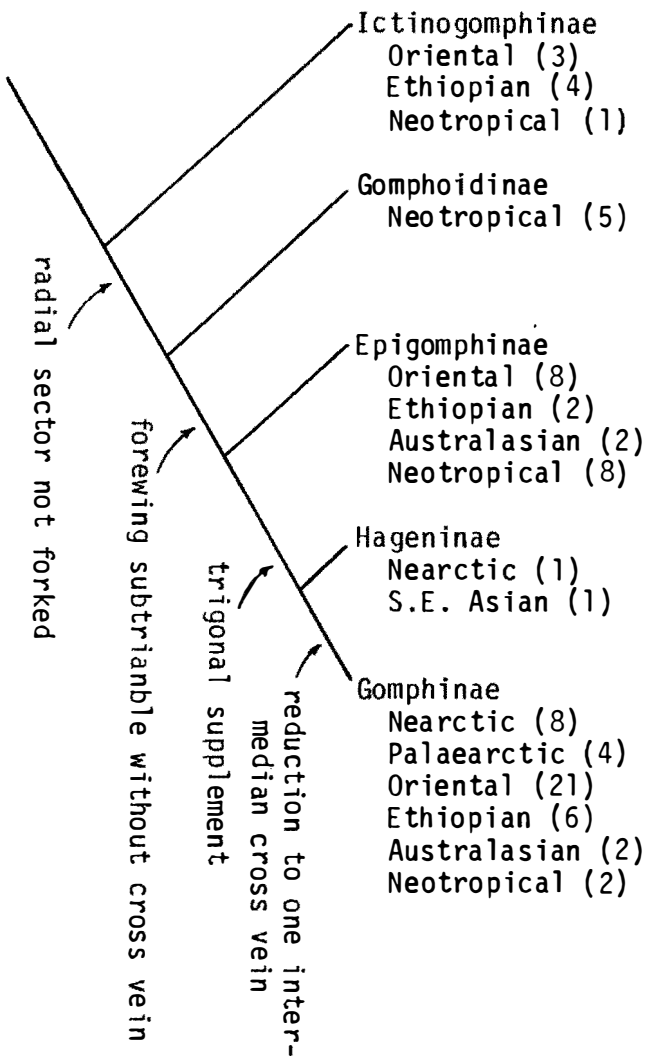


Figure 150. Cladogram of subfamilies of Gomphidae. Modified from Fraser (1940, 1957), Williamson (1920), and Belle (1979).

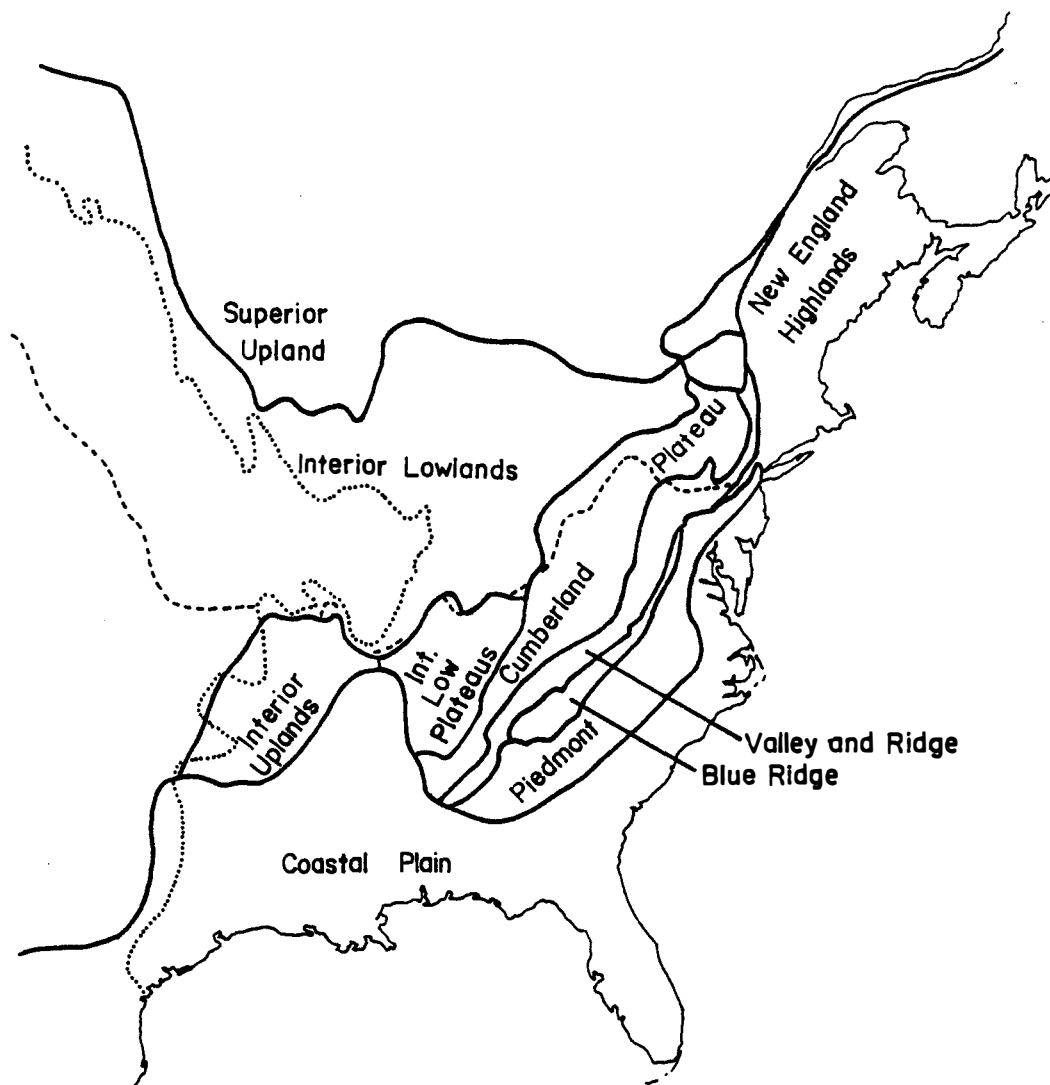


Figure 151. Base map showing physiographic provinces, maximum extent of Pleistocene glaciation (dashed line), and eastern margin of prehistoric prairie (dotted line).

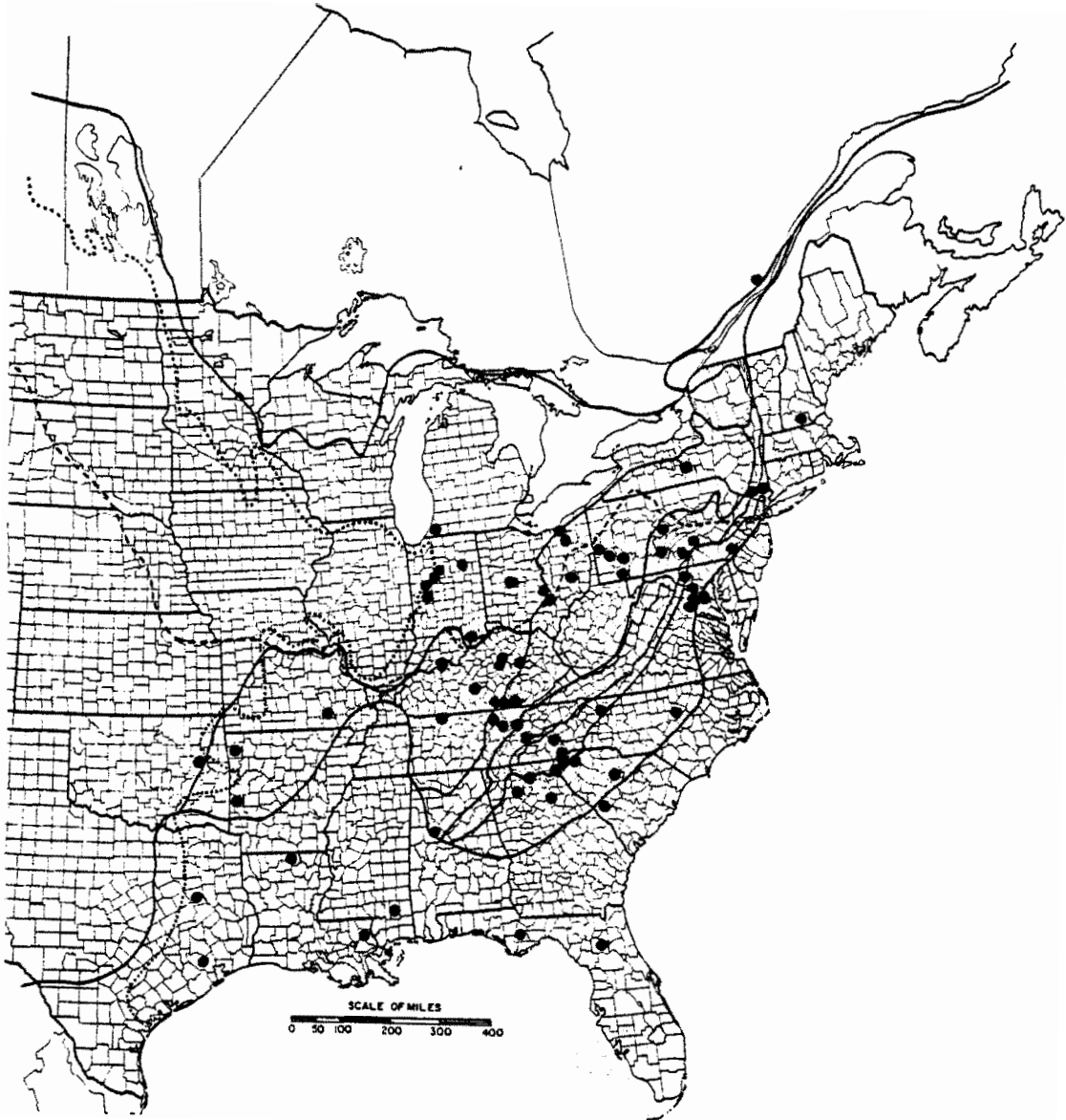


Figure 152. Range of *Tachopteryx thoreyi*.

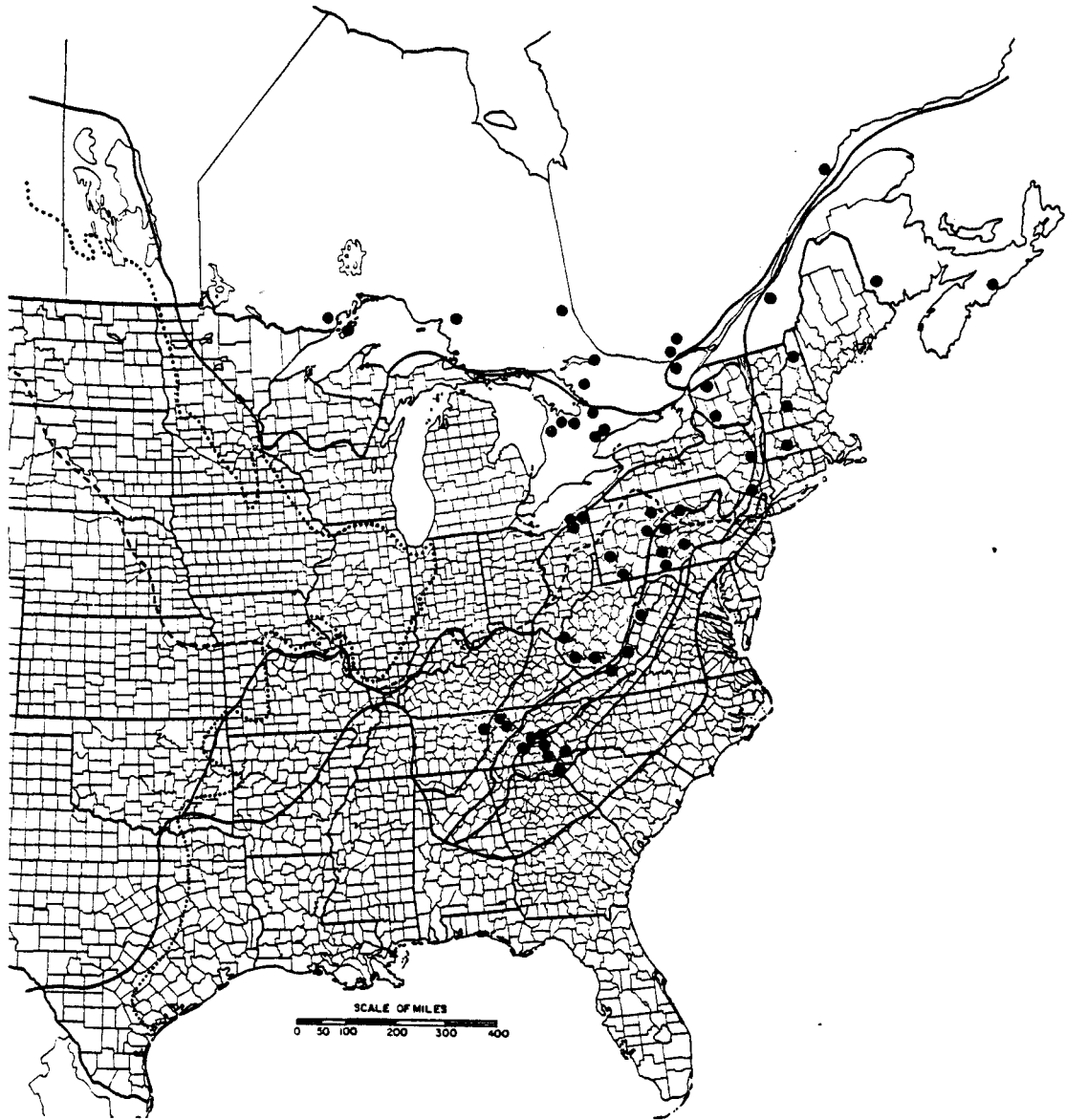


Figure 153. Range of *Boyeria grafiana*.

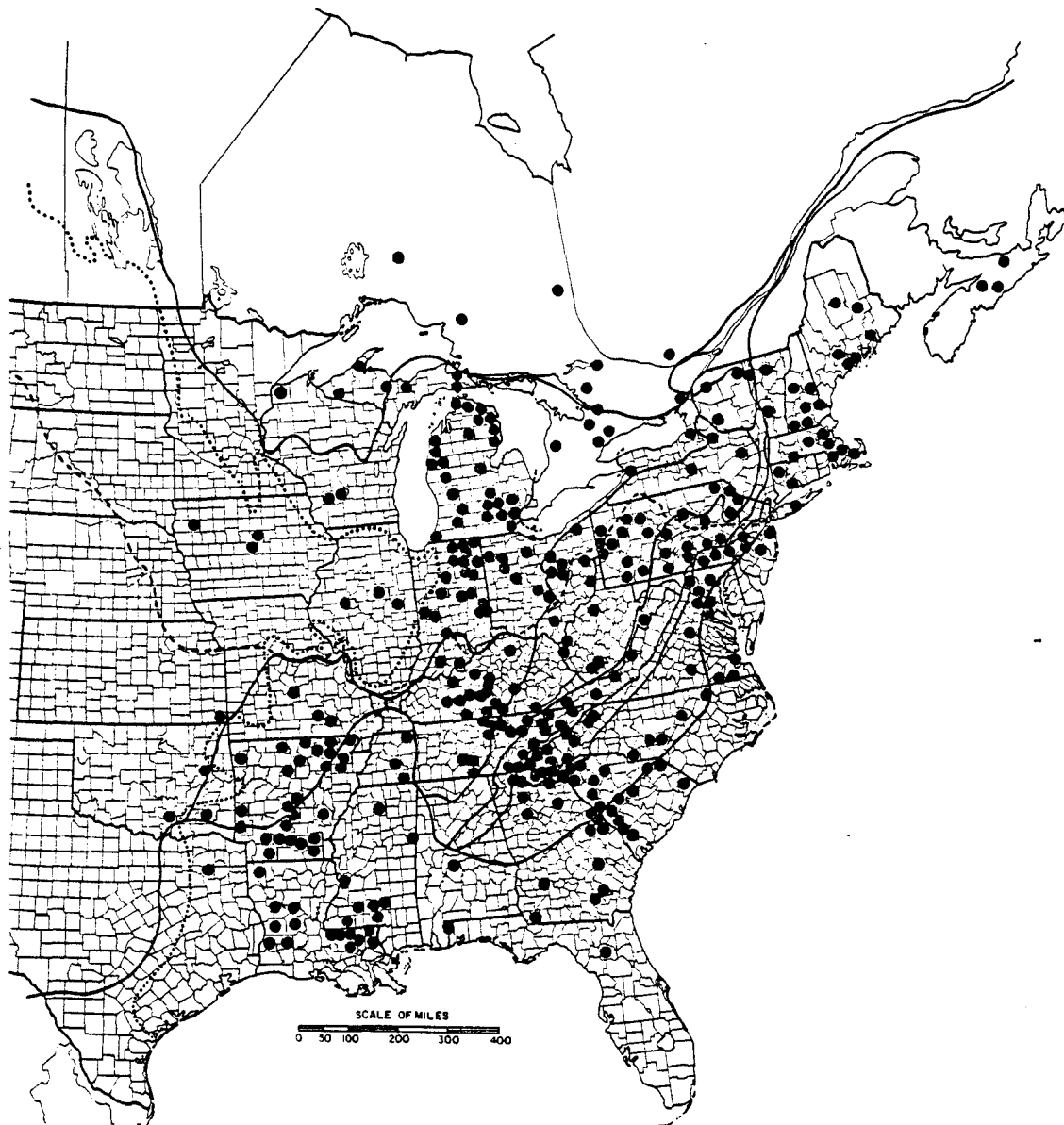


Figure 154. Range of *Boyeria vinosa*.

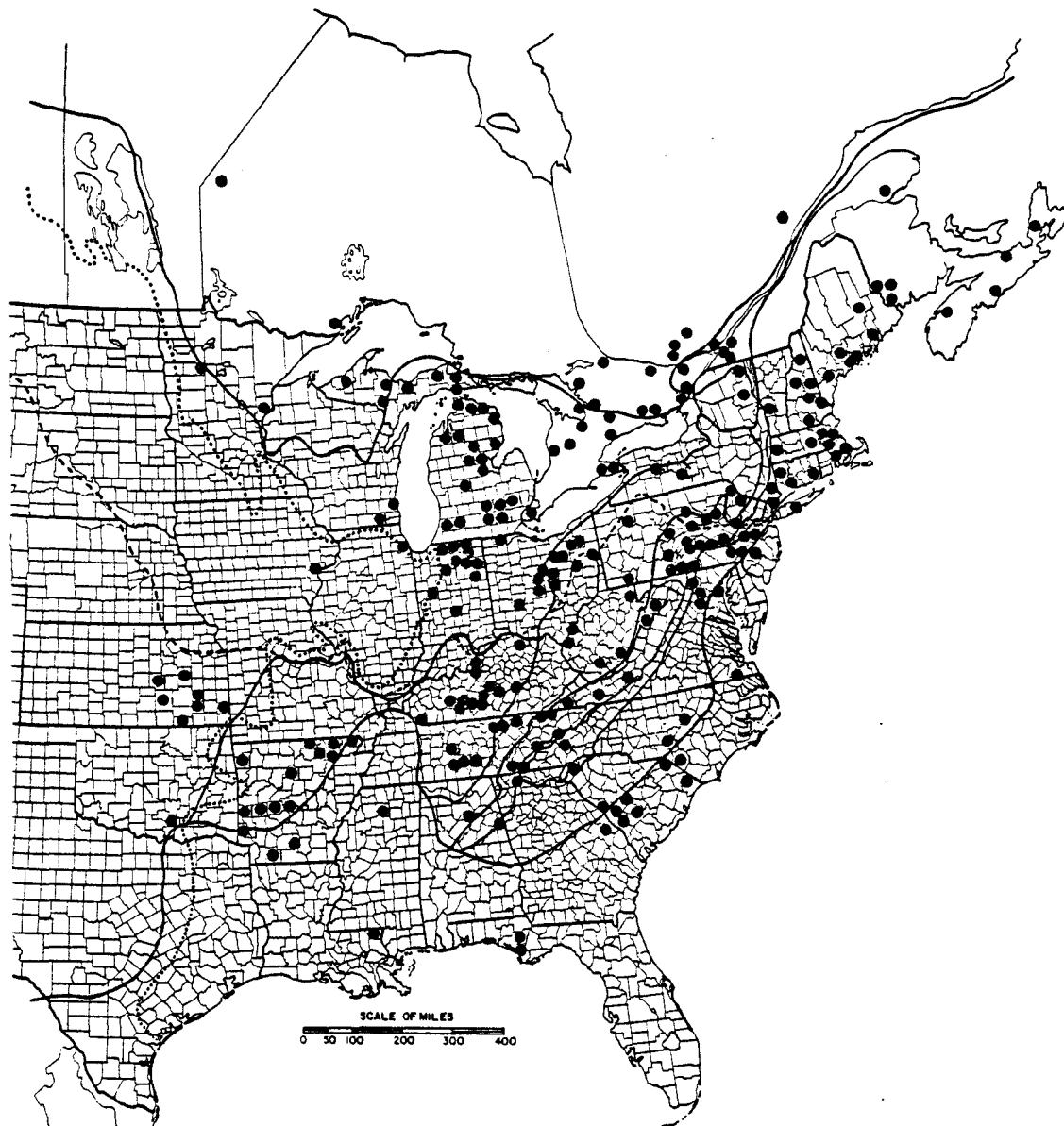


Figure 155. Range of *Basiaeshna janata*.

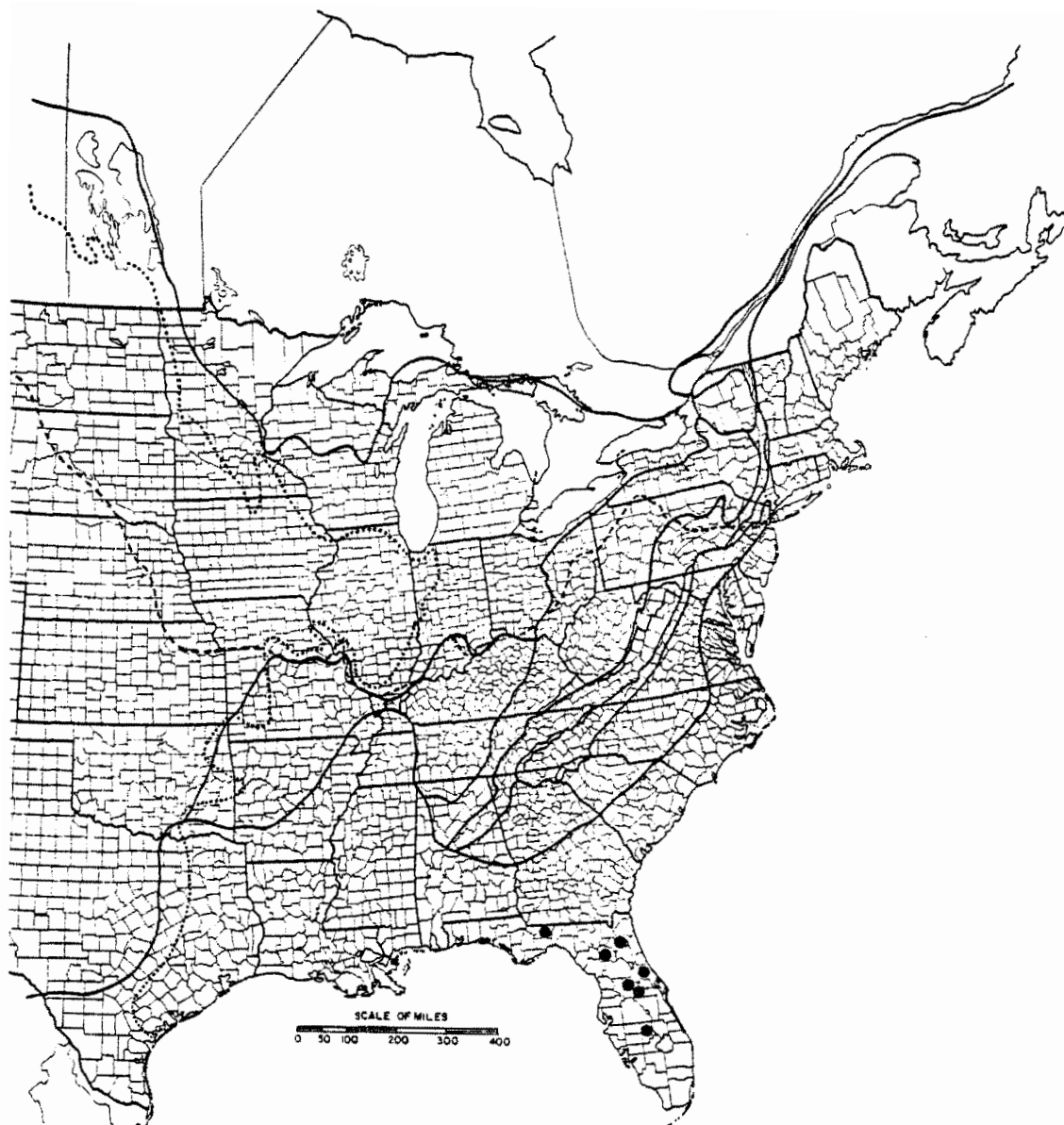


Figure 156. Range of *Progompheus alachuensis*.

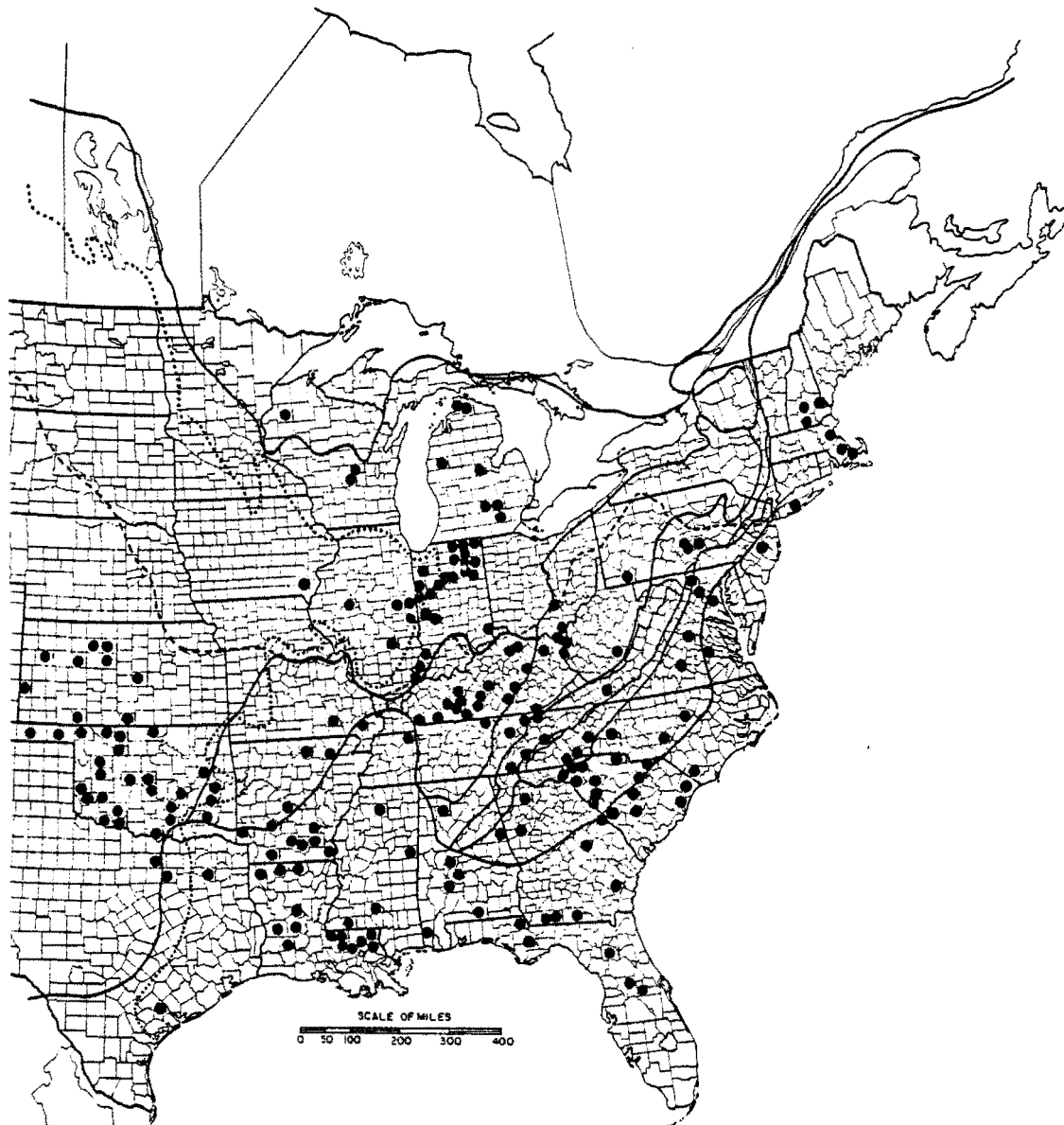


Figure 157. Range of *Progomphus obscurus* (range extends westward to Colorado and Arizona).

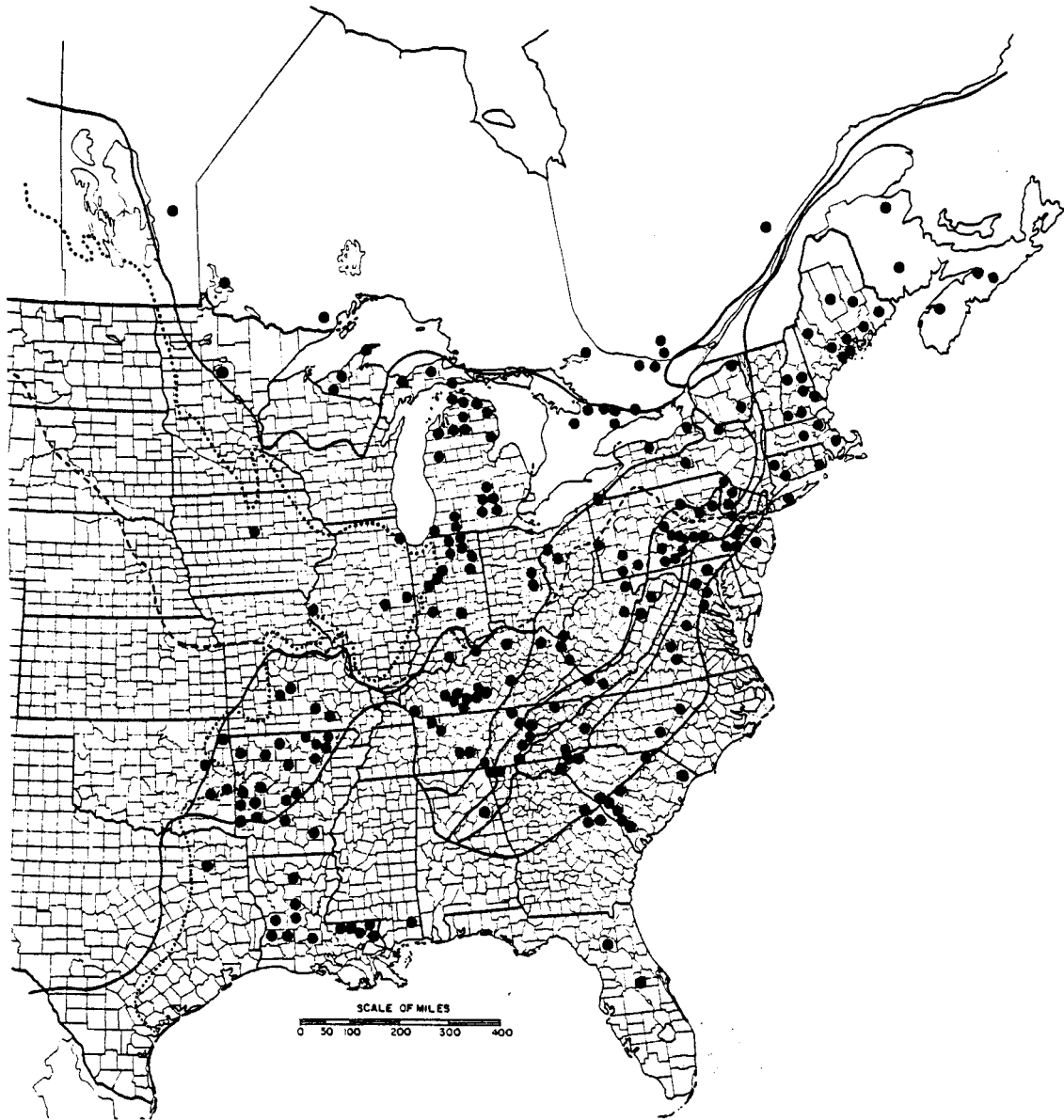


Figure 158. Range of *Hagenius brevistylus*.

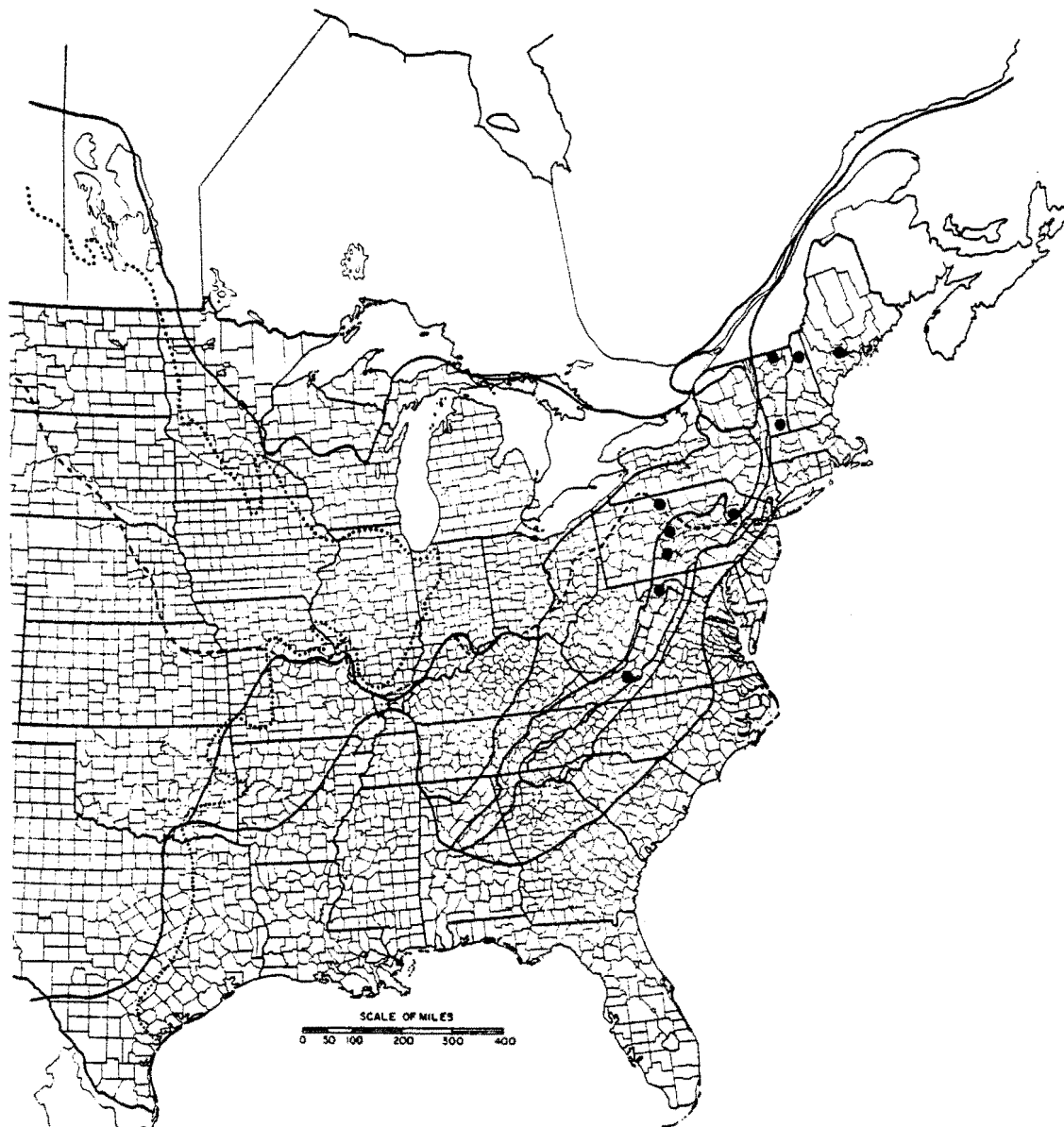


Figure 159. Range of *Lanthus parvulus*.

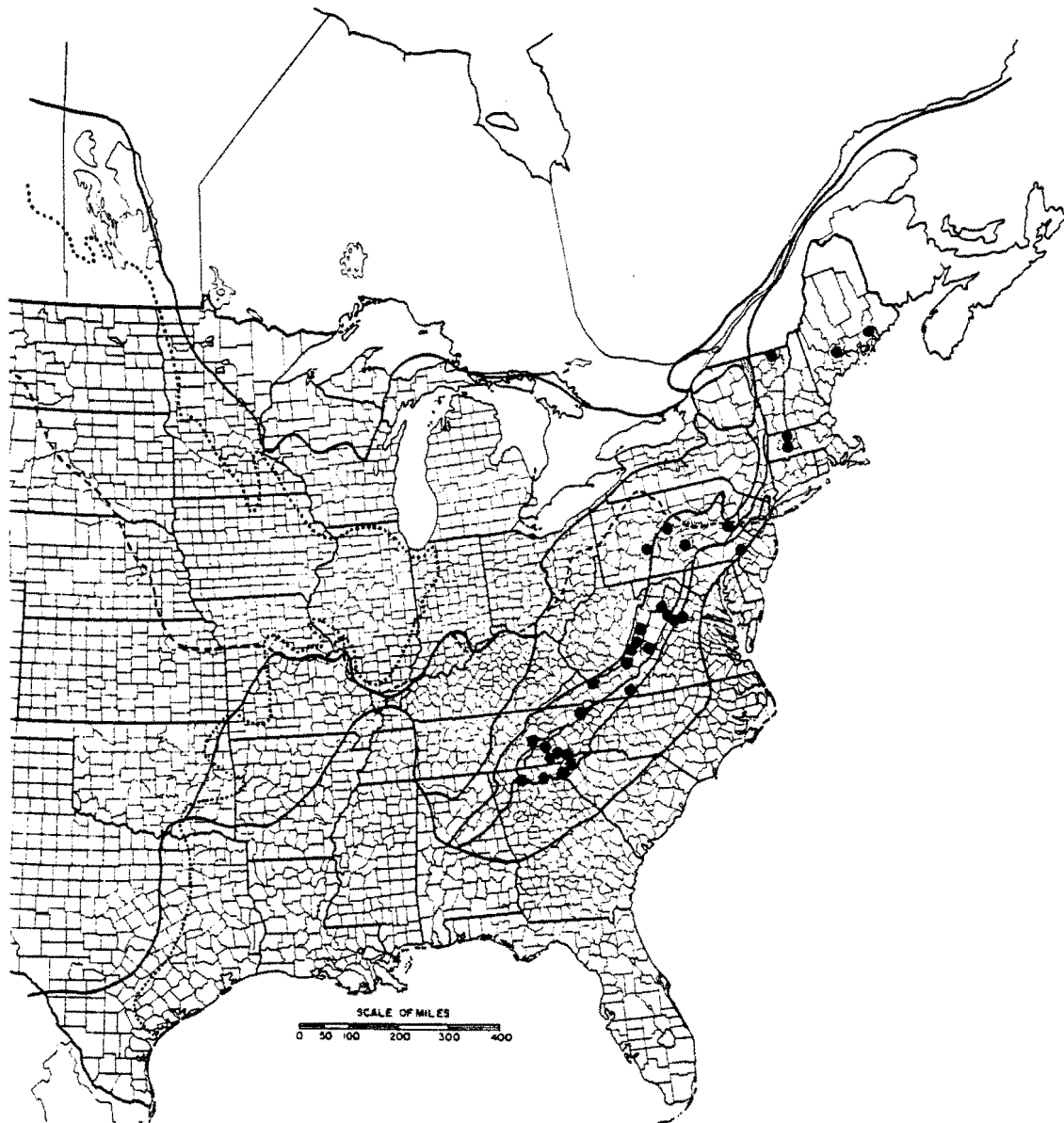


Figure 160. Range of *Lanthus vernalis*.

