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MACROMIA ILLINOIENSIS AND *GEORGINA*: A STUDY OF THEIR VARIATION AND APPARENT SUBSPECIFIC RELATIONSHIP (ODONATA: CORDULIIDAE)

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ABSTRACT

A study of more than 1200 male specimens of ***Macromia illinoiensis*** and ***georgina*** reveals extensive intergradation between the two taxa, which should now be regarded as subspecies of the senior species ***illinoiensis***. The antehumeral stripe shows the relationships less clearly because this variable tends to be less continuous than structural characters (length of hamule tip and relative length of mesotibial keel). ***Illinoiensis*** s. str. occupies the area north and west of the Appalachians and north of northern Alabama, and also occurs in Iowa and South Dakota. ***Georgina*** is a coastal plain and Mississippi Valley subspecies. There is structural intergradation along a fairly narrow zone between the two east of the Mississippi River, but this zone broadens west of the Mississippi to include the entire Ozark Plateau and adjacent upland regions of eastern Kansas. ***Georgina*** has a long antehumeral stripe in the east, but a much shorter stripe to the west. Larvae are diagnosed and compared to those of ***alleghaniensis*** and ***margarita***.

INTRODUCTION

In the eastern United States (west to South Dakota, Iowa, Kansas, Oklahoma, and Texas, and including Quebec and Ontario) the most commonly encountered ***Macromia*** are ***illinoiensis*** Walsh and ***georgina*** (Selys). These taxa are separated both by geographic distribution and larval ecology: ***illinoiensis*** is characteristic of sandy to rocky northern small streams to medium-sized rivers, and ***georgina*** is found in sluggish and muddy medium streams to large rivers in the coastal plain from New Jersey to Texas and in the Mississippi embayment north to Illinois and Missouri. For more than a century odonatists have confidently identified these two species over the broad core areas of their ranges.

During recent studies of specimens of ***Macromia*** from certain localities, however, both KT and TD concluded that the most commonly used criteria for differentiating the species ***illinoiensis*** and ***georgina*** did not always yield reliable discrimination of the two species. Accordingly, a study of a long series of these taxa was undertaken to clarify the distinction between them. Eventually more than 1200 male specimens were examined, and for most of these the hamule tip, mesotibial keel, and antehumeral stripe were measured, and the character of the pale rings on abdominal segments 2 and 7 was recorded. One of the early results of the study was to show that color pattern characters were less reliable for discrimination than structural characters. A further result was that structural criteria for the differentiation of these two taxa were less clear than we had anticipated.

This study aims to clarify the status of ***illinoiensis*** and ***georgina***. East of Alabama and north of southern Illinois the distinction between ***georgina*** and ***illinoiensis*** is generally fairly clear. As the study progressed it became apparent that many specimens geographically intermediate between the core areas for these two taxa, and many trans-Mississippi specimens, could not be reliably named as species, even by structural characters. Thus, we have concluded that the two "species" are not genetically distinct, and that they should at best be considered subspecies. Because this study does not seek to validate either species *per se*, no examination of type material was undertaken. Indeed, such an examination would have been pointless: the characters which we have found to discriminate the two species are available only in male specimens, and the types of both ***illinoiensis*** and ***georgina*** are females. Also, the type of ***illinoiensis*** is lost. The status of the taxon ***australensis*** Williamson is not germane to the present study. We agree with earlier authors that it is a synonym of ***georgina*** and study of the type would serve no purpose for this study.

At an early stage in the study, numerous specimens were borrowed with labels "***georgina*** X