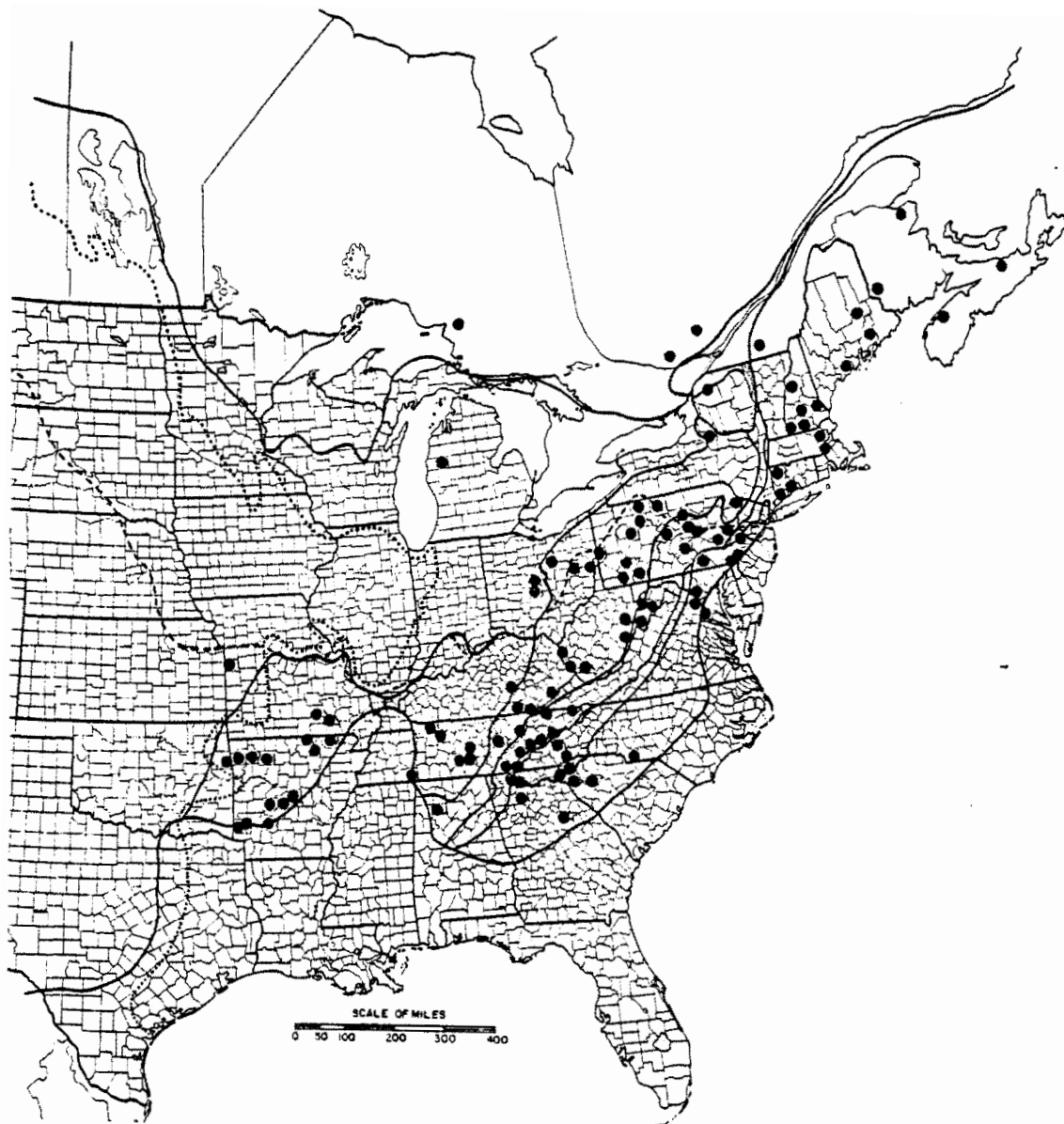


Figure 161. Range of *Stylogomphus albistylus*.



Figure 162. Range of *Ophiogomphus anomalus*.

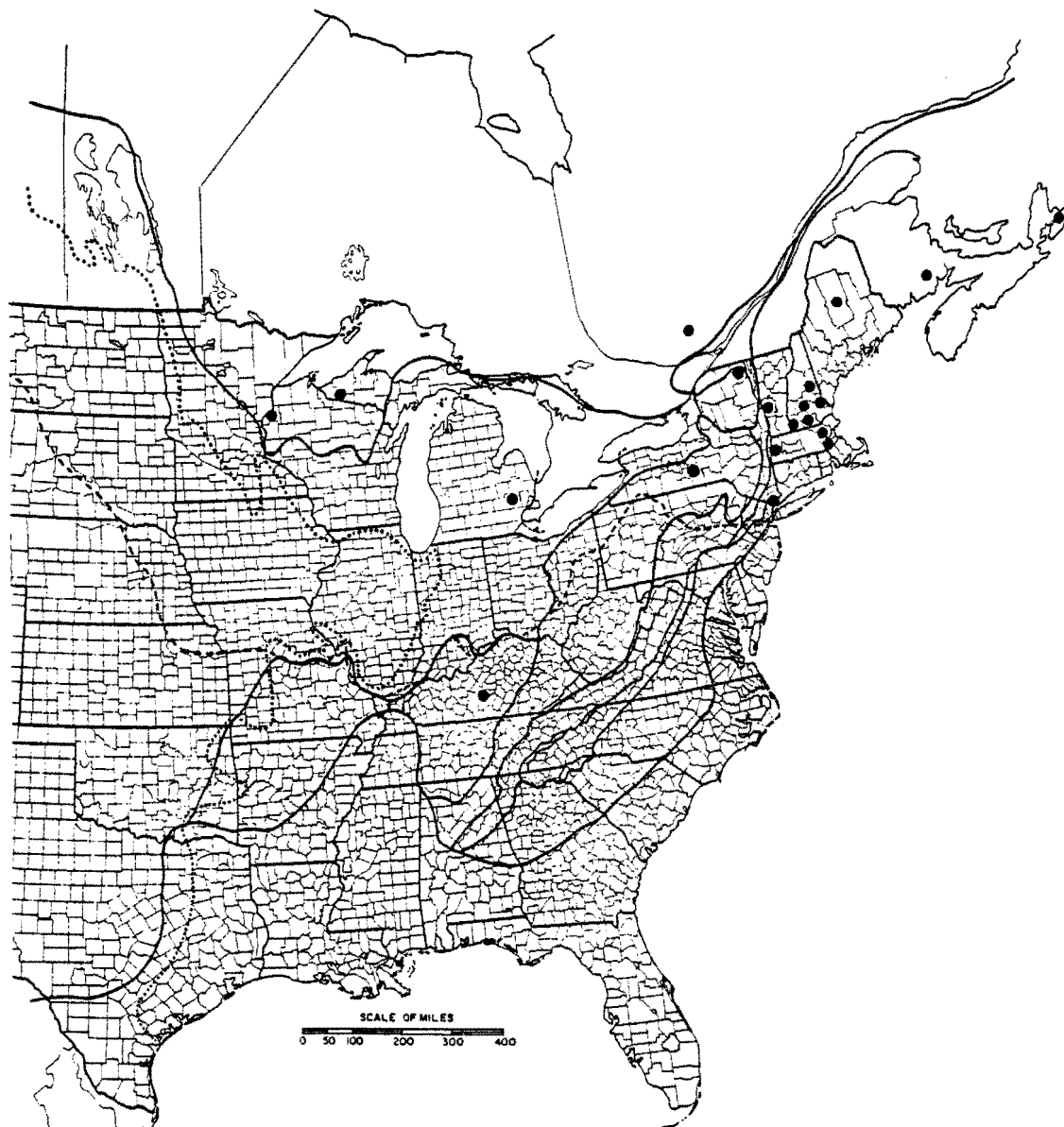


Figure 163. Range of *Ophiogomphus aspersus*.



Figure 164. Range of *Ophiogomphus carolus*.

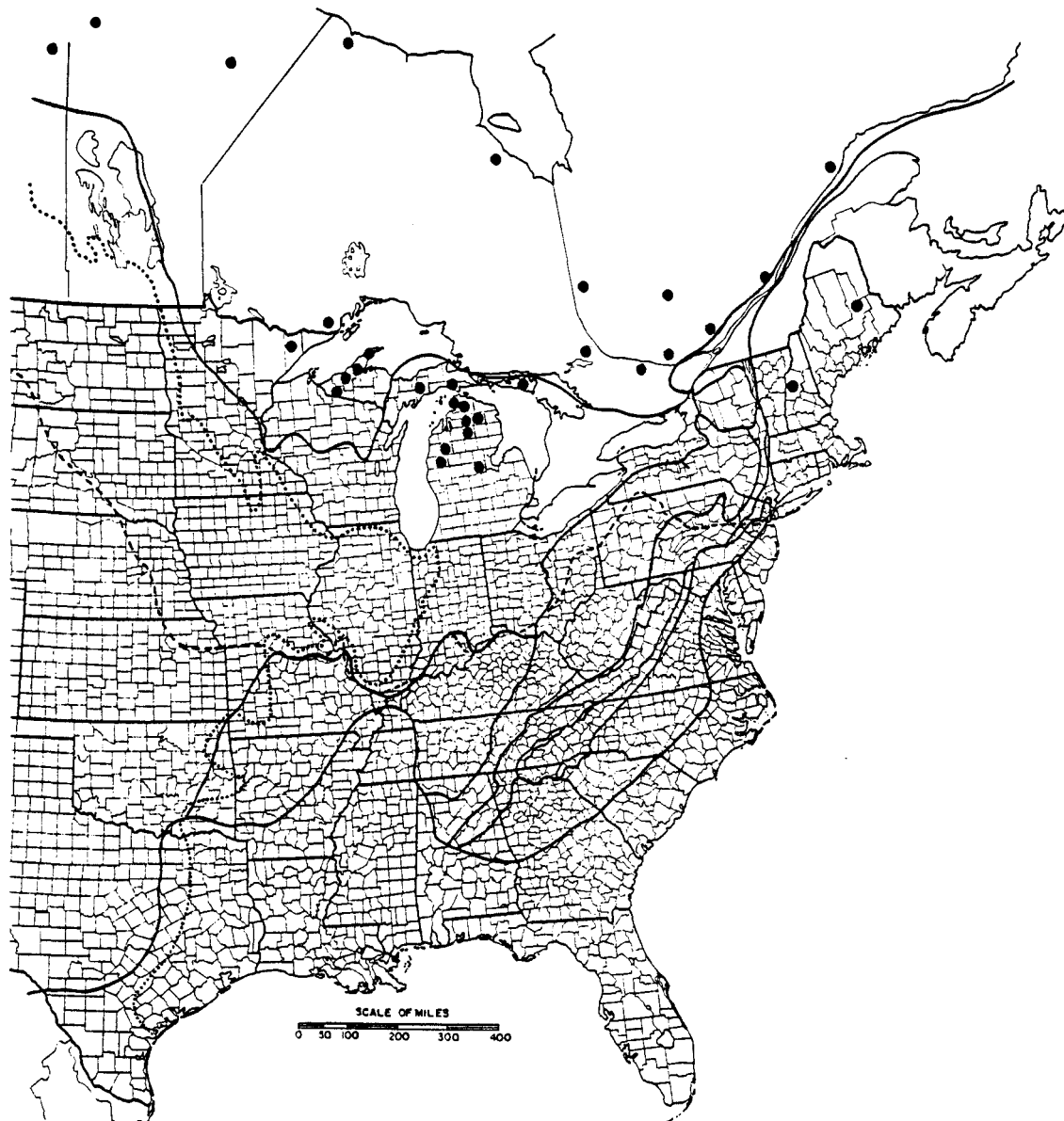


Figure 165. Range of *Ophiogomphus colubrinus* (range extends northward to Northwest Territories, Canada).

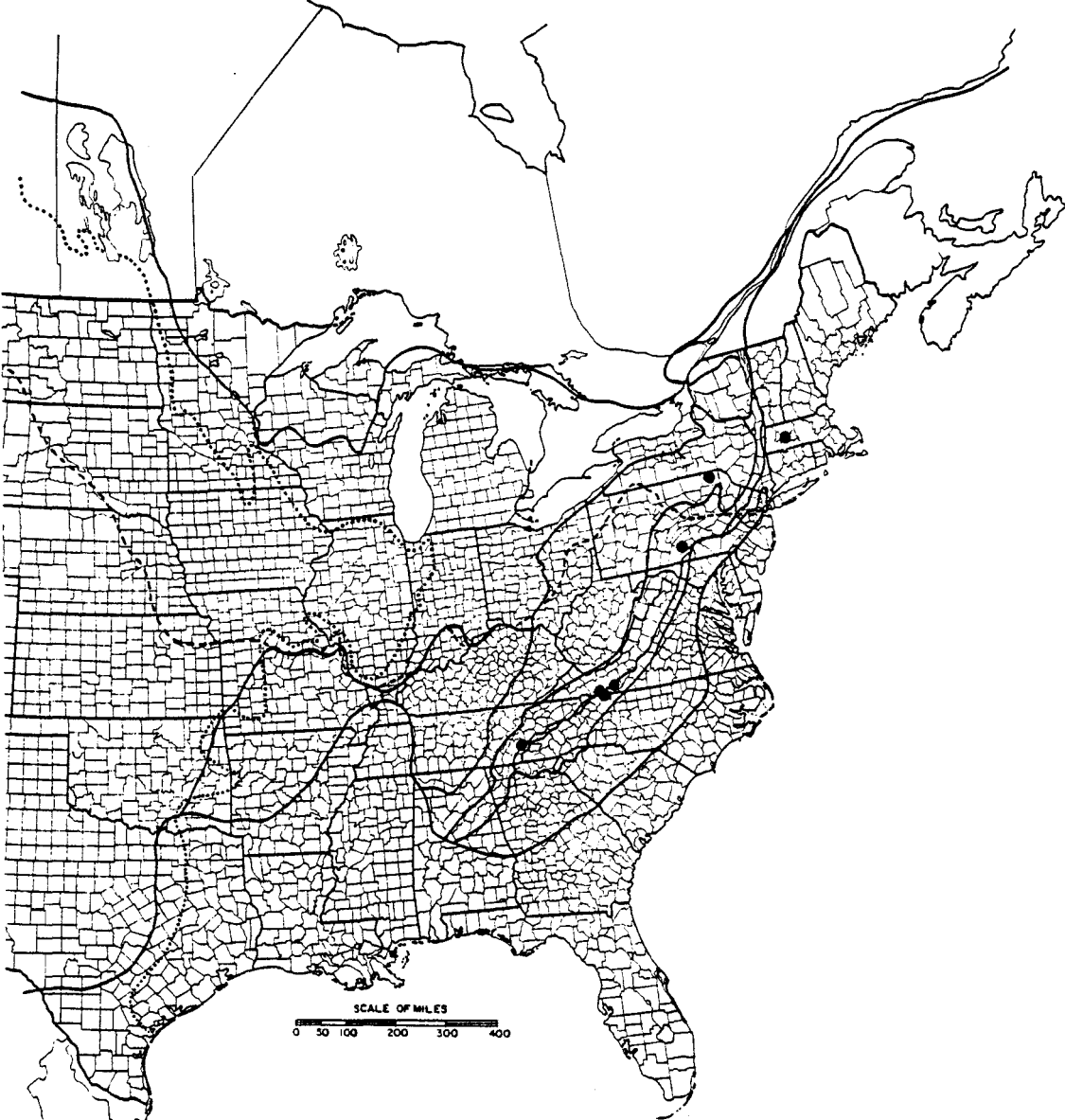


Figure 166. Range of *Ophiogomphus howei*.

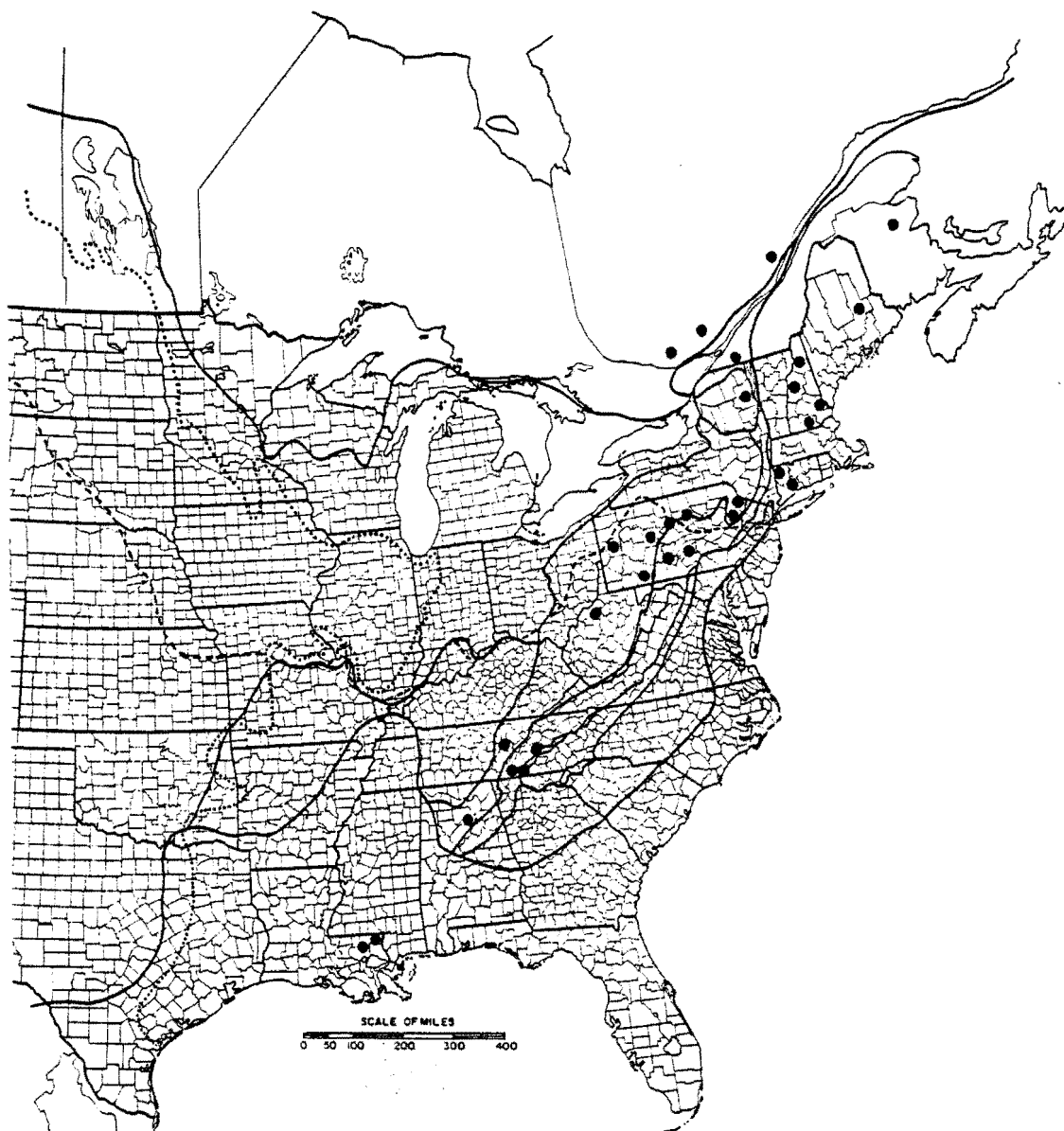


Figure 167. Range of *Ophiogomphus mainensis*.

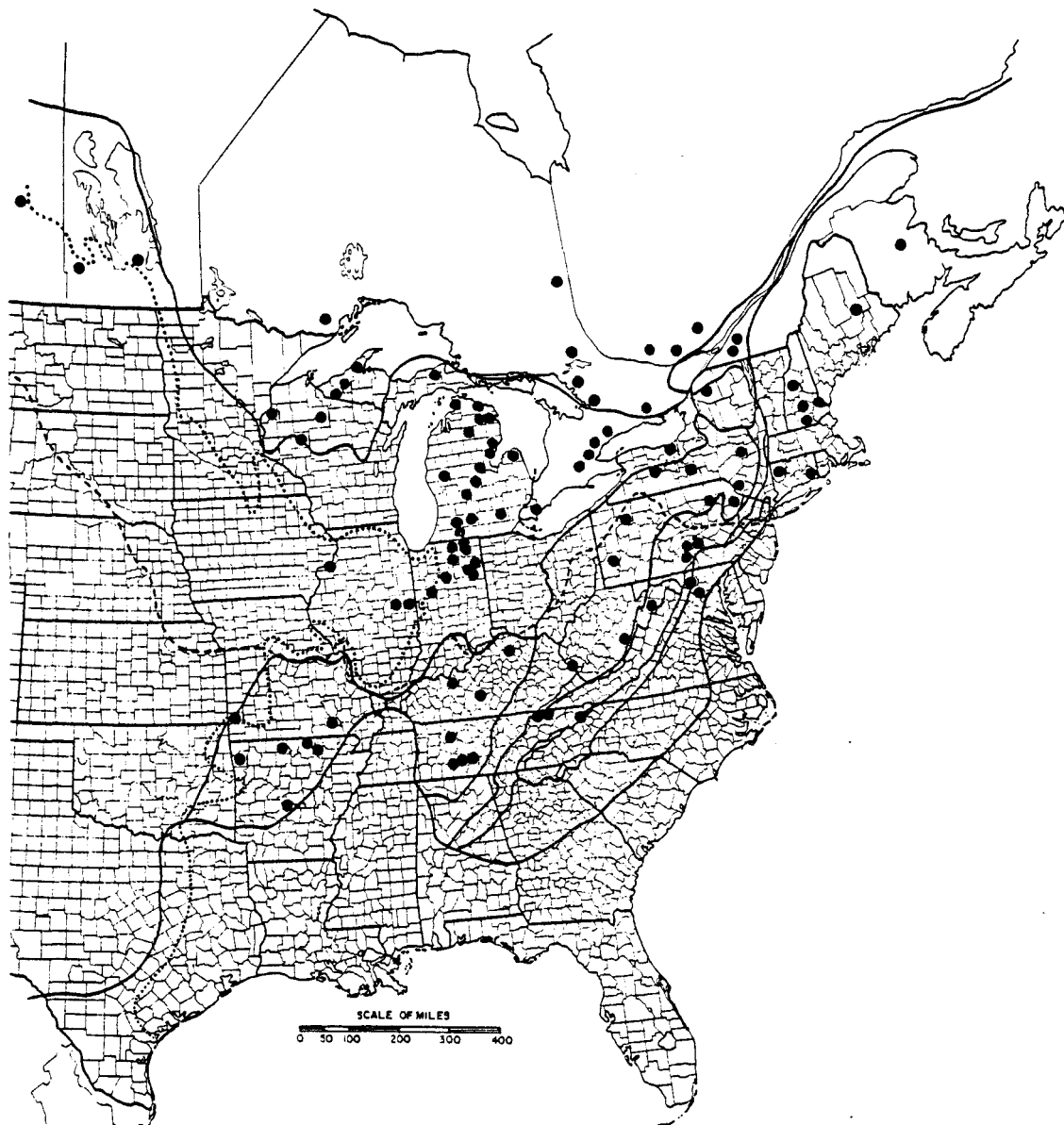


Figure 168. Range of *Ophiogomphus rupinsulensis*.

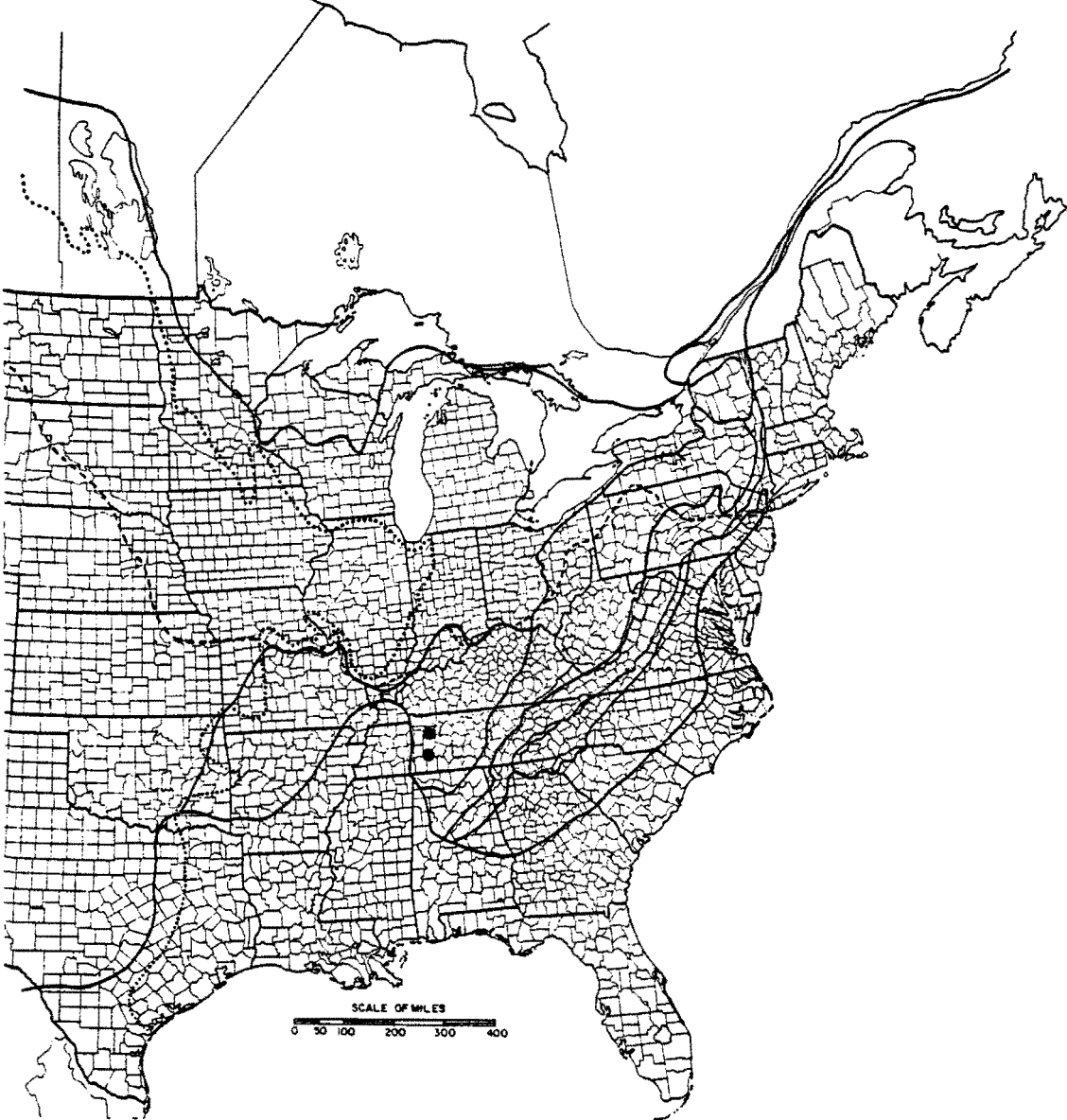


Figure 169. Range of *Ophiogomphus* sp. A.

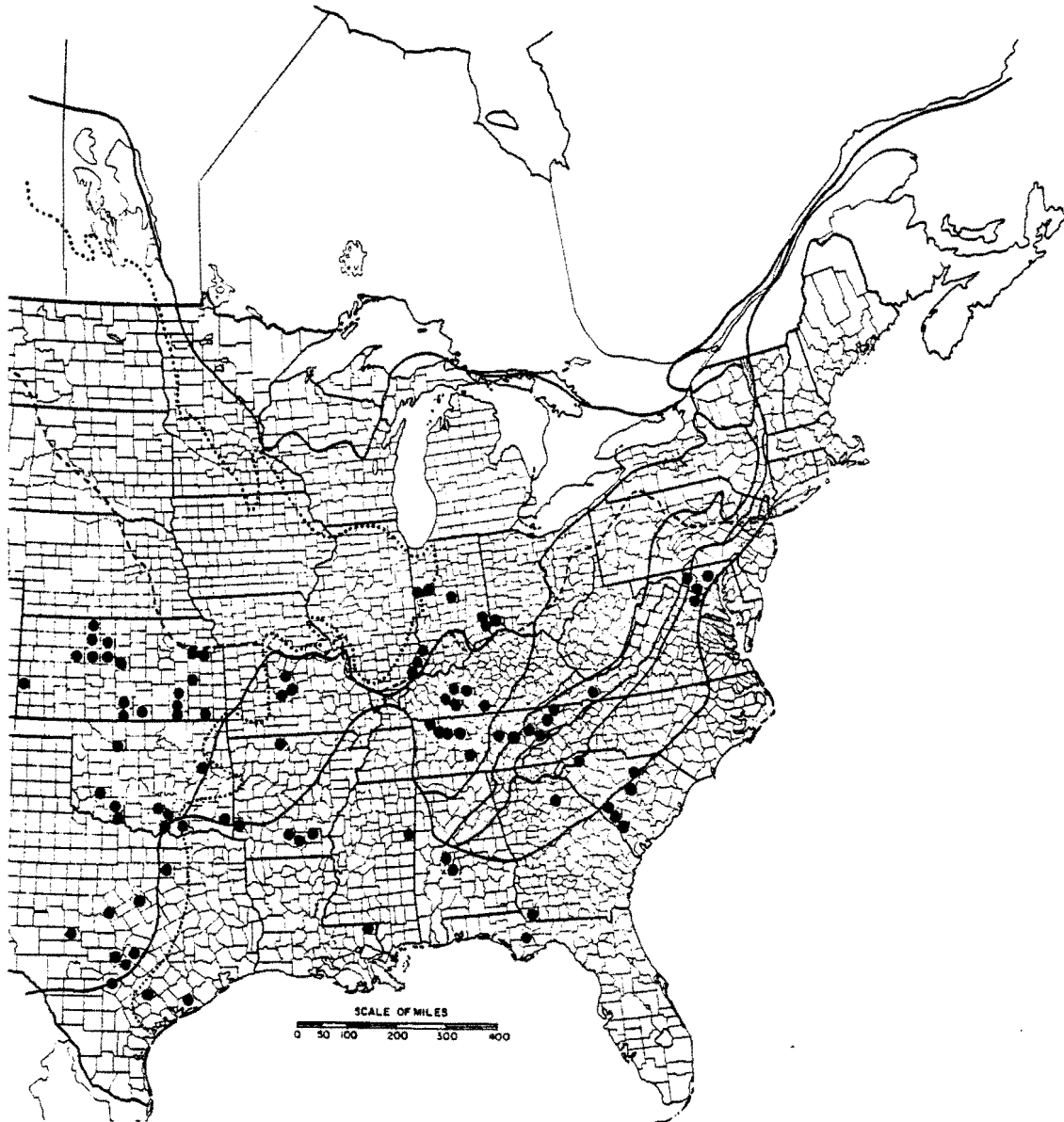


Figure 170. Range of *Erpetogomphus designatus* (" . . . also from Mexico," Needham and Westfall, 1955).

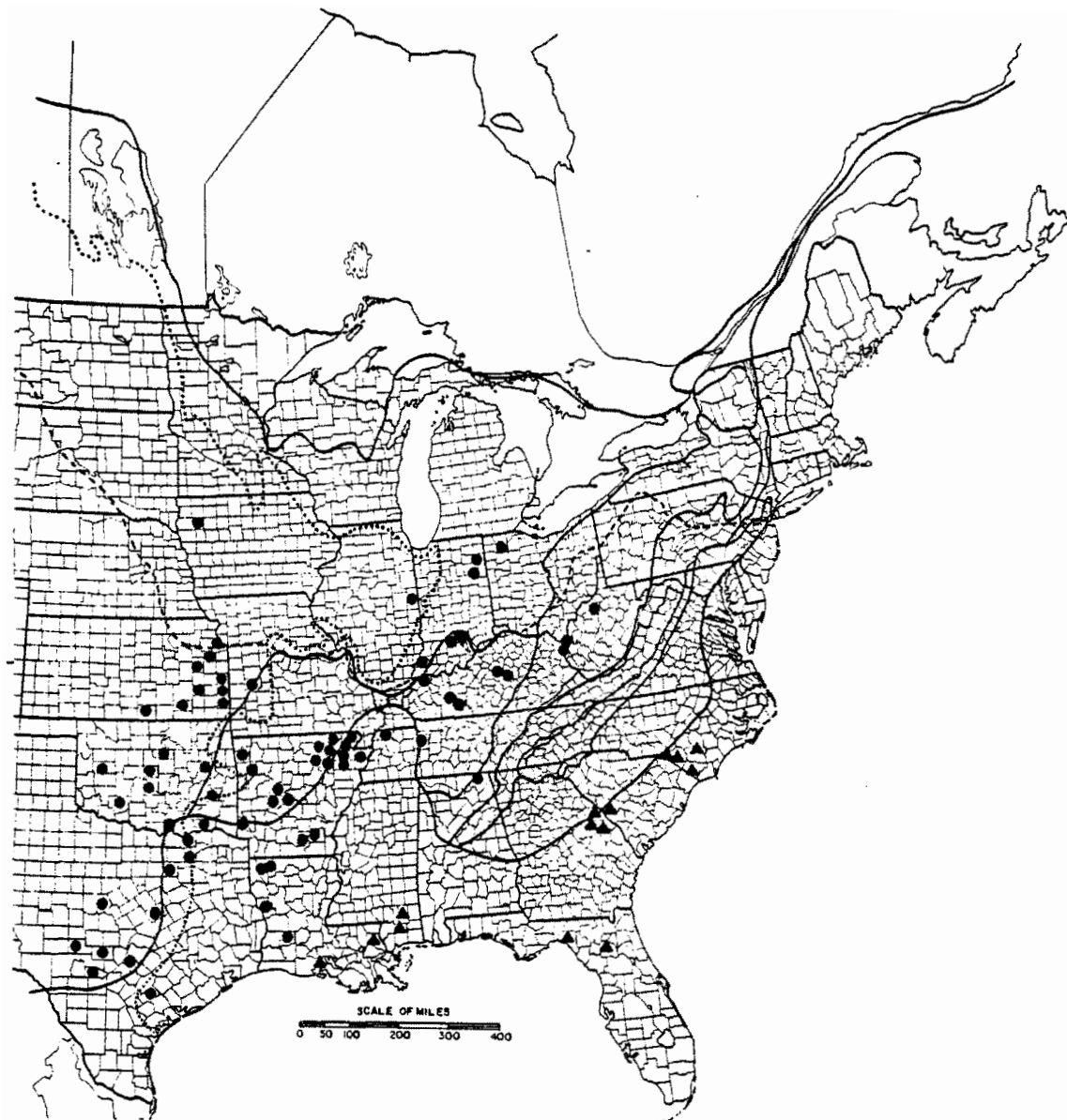


Figure 171. Ranges of *Dromogomphus armatus* (triangles) and *Dromogomphus spoliatus* (dots).

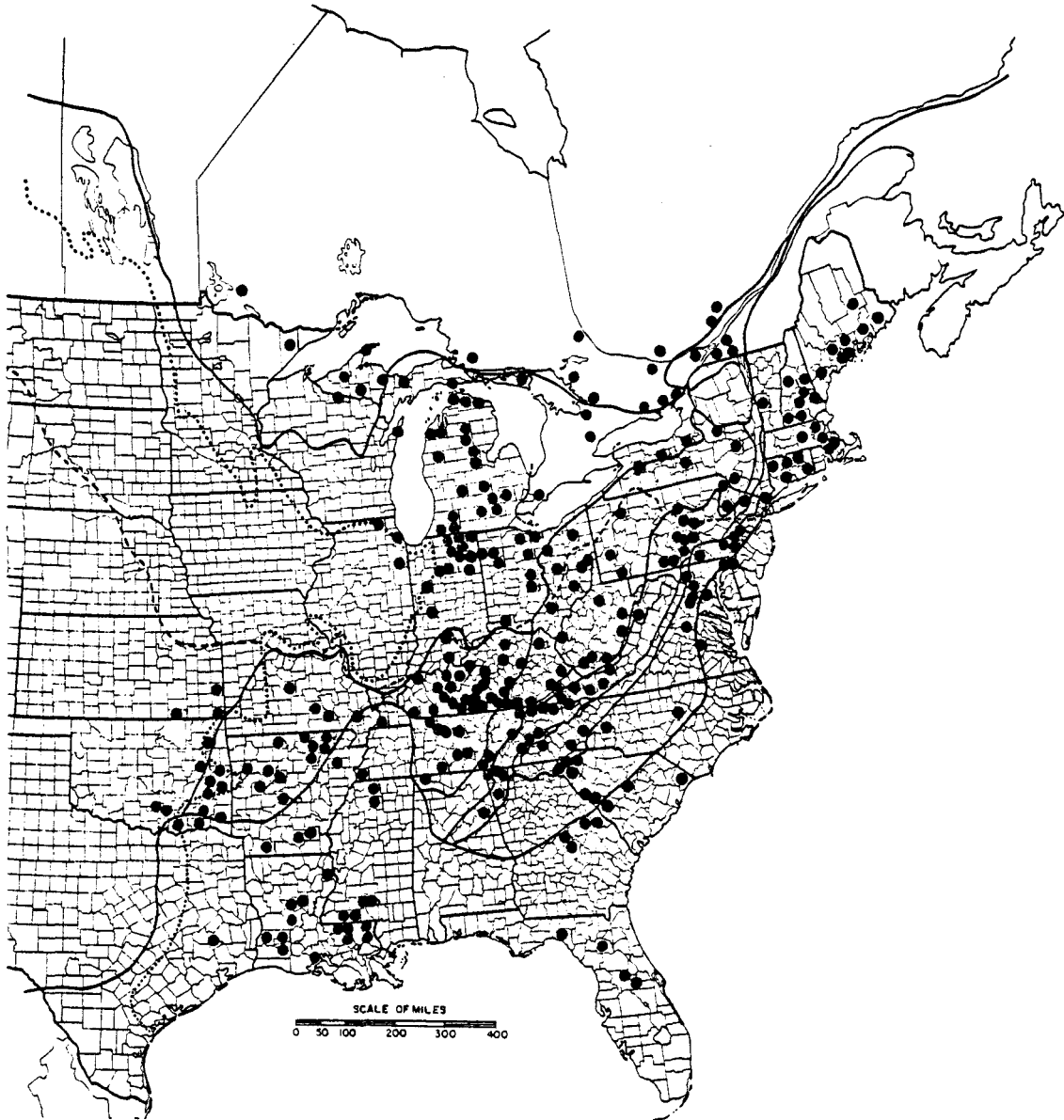


Figure 172. Range of *Dromogomphus spinosus*.



Figure 173. Range of *Gomphus descriptus*.

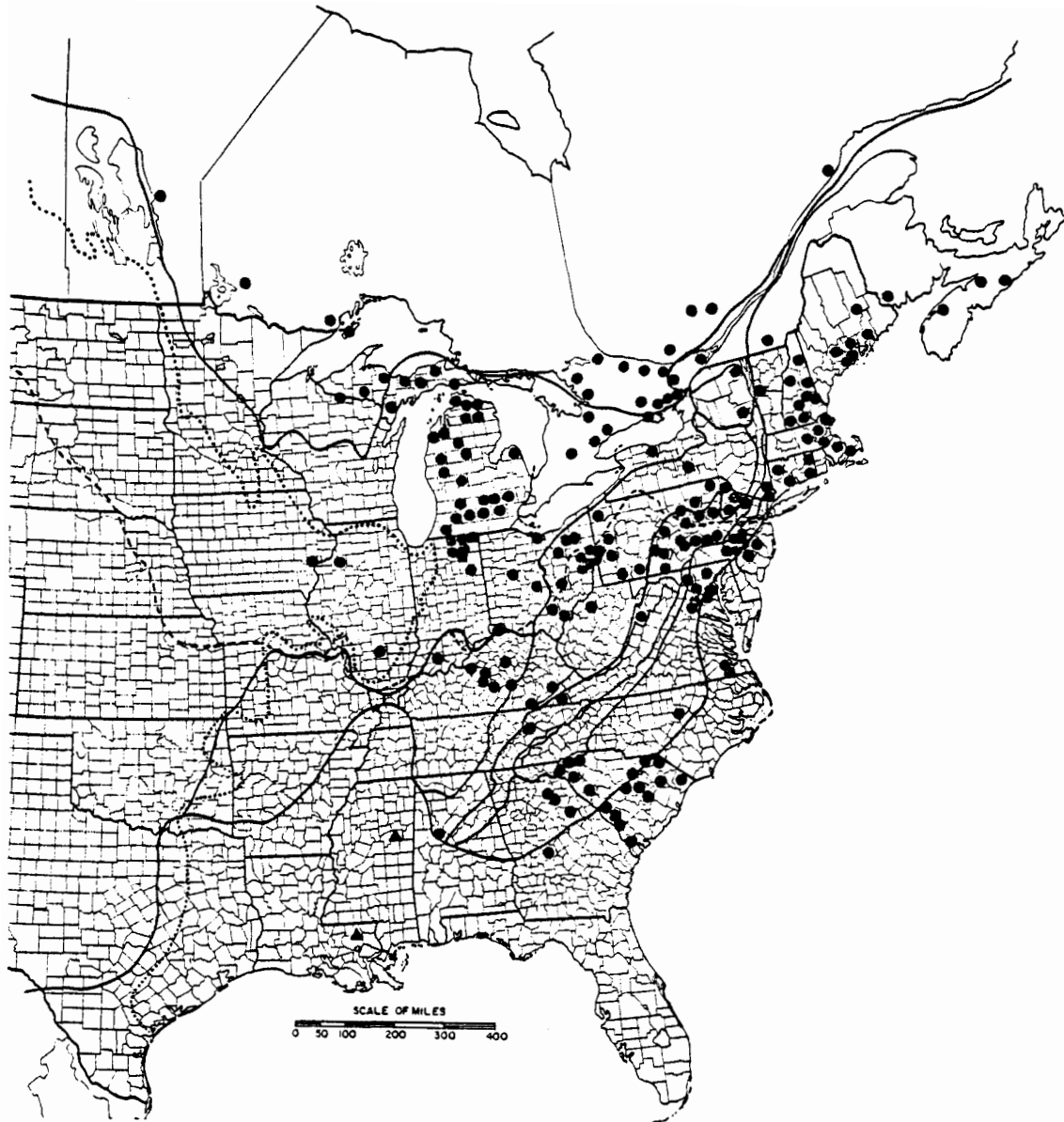


Figure 174. Ranges of *Gomphus exilis* (dots) and *Gomphus flavocaudatus* (triangles).