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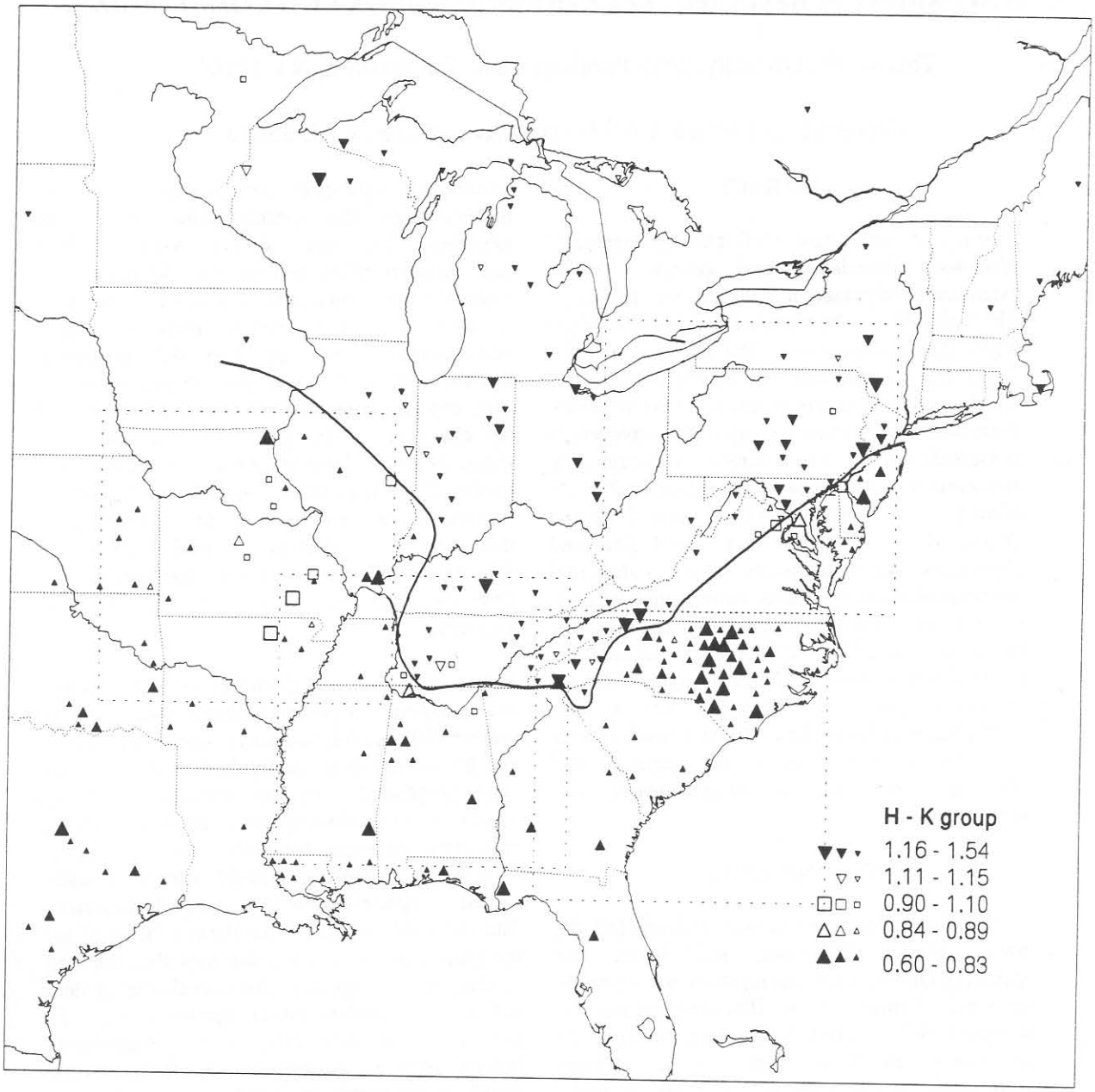

Fig. 1 Map of the eastern United States, showing the area studied. Individual counties are shown as symbols, which represent values of the H - K index (explained below). The size of the symbols show the number of male specimens from each county: small (1 to 3 specimens); intermediate (4 - 9 specimens); large (10 or more specimens). The symbols represent county averages only. The black triangles represent typical ***georgina***, inverted triangles represent typical ***illinoiensis*** , and the open symbols represent various intermediate populations. The dashed line boxes show areas enlarged in figures 2 to 5. The solid line represents the approximate southern boundary of structurally typical ***illinoiensis*** specimens.

alleghaniensis" (or a similar designation) implying hybrids between these two taxa. These specimens caused us to enlarge our investigation to ***alleghaniensis*** Williamson and its rare sibling species ***margarita***. We are confident that both ***alleghaniensis*** and ***margarita*** Westfall are distinct species but that their diagnosis must be based on structural characters, and not color pattern. A surprising result was that most ***alleghaniensis*** specimens commonly have a short pale antehumeral stripe, contrary to the original description and to subsequent keys to species in the genus.

The area of this study is shown in figure 1, which covers the United States east of the Great Plains. We examined specimens from more than 250 counties of the United States, and two in Canada. The "core" area of concentration is approximately south of central Michigan, west of eastern New York, north of the Gulf of Mexico, and east of Nebraska. Figures 2, 3, 4, and 5 show enlargements of four sub areas , with counties of extensive collections named. A black line in several figures separates the conventionally understood ***illinoiensis*** populations to the north from ***georgina*** and mixed populations to the south. The symbols are explained later in the text.

HISTORICAL

We have included the original descriptions of ***illinoiensis*** (Walsh, 1862) and ***georgina*** (de Selys, 1878; translation) in Appendix I, along with excerpts from the original descriptions of ***australensis*** and ***alleghaniensis*** and accompanying descriptive comments on ***georgina*** and ***illinoiensis*** (Williamson 1909).

Walsh (1862) described ***Macromia illinoiensis*** on the basis of a female from Illinois. The type female is reported to be missing, probably as a result of the great fire of Chicago which destroyed many valuable collections, including Walsh's.

Subsequently de Selys (1878) described ***Epophthalmia georgina*** from a female from Georgia. The assignment of this species (along with ***taeniolata***) to the genus ***Epophthalmia*** was based on the crossing of the triangles in both wings. It is not clear why de Selys did not include ***illinoiensis*** in ***Epophthalmia***; Walsh had stated that three of four triangles of his female were crossed.

Calvert (1893) demurred from de Selys's generic assignment, stating,

> "The absence or presence of cross-veins in the triangle, by which de Selys has separated ***Macromia*** and ***Epophthalmia***, is not a constant character. It remains to be seen whether ***georgina*** and ***illinoiensis*** are otherwise distinct, and whether both are variations of ***taeniolata***."

His judgment as to generic placement has prevailed, and subsequent authors have reserved ***Epophthalmia*** for Asiatic species separated from ***Macromia*** on a variety of structural characters. Calvert's remark about the distinctness of ***georgina*** and ***illinoiensis*** could have been prescient, but he provided no further information (nor did he do so in subsequent papers.).

Martin (1906), provided the first monographic treatment of the family; however, he followed de Selys completely on the generic assignments, and provided no new information or insights on the species themselves.

Williamson (1909) undertook an extensive revision of North American species of ***Macromia.*** He began by rejecting the assignment of North American species to ***Epophthalmia.*** Also in this paper he described a new species, ***australensis***, which was similar to ***georgina*** but had a shorter antehumeral stripe, reserving the name ***georgina*** for specimens from North Carolina with longer stripes. He also described the new species ***alleghaniensis***, which had been confused in the past with ***illinoiensis***. Williamson provided no key in this seminal paper, but his emphasis on color characters was followed by subsequent authors. In his discussion of ***illinoiensis***, he noted that a Pennsylvania specimen had the mesotibial keels shorter than normal, which is the first note of structural variation in the species.

Williamson remained deeply interested in ***Macromia*** throughout his entire life. in 1929 and 1930 he went to central Missouri, where he devoted considerable attention to this genus. He collected more than 200 ***illinoiensis*** from Carter County, Missouri, alone and wrote (1932),