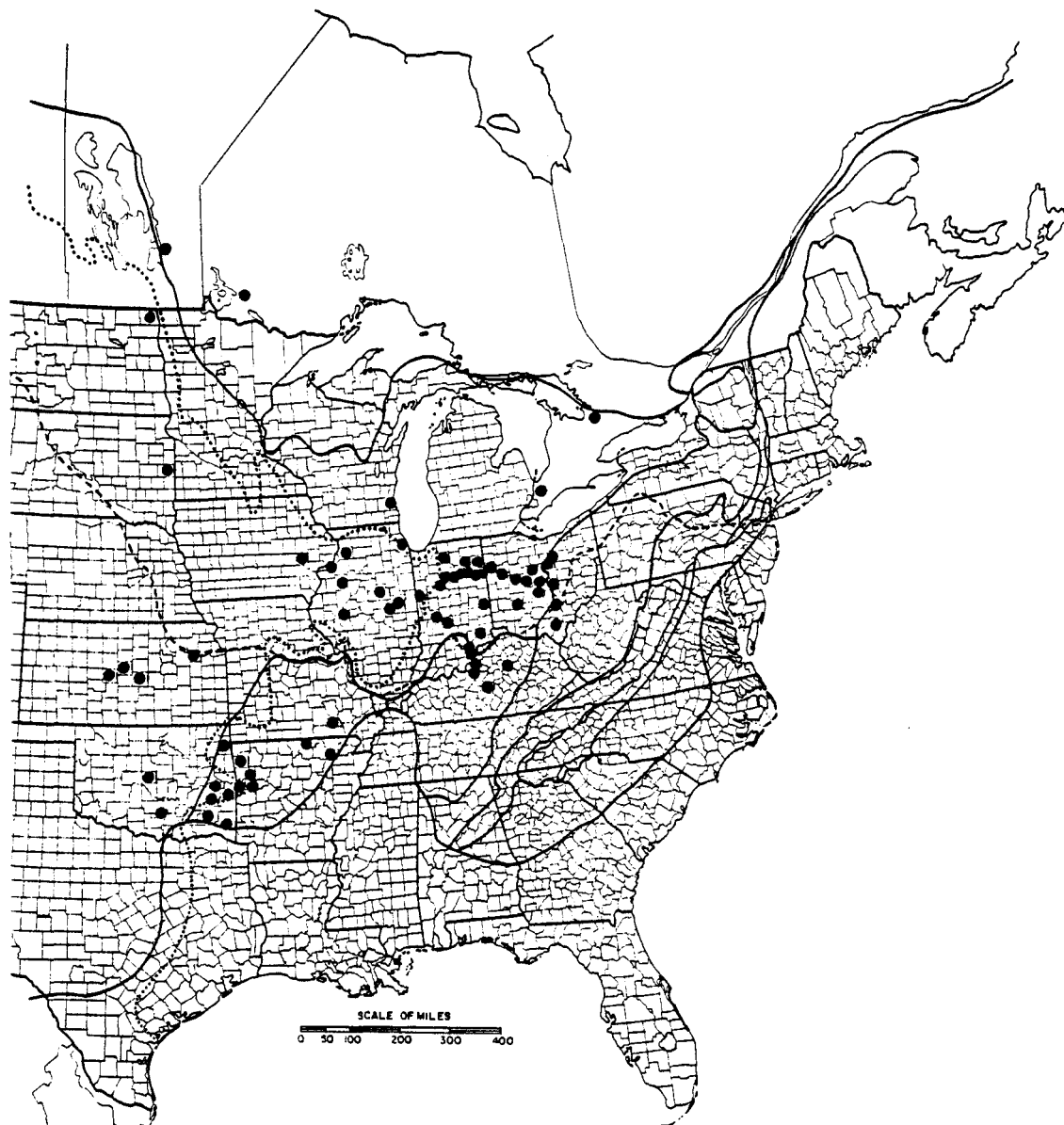


Figure 175. Range of *Gomphus graslinellus*.

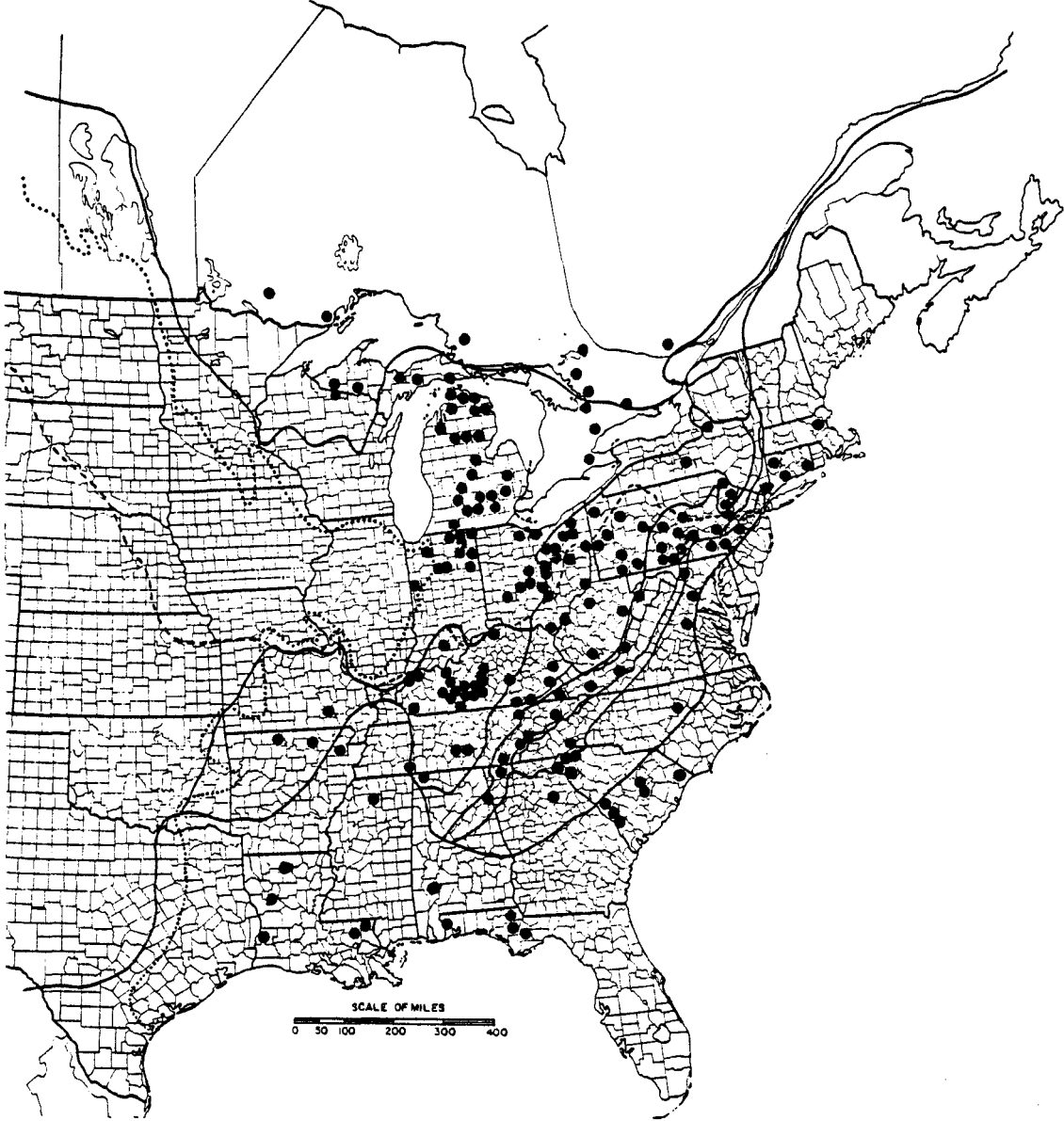


Figure 176. Range of *Gomphus lividus*.



Figure 177. Range of *Gomphus minutus*.

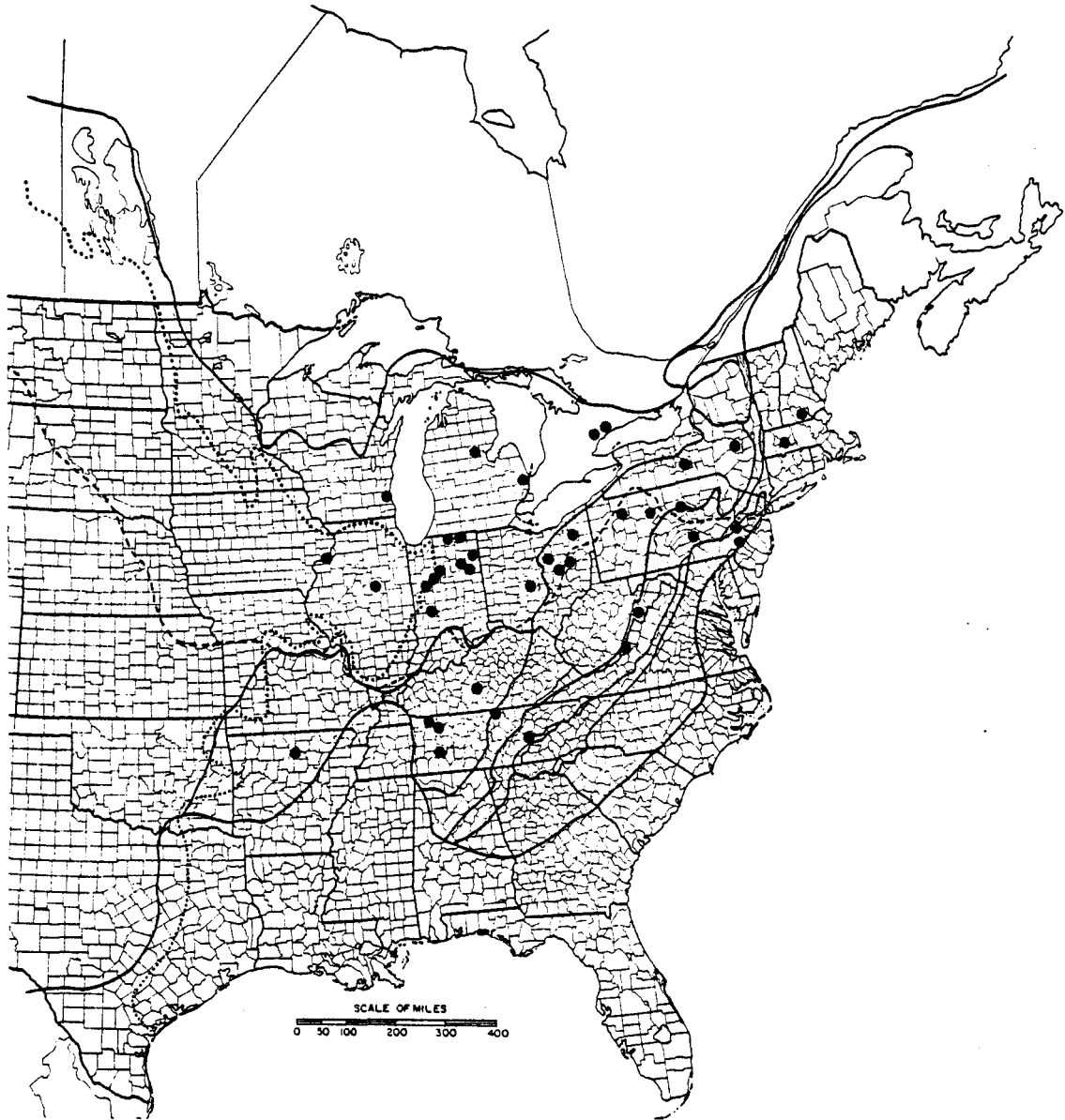


Figure 178. Range of *Gomphus quadricolor*.

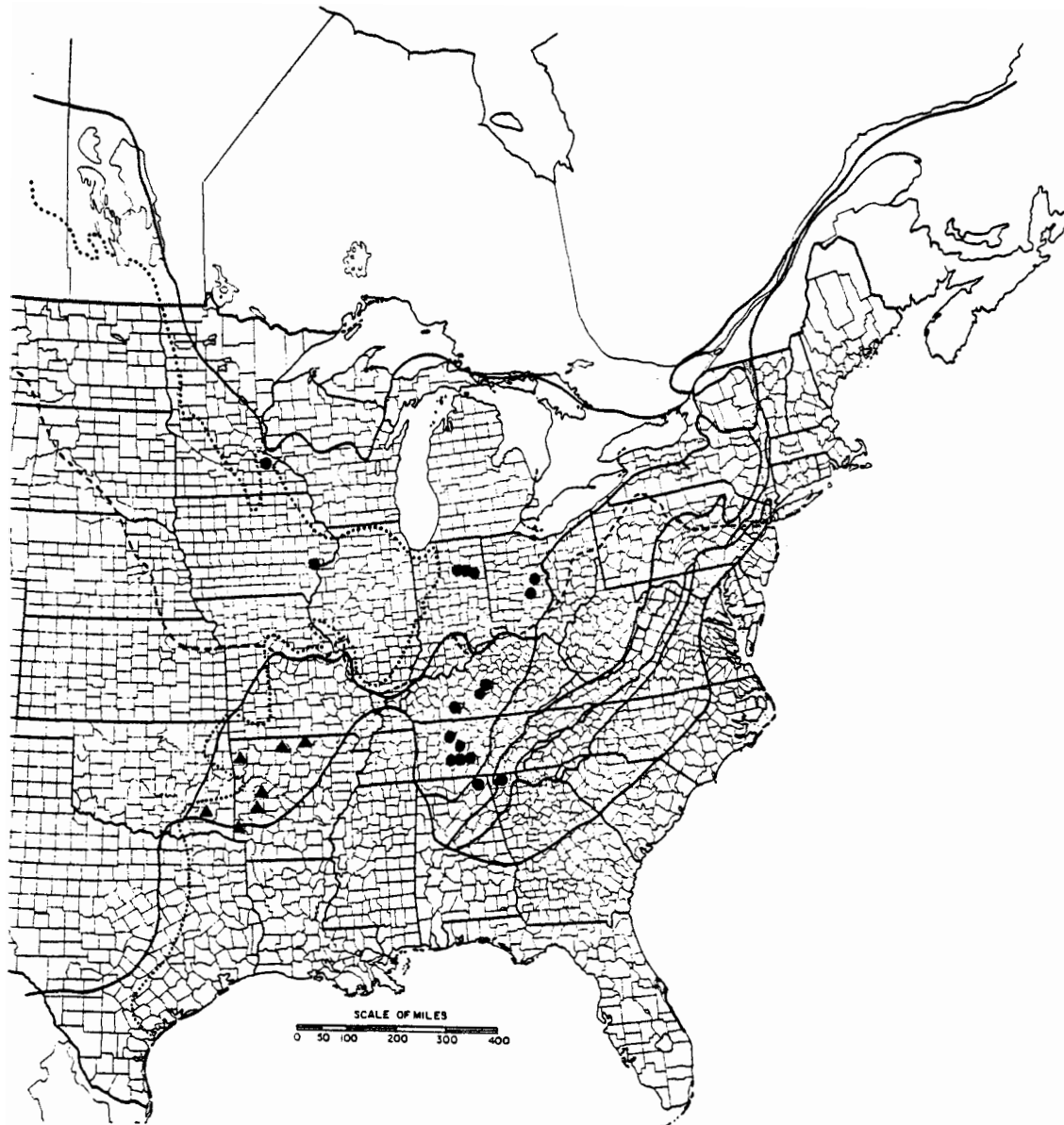


Figure 179. Ranges of *Gomphurus crassus* (dots) and *Gomphurus ozarkensis* (triangles).



Figure 180. Ranges of *Gomphurus dilatatus* (dots) and *Gomphurus modestus* (triangles).

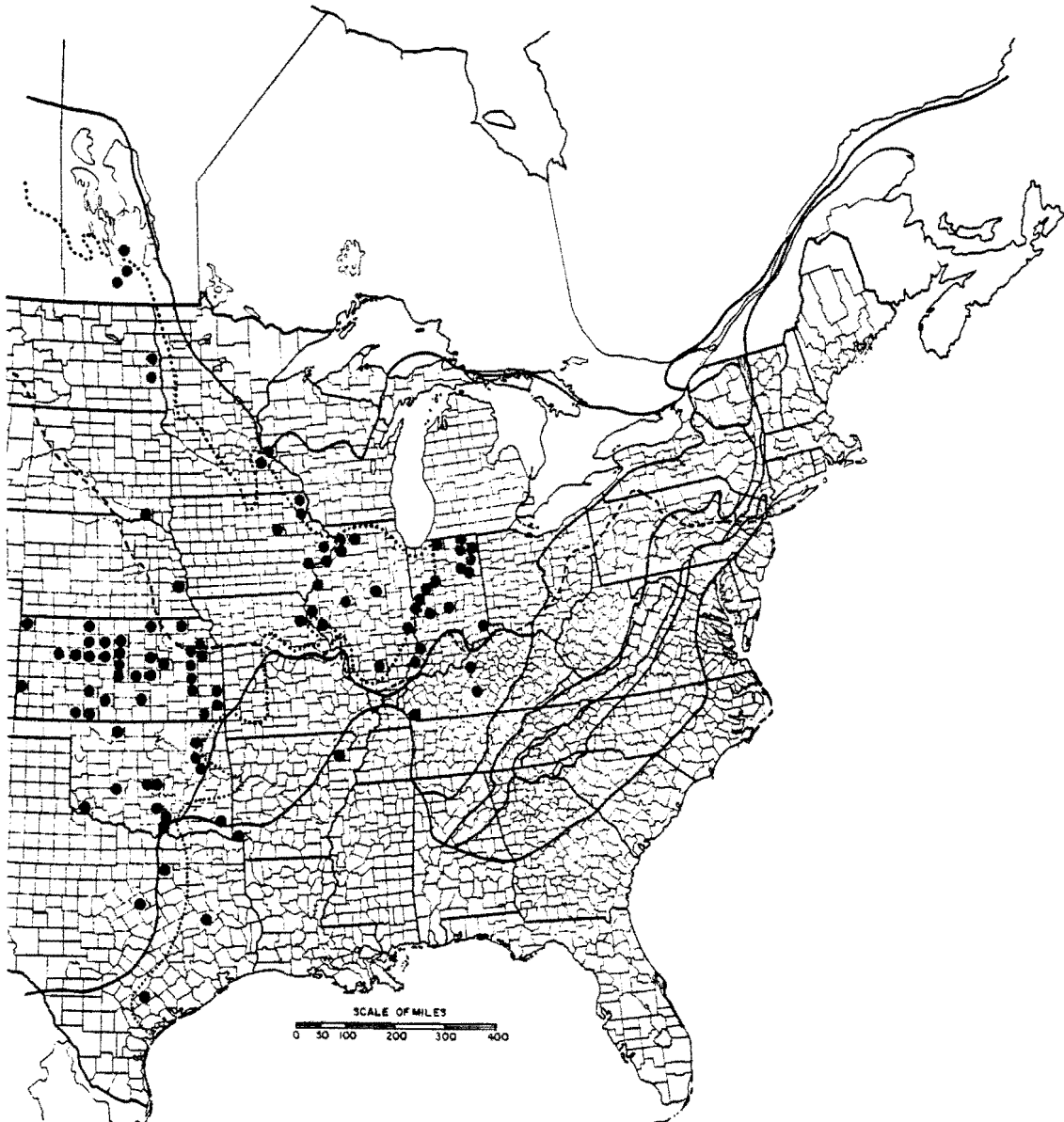


Figure 181. Range of *Gomphurus externus* (range extends westward to Utah).

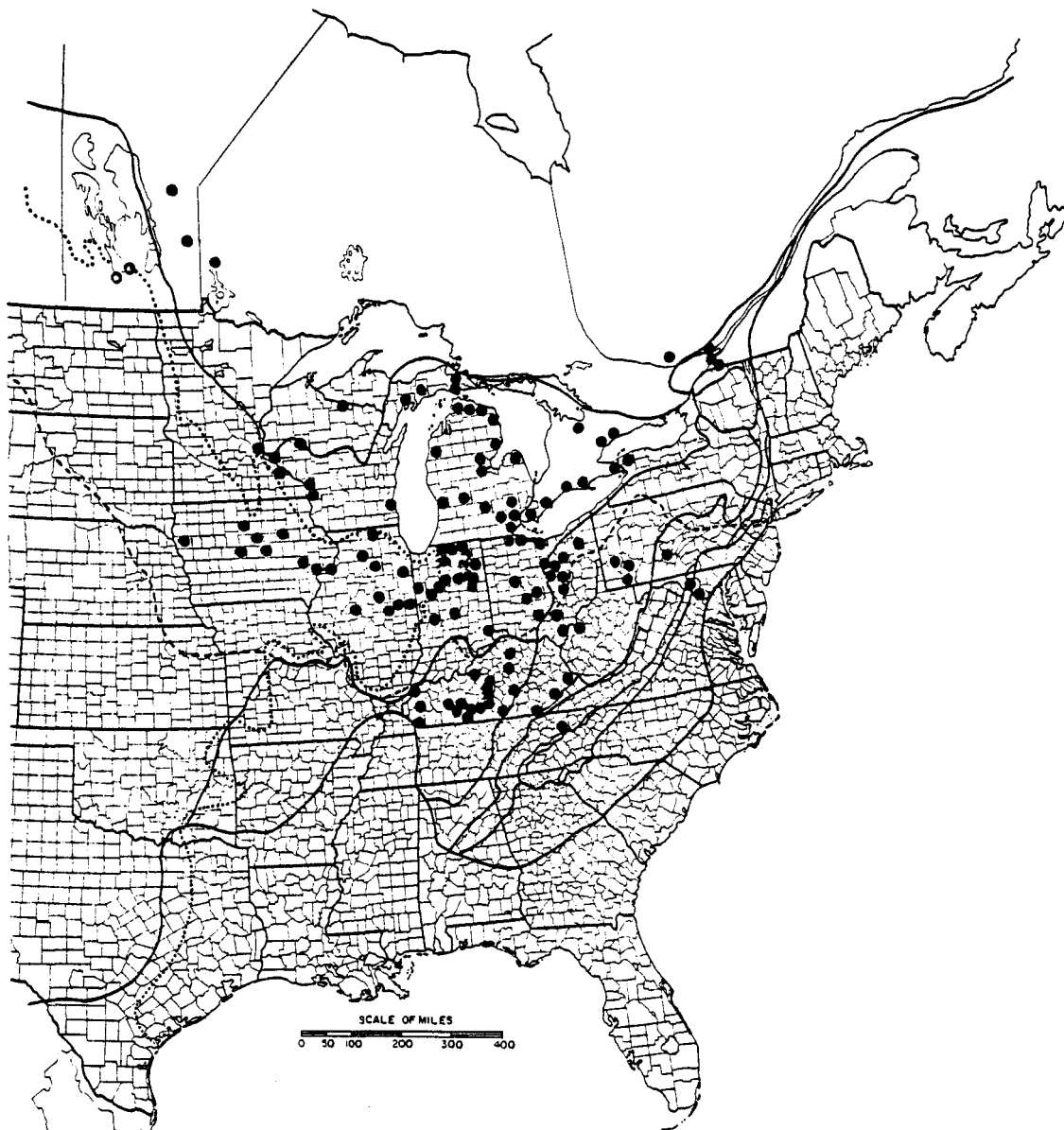


Figure 182. Range of *Gomphurus fraternus*.

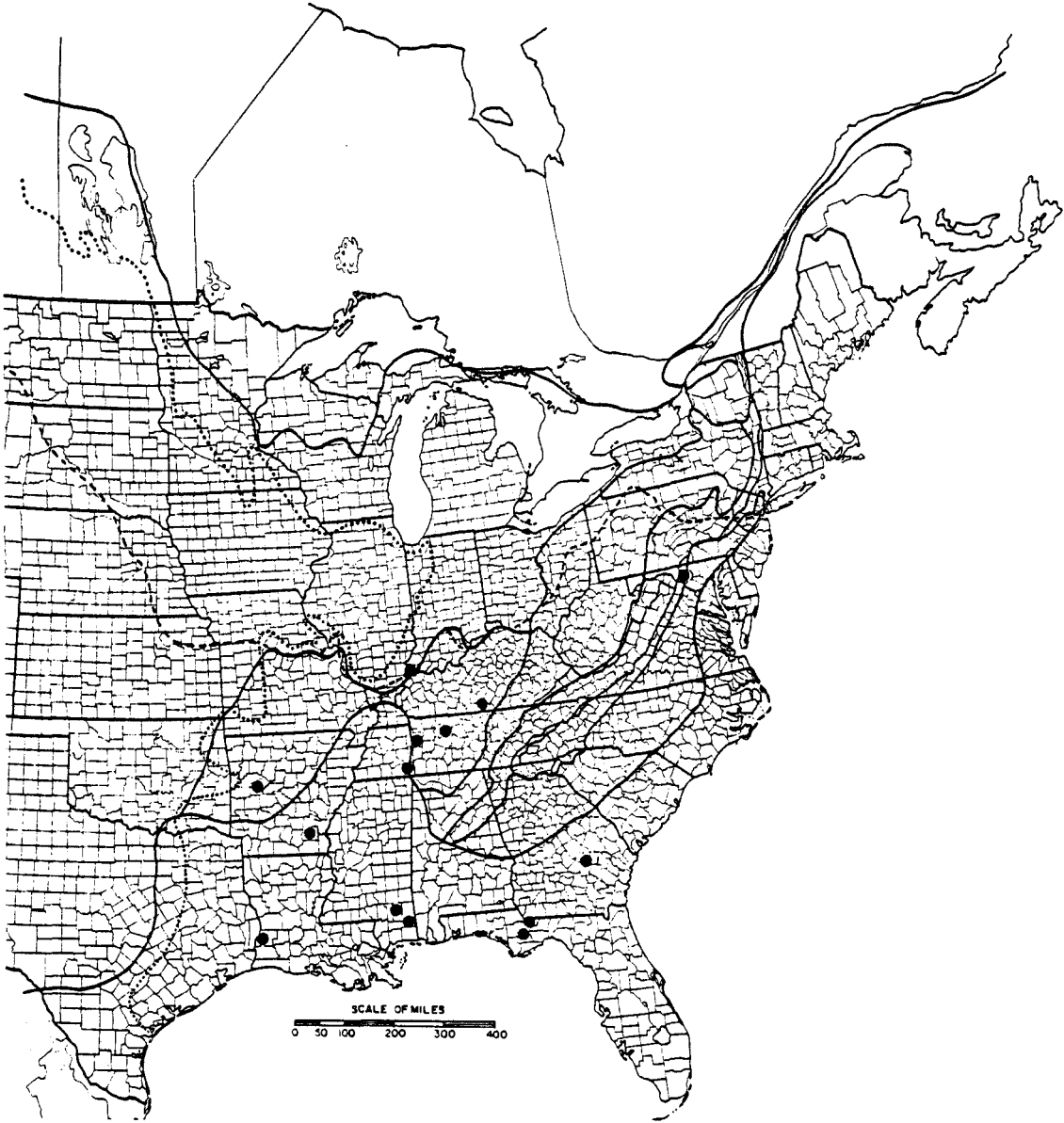


Figure 183. Range of *Gomphurus hybridus*.

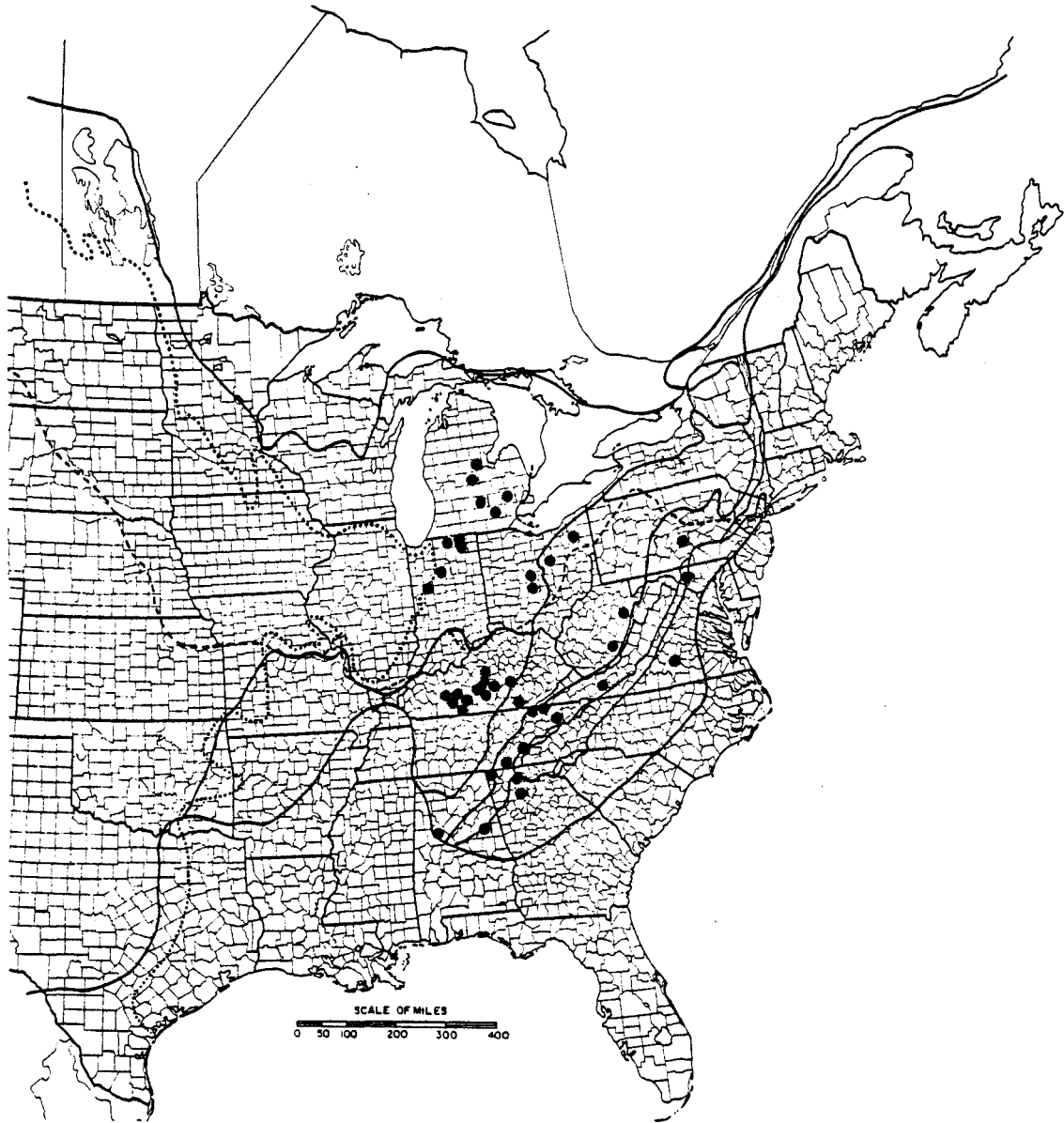


Figure 184. Range of *Gomphurus lineatifrons*.



Figure 185. Range of *Gomphurus septima*.

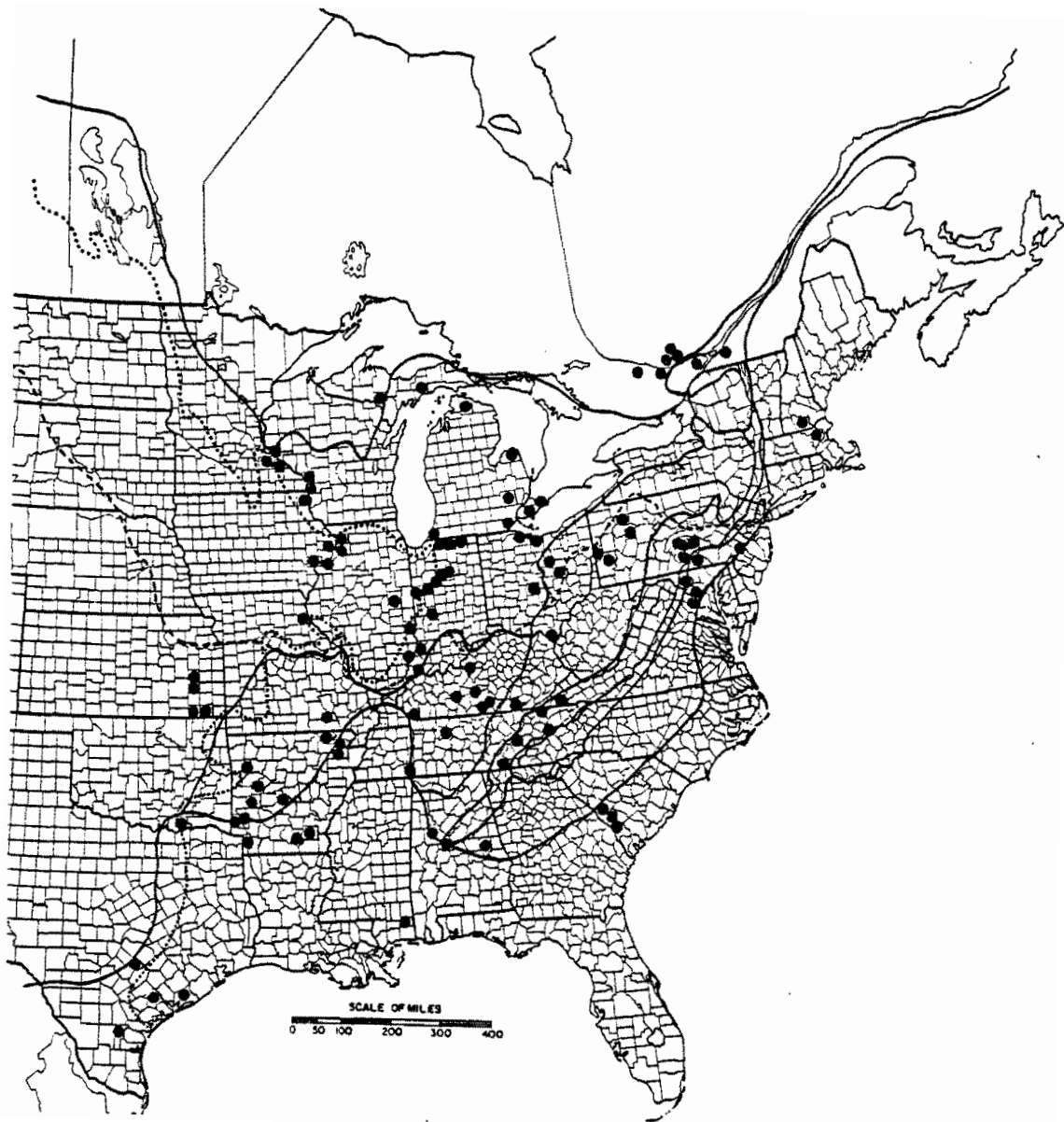


Figure 186. Range of *Gomphurus vastus*.

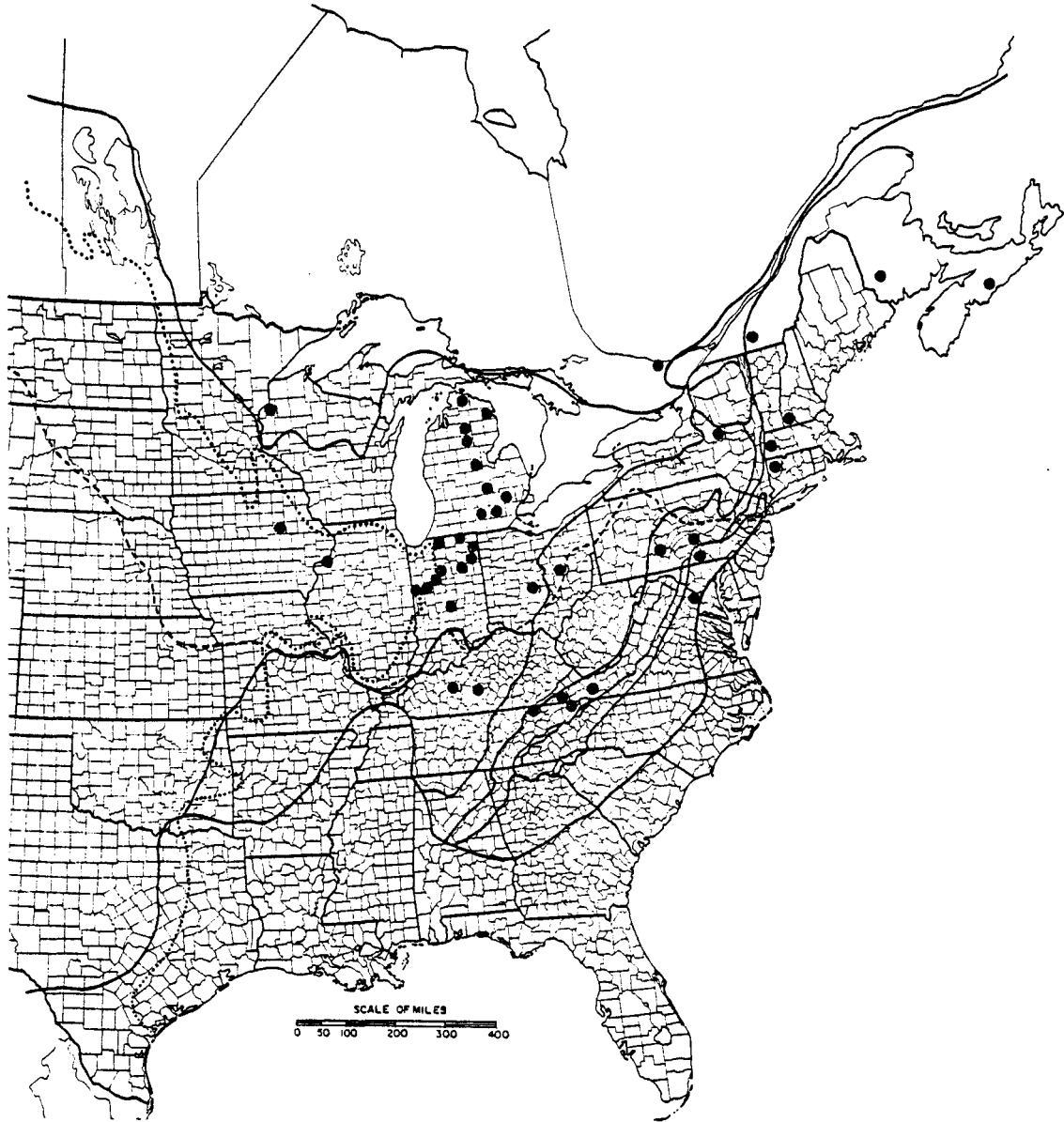


Figure 187. Range of *Gomphurus ventricosus*.



Figure 188. Ranges of *Hylogomphus abbreviatus* (dots) and *Hylogomphus apomyius* (triangles).