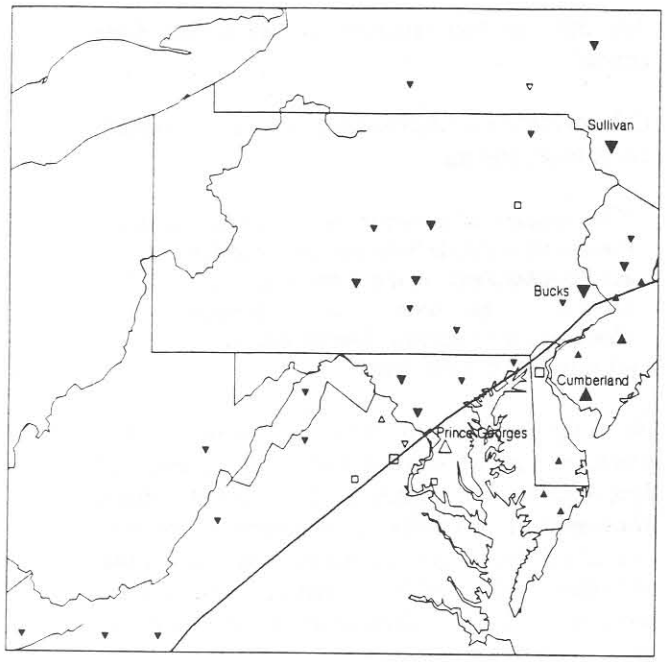

Fig. 2. Map of Pennsylvania to Virginia, showing several named counties, and a line separating ***illinoiensis*** from ***georgina***.

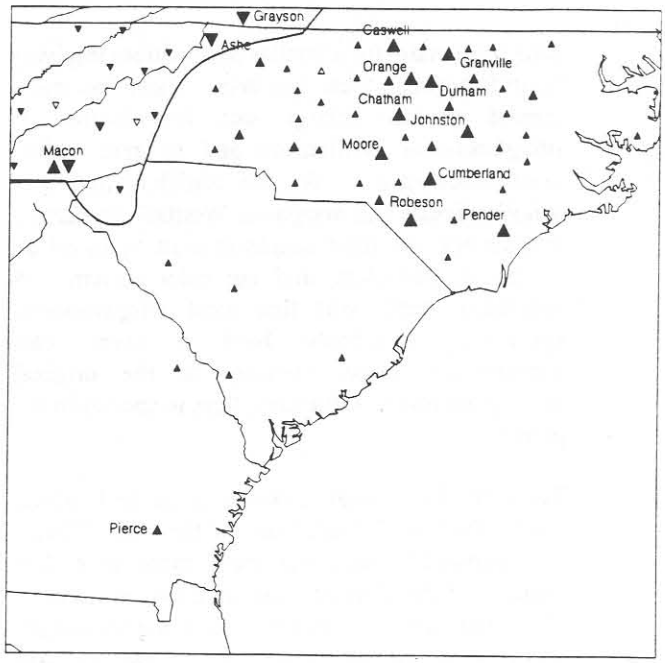

Fig. 3. Map of North Carolina to Georgia, as for Fig. 2. Note that there are two symbols for Macon Co. NC, representing two populations (discussed below).

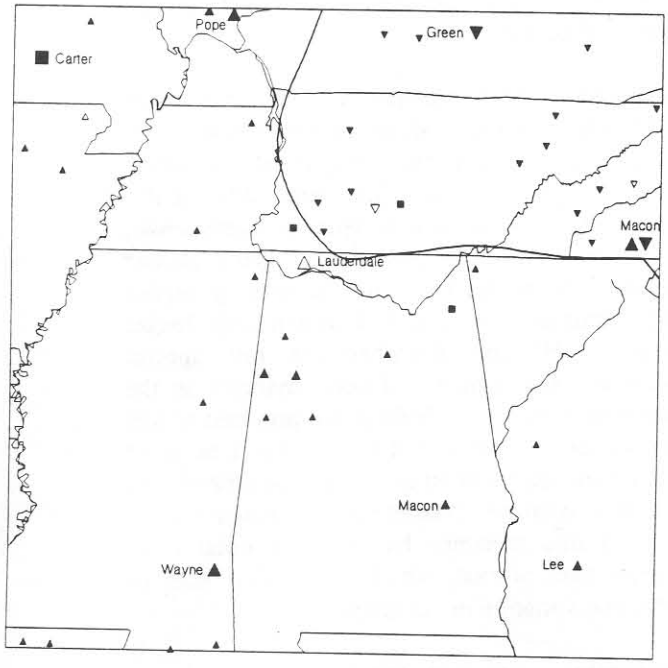

Fig. 4. Map of Tennessee., Alabama, and Mississippi, as for Fig. 2.