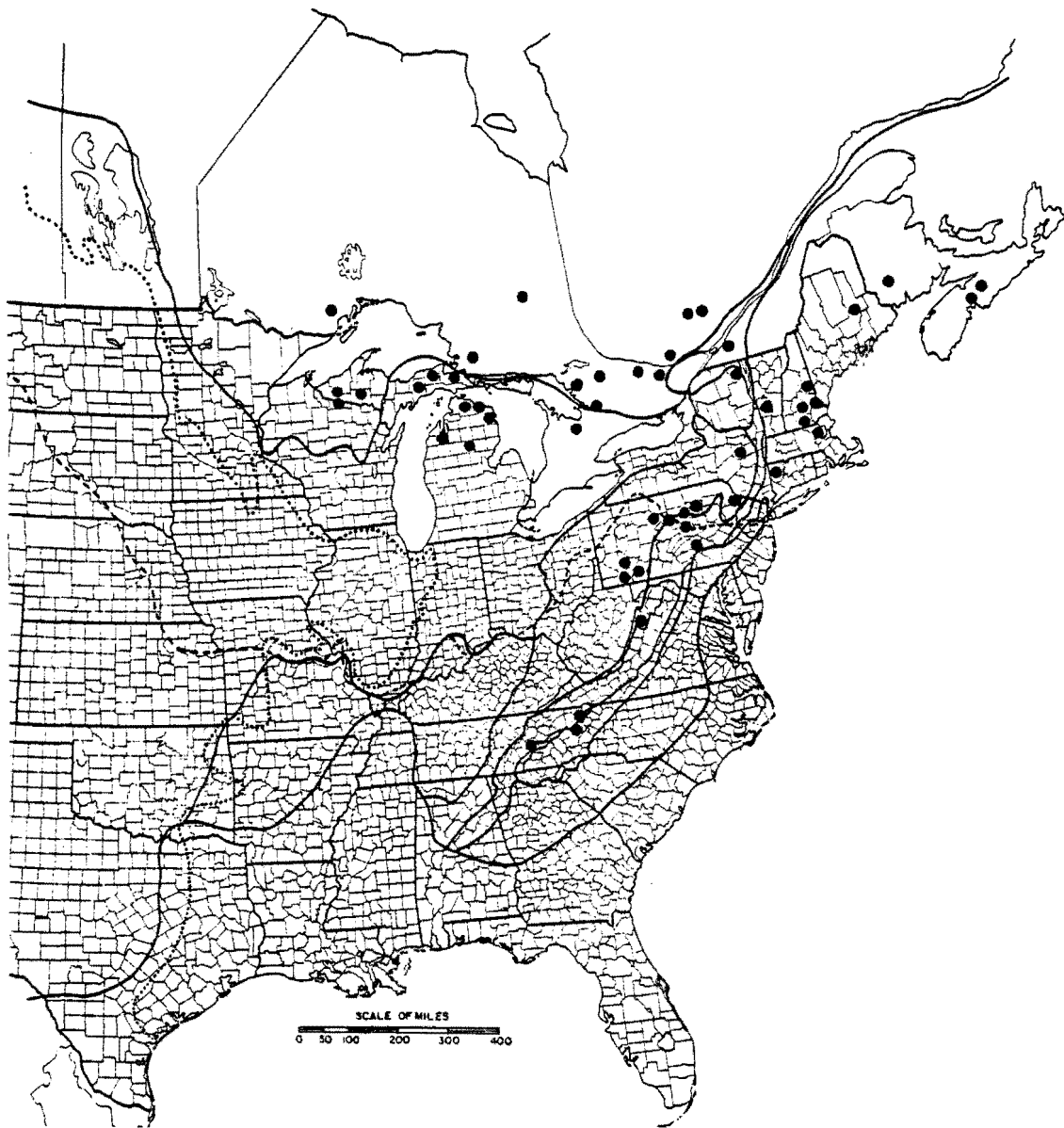


Figure 189. Range of *Hylogomphus brevis*.

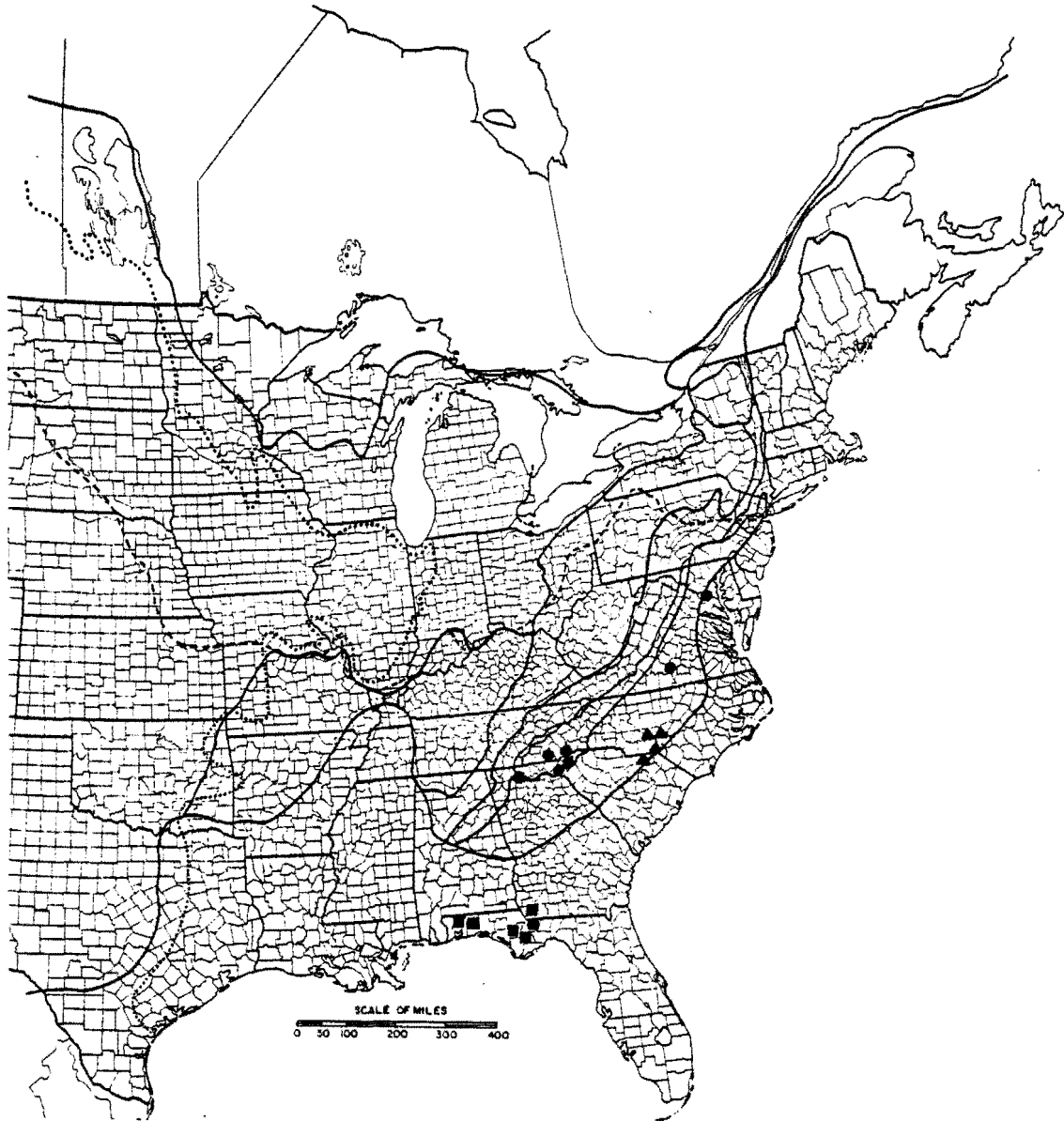


Figure 190. Ranges of *Hylogomphus carolinus* (triangles), *Hylogomphus geminatus* (squares) and *Hylogomphus parvidens* (dots).

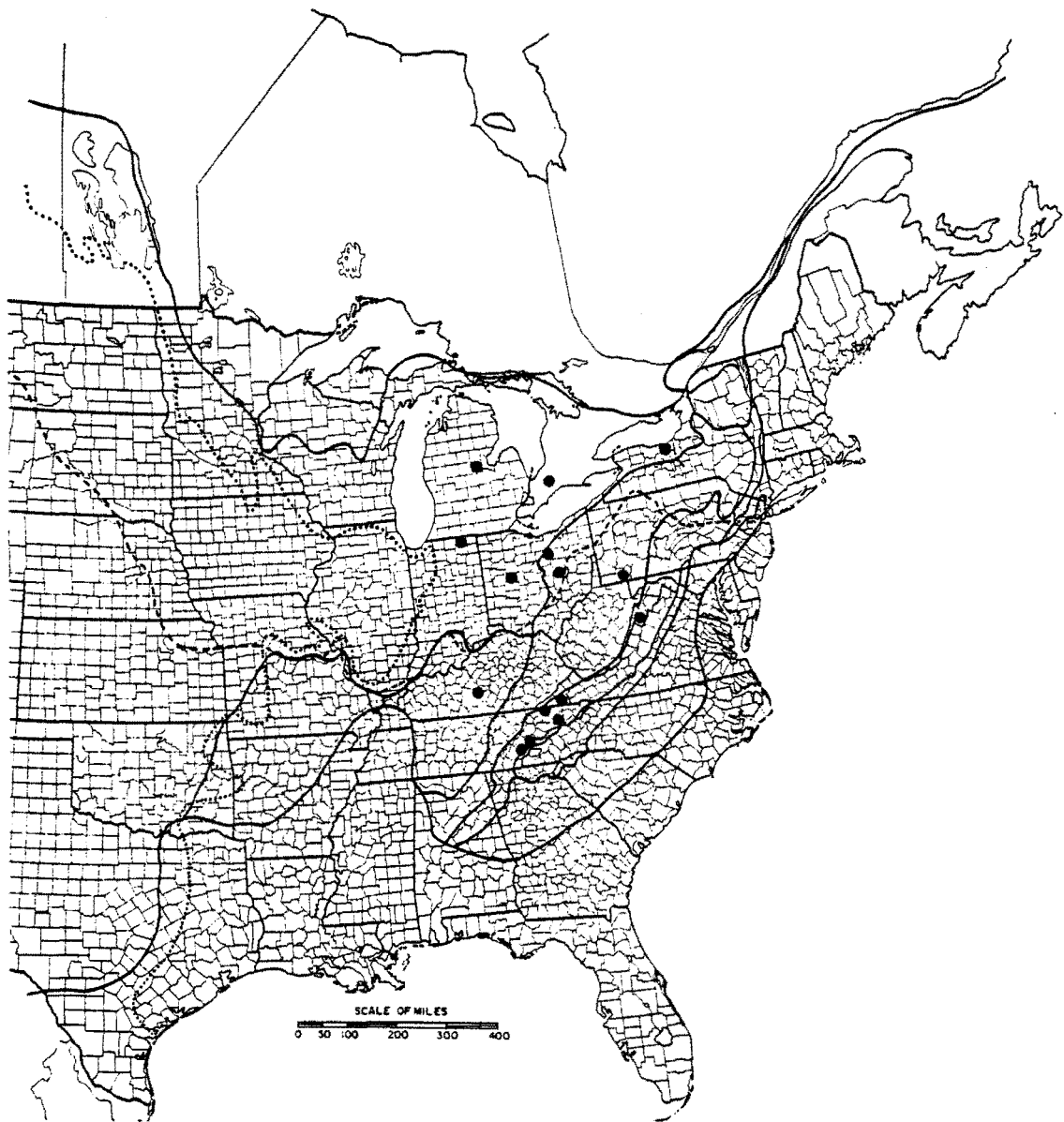


Figure 191. Range of *Hylogomphus viridifrons*.



Figure 192. Range of Genus *A consanguis*.

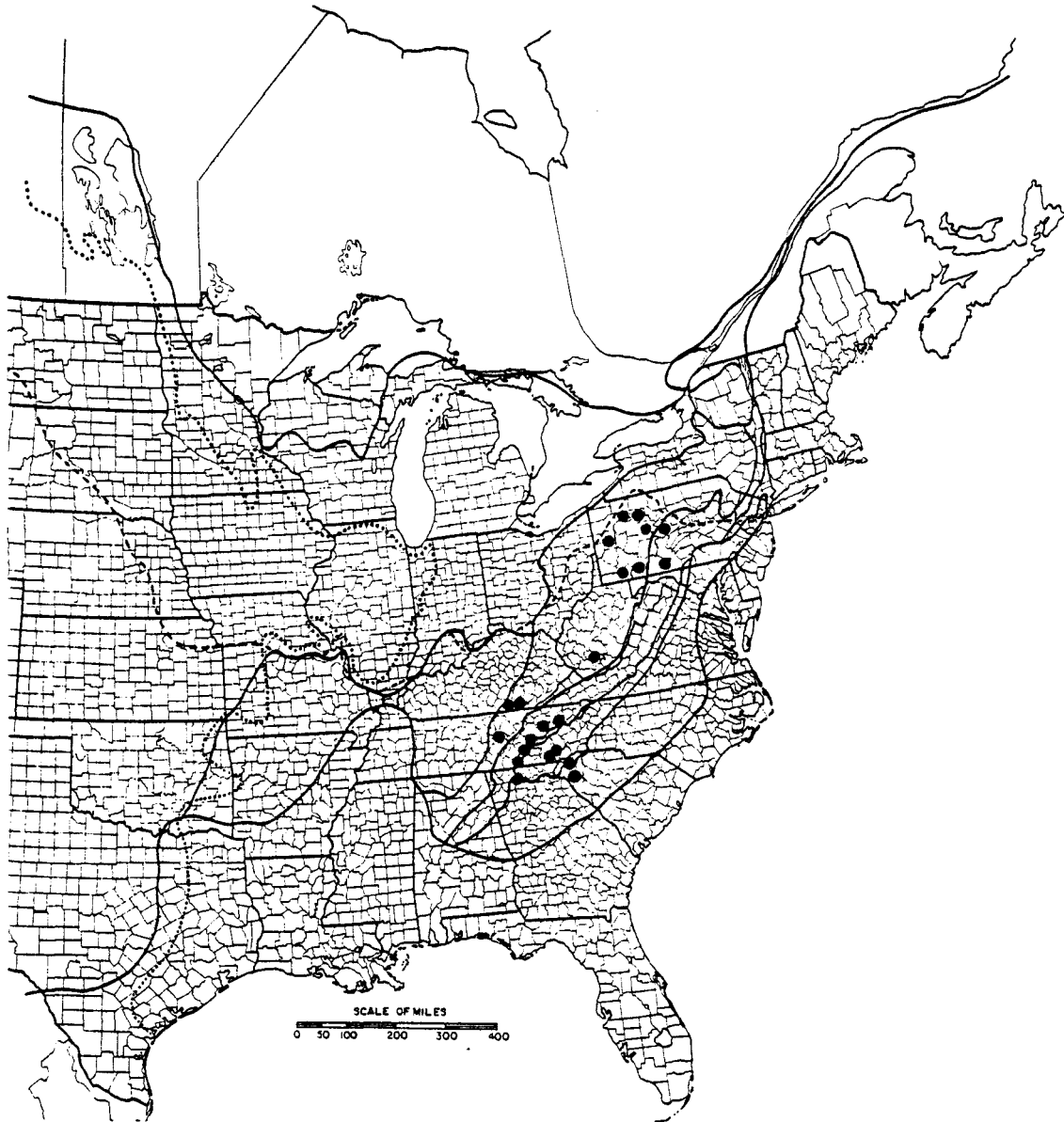


Figure 193. Range of Genus *A. rogersi*.

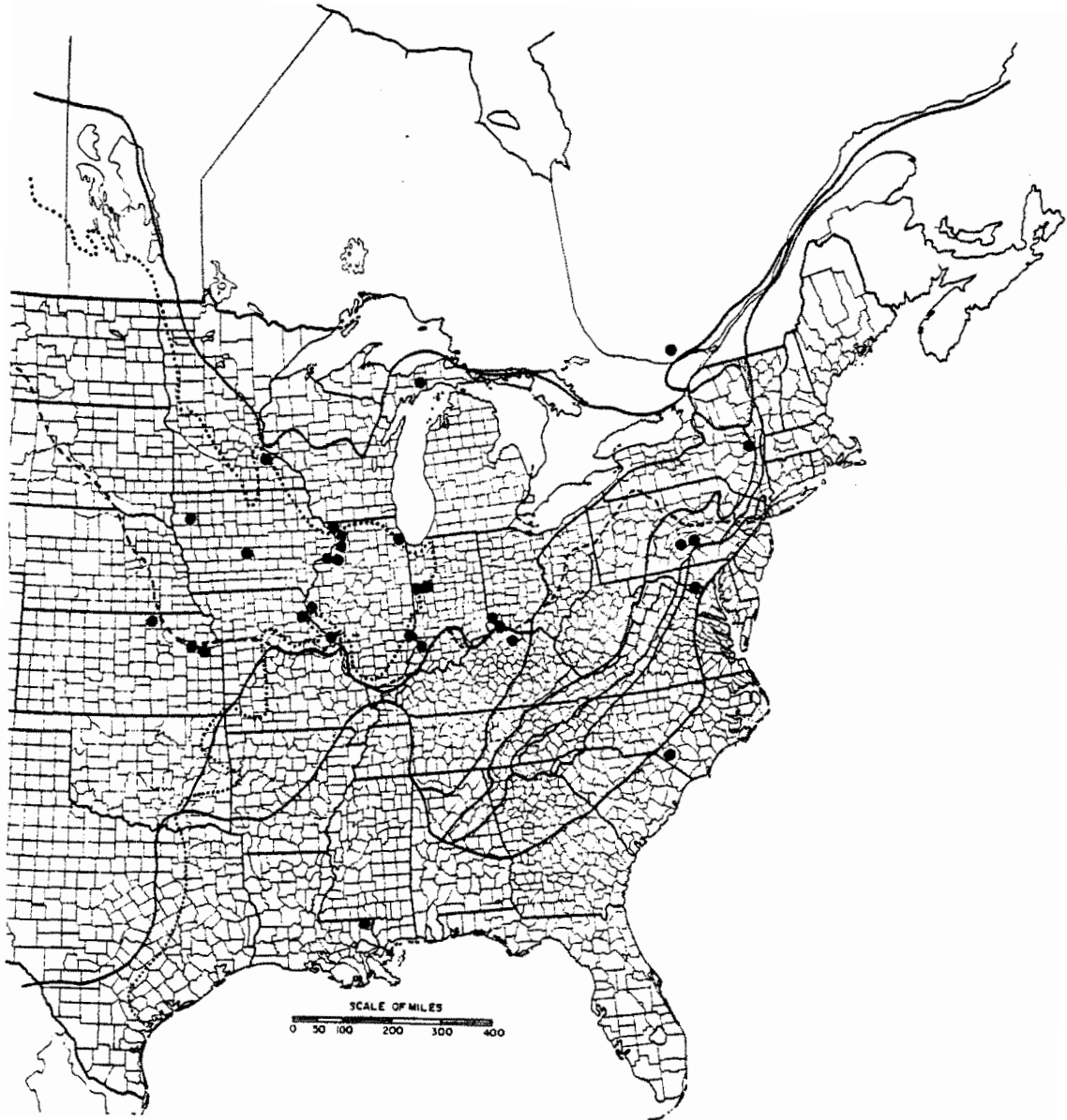


Figure 194. Range of *Stylurus amnicola*.

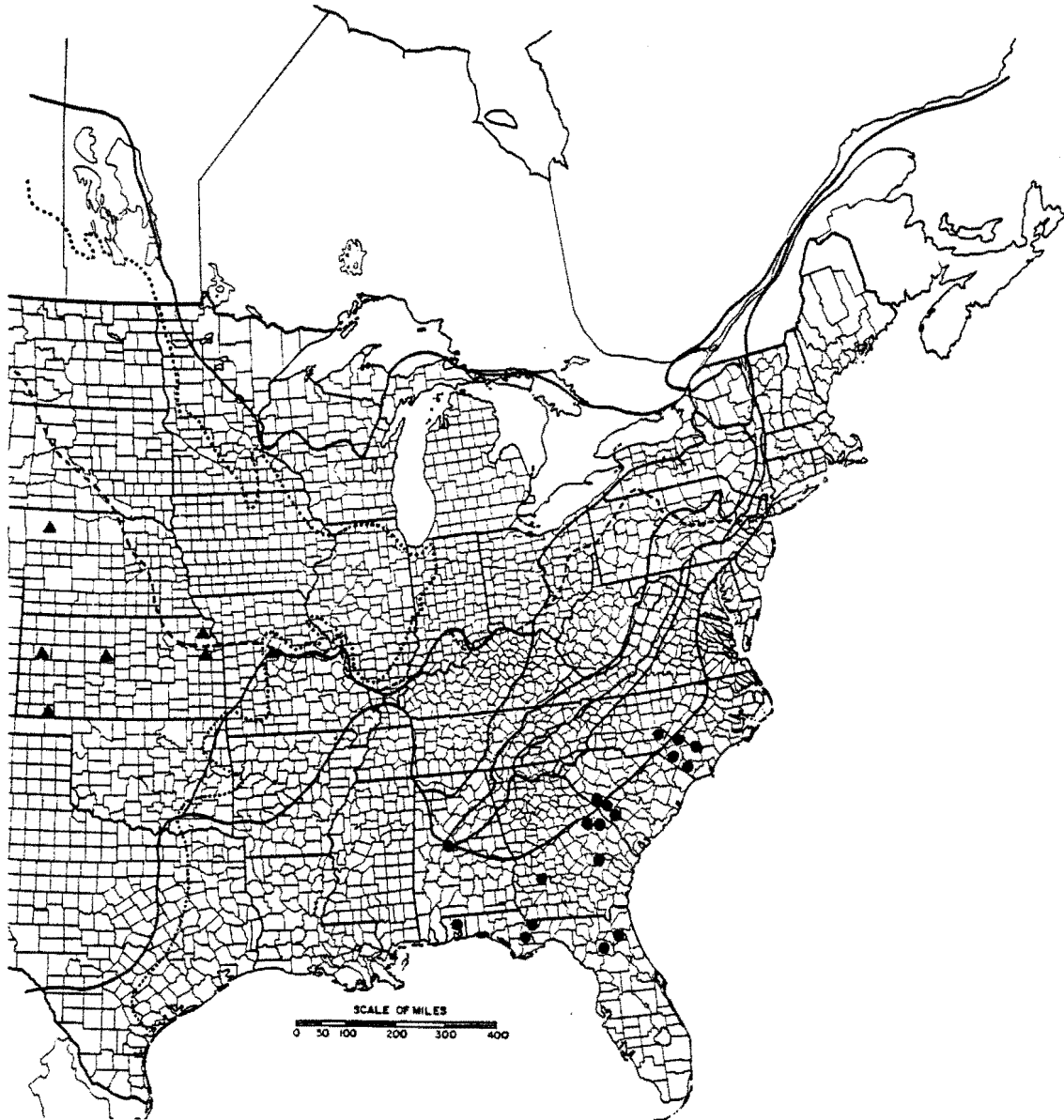


Figure 195. Ranges of *Stylurus intricatus* (triangles, range extends westward to Utah) and *Stylurus ivae* (dots).

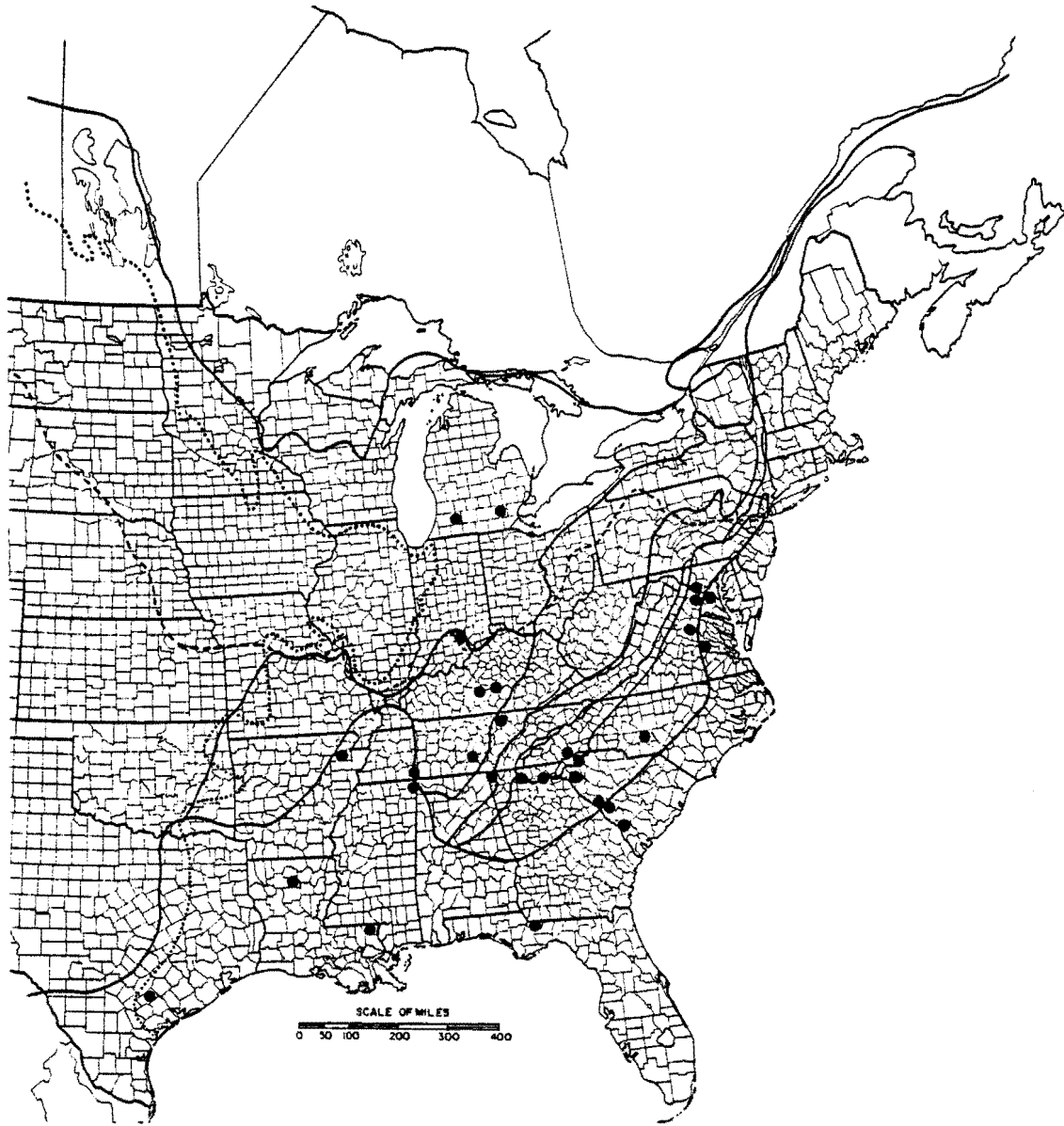


Figure 196. Range of *Stylurus laurae*.

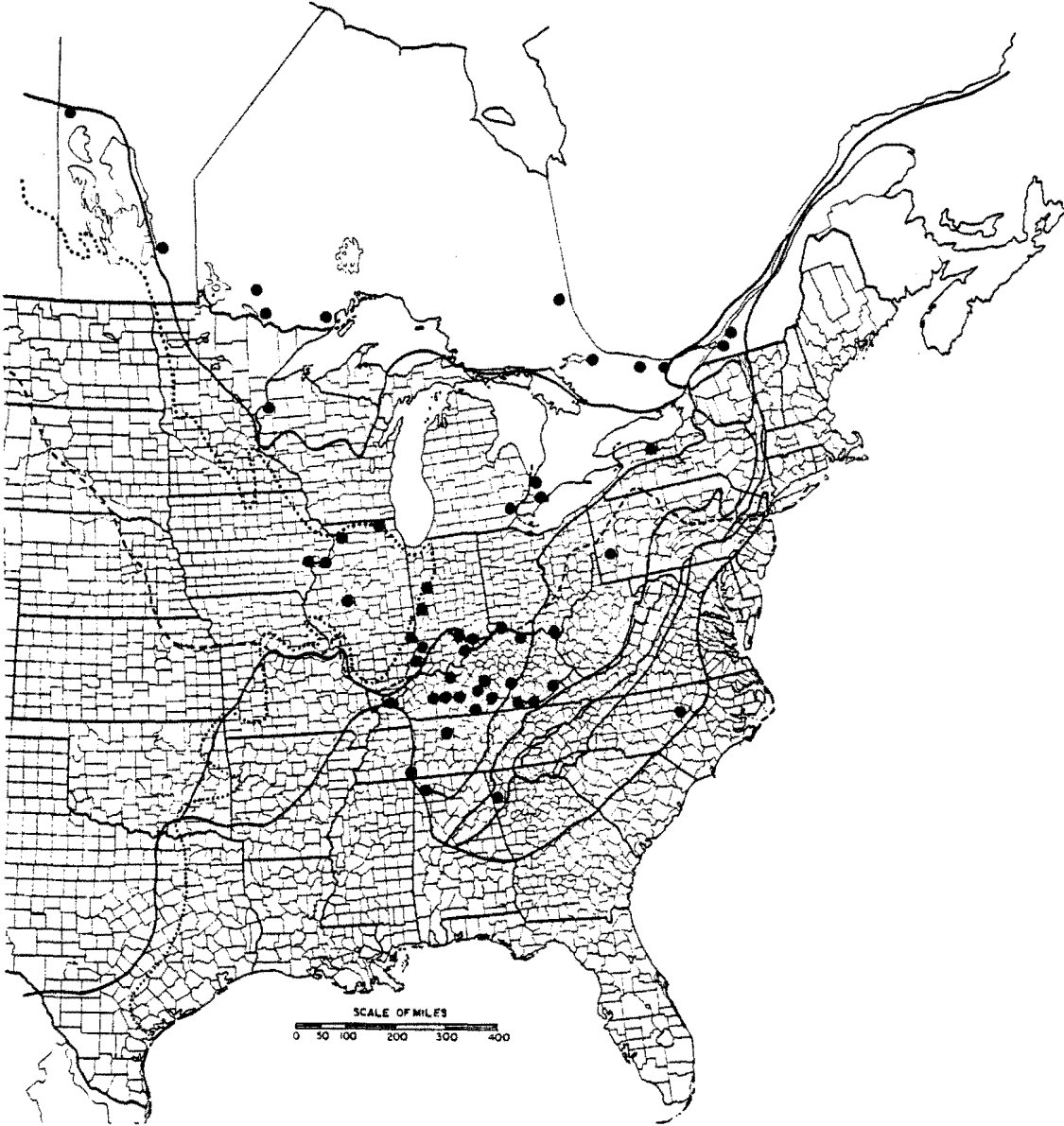


Figure 197. Range of *Stylurus notatus*.

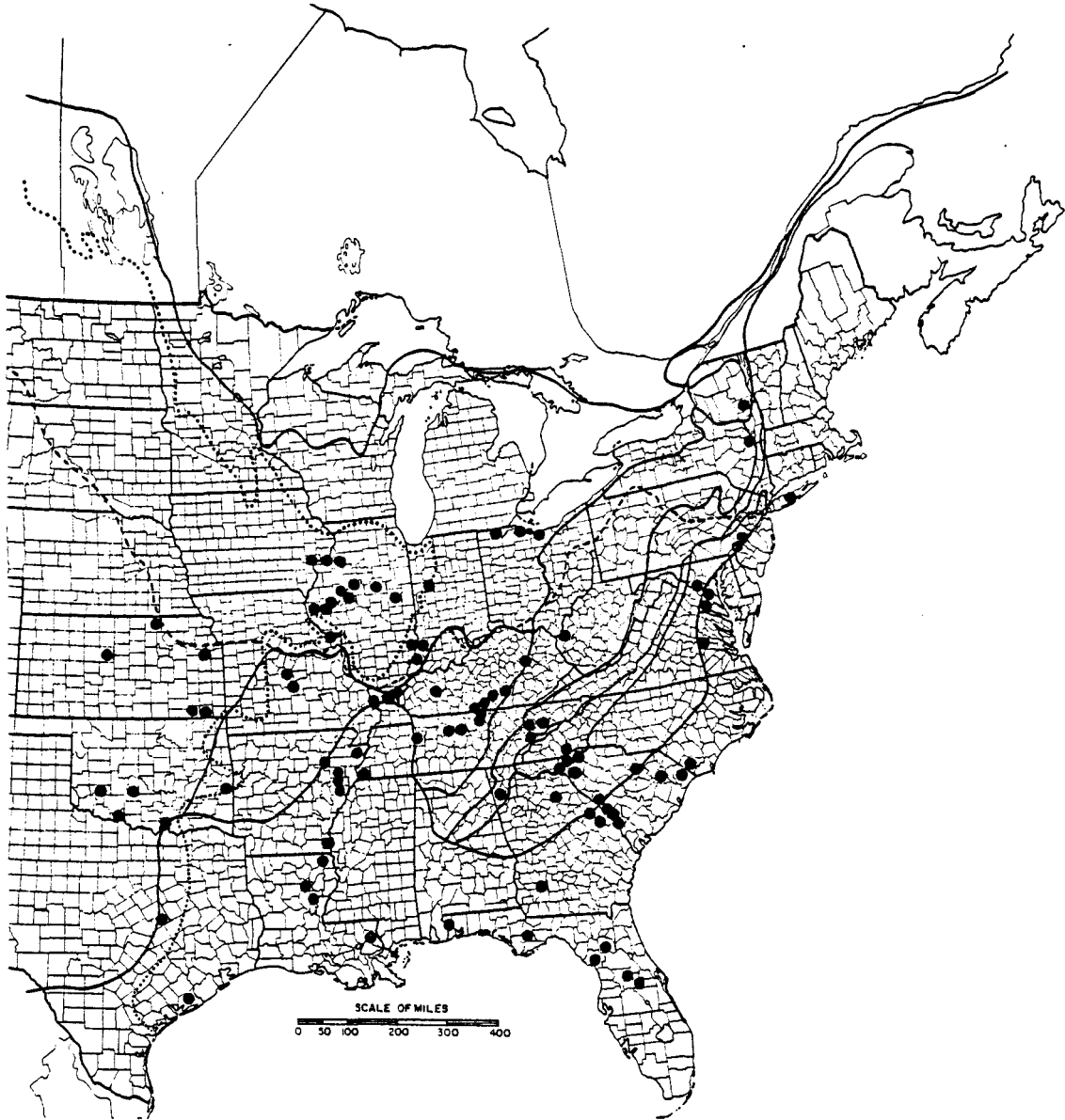


Figure 198. Range of *Stylurus plagiatus*.

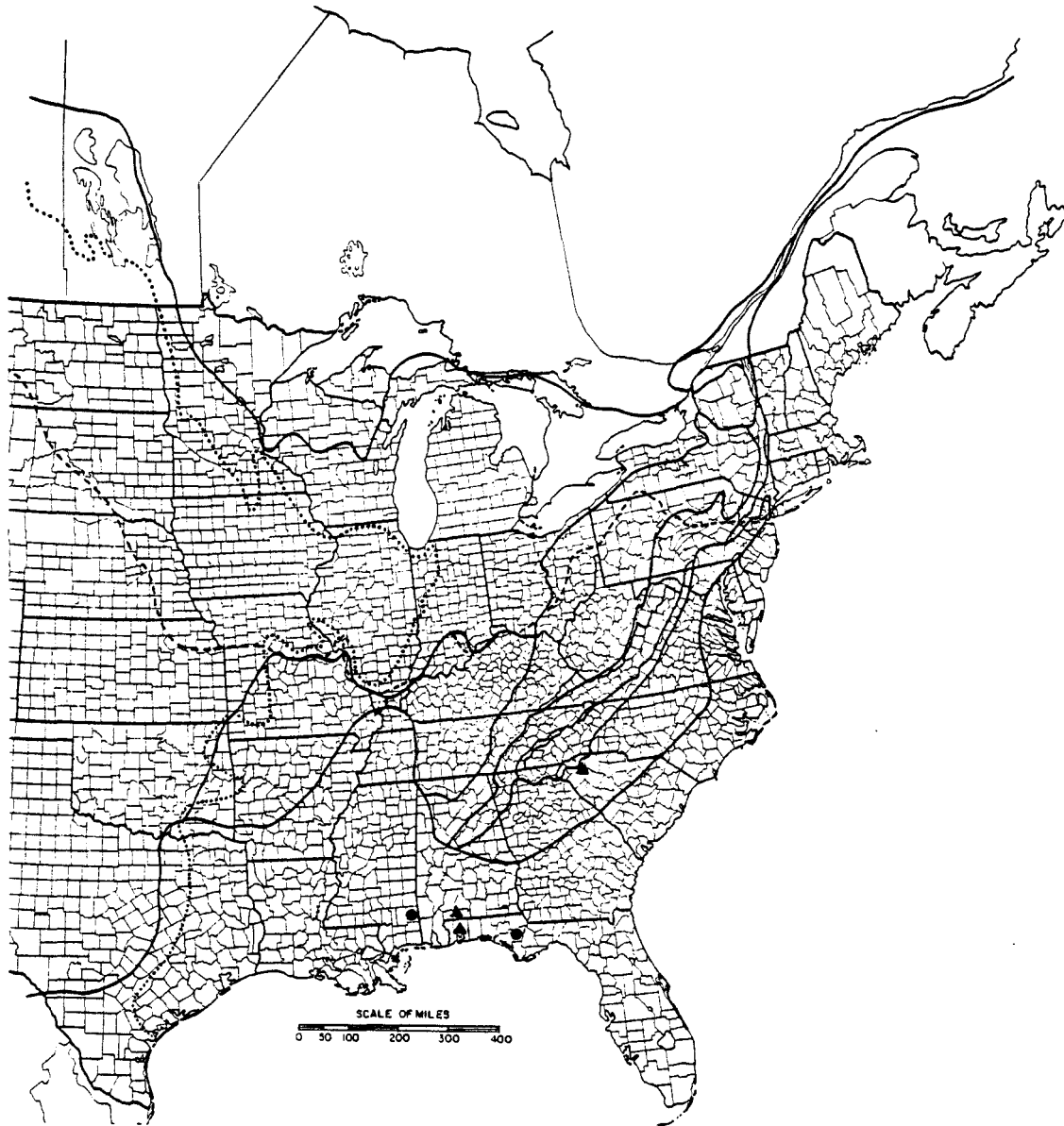


Figure 199. Ranges of *Stylurus potulentus* (dots) and *Stylurus townesi* (triangles).

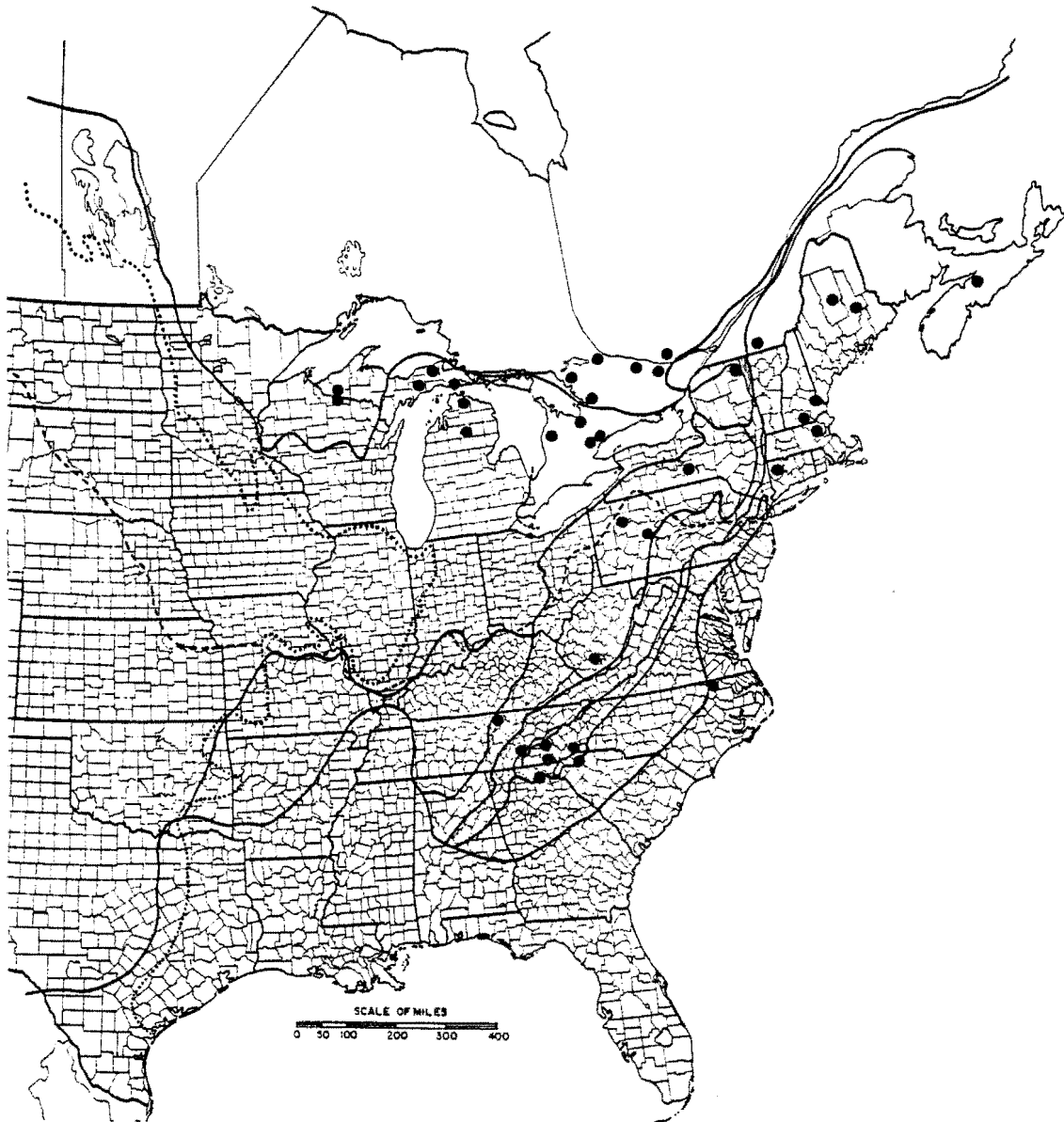


Figure 200. Range of *Stylurus scudderi*.

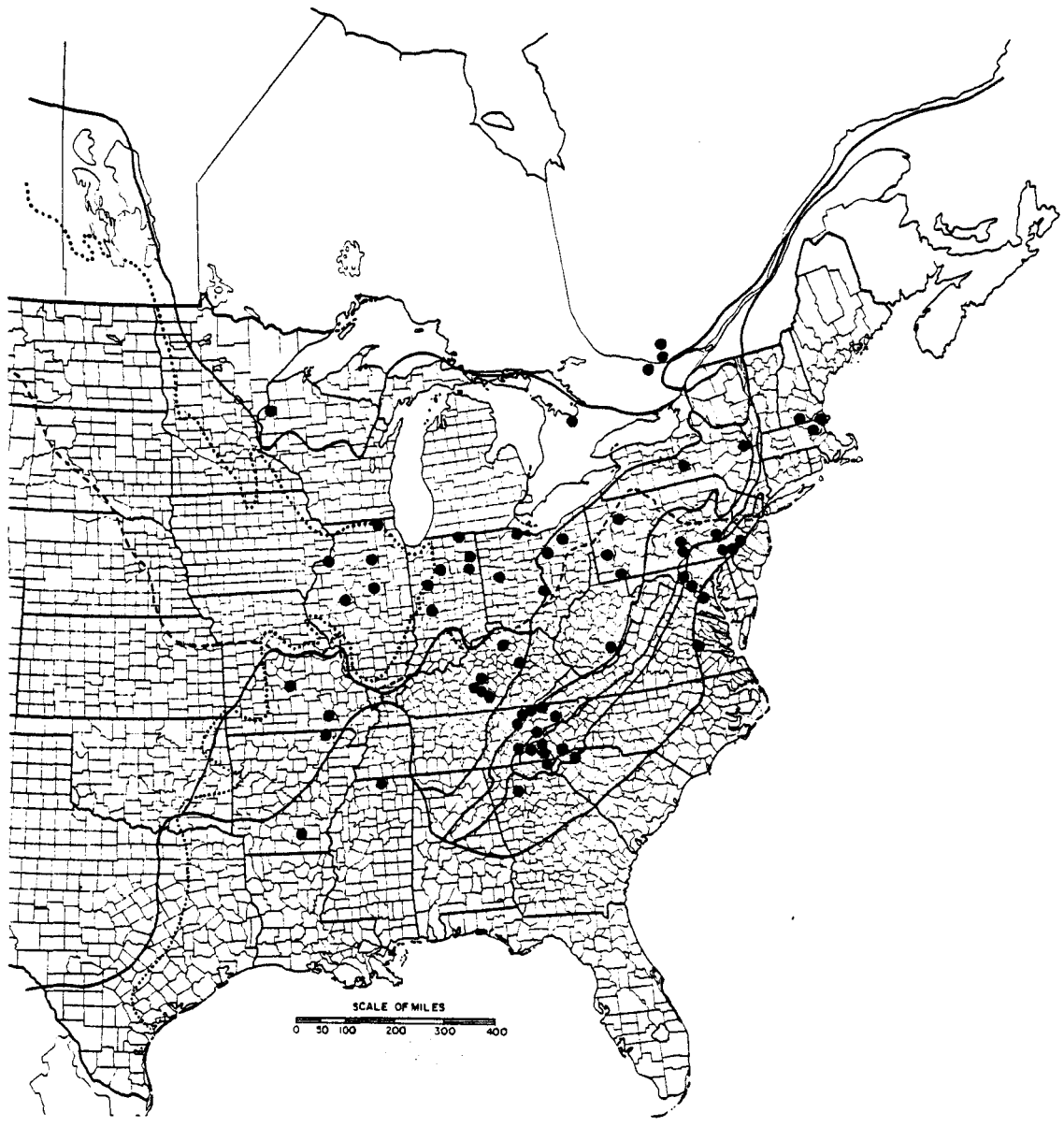


Figure 201. Range of *Stylurus spiniceps*.

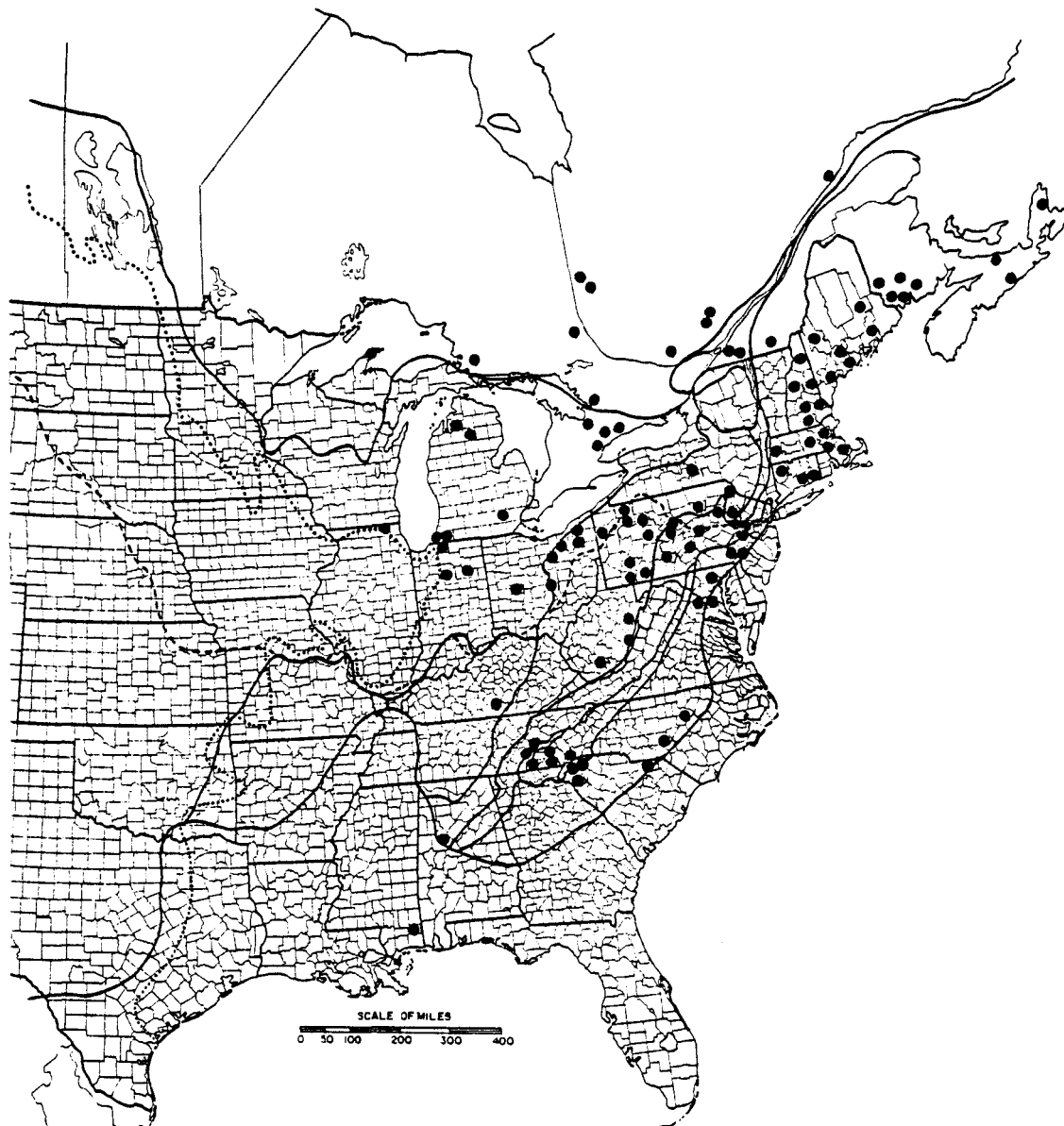


Figure 202. Range of *Cordulegaster diastatops*.

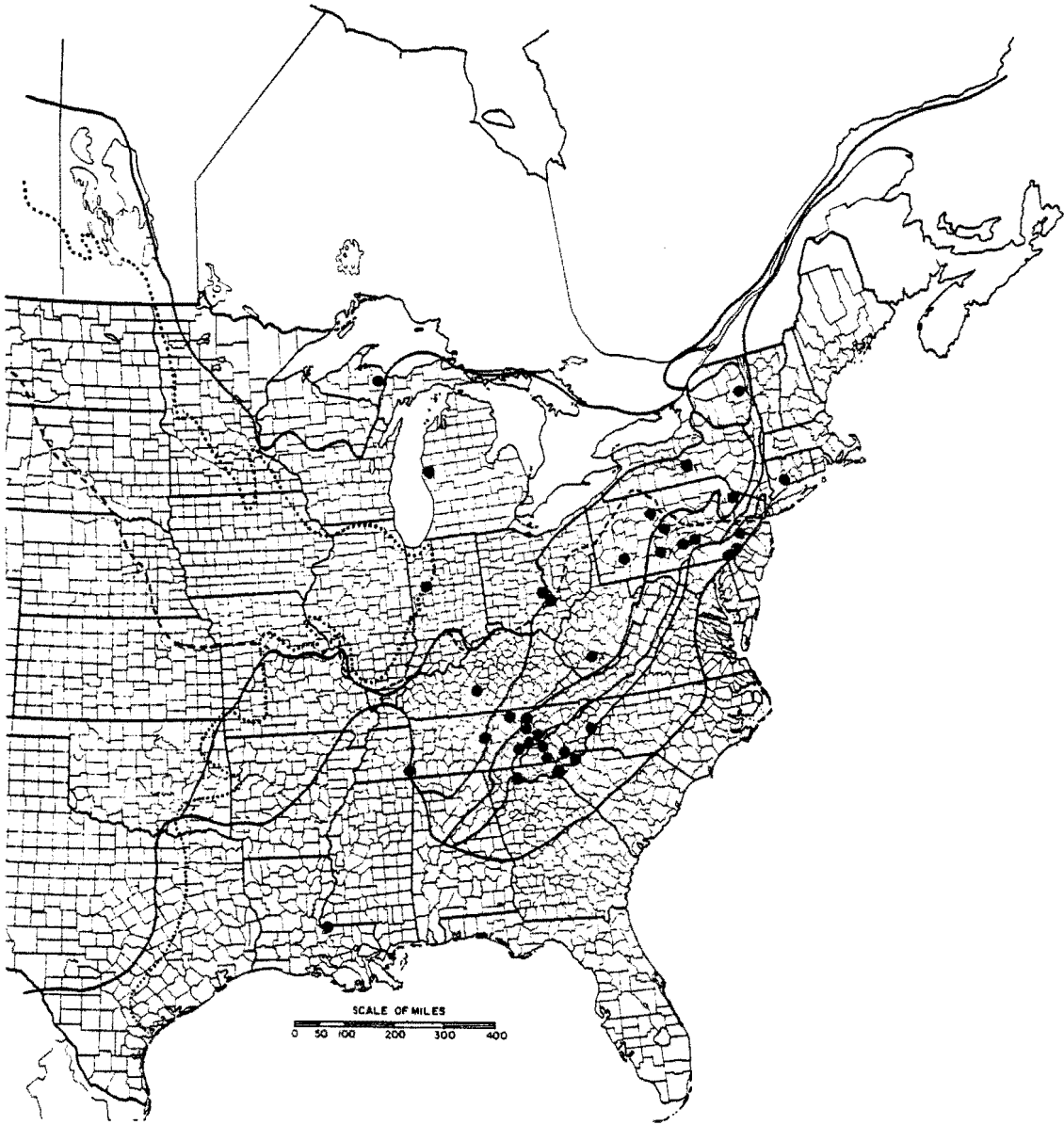


Figure 203. Range of *Cordulegaster erronea*.

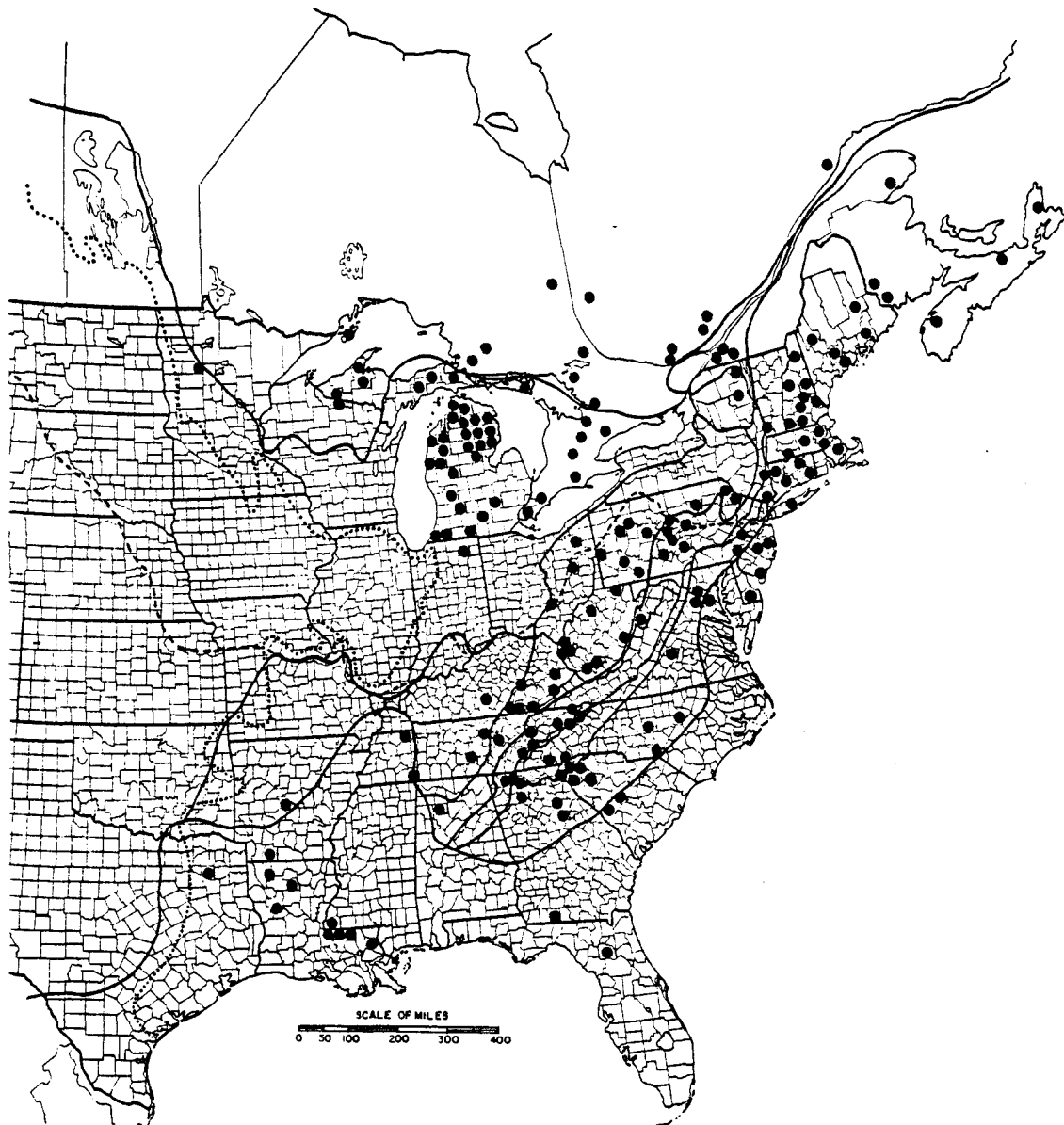


Figure 204. Range of *Cordulegaster maculata* (records in Louisiana and possibly Texas and Arkansas referable to *C. maculata* ssp. A, see text).

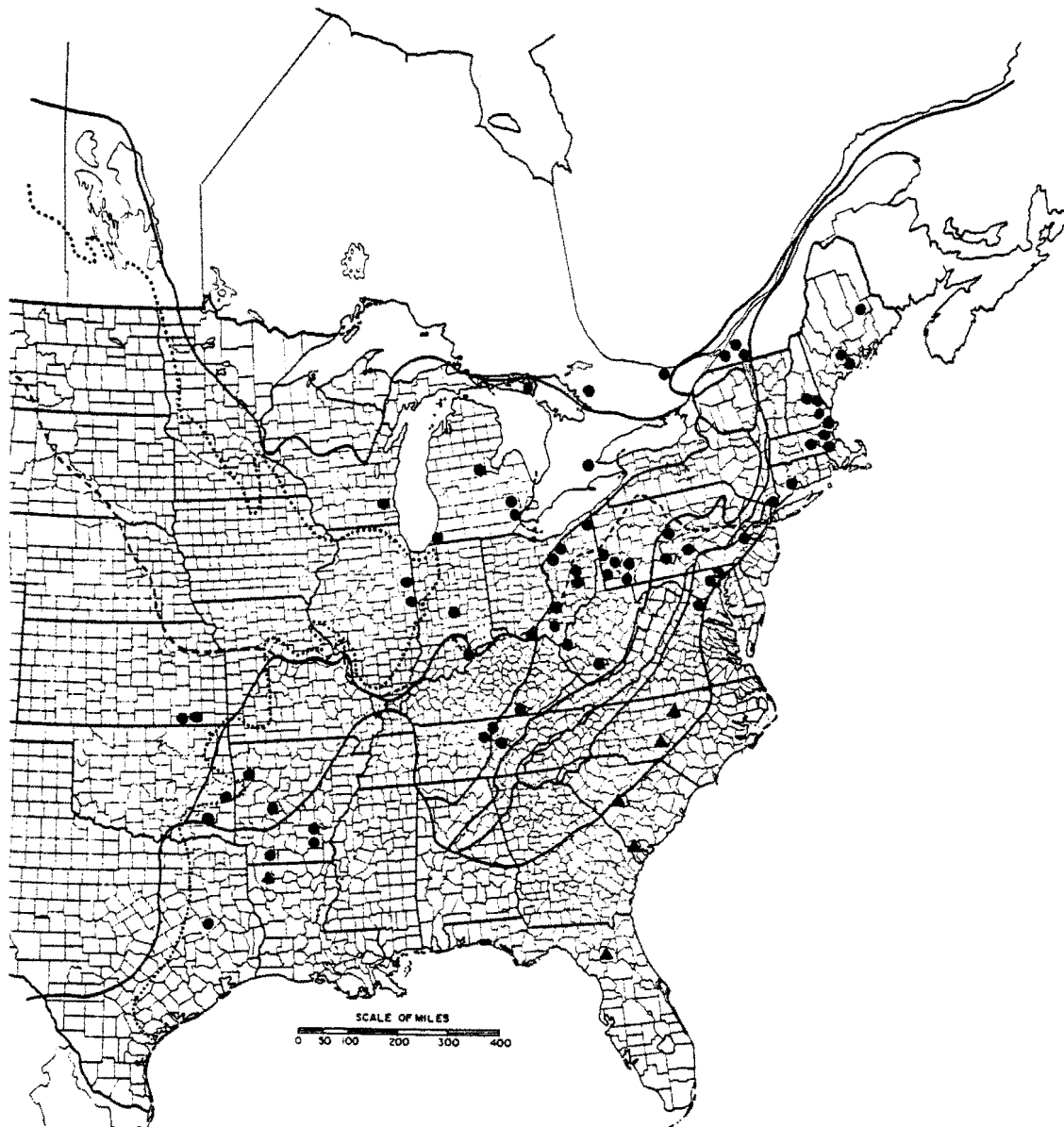


Figure 205. Ranges of *Cordulegaster obliqua obliqua* (dots) and *Cordulegaster obliqua fasciata* (triangles).



Figure 206. Range of *Cordulegaster sayi*.

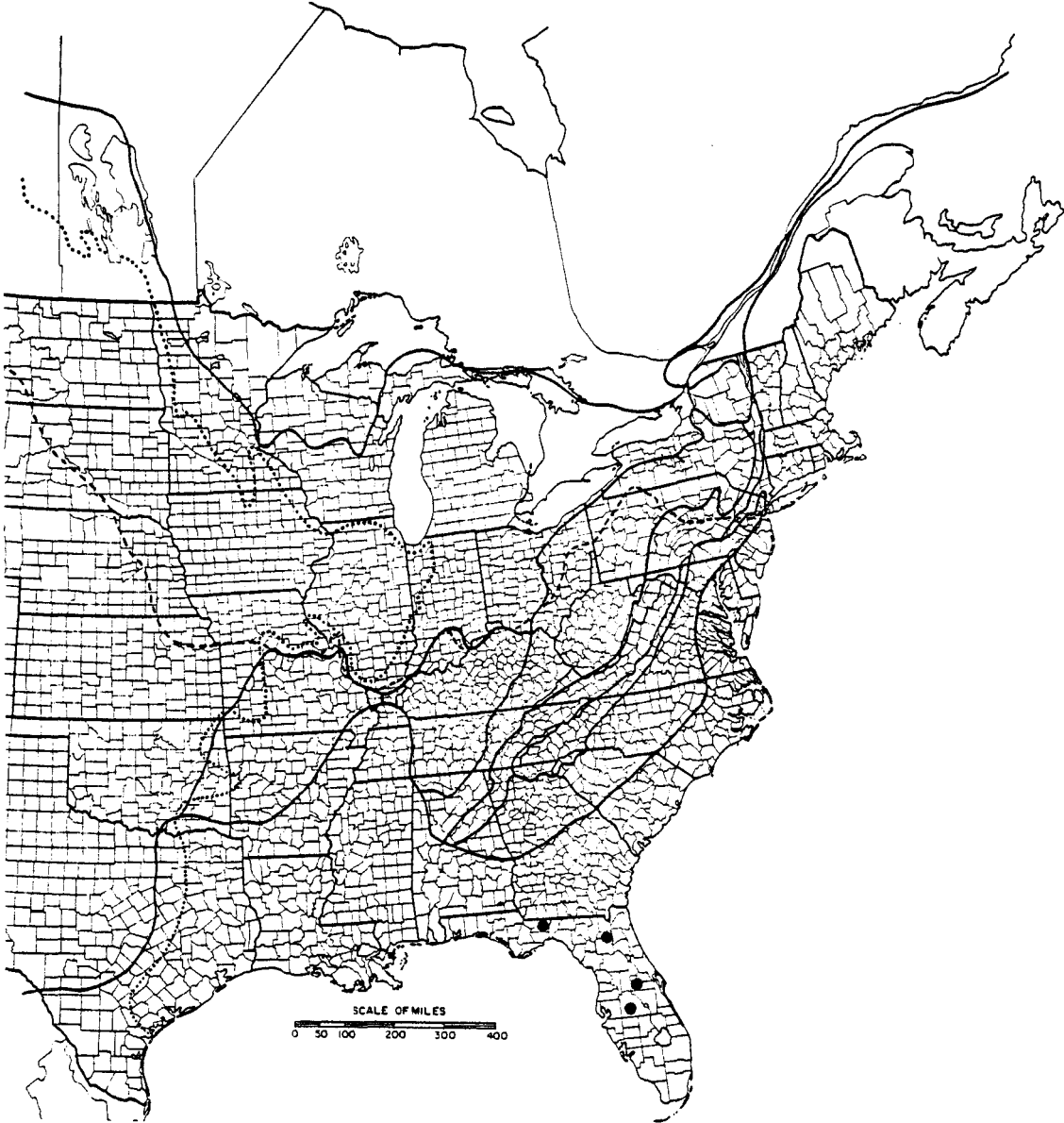


Figure 207. Range of *Didymops floridensis*.

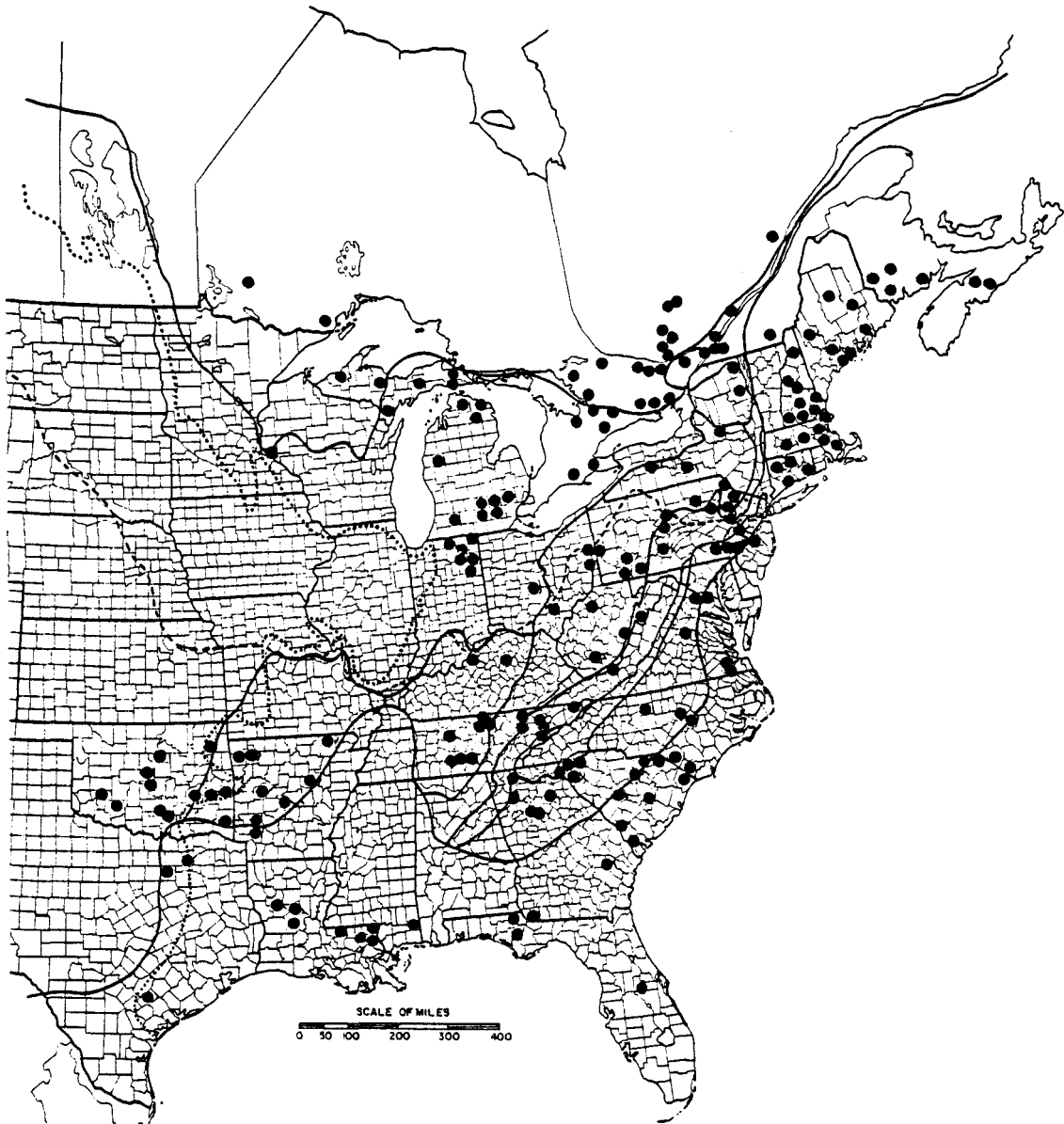


Figure 208. Range of *Didymops transversa*.

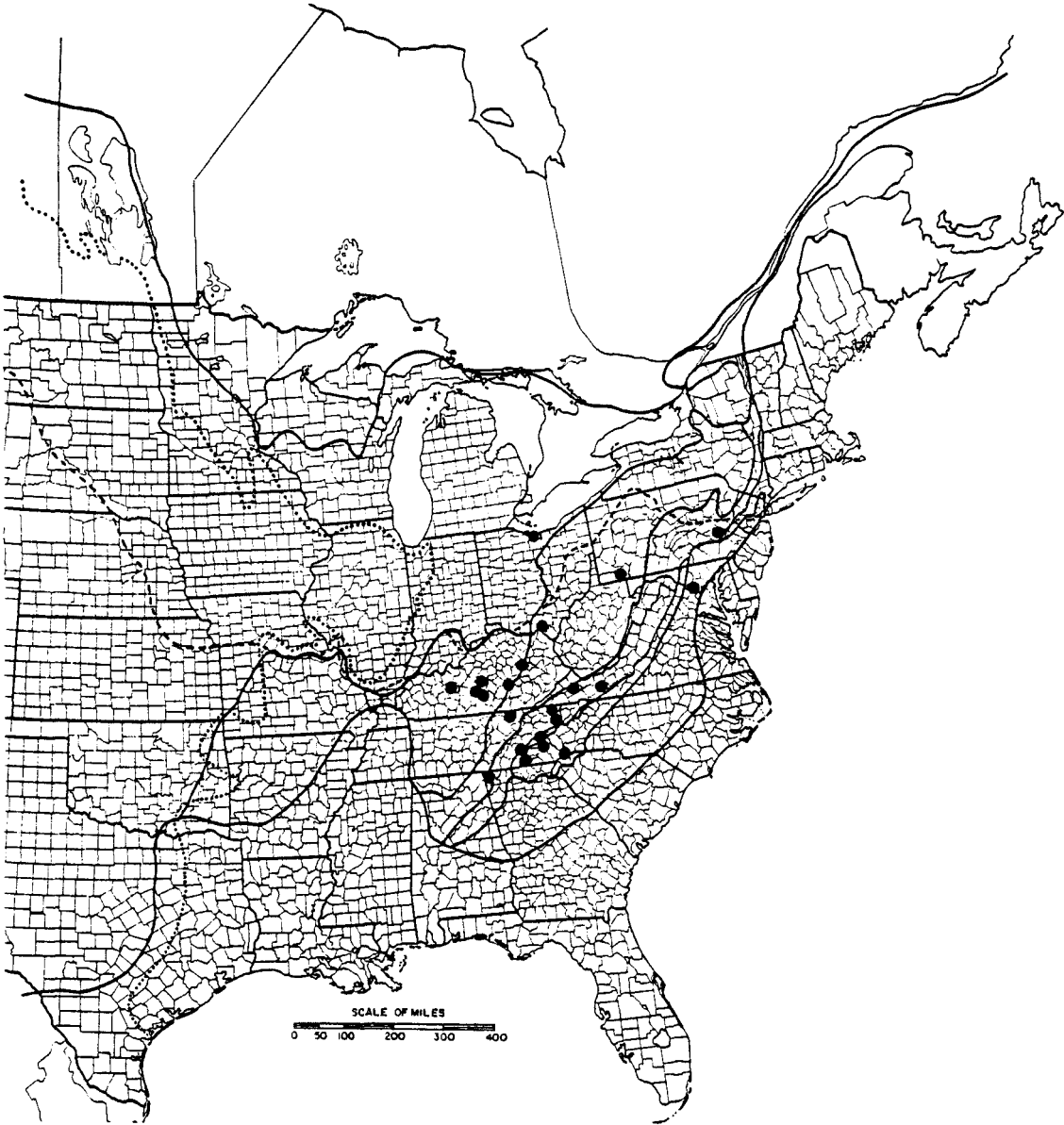


Figure 209. Range of *Macromia alleghaniensis*.

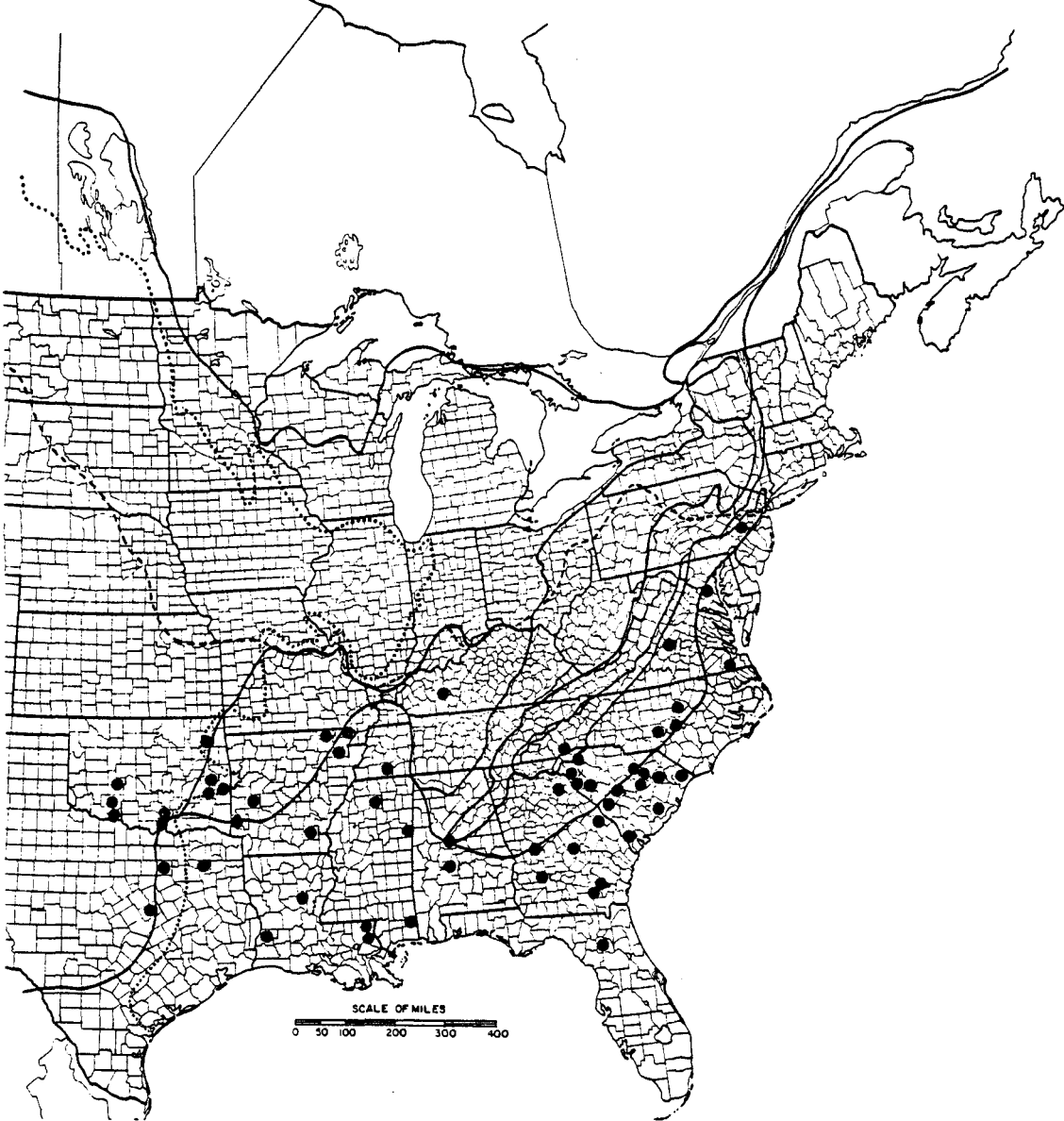


Figure 210. Range of *Macromia georgina*.

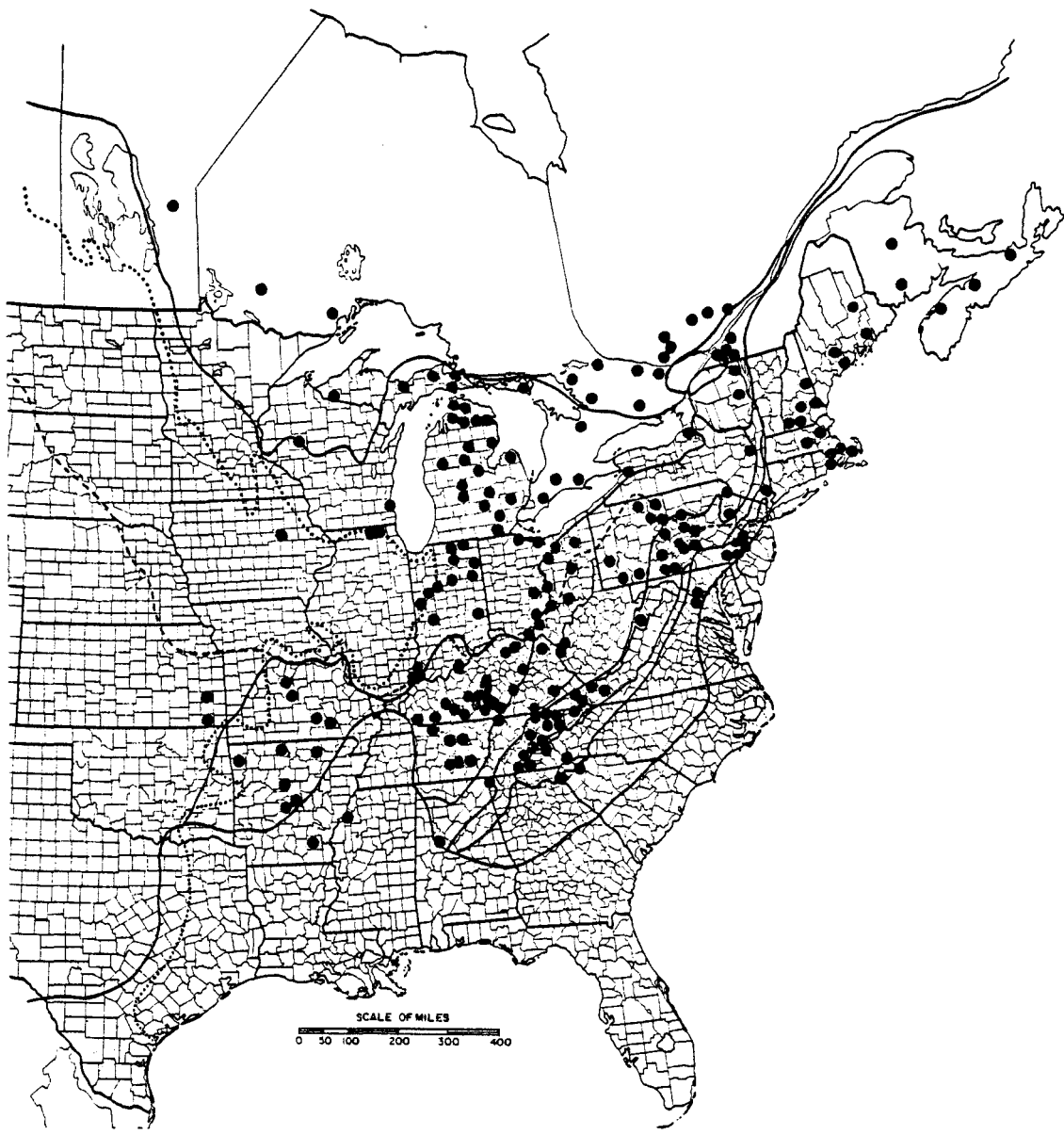


Figure 211. Range of *Macromia illinoiensis*.