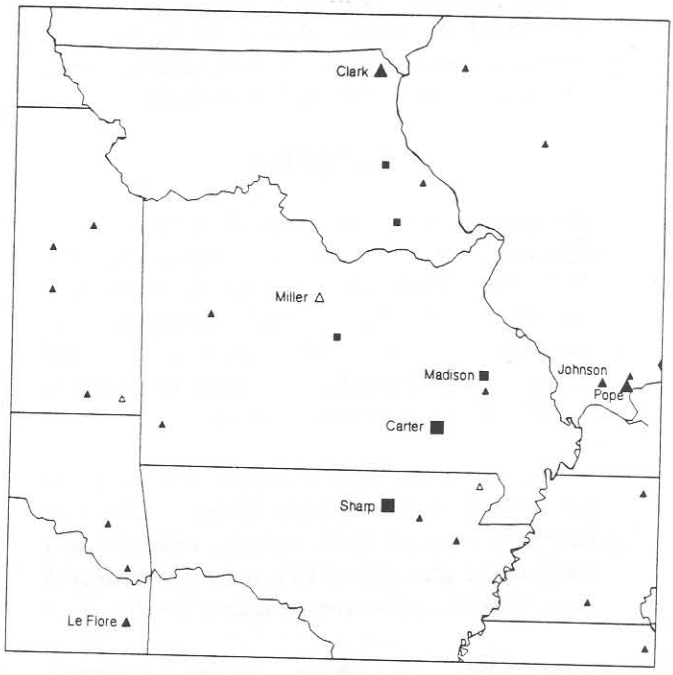

Fig. 5. Map of Missouri and adjacent states, as for Fig. 2. Le Flore Co. OK is the type locality for ***M. australensis***.

"This fine series of specimens has been retained intact pending a thorough study. If only one species is represented, there is greater individual variation than has ever been detected or suspected in any North American species of *Macromia*. If two or more species are included, their detection and definition will require some high powers of discrimination. If the species represents a hybrid population, analysis will be difficult and may prove to be impossible."

These words have turned out to be prophetic, and this study attempts to pursue Williamson's concerns. We have examined a long series of the specimens remaining in the Michigan collection. (Curiously, handwritten labels on the triangles are either "*illinoiensis*" or "*taeniolata*"). Williamson continued to collect ***Macromia*** vigorously.

Needham and Heywood (1929) provided the first key to North American ***Macromia*** that included all the species recognized today. They keyed ***australensis*** incorrectly (transverse ring on 2 interrupted dorsally) but described the character correctly in the text. They also characterized ***alleghaniensis*** as having no pale antehumeral stripes, following Williamson in this regard and unintentionally perpetuating confusion which has persisted to the present. (These authors evidently did not count the yellow spot on the katepisternum as part of an antehumeral stripe.)

Walker (1937), implicitly rejecting Needham and Heywood's earlier key, provided another key to the species of ***Macromia.*** In this paper he synonymized ***australensis,*** stating,

"I have omitted Williamson' species ***australensis*** as this name seems to be a synonym of ***georgina*** . Mrs. Gloyd drew my attention to this point in a letter and, after an examination of the specimens in the Williamson collection, I am convinced she is right. Williamson noted the similarity of ***M. georgina*** to his new species ***australensis*** in all but the length of the antehumeral stripe but did not suggest that the two forms might be conspecific. In the absence of differential characters other than the length of the antehumeral stripe we are not justified in retaining ***australensis*** as a separate species."

Walker presented a key to the North American species based mainly on color pattern, as had become customary for all North American workers. Walker also described a new western species, ***rickeri***, which is now regarded as the dark, northern form of the widespread western species ***magnifica***.

Montgomery (1941) recorded ***georgina*** from Indiana, but was not satisfied with the specific diagnosis:

"These specimens agree rather well with Williamson's description of the species (1908) [sic], except that two of them have the antehumeral stripe shorter than described. However, a careful study of the North American species of this genus is much needed and final classification of individual specimens, especially in the ***illinoiensis*** - ***georgina*** group must await such monographic work."

Westfall (1947) described the new species ***margarita*** from North Carolina. This species, which he had previously confused with ***alleghaniensis***, remains an elusive species in western North Carolina to central Tennessee. An important innovation in this paper is the first use of illustrations of the distinctive hamule tips of the species. Even though they were reproduced at very small size, the illustrations show that, for the species ***illinoiensis***, ***georgina***, ***alleghaniensis***, and ***margarita,*** their distinctive character is quite evident .

Needham and Westfall (1955) presented a key to ***Macromia*** which was based entirely on color pattern and wing venation. Their treatment was similar to that of Needham and Heywood (1929), except that additional taxa were discussed.

The larvae of ***Macromia*** were first diagnosed by Needham and Westfall (1955). Our results agree with this study in that the dorsal abdominal spines of ***illinoiensis*** have a peculiar flattened appearance ("bird's head"). We disagree in that ***georgina*** shares this character and has similar lateral abdominal spines, thus vitiating their key for these species. We discuss the larval characters in Appendix II.

The two species were mentioned and even described in additional papers (e.g., Garman, 1927). However no additional descriptive information has been published. Some authors have cited ***australensis*** (e.g., Kennedy, 1917 for Kansas; Bird, 1932, for Oklahoma). Byers (1930) did not list any species for Florida but described ***illinoiensis***, thinking it the most probable to occur in that state. Numerous additional citations of

illinoiensis and ***georgina*** in other lists are not noteworthy.

In summary, although these species have been well known and widely collected for a century, there has been no critical study of the characters by which they are differentiated, in spite of at least two suggestions that such a study was needed, and several authors have questioned their identity.

Because color characters were presented by each author, it was possible to diagnose both male and female specimens. Some structural characters were also presented (the mesotibial keel by Williamson, 1909; hamule tip, Westfall, 1947), but none for females.

Very likely the widespread satisfaction with the status of the two species results from the fact that problematical specimens are found in a fairly narrow region where the ranges of the two taxa overlap and in the less thoroughly collected region west of the Mississippi River.

THE BIOLOGICAL SPECIES CONCEPT AND *MACROMIA*

Initially we did not consider that the problem of ***Macromia*** would impinge on the larger and more diffuse problem of the species concept. However, our results lead us down paths that are little traveled in the world of Odonata, and we feel compelled to comment on the species concept as it applies in this case.

We accept the biological species concept, as outlined and discussed by Mayr (1982), whose definition is

> "A species is a reproductive community of populations (reproductively isolated from other species) that occupies a specific niche in nature." This concept is parallel to, but not identical with the typological species, which is defined by a holotype specimen, against which other putative members of the same species are compared, and either included or excluded, depending largely on the whim and instinct of the person doing the comparison."

The concept of reproductive isolation is largely theoretical. In the entire animal kingdom it has been put to a rigorous test in only a handful of cases. The best we can do to prove or disprove this necessary concept is to search for hybrid specimens, or present circumstantial or morphological evidence that is best interpreted as proof for or against this concept. In the present case we believe that our morphological results strongly suggest a lack of reproductive isolation. From this we conclude that designation of ***illinoiensis*** and ***georgina*** as distinct species is untenable, and we suggest that the two taxa be regarded as subspecies.

METHODS

Because it became apparent at an early stage in our investigation that structural characters alone would be reliable for the separation of the two species, and because we could find no structural character for the females, we studied only male specimens. We examined and measured more than 1200 male specimens of ***illinoiensis*** and ***georgina,*** mainly for the hamule and mesotibial keel. An additional few dozen provided color pattern information but could not be used for structural analysis because the hamule tips had been broken off, presumably during mating. Because we obtained a very generous loan of the extensive material collected by R. Duncan Cuyler, our collection consists of 539 specimens from North Carolina, with 174 of these from Orange Co. alone! Apart from the North Carolina material, our specimens are distributed unevenly, but with a fairly thorough distribution in the zone of apparent overlap of the two species.

The receipt of specimens troublesomely labeled "***georgina*** X ***alleghaniensis***" prompted us to examine ***alleghaniensis*** also in order to satisfy ourselves of the status of this species. Accordingly, we examined 196 male specimens, with 177 from North Carolina, and 154 of these from Orange Co. Of the 196, we measured 107 hamules and mesotibial keels, and tabulated color characters for the remainder. Although our material of this species was very highly concentrated in North Carolina, we feel that our material is representative of the species over its entire range.