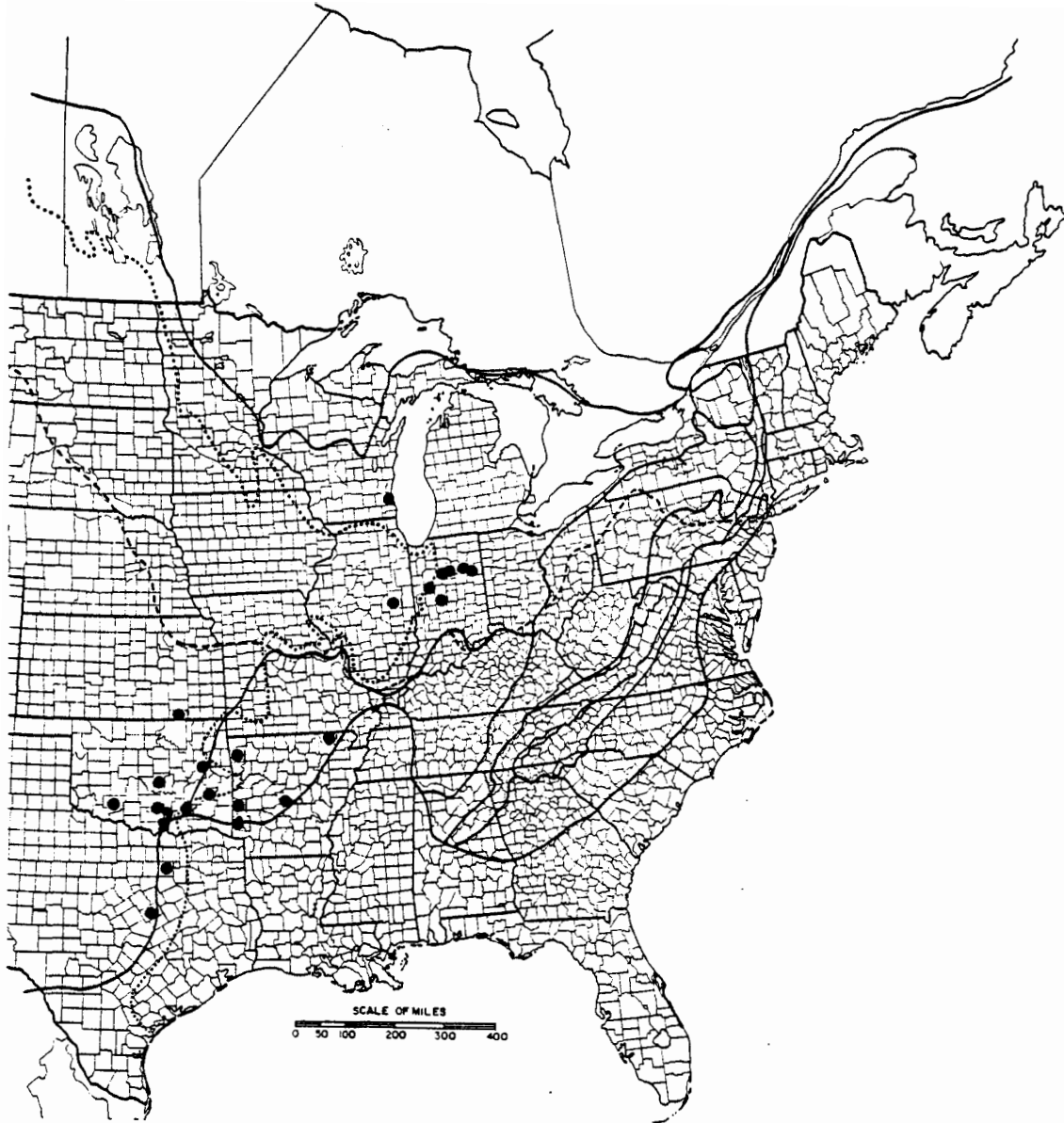


Figure 212. Range of *Macromia pacifica*.

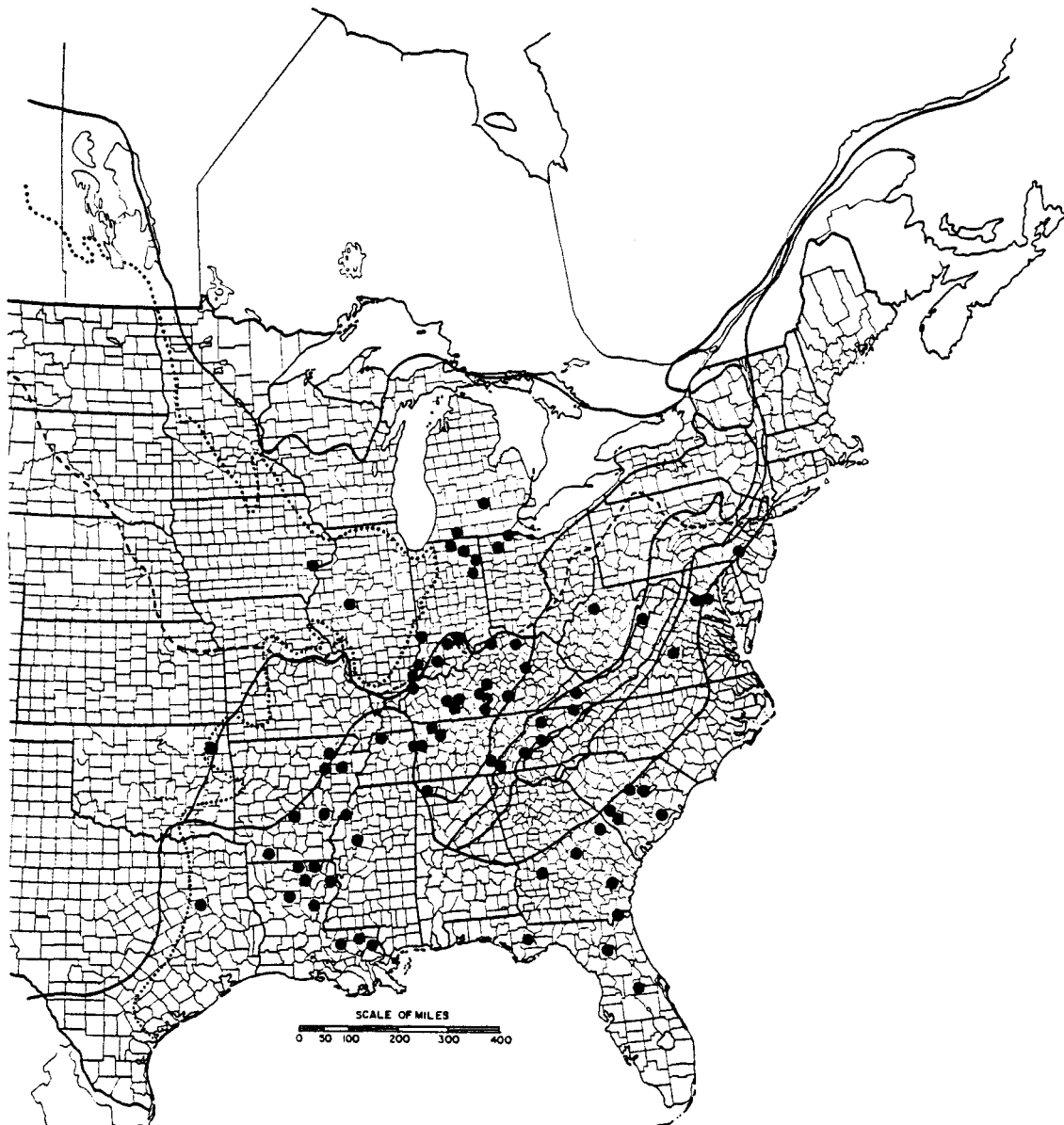


Figure 213. Range of *Macromia taeniolata*.

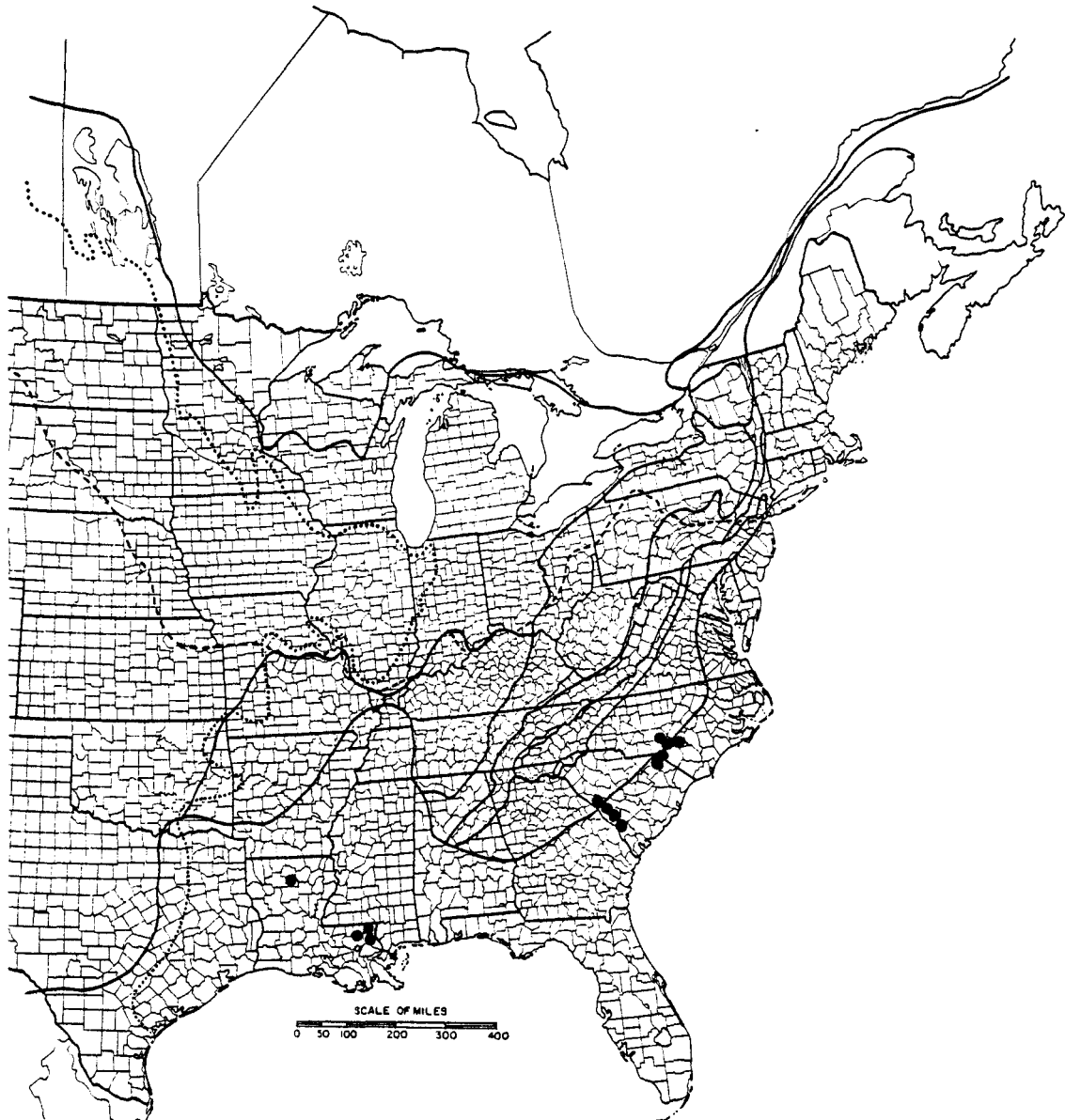


Figure 214. Range of *Neurocordulia alabamensis*.

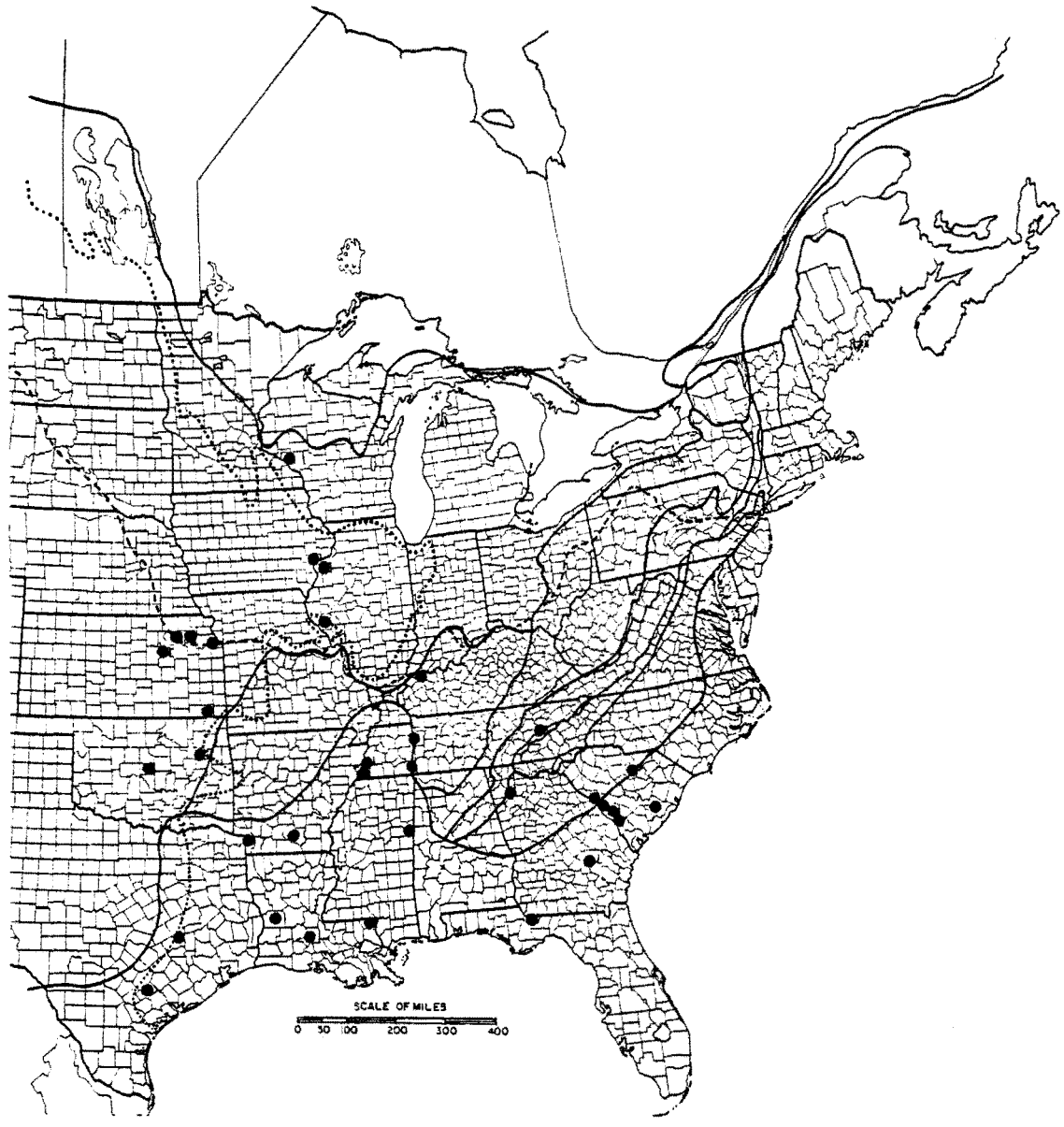


Figure 215. Range of *Neurocordulia molesta*.

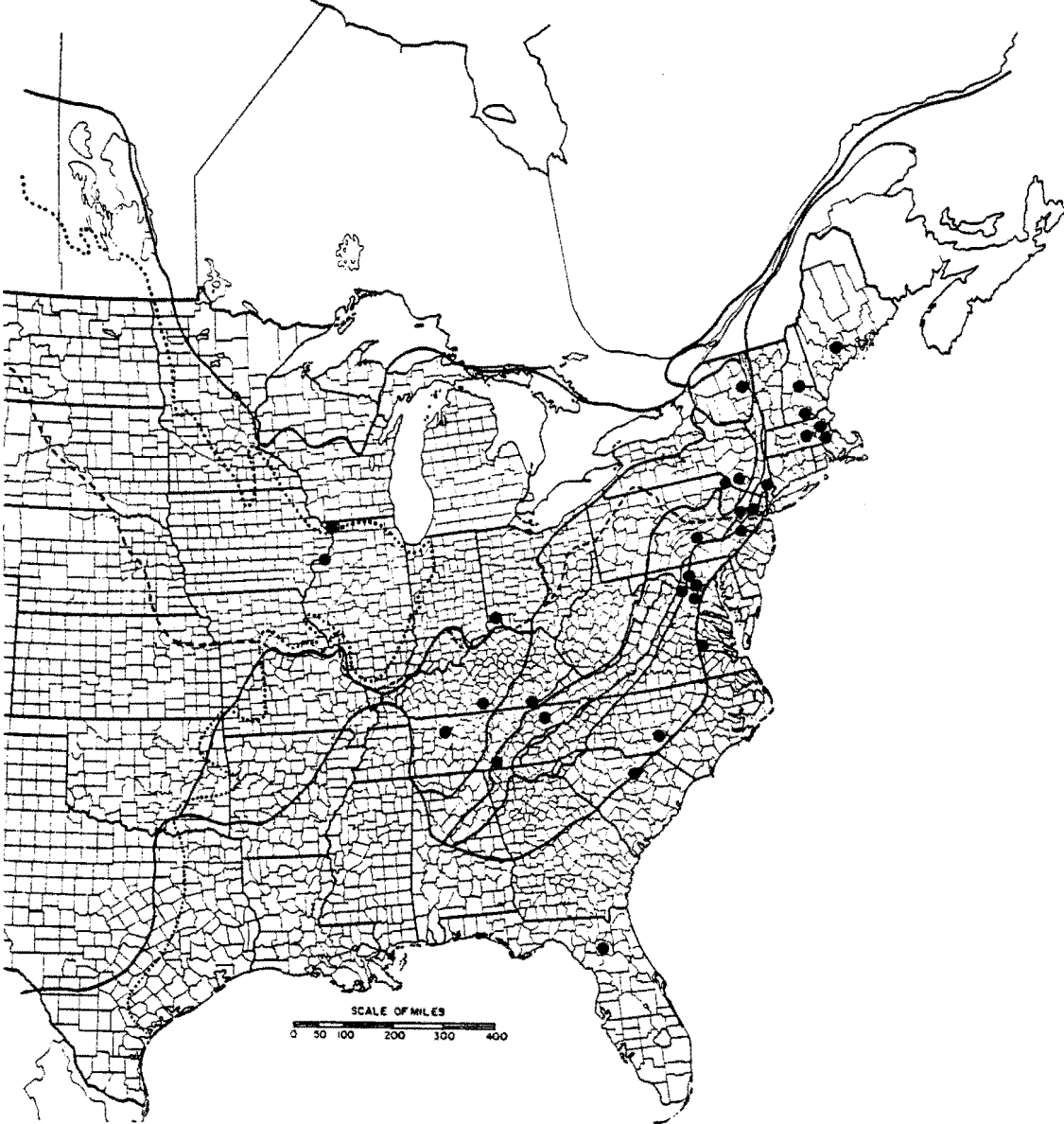


Figure 216. Range of *Neurocordulia obsoleta*.

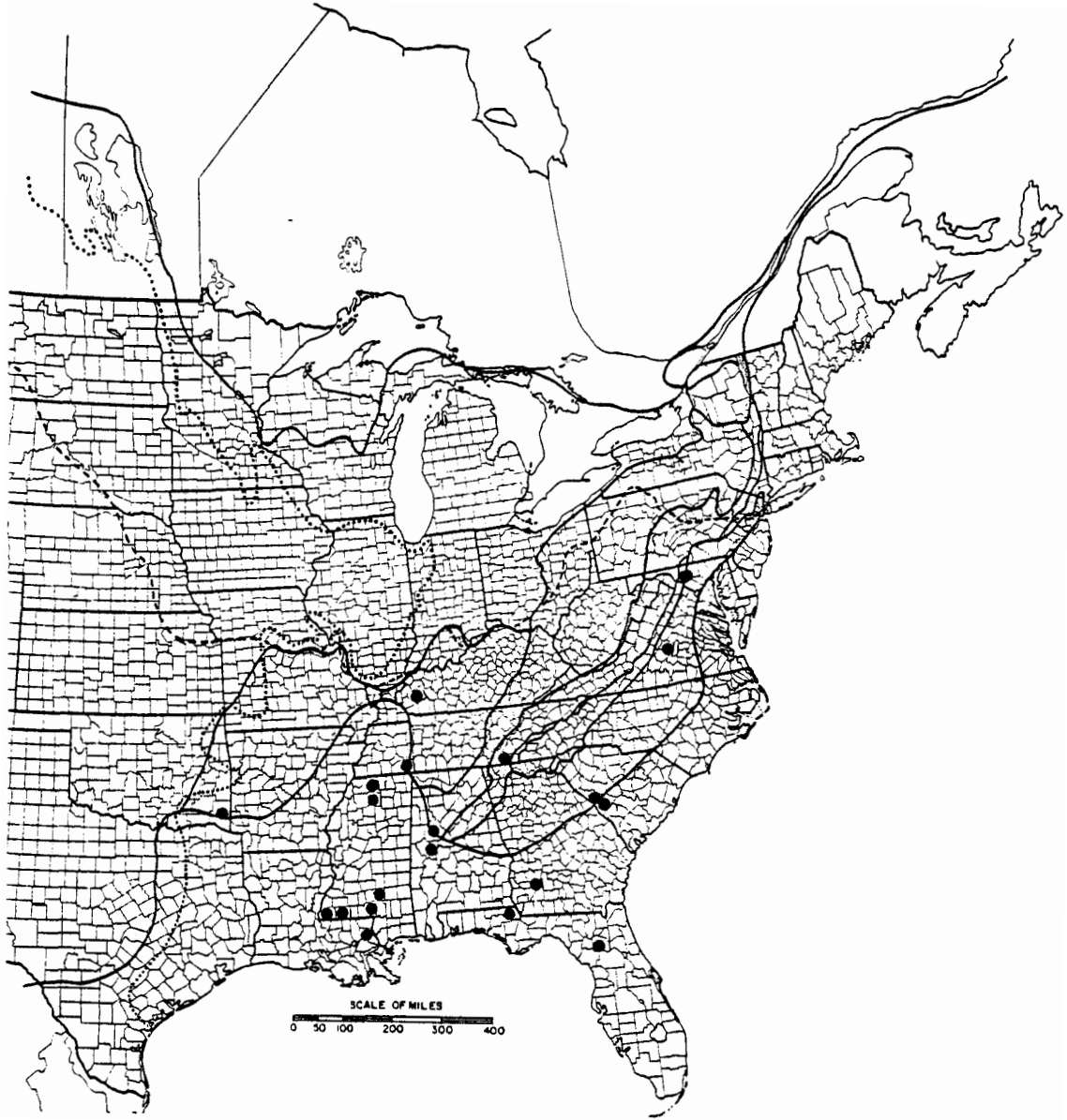


Figure 217. Range of *Neorocordulia virginensis*.

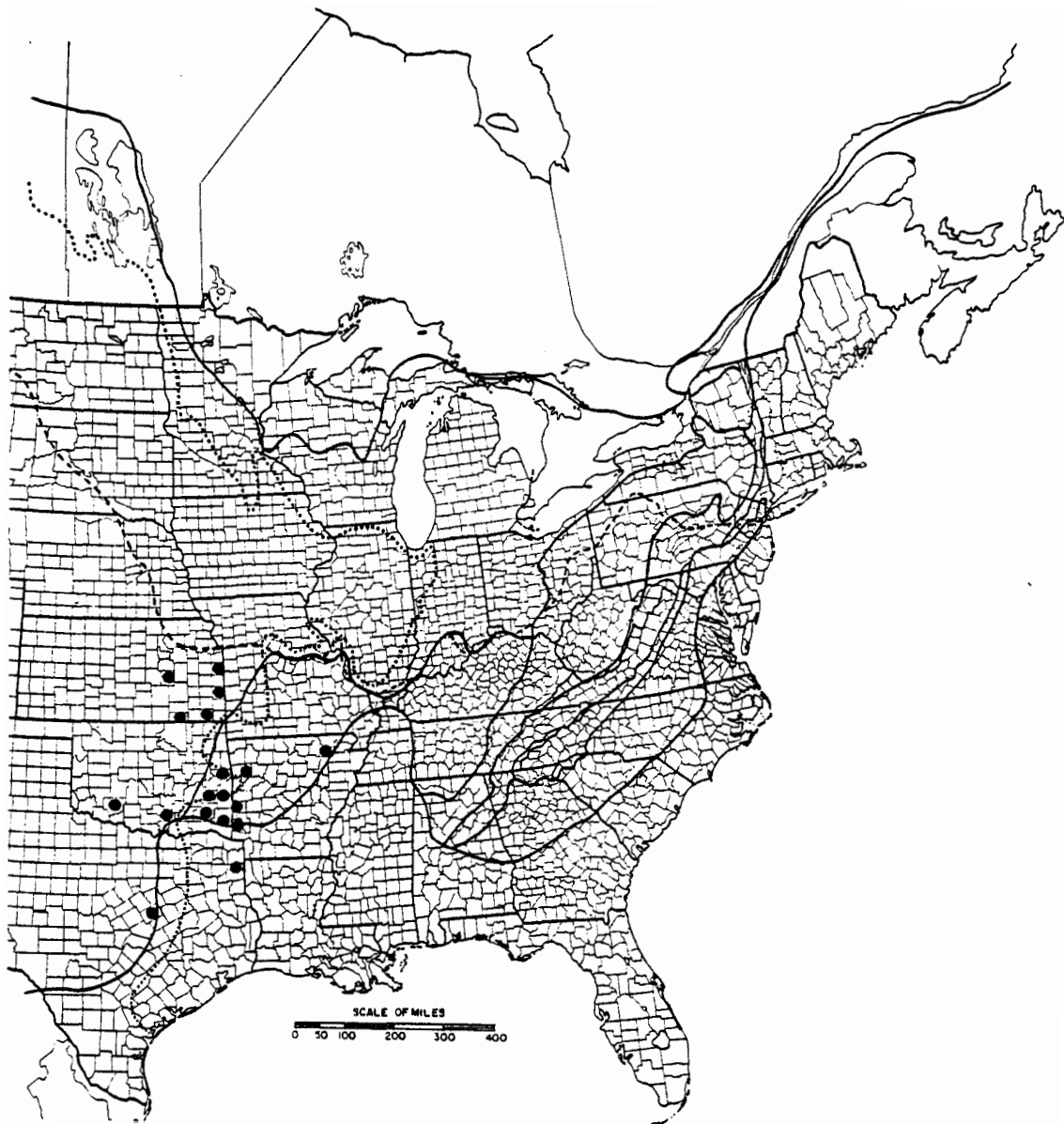


Figure 218. Range of *Neurocordulia xanthosoma*.

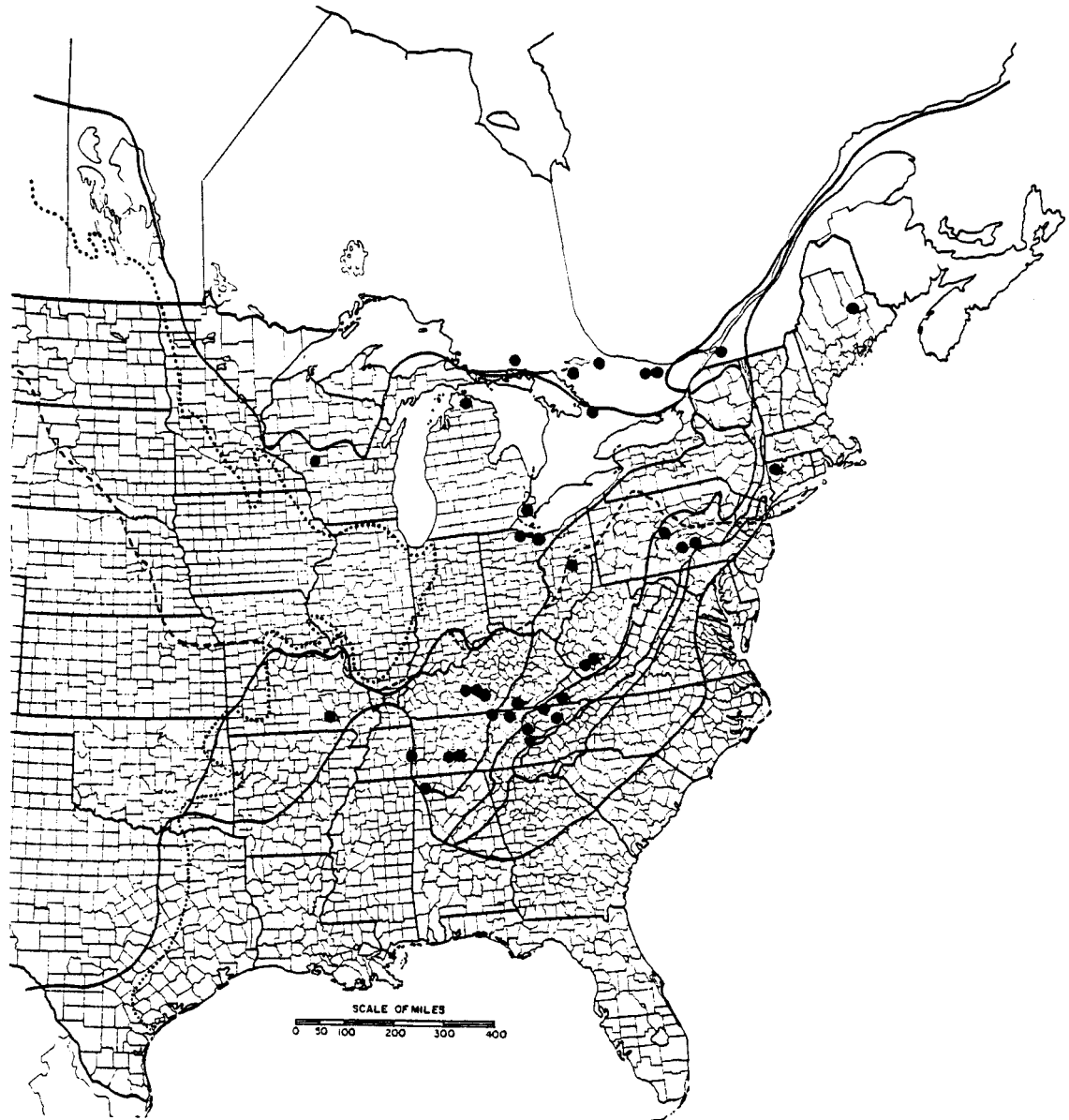


Figure 219. Range of *Neurocordulia yamaskanensis*.

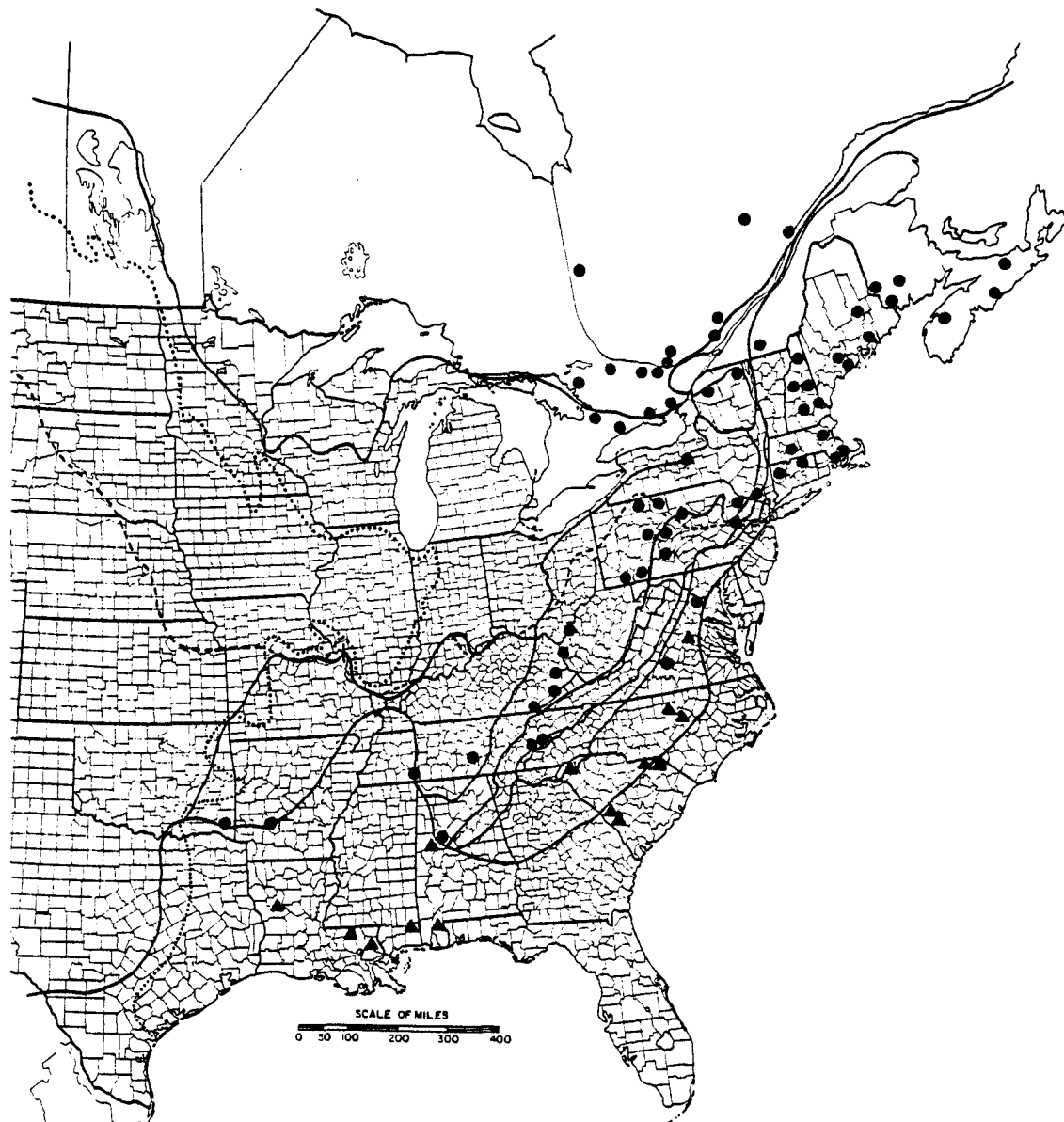


Figure 220. Ranges of *Helocordulia selysii* (triangles) and *Helocordulia uhleri* (dots).

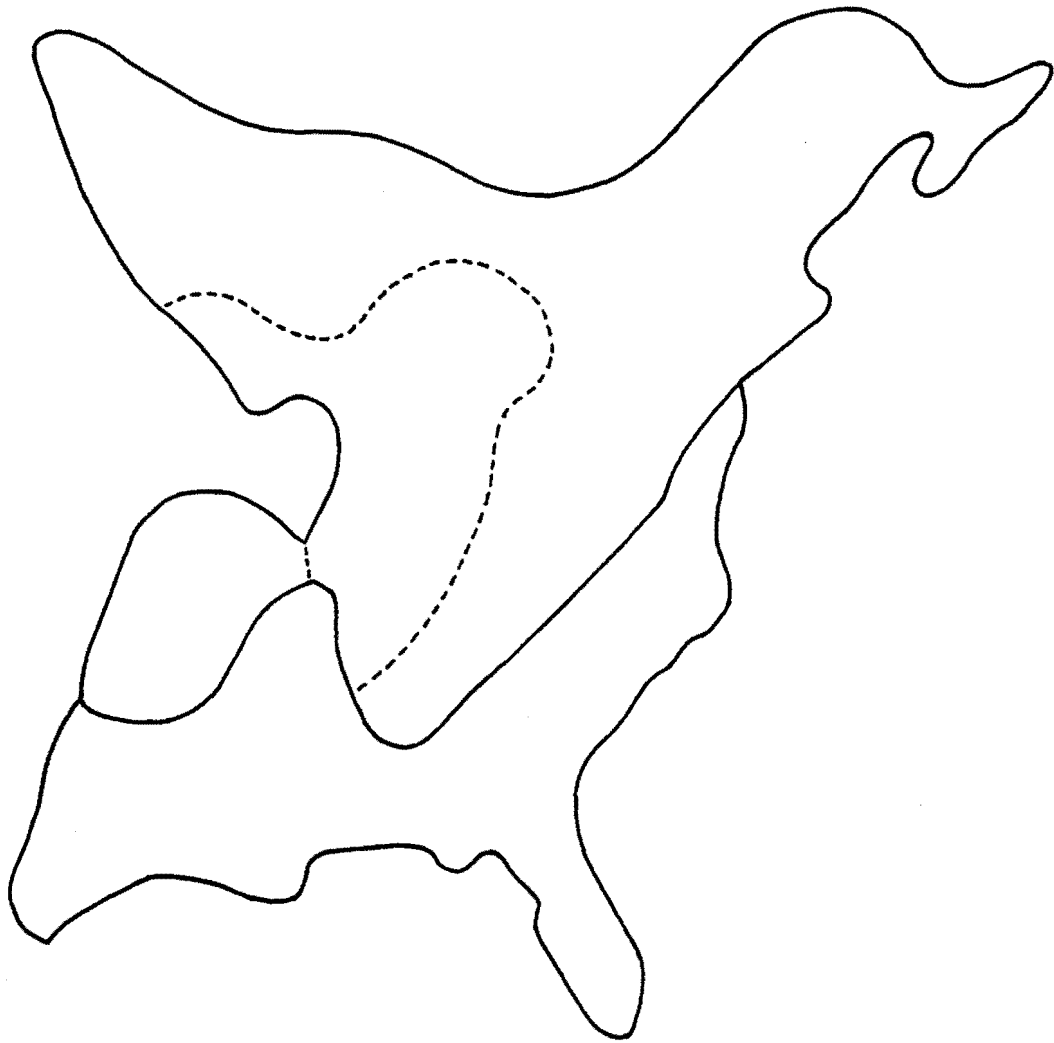


Figure 221. Regions of endemism for lotic Anisoptera.

	<u>species</u>
Eastern ubiquitous	17
Eastern Uplands	18
Gt. Lakes-Appalachian	16
Interior low plateaus	2
Interior Highlands	1
Coastal Plain	19
Prairie	6



Figure 222. Generic distribution of eastern *Ophiogomphus*.



Figure 223. Generic distribution of *Dromogomphus* (*D. spinosus* with dashed boundary).



Figure 224. Generic distribution of *Gomphurus*, all species.

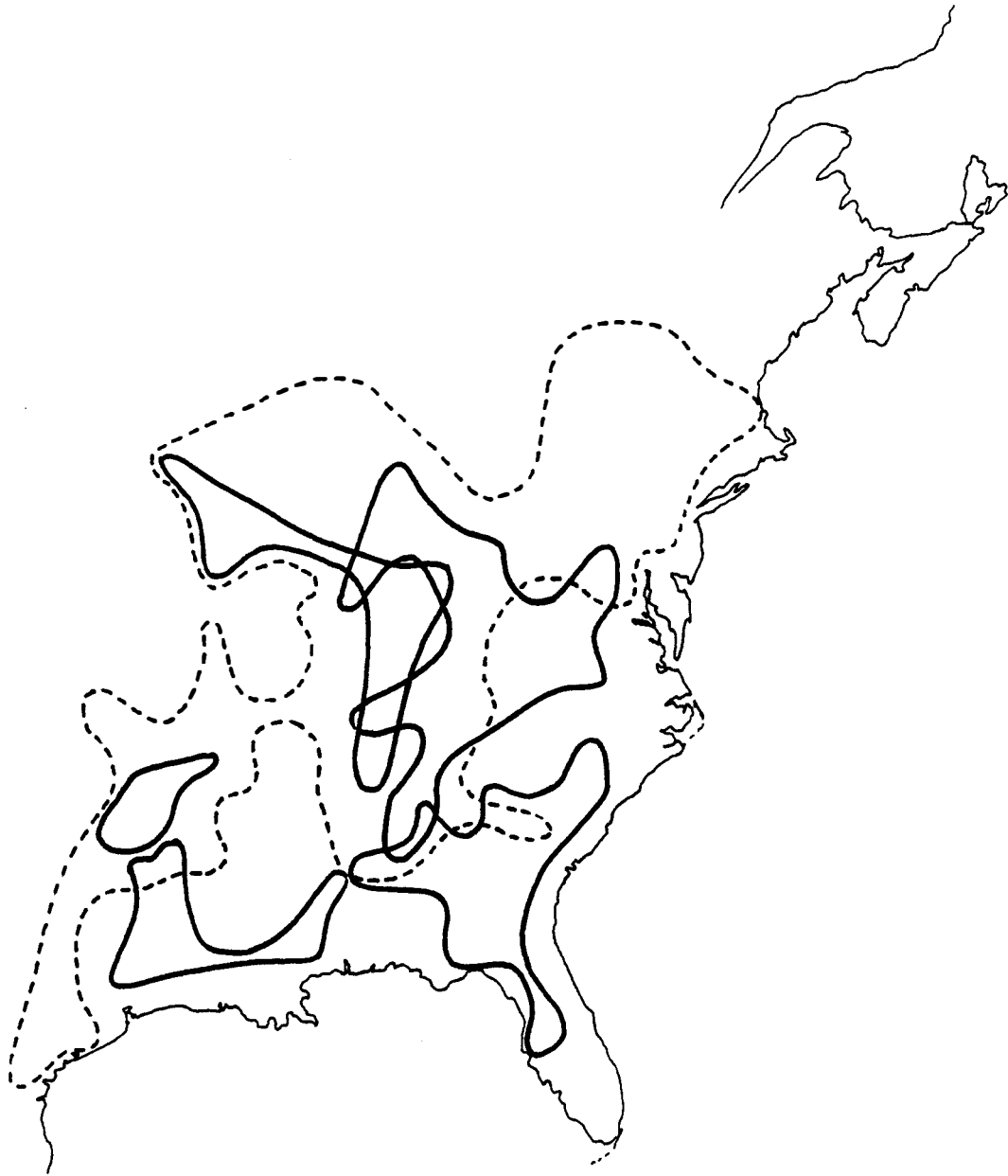


Figure 225. Distribution of *Gomphurus vastus*-group (*G. vastus* with dashed boundary).

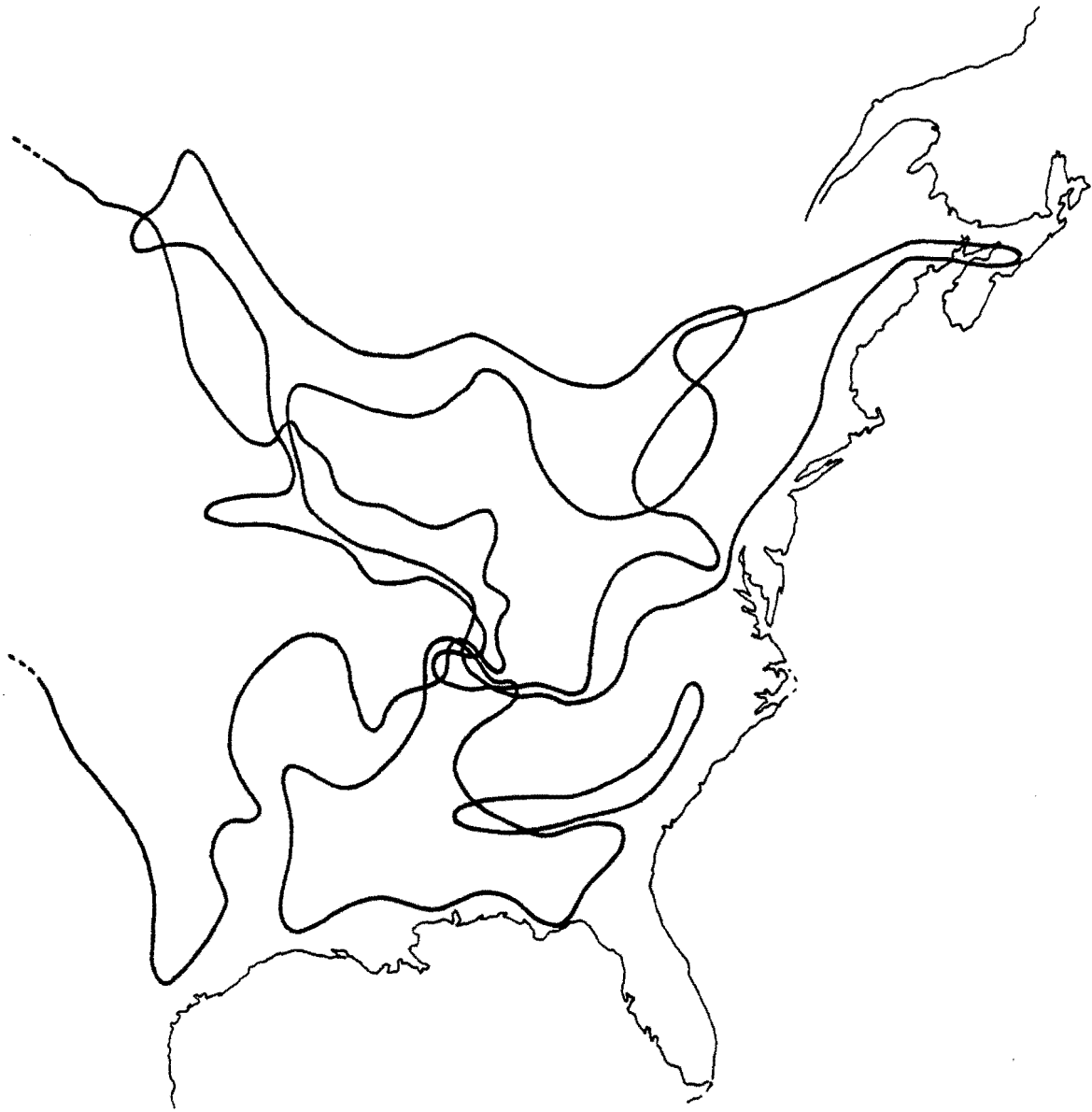


Figure 226. Distribution of *Gomphurus fraternus*-group.



Figure 227. Generic distribution of *Hylogomphus* (*H. abbreviatus*-group with solid boundary, *H. parvidens*-group with dashed boundary).

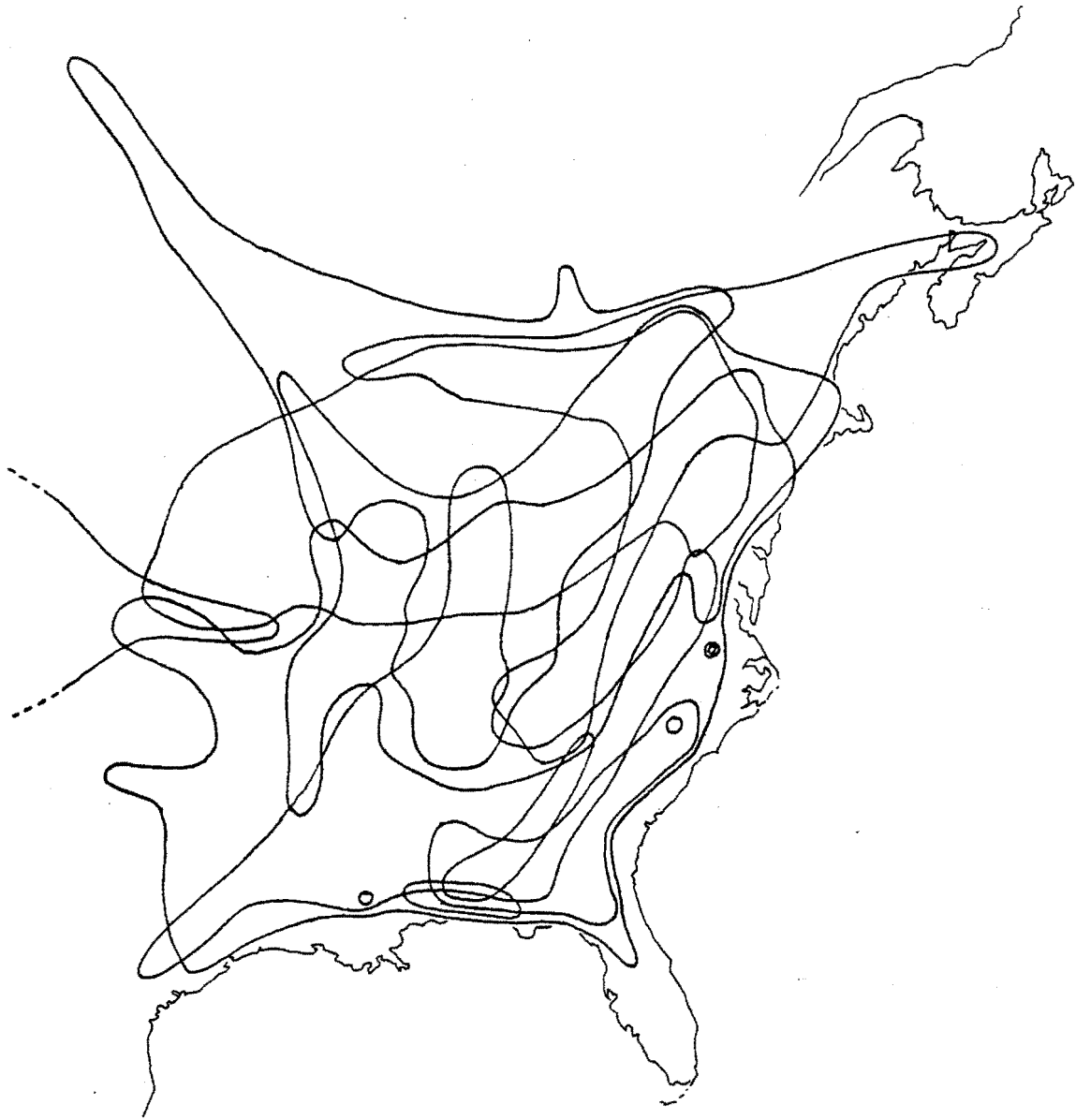


Figure 228. Generic distribution of *Stylurus*, all species.



Figure 229. Distribution of *Stylurus intricatus*-group.

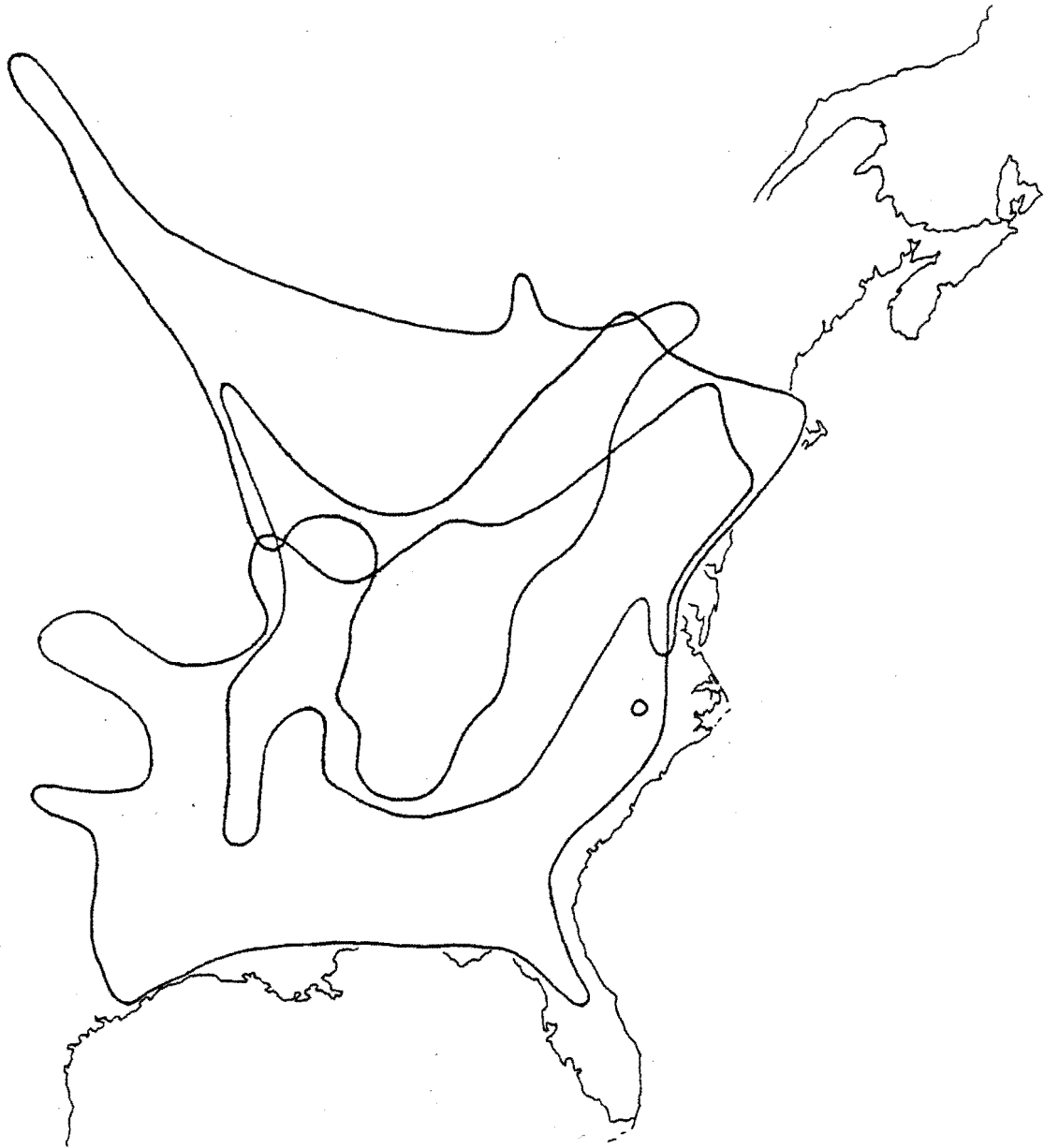


Figure 230. Distribution of *Stylurus plagiatus*-group.

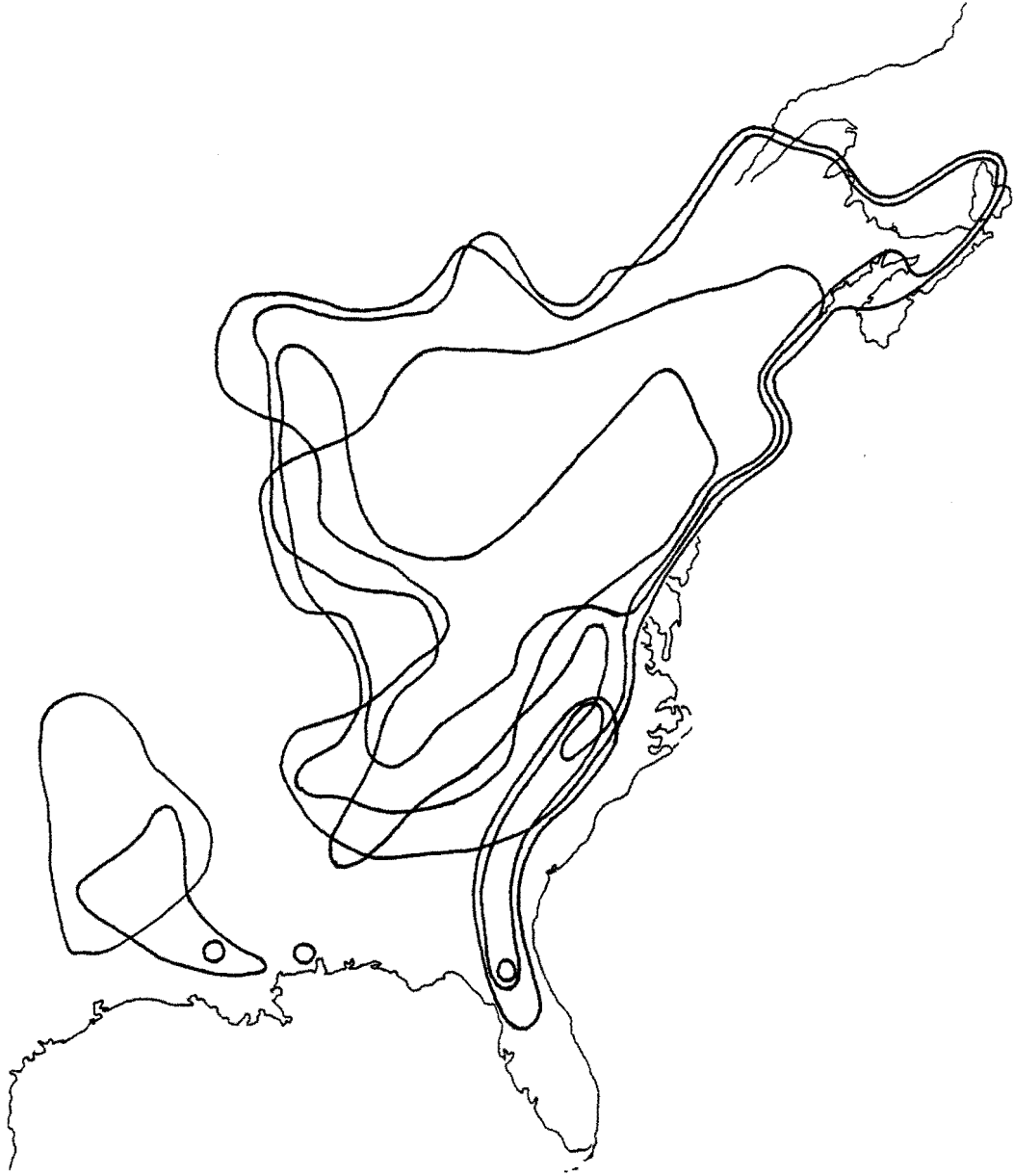


Figure 231. Distribution of eastern *Cordulegaster*.

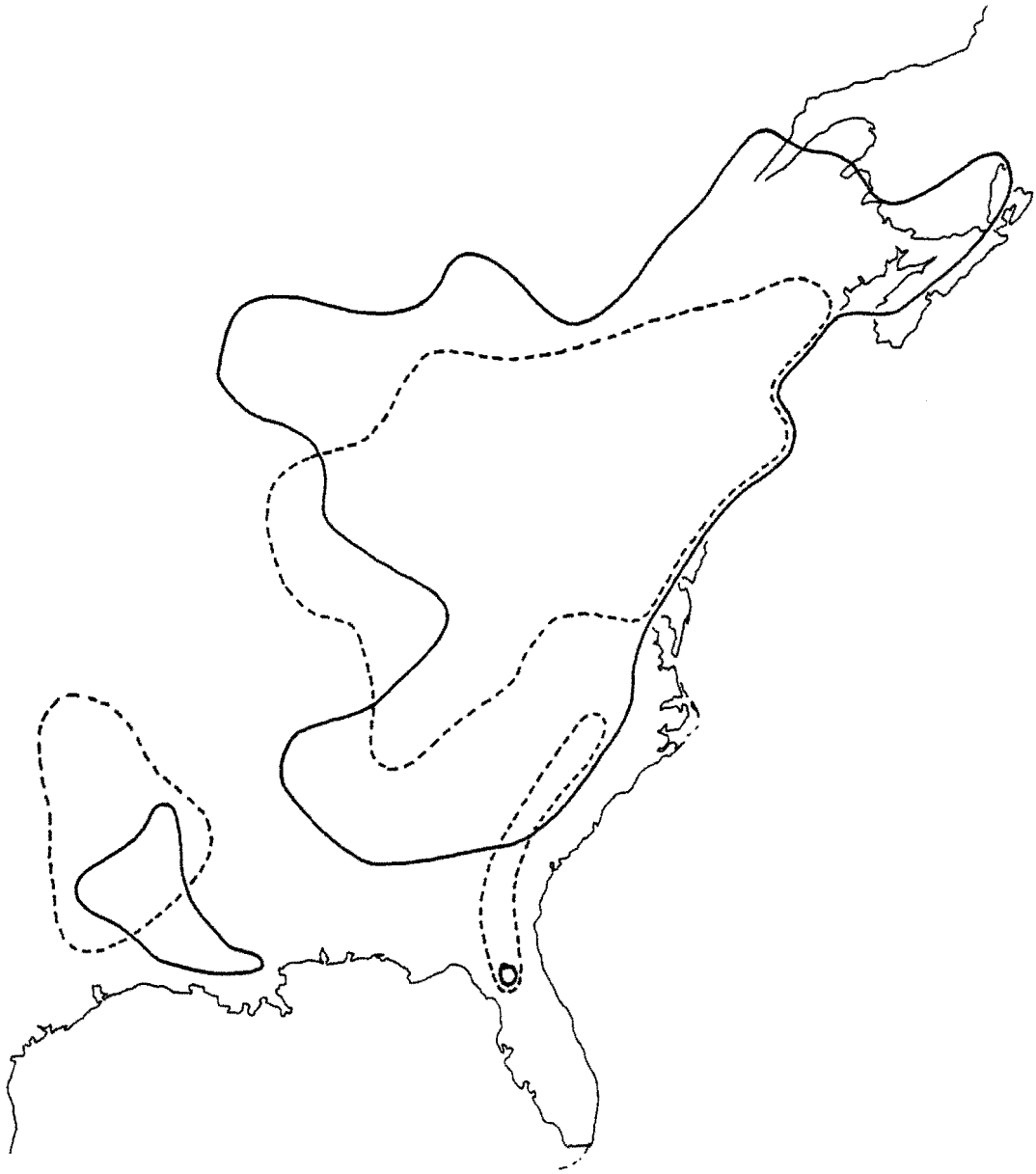


Figure 232. Distribution of *Cordulegaster maculata* (solid boundary), *Cordulegaster obliqua obliqua* and *Cordulegaster obliqua fasciata* plotted together (dashed boundary).

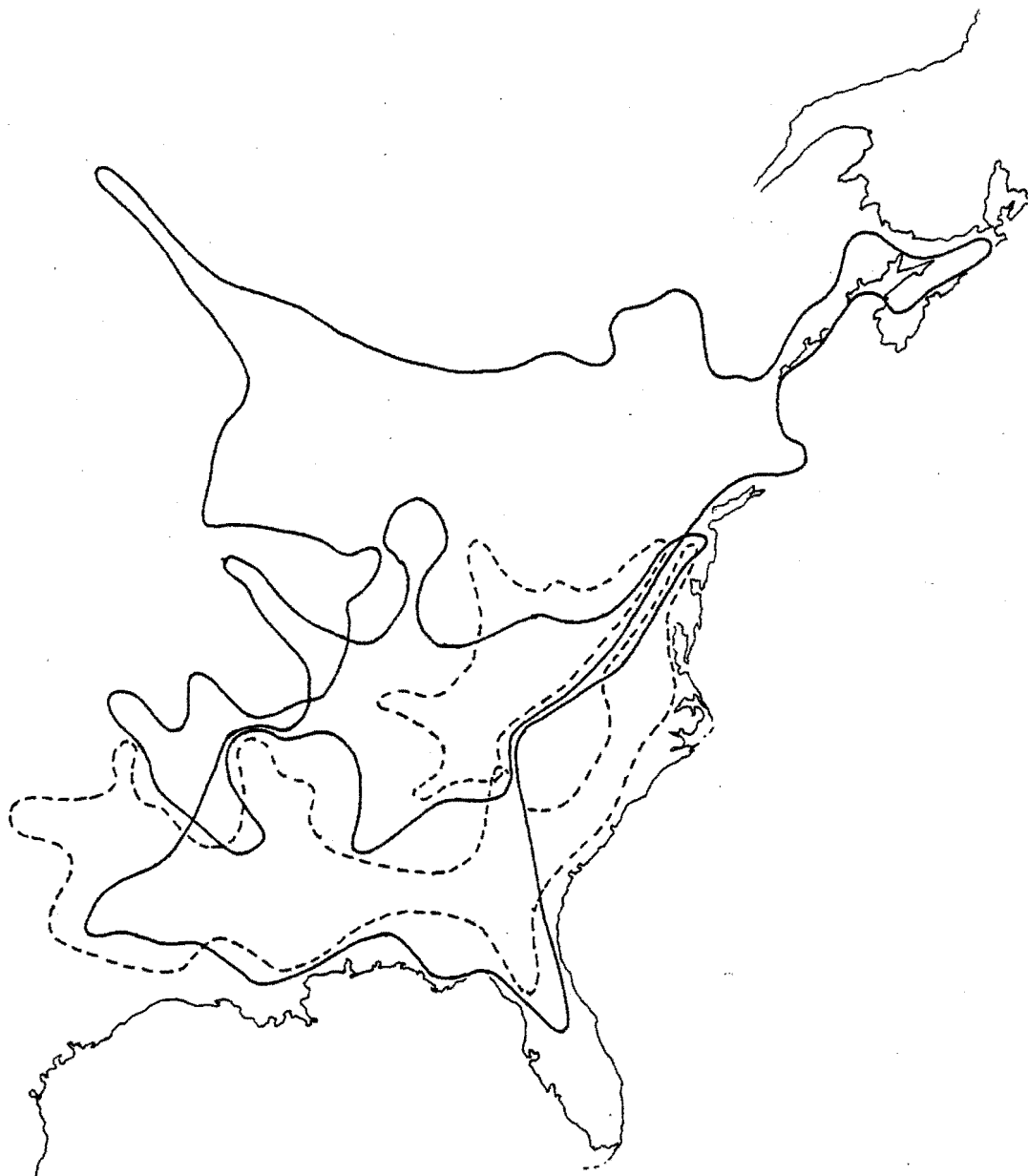


Figure 233. Distribution of *Macromia* vicariad pairs (*Macromia illinoensis* and *Macromia taeniolata* with solid boundaries, *M. alleghaniensis* and *M. georgina* with dashed boundaries).



Figure 234. Generic distribution of *Neurocordulia*.



Figure 235. Distribution of *Neurocordulia virginiensis* and *Neurocordulia yamaskanensis*.

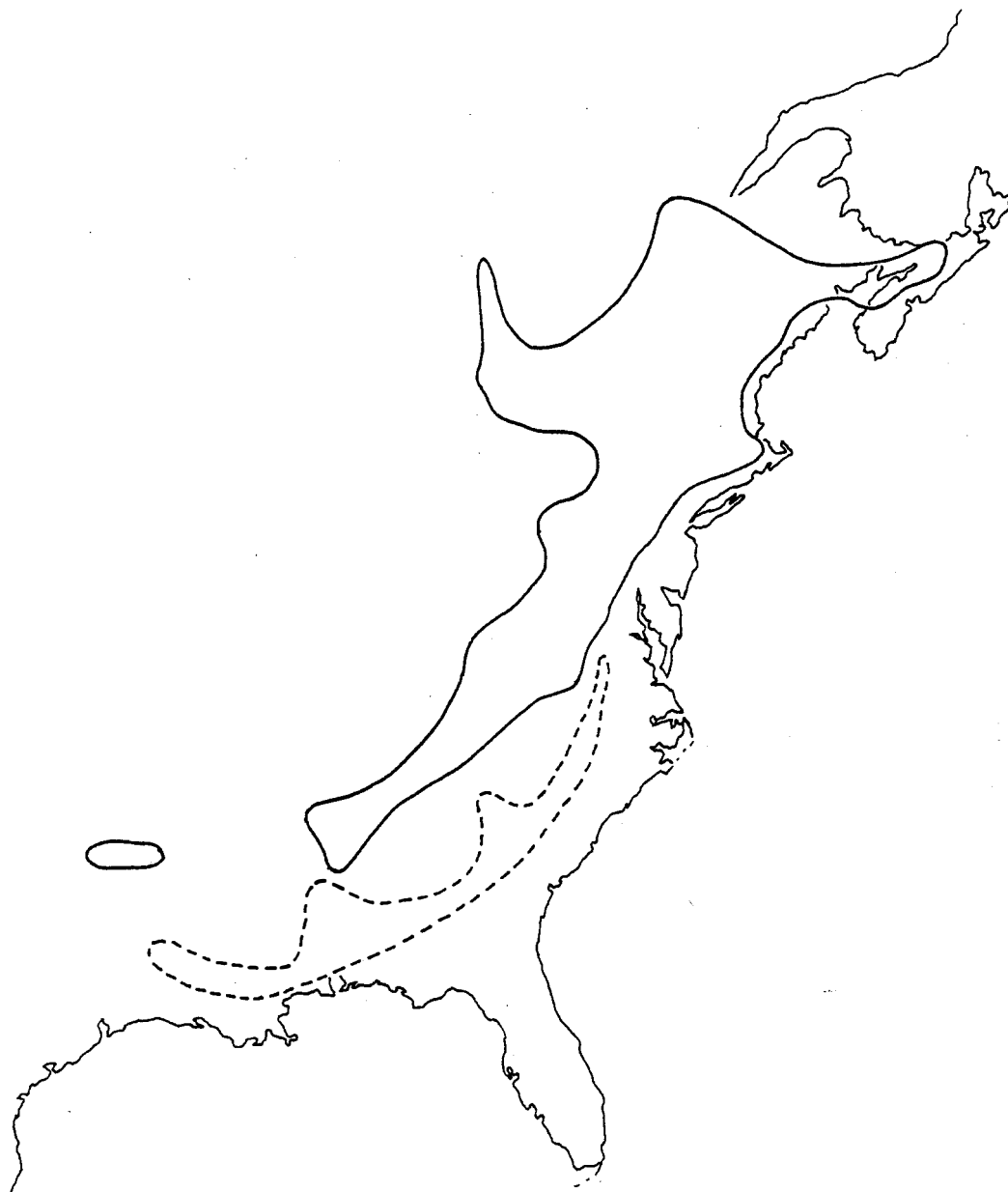


Figure 236. Generic distribution of *Helocordulia* (*Helocordulia uhleri* with solid boundary, *Helocordulia selysii* with dashed boundary).

APPENDIX B

MATERIAL EXAMINED

Tachopteryx thoreyi (Hagen)

KENTUCKY, Whitley Co., Bark Creek, Daniel Boone National Forest, VI-17-1976, 1 male. TENNESSEE, Anderson Co., Norris, VI-4-1976, 1 male. Clear Creek, V-13-1978, 1 nymph. Blout Co., Cades Cove Gum Swamp, Great Smoky Mountains National Park, VI-24-1976, 1 male. Seepage to Parsons Branch, IV-8-1978, 7 nymphs. Seepage to Husky Branch, IV-8-1978, 14 nymphs. 5 miles E. Walland, VII-23-1976, 1 male. Seepage to Huskey Branch, VII-23-1976, 1 female. Seepage to headwaters of Reed Cr., IV-21-1978, 1 nymph. Same locality, VI-3-1980, 3 nymphs.

Boyeria grafiiana Williamson

NORTH CAROLINA, Transylvania Co., Davidson R., Brevard, IV-8-1979, 1 nymph. North Fork French Broad R., St. Rt. 1322, VI-20-1979, 2 nymphs. TENNESSEE, Monroe Co., Turkey Cr., 1 mile NE confl. Tellico R., Cherokee National Forest, IV-19-1978, 3 nymphs.

Boyeria vinosa (Say)

ALABAMA, Perry/Dallas Cos., Oakmulgee Cr., AL Hwy. 219, X-24-1980, 1 nymph. ARKANSAS, Polk Co., Ouchita R., McGuire Access, IX-11-1978, 1 nymph. FLORIDA, Alachua Co., Hackett Cr., FL Hwy. 26, XI-13-1979, 5 nymphs. GEORGIA, Cherokee Co., Etowah R., confl. Board Tree Cr., IX-21-1980, 1 male. Columbia Co., Kiokee Cr., GA Hwy. 104, V-8-1980, 3 nymphs. Gilmer Co., Mountain Town Cr., GA Hwy. 52, 7 nymphs. Murray Co., Sumac Cr., US 411,

V-17-1980, 1 nymph. Richmond Co., Little Spirit Cr., US Hwy. 25,
V-20-1980, 1 nymph. Toombs/Tattnall Cos., Ochoopee R., GA Hwy. 152,
V-21-1980, 1 nymph. LOUISIANA, Beauregard Parish, Bundick Cr.,
LA Hwy. 26, VI-2-1972, 1 female. East Feliciana Parish, Karr Cr.,
LA Hwy. 61, XI-5-1972, 1 female. Jefferson Davis Parish, Marsh
Bayou, Parish Rd. 3-01, VI-19-1972, 1 male. Natchitoches Parish,
Little Bayou Pierre, VI-15-1974, 1 male. MINNESOTA, Clearwater
Co., Ithasca State Park, VI-20-1962, 1 nymph. MISSISSIPPI, Lincoln
Co., Homochitto R., MS Rt. 550, IV-24-1976, 1 reared female and
exuviae, emerged V-24. Lowndes Co., Tombigbee R., MS Hwy. 82,
V-23-1976, 1 reared male and exuviae, emerged VI-20. NORTH
CAROLINA, Moore/Montgomery Cos., Drowning Cr., NC Hwy. 73,
V-22-1980, 5 nymphs. Union Co., Creek on Co. Rd. 1107, .8 mi. S.
St. Hwy. 75, V-23-1980, 3 nymphs. SOUTH CAROLINA, Aiken Co., Cedar
Cr., Upper Three Runs System, V-19-1980, 3 nymphs. Lexington Co.,
Rawls Cr., SC Hwy. 6, V-22-1980, 5 nymphs. TENNESSEE, Bedford Co.,
Duck R., Anchor Mill, V-20-1978, 2 nymphs. Blount Co., Hesse
Cr., confl. Little R., V-24-1969, 1 reared female and exuviae,
emerged VI-5. Bradley Co., Conasauga R., TN Hwy. 74, Coffee Co.,
Duck R., confl. Perry Cr., VI-25-1977, 1 nymph. Franklin Co.,
Boiling Fork Cr., Co. Rd. 4403, V-5-1977, 1 nymph. Hancock Co.,
Clinch R., Frost Ford, IV-22-1978, 1 nymph. Lawrence Co., D.
Crockett St. Pk., 1 nymph. Madison Co., Turk Cr., US Hwy. 45,
V-16-1978, 1 nymph. Monroe Co., Turkey Cr., 1 mi. upstream confl.
Tellico R., IV-19-1978, 2 nymphs. Polk Co., Greasy Cr., TN Hwy. 30,
V-17-1980, 3 nymphs. Sullivan Co., Muddy Cr., Blountville,

IV-4-1980, 3 nymphs. VIRGINIA, Giles Co., Sinking Cr., Newport,
VIII-3-1979, 1 nymph. Scott Co., Copper Cr., Spivey Mill,
IV-5-1980, 6 nymphs.

Basiaeschna janata (Say)

ALABAMA, Blount Co., Village Cr., AL Hwy. 75, IX-22-1980,
2 nymphs. Cleburne Co., Little Shoal Cr., Forest Svc. Rt. 531,
IX-16-1980, 1 nymph. ARKANSAS, Polk Co., Ouchita R., McGuire
Access, IX-11-1978, 1 nymph. GEORGIA, Murray Co., springs at
junct. GA Hwys. 225 and 2, IV-25-1976, 1 male. LOUISIANA,
Washington Parish, III-30-1974, 2 males. MINNESOTA, Clearwater
Co., Itasca St. Pk., VII-5-1962, 2 nymphs. Pine Co., Snake R.,
10 mi. E. Pine City, V-24-1964, 1 nymph. TENNESSEE, Bedford Co.,
Duck R., Anchor Mill, V-20-1978, 1 male. Bedford Co., Garrison
Fork Cr., 7 mi. E Shelbyville, XII-14-1977. 6 nymphs. Blount Co.,
Reed Cr., 4 mi. E Walland, IV-1-1976, 1 reared female and exuviae,
emerged IV-3. Bradley Co., Conasauga R., TN-GA state line,
II-22-1970, 1 reared female and exuviae. Coffee Co., Duck R.,
confl. Bashaw Cr., III-23-1978, 1 nymph. Claiborne Co. (no
locality), XI-7-1965, 1 nymph. Hancock Co., Big War Cr., confl.
Clinch R., X-30-1975, 1 nymph. Marshall Co., Duck R., 2.5 mi. SE
Chapel Hill, III-24-1978, 2 nymphs. Polk Co., Minnewauga Cr.,
confl. Conasauga R., XI-2-1975, 2 nymphs.

Progomphus obscurus (Rambur)

ALABAMA, Dallas Co., Cedar Cr., AL Hwy. 41, X-24-1980, 8
nymphs. Perry/Dallas Co., Oakmulgee Cr., AL Hwy. 219, X-24-1980,

7 nymphs. Randolph Co., Pinewood Cr., Co. Rd. 19, XI-16-1980,
 1 nymph. Wilcox Co., Cedar Cr., AL Co. Rd. 63, X-24-1980, 15
 nymphs. ARKANSAS, Clark Co., Little Missouri R., AR Hwy. 53,
 V-28-1977, 1 exuviae. GEORGIA, Cherokee Co., Etowah R., at Board
 Tree Cr., IX-21-1980, 2 nymphs. Richmond Co., Little Spirit Cr.,
 US Hwy. 25, V-20-1980, 7 nymphs and 2 exuviae. Beauregard Parish,
 Bundick Cr., VI-5-1972, 1 reared female and exuviae, 1 male.
 LaSalle Parish, Trout Cr., VII-29-1973, 1 male. Natchitoches
 Parish, Little Bayou Pierre, VI-15-1974, 1 male, 1 female. St.
 Tammany Parish, Talisheek Cr., LA Hwy. 41, XII-15-1973, 1 nymph.
 Vernon Parish, Pearl Cr., V-18-1972, 5 males. Washington Parish,
 Crains Cr., VI-8-1974, 1 male. NORTH CAROLINA, Columbus Co.,
 Lumber R. at Fair Bluff, VII-16-1978, 4 nymphs. TENNESSEE,
 Bradley Co., Conasauga R., TN Hwy. 74, V-15-1977, 1 nymph.
 Claiborne Co., Powell R., US Hwy. 25E, IV-22-1978, 1 nymph. Henry
 Co., Holly Fork Cr., 4 mi. N Nobles, XII-6-1973, 2 nymphs. Morgan
 Co., Crooked Fork Cr., TN Hwy. 62, V-5-1969, 1 nymph, 1 reared
 female and exuviae, emerged VI-1. Sevier Co., Gists Cr.,
 X-11-1966, 1 nymph.

Hagenius brevistylus Selys Longchamps

FLORIDA, Alachua Co., Hackett Cr., FL Hwy. 26, X-13-1979, 1
 nymph. GEORGIA, Catoosa Co., Little Chicamauga Creek, Co. Rd.
 179, X-26-1979, 2 nymphs. Dade Co., Lookout Cr., 2 mi. downstream
 Easley Cemetery, VII-19-1980, 1 male. LOUISIANA, Allen Parish,
 Whiskey Chitto Cr., LA Hwy. 377, VI-4-1972, 1 male. Beauregard
 Parish, Sugar Cr., VI-23-1972, 1 male. Jackson Parish, Mill Cr.,

VIII-25-1973, 1 male. Vernon Parish, Cypress Cr., VI-24-1972, 1 male. TENNESSEE, Bedford Co., Duck R., Anchor Mill, V-20-1978, 1 reared male and exuviae. Blount Co., Little R., Co. Rd. 2498, IV-19-1980, 1 nymph. Hancock Co., Clinch R., Frost Ford, V-7-1976, 1 reared male and exuviae, emerged V-28. Powell R., McDowell Ford, VI-14-1977, 1 nymph. Knox Co., Knoxville, VIII-15-1980, 1 male. Polk Co., no further data, X-25-1965, 1 nymph.

Lanthus vernalis Carle

GEORGIA, Gilmer Co., Big Turniptown Cr., GA St. Hwy. 5, 3 mi. NE Ellijay, IV-13-1980, 1 reared male and exuviae, emerged V-2. TENNESSEE, Blount Co., Reed Cr., 5 mi. E Walland, IV-18-1976, 1 reared male, 2 reared females and exuviae, emerged V-5-7. Carter Co., Doe R., Roane Mtn. St. Pk., V-8-1978, 1 reared male and exuviae in transformation.

Stylogomphus albistylus (Hagen)

ARKANSAS, Sevier Co., Saline R., AR Hwy. 24, V-28-1977, 1 male. GEORGIA, Cherokee Co., Conn Cr., Co. Rd. 775, V-18-1980, 5 nymphs. Etowah R., confl. Board Tree Cr., IX-21-1980, 2 nymphs. Gilmer Co., Mountaintown Cr., GA St. Hwy. 52, IV-12-1980, 2 nymphs. Greene Co., Richland Cr., Hwy. 278, V-18-1980, 1 nymph. Murray Co., Sumac Cr., US Hwy. 411, V-17-1980, 1 nymph. KENTUCKY, Whitley Co., South Fork Little Dog Slaughter Cr., Daniel Boone National Forest, VII-17-1976, 1 male and 2 females. NORTH CAROLINA, Union Co., unnamed creek, Co. Rd. 1107, .8 mi. S St. Hwy. 75, V-23-1980, 5 nymphs. SOUTH CAROLINA, Oconee Co., Chatoga R., Hwy. 28,

IV-30-1976, 2 nymphs. TENNESSEE, Anderson Co., Oak Ridge,
 V-16-1970, 2. males and exuviae. Bedford Co., Thompson Cr., 4 mi.
 SW Normandy, XII-13-1977, 1 nymph. Blount Co., Little R., Townsend,
 IV-15-1976, 1 male and exuviae, emerged V-17. Reed Cr., 2.7 mi.
 E Walland, V-14-1976, 1 nymph. Bradley Co., Conasauga R., TN Hwy.
 74, V-15-1977, 2 nymphs. Cannon Co., McMahan Cr., 2 mi. NE Ivy
 Bluff, VI-25-1977, 1 male. Coffee Co., Garrison Fork Cr., US 41,
 XII-14-1977, 3 nymphs. Duck R., mouth of Bashaw Cr., III-23-1978,
 15 nymphs. Cumberland Co., Caney Fork R., 1.3 mi. NNE Pleasant
 Hill, IV-14-1976, 1 nymph, 4 reared males and 3 reared females
 and exuviae, emerged V-14 to V-23. Hancock Co., Clinch R., 3.7 mi.
 NE TN Hwy. 31 bridge, V-8-1976, 2 nymphs, 2 reared males and 3
 reared females and exuviae, emerged V-11 to V-17. Monroe Co.,
 Spicewood Br., Frozenhead St. Pk., II-12-1979, 1 nymph. Polk
 Co., Greasy Cr., TN Hwy. 30, V-17-1980, 2 nymphs. Sevier Co.,
 Walden Cr., approx. 8 mi. E Walland, VI-6-1976, 1 male. Sullivan
 Co., Muddy Cr., Blountville, IV-4-1980, 7 nymphs. VIRGINIA, Scott
 Co., North Fork Holston R., 5 mi. upstream from Weber, IV-6-1976,
 1 reared male and exuviae, emerged V-22.

Ophiogomphus howei Bromley

TENNESSEE, Monroe Co., Tellico R., Co. Rd. 2510, V-4-1971,
 1 male and exuviae, emerged V-17.

Ophiogomphus mainensis Packard

ALABAMA, Blount Co., Copeland Cr., III-23-1973, 1 reared
 female and exuviae, emerged IV-2. TENNESSEE, Blount Co., Four

Mile Cr., III-5-1978, 1 nymph. Bradley Co., Conasauga R., TN Hwy. 74, XI-2-1975, 4 nymphs. Same location, VI-25-1976, 1 female. Cumberland Co., Caney Fork R., 1.3 mi. NNE Pleasant Hill, IV-14-1976, 1 reared male and exuviae, emerged V-7. Polk Co., X-25-1965, 1 nymph.

Ophiogomphus rupinsulensis (Walsh)

TENNESSEE, Bedford Co., Duck R., Anchor Mill, V-20-1978, 2 reared males and exuviae, emerged V-27 and VI-1. Carter Co., Elk R., above Watauga reservoir, IV-14-1978, 1 nymph. Claiborne Co., Powell R., US Hwy. 25E, IV-22-1978, 1 reared female and exuviae, emerged V-18. Coffee Co., Duck R. at Bashaw Cr., III-23-1978, 2 nymphs. Hancock Co., Powell R., mouth Mountain Cr., III-18-1971, 1 reared female and exuviae, emerged IV-29-1971. Clinch R., 3.7 mi. NE TN Hwy. 31. bridge, V-8-1976, 2 nymphs, 5 reared males and exuviae, 2 reared females and exuviae, emerged V-10 to V-29. Same location IV-12-1976, 1 nymph, 1 female and exuviae, emerged V-14. Marshall Co., Duck R., 2.5 mi. SE Chapel Hill, III-24-1978, 4 nymphs, 1 female and exuviae, emerged V-23.

Ophiogomphus sp. A

TENNESSEE, Dickson Co., Will Hall Cr., US Hwy. 70, Montgomery Bell St. Pk., III-26-1971, 1 reared female and exuviae. Same location, IX-25-1980, 5 nymphs. Same location, III-21-1981, 8 reared males and exuviae, 6 reared females and exuviae, emerged IV-13 to IV-29. Lewis Co., Little Swan Cr., Natchez Trace Pkwy., III-20-1979, 1 nymph.

Erpetogomphus designatus Hagen

ALABAMA, Dallas Co., Cedar Cr., AL Hwy. 41, X-24-1980, 15 nymphs. Perry/Dallas Cos., Oakmulgee Cr., AL Hwy. 219, X-24-1980, 1 nymph. ARKANSAS, Bradley/Drew Co., Saline R., 7 mi. SSE Warren off AR. Hwy. 8, V-21-1977, 23 nymphs. MISSISSIPPI, Lowndes Co., Tombigbee R., MS Hwy. 82, V-23-1976, 2 nymphs. TENNESSEE, Coffee Co., Duck R. at Bashaw Cr., III-23-1978, 1 nymph. Knox Co., Holston R., 1.5 mi. S US 11E, VIII-1-1967, 3 nymphs.

Dromogomphus armatus Selys Longchamps

FLORIDA, Taylor Co., Econfina R., St. Hwy. 15, VI-23-1977, 1 nymph. LOUISIANA, St. Tammany Parish, Talisheek Cr., St. Hwy. 41, XII-15-1973, 1 nymph. MISSISSIPPI, Perry Co., Beaver Cr., St. Rt. 15, V-25-1977, 1 exuviae and 2 nymphs. SOUTH CAROLINA, Aiken Co., Upper Three Runs Cr., Co. Rd. 114, V-19-1980, 1 nymph.

Dromogomphus spinosus Selys Longchamps

ARKANSAS, Bradley/Drew Cos., Saline R., 7 mi. SSE Warren, V-21-1977, 1 nymph. Drew Co., Saline R., St. Hwy. 172, V-21-1977, 2 exuviae. FLORIDA, Lake Co., Alexander Spring Run, St. Rt. 445, VI-19-1977, 1 nymph. Taylor Co., Steinhatchie R. at US Hwy. 19, VI-23-1977, 2 nymphs. GEORGIA, Catoosa Co., S. Chickamauga Cr., Graysville Mill Dam, VIII-8-1980, 1 female. Dade Co., Lookout Cr., Co. Rd. 201, V-10-1980, 1 nymph. Murray Co., Conasauga R., Co. Rd. 132, VI-24-1980, 6 exuviae. LOUISIANA, Allen Parish, Whiskey Chitto Cr., LA Hwy. 377, II-1-1975, 1 nymph. Beauregard Parish, Sugar Cr., VI-26-1972, 1 male. Jefferson Davis Parish,

Marsh Bayou, Parish Rd. 3-01, VI-19-1972, 1 male. Lasalle Parish, Trout Cr., VII-29-1973, 1 male. Washington Parish, Crains Cr., VI-8-1974, 1 male. MINNESOTA, Lake Co., Saganaga R., Saganaga Falls, VII-20-1976, 1 male. OKLAHOMA, Leflore Co., Kiamichi R., Hwy. 259, IX-8-1979, 2 nymphs. Pushmataha Co., Little R., 5 mi. E Cloudy, V-27-1977, 1 nymph. TENNESSEE, Bedford Co., Duck R., Anchor Mill, V-20-1978, 8 nymphs. Blount Co., Little R., Melrose, VI-27-1976, 1 male. Coffee Co., Duck R., confl. Bashaw Cr., III-23-1978, 1 nymph. Hancock Co., Powell R., McDowell Ford, VI-14-1977, 1 exuviae. Claiborne Co., Powell R., Buchanan Ford, VI-14-1977, 1 exuviae.

Dromogomphus spoliatus (Hagen)

LOUISIANA, Sabine Parish, Hodges Gardens Lake, VIII-12-1973, 2 reared females and exuviae (taken in transformation), 1 female. TEXAS, Bandera Co., Medina R., TX Hwy. 16, VII-5-1974, 1 exuviae. Gillespie Co., Pedernales R., St. Hwy. 16, V-26-1977, 1 nymph. Hays Co., San Marcos R., San Marcos, V-24-1977, 1 exuviae.

Gomphus exilis Selys Longchamps

TENNESSEE, Knox Co., Knoxville, V-9-1978, 1 male. Rhea Co., Richland Cr., at mouth of Payne Cr., V-13-1978, 1 male. VIRGINIA, Scott Co., Conservation League Lake, IV-18-1975, 1 female and exuviae.

Gomphus graslinellus Walsh

CANADA, ONTARIO, New Lewis Island, Lake Sagnaga, VII-7-1978, 1 male, 1 female. ARKANSAS, Montgomery Co., Collier Cr., Ark. Hwy. 8, V-27-1977, 1 male.

Gomphus lividus Selys Longchamps

ALABAMA, Cherokee Co., trib. to Little R., III-26-1974, 1 male and exuviae, emerged III-30. Clarke Co., W Whatley, V-14-1975, 1 male. Lauderdale Co., Lindsey Cr., Co. Rds. 15 & 6, III-10-1979, 1 nymph. ARKANSAS, Craighead Co., Thompson Cr., AR Rt. 1, V-17-1978, 1 reared male and exuviae. GEORGIA, Whitfield Co., E Chickamauga Cr., GA Rt. 336, V-10-1980, 5 males. KENTUCKY, McCreary Co., Cal Cr., at KY Rt. 592, IV-16-1977, 1 female and exuviae. LOUISIANA, Beauregard Parish, Sugar Cr., IV-8-1972, 2 males. Natchitoches Parish, Little Bayou Pierre, IV-5-1974, 2 males. Washington Parish, Crains Cr., at LA Hwy. 62, IV-22-1976, 2 males. TENNESSEE, Bedford Co., Duck R., at Anchor Mill, V-20-1978, 2 males. Blount Co., Little R. at Walland, IV-7-1978, 1 female and exuviae, emerged VI-17. Bradley Co., Conasauga R., TN Hwy. 74, IV-25-1976, 1 male. Campbell Co., Ollis Cr., VI-15-1976, 1 male. Coffee Co., Duck R., confl. Bashaw Cr., III-23-1978, 1 male and exuviae, emerged IV-10. Cumberland Co., Caney Fork R., 1.3 mi. NE Pleasant Hill, IV-14-1976, 1 female and exuviae. Same location, VI-26-1976, 1 male. Feutress Co., Little Jack Cr., 4 mi. SE Fairview, V-7-1980, 5 reared females and exuviae. Hardin Co., Walker Br. of Mud Cr., 3.2 mi. S Savannah, V-16-1978, 2 reared males and exuviae. Monroe Co., Turkey Cr., Cherokee National Forest, IV-19-1978, 1 reared male and exuviae, emerged IV-25.

Gomphus minutus Rambur

FLORIDA, Alachua Co., Hatchet Cr., FL Hwy. S-225, IV-11-1974, 1 male. Glades Co., Fisheating Cr., FL Hwy. 27, III-29-1974,

1 male, 1 female. Hernando/Sumpter Cos., Little Withlacoochee R., US Hwy. 301, III-26-1980, 1 female and exuviae. GEORGIA, Burke Co., Rocky Cr., GA Hwy. 56, V-20-1980, 1 male. Chadler Co., Fifteen Mile Cr., GA Hwy. 46, V-21-1980, 3 males.

Gomphus quadricolor Walsh

TENNESSEE, Blount Co., Little R., Walland, IV-7-1978, 1 female and exuviae, Marshall Co., Duck R., 2.5 mi. SE Chapel Hill, III-24-1978, 2 reared males and 1 reared female and exuviae. Pickett Co., Wolf R. at Town Br., V-7-1980, 1 reared male and exuviae, emerged V-8.

Gomphurus crassus (Hagen)

TENNESSEE, Bedford Co., Duck R., Anchor Mill, V-20-1978, 2 reared males and exuviae, 1 reared female and exuviae, emerged V-24, 5 exuviae, 8 nymphs. Coffee Co., Duck R., at Bashaw Cr., III-23-1978, 2 nymphs. Marshall Co., Duck R., 2.5 mi. SE Chapel Hill, III-24-1978, 2 nymphs. Same location, IV-1-1978, 1 nymph, 1 reared female and exuviae, emerged V-17. Rutherford Co., Stones R., US Hwy. 231, IV-1-1978, 1 nymph.

Gomphurus dilatatus (Hagen)

FLORIDA, Alachua Co., Newman's Lake, V-24-1975, 1 male. Hogtown Cr., SW Gainesville, V-11-1975, 1 exuviae. Pasco Co., Hillsborough R., St. Hwy. 39 bridge, III-26-1980, 2 exuviae. Sumter Co., Jumper Cr., US 301, III-26-1980, 1 female, 3 exuviae. GEORGIA, Murray Co., Conasauga R., Co. Rd. 132, VI-24-1980, 13 exuviae.

Gomphurus externus (Hagen)

ILLINOIS, Clark Co., Wabash R., at riffle 1.7 mi. below Breeder Plant, VI-23-1978, 6 exuviae.

Gomphurus fraternus (Say)

TENNESSEE, Greene Co., Nolichucky R., at Steele Island (river mile 19.7), IV-13-1978, 1 nymph, 1 female and exuviae, emerged V-7.

Gomphurus hybridus (Williamson)

ARKANSAS, Drew Co., Saline R., at AR Hwy. 172, V-21-1977, 1 male. GEORGIA, Jeff Davis/Montgomery Cos., Altamaha R., US Hwy. 221, V-21-1980, 2 males, 2 females. INDIANA, Posey Co., Wabash R., New Harmony, XI-11-1978, 1 nymph. LOUISIANA, Beauregard Parish, Sabine R., US Hwy. 190, IV-29-72, 2 males, 1 female. TENNESSEE, Hardin Co., Tennessee R., at Diamond Island, 5 mi. SW Savannah, V-16-1978, 1 male, 1 exuviae. Humphreys Co., Duck R. confl. Hurricane Cr., 7.3 mi. NNE Buffalo, X-21-1978, 3 nymphs. Duck R., 3.4 mi. N Buffalo, X-21-1978, 2 nymphs.

Gomphurus lineatifrons (Calvert)

ALABAMA, Clay Co., Cheaha Cr., XI-12-1978, 1 nymph. GEORGIA, Cherokee Co., Etowah R., St. Rt. 1018, IX-22-1980, 1 nymph. Dade Co., Lookout Cr., Co. Rd. 201, V-10-1980, 1 female and exuviae, emerged V-19. Gilmer Co., Ellijay R., IX-1-1978, 1 nymph. TENNESSEE, Bradley Co., Conasauga R., TN Hwy. 74, XI-21-1976, 1 nymph. Claiborne Co., Powell R., Buchanan Ford (river mile 99),

VI-14-1977, 1 exuviae. Greene Co., Nolichucky R., Steele Island (river mile 19.7), IV-13-1978. Hancock Co., Clinch R., Kyles Ford, IV-9-1978, 1 nymph. Powell R., McDowell Ford, 1.5 mi. NE Atlanthus Hill confl. Four Mile Cr., IV-22-1978, 1 nymph. Monroe Co., Tellico R., 4.5 mi. downstream Tellico Plains, X-12-1980, 3 nymphs. VIRGINIA, Giles Co., Sinking Cr., Sec. Hwy. 700 off US Hwy. 460 E Newport, VIII-3-1979, 1 nymph.

Gomphurus modestus (Needham)

ARKANSAS, Clark Co., Little Missouri R., AR Hwy. 53, V-28-1977, 4 exuviae. Sevier Co., Saline R., AR Hwy. 24, V-28-1977, 5 exuviae. LOUISIANA, Washington Parish, Crains Cr., LA Hwy. 62, IV-6-74, 1 female, 1 female and exuviae, emerged V-6. MISSISSIPPI, Jones Co., Leaf R. I-59, V-25-1976, 1 exuviae. TEXAS, Newton Co., Big Cow Cr., TX Rt. 1012, V-22-1977, 4 exuviae. San Jacinto Co., Big Cr., US Hwy. 59, V-23-1977, 4 exuviae.

Gomphurus ozarkensis (Westfall)

ARKANSAS, no further data, 9 exuviae of adults reared by G. Harp.

Gomphurus vastus (Walsh)

ALABAMA, Bibb Co., Cahaba R., Hwy. 27, IV-15-1978, 1 nymph. Tallapoosa Co., Hillabee Cr., AL Hwy. 22, XI-16-1980, 1 nymph. ARKANSAS, Bradley/Drew Cos., Saline R., 7 mi. SSE Warren, V-21-1977, 2 exuviae. Drew Co., Saline R., AR Hwy. 172, V-21-1977, 3 exuviae. Montgomery Co., N. Collier Cr., AR Hwy. 8, V-28-1977, 1 male. Ouchita R., US Hwy. 270, IX-14-1978, 3 nymphs. Randolph

Co., Current R., V-19-1979, 2 nymphs. ILLINOIS, Clark Co., Wabash R., 1.7 mi. below Breeder Plant, VI-23-1978, 1 exuviae. MICHIGAN, Dickinson Co., Menominee R., Kingsford, VI-7-1978, 1 female and 3 exuviae. TENNESSEE, Bradley Co., Conasauga R., Hwy. 74, XI-2-1975, 1 nymph. Cocke Co., Nolichucky R., Johnson Island, VI-12-1976, 1 female. Cocke/Greene Cos., Nolichucky R., 12 mi. N Newport, VI-25-1976, 1 male. Greene Co., Nolichucky R., Steele Island (river mile 19.7), IX-14-1977, 2 nymphs. Same location, IV-13-1978, 5 nymphs. Hancock Co., Clinch R., 3.7 mi. NE TN Hwy. 31 bridge, V-8-1976, 1 reared female and exuviae, emerged VI-5. Same location, IV-22-1878, 1 nymph, 1 male and exuviae, emerged V-7. Loudon Co., Little Tennessee R., Coytee Sprgs., VIII-16-1973, 1 male. VIRGINIA, Scott Co., North Fork Holston R., 5 mi. upstream from Weber, IV-6-1976, 1 reared male and exuviae, emerged IV-29.

Gomphurus ventricosus (Walsh)

TENNESSEE, Claiborne Co., Powell R., US 25E, V-24-1969, 1 male. VIRGINIA, Scott Co., North Fork Holston R., 5 mi. upstream from Weber, IV-6-1976, 1 male and exuviae, emerged V-7, 1 female and exuviae, emerged IV-27.

Hylonomphus abbreviatus (Hagen)

NORTH CAROLINA, Chatham Co., Rocky R., Hwy. 902, V-2-1980, 2 exuviae. Rocky R., Hwys. 15 and 501, V-3-1980, 9 exuviae. Montgomery Co., Uwharrie R., Hwy. 109, V-4-1980, 4 exuviae.

Hylonomphus brevis (Hagen)

TENNESSEE, Blount Co., Little River, near Walland, IV-15-1976, 2 females and exuviae, emerged IV-25, IV-27. Same

location, IV-7-1978, 2 males and exuviae, emerged IV-17, 1 female and exuviae, emerged IV-17.

Hylogomphus carolinus (Carle)

NORTH CAROLINA, Moore/Montgomery Co., Drowning Cr., NC Hwy. 73, V-22-1980, 2 females and exuviae, emerged V-31, VI-1. Richmond Co., Rocky Fork Cr. 5 mi. E Ellerbe, IV-28-1979, 1 nymph.

Hylogomphus geminatus (Carle)

FLORIDA, Calhoun Co., Juniper Cr., Hwy. 20, III-18-1974, 5 nymphs, 1 male and exuviae, emerged III-23. Gadsden Co., Crooked Cr., Hwy. 270, IV-16-1972, 6 nymphs. Santa Rosa Co., Middle Cr., Blackwater St. Forest, III-16-1973, 3 exuviae, emerged III-23, IV-16.

Hylogomphus parvidens (Currie)

GEORGIA, Gilmer Co., Big Turniptown Cr., GA St. Hwy. 5, IV-13-1980, 1 female and exuviae, emerged V-5.

Hylogomphus viridifrons (Hine)

TENNESSEE, Blount Co., Little River, Walland, IV-7-1978, 1 female and exuviae, emerged IV-17. Little R., US 411, IV-8-1978, 1 male and exuviae, emerged IV-17. Greene Co., Nolichucky R., Steele Island (river mile 19.7), IV-13-1978, 5 males and exuviae, emerged IV-17, IV-18. Hancock Co., Clinch R., 3.7 mi. NE TN Hwy. 31 bridge, IV-12-1976, 1 male and exuviae, emerged IV-27, 1 female and exuviae, emerged IV-27. Powell R., McDowell Ford, IV-22-1978, 1 male and exuviae, emerged IV-23. Monroe Co., Turkey Cr., 1 mi. NE confl. Tellico R., IV-19-1978, 1 male and exuviae, emerged

IV-24. VIRGINIA, Scott Co., Copper Cr., Spivey Mill, IV-5-1980, 1 female and exuviae, emerged V-2. North Fork Holston R., 5 mi. upstream from Weber, IV-6-1976, 3 males and exuviae, emerged IV-19 to IV-21, 1 female and exuviae, emerged IV-20.

Genus *A consanguis* (Selys Longchamps)

ALABAMA, Blount Co., Champion Cr., AL Hwy. 79, III-22-1973, 1 female and exuviae. TENNESSEE, Polk Co., Conasauga R., TN Hwy. 74, V-16-1970, 1 female and exuviae, emerged V-25. Sullivan Co., Muddy Cr., 1.5 mi. upstream from Blountville, IV-4-1980, 6 nymphs, 3 females and exuviae, emerged V-1-6, 1 male and exuviae, emerged V-2. Scott Co., Copper Cr., Spivey Mill, IV-5-1980, 1 male and exuviae, emerged V-1, 1 female and exuviae, emerged V-5.

Genus *A rogersi* (Gloyd)

GEORGIA, Gilmer Co., Big Turniptown Cr., GA St. Hwy. 5, IV-13-1980, 3 nymphs. Boardtown Cr., GA St. Rt. 12, IV-12-1980, 1 nymph. Mountain Town Cr., GA St. Hwy. 52, IV-12-1980, 5 nymphs. Unnamed trib. to Ellijay R., GA St. Rt. 12 ca. 1 mi. N junction with GA St. Hwy. 5, IV-13-1980, 4 nymphs. KENTUCKY, McCreary Co., Cal Cr., KY Hwy. 592, IV-16-1977, 1 male and exuviae, emerged V-2. Whitley Co., South Fork Little Dog Slaughter Cr., Daniel Boone National Forest, VII-17-1976, 3 males. TENNESSEE, Blount Co., Reed Cr., 5 mi. E Walland, VI-6-1976, 2 males. Seepage trib. to Reed Cr., 2.7 mi. upstream Walland, IV-21-1978, 1 male and exuviae, emerged V-10. Cumberland Co., Caney Fork R., 1.3 mi. NNE Pleasant Hill, IV-14-1976, 1 male and exuviae, emerged V-12. Monroe Co.,

North R., North River Campground, Cherokee National Forest,
IV-19-1978, 2 males and exuviae, emerged V-7.

Stylurus amnicola (Walsh)

ILLINOIS, Clarke Co., Wabash R., 1.7 mi. below Breeder Plant,
VI-23-1978, 2 exuviae.

Stylurus intricatus (Hagen)

MISSOURI, Cooper Co., Missouri R., 1 mi. E Wooldridge,
V-25-1979, 2 nymphs.

Stylurus ivae Williamson

ALABAMA, Bibb Co., South Fork Sandy Cr., 15 mi. WNW Center-
ville, IX-11-1980, 1 nymph. GEORGIA, Toombs/Tattnall Cos.,
Ohoopsee R., GA Hwy. 152, V-21-1980, 1 nymph. FLORIDA, Clay Co.,
Bull Cr., Hwy. 21, V-10-1973, 6 nymphs. Gadsden Co., Crooked Cr.,
Hwy. 270, IV-16-1972, 3 nymphs. Liberty Co., Sweetwater Cr., Hwy.
5-270, V-26-1973, 2 exuviae (from reared adults). Santa Rosa Co.,
Pond Cr., Hwy. 191, III-16-1974, 7 nymphs.

Stylurus laurae Williamson

ARKANSAS, Craighead Co., Thompson Cr., AR Rt. 1, V-17-1978,
1 female and exuviae, emerged V-27. GEORGIA, Dade Co., Lookout
Cr., Co. Rd. 201, V-10-1980, 1 male and exuviae, 1 female and
exuviae, emerged VI-21. Gilmer Co., Mountaintown Cr., GA Hwy. 52,
IV-12-1980, 1 male and exuviae, emerged VI-2. LOUISIANA, Jackson
Parish, Mill Cr., VII-28-1973, 1 male and 1 female. Washington
Parish, Crains Cr., LA Hwy. 62, IV-6-1974, 1 male and exuviae,

emerged V-10. NORTH CAROLINA, Moore/Montgomery Cos., Drowning Cr., NC Hwy. 73, V-22-1980, 1 female and exuviae, emerged VI-21. SOUTH CAROLINA, Aiken Co., Upper Three Runs Cr., Co. Rd. 114, V-19-1980, 1 female and exuviae, emerged VI-14. TENNESSEE, Coffee Co., Bashaw Cr., near confl. with Duck R., V-20-1978, 1 female and exuviae, emerged V-30. Hardin Co., Walker Branch of Mud Cr., V-16-1978, 3 females and exuviae, emerged V-21, V-22, 1 male and exuviae, emerged V-25.

Stylurus notatus (Rambur)

ILLINOIS, Clark Co., Wabash R., 1.7 mi. below Breeder Plant, VI-23-1978, 1 exuviae.

Stylurus plagiatus (Selys Longchamps)

ARKANSAS, St. Francis Co., St. Francis R., I-40, VI-15-1978, 1 reared male and exuviae, captured during transformation. FLORIDA, Lake Co., Alexander Spring Run, St. Rt. 445, VI-19-1977, 1 nymph. Levy Co., Waccassassa R., Hwy. 19, VII-1975, 1 exuviae. ILLINOIS, Lawrence Co., Wabash R., 1 mi. below confl. Embarrass R., IX-13-1979, 1 nymph. NORTH CAROLINA, Columbus Co., Lake Waccamaw, IX-2-1978, 1 reared female and exuviae, captured in transformation, 2 exuviae. TENNESSEE, Knox Co., Knoxville, VIII-24-1978, 1 female.

Stylurus scudderi (Selys Longchamps)

NORTH CAROLINA, Transylvania Co., West Fork French Broad R., US Hwy. 64, VI-20-1979, 1 female and exuviae, emerged VI-30. French Broad R., US Hwy. 178, VI-20-1979, 1 male, 2 females and exuviae, all emerged VI-30. French Broad R., St. Rt. 1129,

VI-20-1979, 1 male, 1 female and exuviae, emerged VI-29.

TENNESSEE, Monroe Co., North R., North R. Campground, VII-24-1979,
4 females and exuviae, emerged VIII-3, VIII-4.

Stylurus spiniceps (Walsh)

ARKANSAS, Bradley/Drew Cos., Saline R., AR Hwy. 8, V-21-1977,
1 nymph. GEORGIA, Cherokee Co., Etowah R., confl. Long Swamp Cr.,
IX-22-1980, 1 nymph. NORTH CAROLINA, Macon Co., Little Tennessee
R., confl. Cullasaja R., VII-7-1977, 1 nymph. MISSISSIPPI, Benton
Co., Indian Cr., MS Hwy. 7, VIII-5-1976, 1 male. TENNESSEE, Greene
Co., Nolichucky R., Steele Island, VI-15-1977, 1 male. Same
location, IV-13-1978, 4 nymphs.

Cordulegaster diastatops (Selys Longchamps)

GEORGIA, Dawson Co., spring in swamp S Dawsonville, III-15-1980,
2 nymphs. TENNESSEE, Blount Co., Reed Cr., 5 mi. E Walland,
VI-5-1976, 1 male. Sphagnum bog in Cades Cove, Gt. Smoky Mountains
Nat. Pk., III-5-1976, 1 nymph. Monroe Co., Seepage trib. North R.,
North R. Campground, Cherokee Nat. Forest, VII-31-1976, 3 nymphs.

Cordulegaster erroneus Hagen

GEORGIA, Gilmer Co., Big Turniptown Cr., GA Hwy. 5, IV-13-1980,
4 nymphs. LOUISIANA, West Feliciana Parish, Tunica Bayou headwater
trib. LA Hwy. 66, IV-21-1973, 1 nymph. TENNESSEE, Blount Co.,
Little R., Junct. TN Hwy. 73 and Foothills Pkwy., V-28-1980, 1
female and exuviae taken in transformation. Seepage to Parsons
Branch, IV-8-1978, 1 nymph. Seepage trib. to Reed Cr., 2.7 mi.
E Walland, VI-5-1976, 1 nymph. Hardin Co., Walker Br. of Mud

Creek, 3.2 mi. S Savannah, V-16-1978, 1 reared male and exuviae.
 Knox Co., Seepage at Univ. TN woodlot on Cherokee Trail, V-9-1978,
 1 reared female and exuviae. Monroe Co., Falls Br. of Citico Cr.,
 IV-19-1978, 1 reared male and exuviae. Seepage trib. to North R.,
 North R. Campground, Cherokee Natl. Forest, VII-31-1976, 1 nymph.
 Same location, VII-24-1979, 3 males. Turkey Cr. approx. 1 air mi.
 NE confl. with Tellico R., IV-19-1978, 1 reared female and exuviae.
 Sevier Co., Gt. Smoky Mountains Natl. Pk., 3 mi. SE Tremont,
 VII-24-1976, 3 males. Union Co., Big Ridge St. Pk., VII-12-1978,
 1 male. White Co., Lost Cr. Falls, TN Co. Rd. 4448, approx. 6 mi.
 SE Sparta, VII-5-1980, 8 males.

Cordulegaster maculata (Selys Longchamps)

GEORGIA, Cherokee Co., Conn Cr., Co. Rd. 775, V-18-1980,
 10 nymphs. Gilmer Co., Boardtown Cr., GA Rt. 12, IV-12-1980, 2
 nymphs. Mountain Town Cr., GA Hwy. 52, IV-12-1980, 3 nymphs.
 Greene Co., Richland Cr., GA Hwy. 278, V-18-1980, 4 nymphs.
 Murray Co., Sumac Cr., US Hwy. 411, V-17-1980, 2 nymphs. Whitfield
 Co., East Chickamauga Cr., GA St. Rt. 326, V-10-1980, 1 male.
 KENTUCKY, Jackson Co., Lake Cr., 2 mi. NE Macedonia, III-19-1977,
 2 reared females and exuviae. McCreary Co., confl. Indian Cr. and
 Barren Fork, III-27-1977, 1 reared female and exuviae. Whitley
 Co., Youngs Cr., IV-8-1978, 2 females and exuviae, emerged IV-14.
 MINNESOTA, Clearwater Co., LaSalle Cr., Itasca St. Pk., VII-25-1962,
 4 nymphs. NORTH CAROLINA, Macon Co., Burningtown Cr., 10 mi. NW
 Franklin, XI-15-1977, 1 nymph. Richmond Co., Creek 2.0 mi. S Co.
 Rd. 1425 on Co. Rd. 1424, 5 mi. E Ellerbe, IV-28-1979, 2 nymphs.

Transylvania Co., North Fork French Broad R., St. Rt. 1322,
 VI-20-1979, 1 nymph. SOUTH CAROLINA, Aiken Co., Cedar Cr.,
 V-19-1980, 4 nymphs. Upper Three Runs Cr., Co. Rd. 114, V-19-1980,
 7 nymphs. Lexington Co., Rawls Cr., SC Hwy. 6, V-22-1980, 15
 nymphs. TENNESSEE, Blount Co., Reed Cr., 5 mi. E Walland,
 IV-18-1976, 1 male. Seepage to Huskey Br., 2.7 mi. E Walland,
 IV-8-1978, 7 nymphs. Carter Co., Springs near junct. TN Hwy. 143
 and TN Hwy. 37, IX-2-1977, 4 nymphs. Coffee Co., Duck R. at
 Bashaw Cr., III-23-1978, 1 exuviae. Hardin Co., Spring at
 Pickwick Landing St. Pk. Campground, III-2-1974, 1 nymph. Henry
 Co., Holly Fork Cr., 4 mi. N Nobles, XII-6-1973, 1 nymph. Knox
 Co., I.C. King Pk., Knoxville, III-26-1966, 1 nymph. Monroe Co.,
 North R., North River Campground, Cherokee Natl. Forest, IV-19-1978,
 3 reared females and exuviae, emerged V-2, 1 reared male and
 exuviae, emerged V-5, and 3 nymphs. Sullivan Co., Muddy Cr.,
 Blountville, IV-4-1980, 10 nymphs. Unicoi Co., Indian Cr., junct.
 Hwy. 23 & Hwy. 19, III-30-1974, 1 nymph.

Cordulegaster maculata ssp. A

LOUISIANA, East Feliciana Parish, trib. to McCowen Cr.,
 IV-8-1973, 1 male. Jackson Parish, Schoolhouse Branch Springs,
 III-30-1973, 2 nymphs. Natchitoches Parish, Little Bayou Pierre,
 IV-5-1974, 3 males. West Feliciana Parish, headwater trib. to
 Tunica Bayou, LA Hwy. 66, V-5-1973, 2 nymphs. Same locality,
 I-19-1974, 1 nymph.

Cordulegaster obliqua obliqua (Say)

KENTUCKY, Whitley Co., headwater seep of Martins Fork, 7 mi. SW Corbin, VII-17-1976, 1 nymph. TENNESSEE, Cumberland Co., Daddy's Cr., 1 mi. N Crab Orchard, VI-13-1981, 1 nymph. Long Rockhouse Br., 3.5 mi. NE Crab Orchard, XI-16-1975, 1 nymph. Caney Fork R., 1.3 mi. NNE Pleasant Hill, IV-14-1976, 2 nymphs. Trib. to Clear Br., 3 mi. SW Crab Orchard, VI-13-1981, 1 nymph.

Cordulegaster obliqua fasciata Rambur

NORTH CAROLINA, Moore/Montgomery Cos., Drowning Cr., NC Hwy. 73, V-22-1980, 1 nymph. SOUTH CAROLINA, Lexington Co., Rawls Cr., SC Rt. 6, 2 mi. N Lexington, V-22-1980, 1 nymph.

Cordulegaster sayi Selys Longchamps

FLORIDA, Alachua Co., Seepage to Possum Br., Gainesville, III-4-1972, 1 nymph.

Didymops transversa (Say)

GEORGIA, Murray Cr., trib. to Murray's Lake, III-17-1977, 1 reared male and exuviae. SOUTH CAROLINA, Lexington Co., Rawls Cr., SC Rt. 6, V-22-1980, 1 female. TENNESSEE, Anderson Co., Norris Reservoir, V-3-1969, 1 reared male and exuviae. Bedford Co., Duck R., Shelbyville, XII-13-1977, 1 nymph. Thompson Cr., 4 mi. SW Normandy, XII-13-1977, 1 nymph. Campbell Co., Ollis Cr., V-19-1977, 1 male. Coffee Co., Duck R., at Bashaw Cr., III-23-1978, 1 nymph. Grainger Co., no locality, XI-7-1965, 4 nymphs. Marshall Co., Duck R., 2.5 mi. SE Chapel Hill, III-24-1978, 1 nymph. Sevier Co., Gists Cr., X-11-1966, 1 nymph.

Macromia alleghaniensis Williamson

GEORGIA, Dade Co., Lookout Cr., Co. Rd. 201, V-10-1980, 1 reared male and exuviae, emerged VI-14. Lookout Cr., approx. 1 mi. downstream Easley Cemetery, VIII-18-1980, 2 females. TENNESSEE, Scott Co., Cumberland R., Co. Rd. 2451, VII-22-1976, 1 male.

Macromia georgina (Selys Longchamps)

ALABAMA, Bibb Co., Cahaba R., AL Hwy. 24, VII-26-1977, 1 male. Dallas Co., Cedar Cr. AL Hwy. 41, X-24-1980, 2 nymphs. ARKANSAS, Craighead Co., Thompson Cr., St. Rt. 1, V-17-1978, 1 reared male and exuviae. Sevier Co., Saline R., AR Hwy. 24, V-28-1977, 1 reared male and exuviae. LOUISIANA, Beauregard Parish, Bundick Cr., LA Hwy. 113, V-25-1973, 1 female. Same location, VI-8-1972, 1 male. Same location, VI-23-1972, 1 female. Washington Parish, Crains Cr., IV-27-1974, 1 exuviae. MISSISSIPPI, Lowndes Co., Tombigbee R., US Hwy. 82, V-23-1976, 1 reared male and exuviae, emerged VI-10.

Macromia illinoiensis Walsh

GEORGIA, Dade Co., Lookout Cr., 2 mi. downstream Easley Cemetery, VIII-19-1980, 1 male. Lookout Cr., Co. Rd. 201, V-10-1980, 1 reared male and exuviae. TENNESSEE, Bedford Co., Duck R., Anchor Mill, V-20-1978, 1 reared female and exuviae, 1 reared male and exuviae. Claiborne Co., Powell R., US 25E, V-24-1969, 1 reared male and exuviae, emerged VI-6. Coffee Co., Duck R., confl. Bashaw Cr., V-20-1978, 1 reared female and exuviae, emerged VI-20. Greene Co., Nolichucky R., Steele Island,

IV-13-1978, 1 reared male and exuviae. Hancock Co., Clinch R., Frost Ford, IV-15-1978, 1 reared female and exuviae, emerged V-30. Same location, IV-22-1978, 2 reared males and 1 reared female and exuviae, emerged V-20 and V-30. Same location, V-8-1976, 2 reared males and exuviae, emerged V-15 and VI-9. Powell R., confl. Four Mile Cr., IV-22-1978, 2 reared males and exuviae, emerged VI-7. Marshall Co., Duck R., 2.5 mi. SE Chapel Hill, III-24-1978, 1 reared female, emerged VI-15. Monroe Co., North R., North R. Campground, IV-19-1978, 1 reared male and exuviae. Pickett Co., Wolf R., confl. Town Br., V-7-1980, emerged VI-5. Polk Co., Conasauga R., TN Hwy. 74, V-16-1970, 1 male and exuviae emerged V-20.

Macromia taeniolata Rambur

LOUISIANA, East Baton Rouge Parish, Baton Rouge, VII-10-1974, 1 male. St. Tammany Parish, Mill Cr., LA Hwy. 40, VIII-24-1974, 1 male. Winn Parish, Winnfield, VII-28-1973, 1 male. TENNESSEE, Monroe Co., Turkey Cr., 1 mi. NE confl. Tellico R., IV-19-1978, 1 reared female and exuviae.

Neurocordulia alabamensis Hodges

LOUISIANA, Jackson Parish, Schoolhouse Br. Springs, VII-7-1973, 1 nymph. St. Tammany Parish, Talisheek Cr., LA Hwy. 41, XII-15-1973, 1 nymph. Washington Parish, Crains Cr., LA Hwy. 62, I-18-1975, 1 nymph. Same location, IV-22-1976, 1 reared male and exuviae, emerged VI-8, 1 nymph. NORTH CAROLINA, Moore/Montgomery Cos., Drowning Cr., NC Hwy. 73, V-22-1980, 1 nymph. SOUTH CAROLINA, Aiken Co., Cedar Cr., Upper Three Runs Cr., V-19-1980, 14 nymphs.

Neurocordulia molesta Walsh

ARKANSAS, Bradley, Drew Cos., Saline R., 7 mi. SSE Warren, V-21-1977, 1 nymph. GEORGIA, Bartow Co., Etowah R., GA Hwy. S-831, X-26-1979, 2 nymphs. Jeff Davis/Montgomery Cos., Altamaha R., US Hwy. 221, V-21-1980, 3 exuviae. LOUISIANA, Vernon Parish, Sabine R., LA Hwy. 8, V-22-1977, 2 nymphs. MISSISSIPPI, Lowndes Co., Tombigbee R., US Hwy. 82, V-23-1976, 1 nymph, 1 reared female and exuviae. TENNESSEE, Humphreys Co., Duck R., 3.4 mi. N Buffalo, X-21-1978, 1 nymph. Sevier Co., French Broad R., TN Hwy. 2420, IV-26-1976, 1 nymph. TEXAS, Brazos Co., Little Brazos R., TX Hwy. 21, V-23-1977, 1 male.

Neurocordulia obsoleta (Say)

FLORIDA, Alachua Co., Santa Fe Lake, IV-7-1972, 1 reared male and exuviae, emerged IV-8.

Neurocordulia virginiana Davis

ALABAMA, Hale Co., Five Mile Cr., Co. Rd. 52, IX-11-1979, 4 nymphs. TENNESSEE, Bradley Co., Conasauga R., TN Hwy. 41, XI-2-1972, 1 nymph.

Neurocordulia xanthosoma (Williamson)

ARKANSAS, Sevier Co., Saline R., AR Hwy. 24, V-28-1977, 3 exuviae. OKLAHOMA, Pushmataha Co., Little R., 5 mi. E Cloudy, V-27-1977, 3 exuviae.

Neurocordulia yamaskanensis (Provancher)

TENNESSEE, Blount Co., Townsend, VII-8-1977, 1 female. Same location, VII-28-1977, 1 female. Greene Co., Nolichucky R.,

Steele Island, IV-13-1978, 1 nymph. Hancock Co., II-13-1978, 1 nymph. Knox Co., Knoxville, VII-6-1977, 1 male. Marshall Co., Duck R., 2.5 mi. SE Chapel Hill, IV-1-1978, 1 nymph. Maury Co., Duck R., Sowell Ford, V-21-1979, 2 exuviae. Pickett Co., Wolf R., confl. Town Br., V-7-1980, 1 reared female and exuviae. Scott Co., Big South Fork Cumberland R. at Station Camp Cr., XI-1-1977, 2 nymphs.

Helocordulia selysii (Hagen)

LOUISIANA, Natchitoches Parish, Little Bayou Pierre, III-23-1974, 1 male and 1 female. Same location, IV-5-1974, 3 males and 1 female. SOUTH CAROLINA, Aiken Co., Upper Three Runs Cr., Co. Rd. 114, V-19-1980, 1 nymph.

Helocordulia uhleri (Selys)

TENNESSEE, Blount Co., Reed Cr., 4 mi. W Walland, V-14-1976, 1 nymph. Little R., US Hwy. 411, IV-7-1978, 1 nymph. Little R., III-30-1979, 1 nymph. Coffee Co., Duck R., confl. Bashaw Cr., III-23-1978, 1 nymph. Hardin Co., Barbwood Br. of Hatley Cr., 2.5 mi. NNE Counce, V-16-1978, 2 nymphs. Sevier Co., small stream at Kodak, TN Hwy. 66, II-20-1973, 1 reared male and exuviae, emerged III-15-1973.

VITA

Jerry Louton was born in Lake Charles, Louisiana on August 5, 1944 and attended public schools nearby. After serving in the U.S. Army he attended and graduated from McNeese State University. He received a Master of Science from Louisiana State University and thereafter was employed in various environmental consulting positions. He is a member of The American Association for the Advancement of Science, The Society of Systematic Zoology, The North American Benthological Society, The Ecological Society of America, The Biological Society of Washington and Phi Kappa Phi.