In the early stages of our investigation we measured and tabulated several characters which we later dropped from the study. Some of these proved to be too variable because of varied preservation or because they varied with age of the individual (e.g., brown vs. black ground color of the abdomen). Some apparently varied for other reasons (e.g., shape of male superior abdominal appendage, which may be inflated during ecdysis

to different degrees, leaving it fatter and straighter, or thinner and more curved). One character (development of band on 7th abdominal segment) was not measured initially but became important in the distinction of ***georgina*** and ***alleghaniensis***, and was tabulated systematically for the latter part of the investigation (more than 1000 specimens of ***illinoiensis*** and ***georgina*** and all ***alleghaniensis***). For some specimens, assessment of color characters was not meaningful, either because of teneral development, or because poor preservation resulted in an unclear delineation of the pale areas.

Specimens were removed from transparent envelopes or triangles for all observations; pinned specimens were not used because of the difficulty of examining the hamules in profile. Many specimens were covered with dried mold spores and/or droppings and dried, molted larval instars of dermestid beetles. The specimens were often partially cleaned off by a light application of compressed gas from a small can used by photographers to remove dust from film surfaces or camera lenses. In some cases the specimens were lightly and gently painted with reagent-grade acetone to remove mold spores and to increase the color contrast of badly preserved specimens.

Antehumeral Stripe. - We retain this term, but the stripe is more anterior and dorsal than for most other odonates to which this term is applied. In this report its measurement includes the extension to the katepisternum (mesinfraepisternum), but does not include any further extension to the fore coxa (fig. 6). In most specimens of ***alleghaniensis*** the katepisternum is pale, and the extension of the pale color to the mesepisternum is minimal; these, in the narrow sense lack an antehumeral stripe. The measurement of this stripe is subjective, because the posterior (upper) end of the stripe tapers and fades into the dark color of the mesepisternum. Also, the dark (ground) color of this sclerite is often sufficiently pale (in teneral and badly preserved specimens, and for many western specimens), that the stripe lacks contrast. In many specimens of both ***alleghaniensis*** and ***georgina*** (especially, in the latter taxon, northern specimens) the portion of the stripe on the mesepisternum is thin and even divided into two spots.

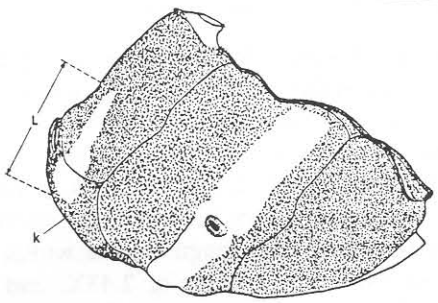

Fig 6. Sketch of pterothorax, showing the antehumeral stripe. "k" is the katepisternum.

In reviewing our character tabulations, we found that one of us (TD) had systematically recorded, for many specimens with no apparent antehumeral stripe, a tiny stripe on the katepisternum which was not recorded by the other (KT). The KT specimens with a measured antehumeral stripe were later adjusted to remove the difference. KT specimens with no antehumeral stripe were not adjusted. Our category of minimally marked forms includes specimens with the stripe 0 to 0.5 mm, which merges our independent observations into the same group, and also recognizes the unavoidable ambiguity in identifying the tiny pale mark on the katepisternum for many ***illinoiensis*** specimens.

Pale ring on abdominal segment 2. - This ring was tabulated as being broadly connected, narrowly connected, or clearly divided both laterally and dorsally. In many poorly preserved specimens the stripe is badly faded, especially on the auricle, and difficult to categorize.

Pale ring on abdominal segment 7. - This ring was tabulated as being completely broken laterally, broadly connected laterally, or barely connected laterally. However, the connection is often unclear because of poor preservation.

Color of pterostigma. - The color of the ventral surface of the fore wing pterostigma was recorded, scaling from 2 (black) to 9 (yellow). The pterostigma varies in color with the age of the specimens, being pale in teneral specimens and darkening with age.

Color of costa. - The anterior groove in the fore wing costa was examined in the portion adjacent to the pterostigma and coded as for the pterostigma. We found that many older specimens have this pale groove darkened, evidently as part of the aging process.

Length of mid-tibial and mesotibial keel. - The tibia and keel were measured with an eyepiece micrometer and recorded to the nearest 0.01 mm. The measurement includes the curved proximal portion articulating with the femur, and the measurement cannot be done accurately on an extended leg. The vast majority of specimens examined had this middle leg flexed tightly against the thorax, making the observation of the keel very difficult. In these specimens the leg was gently opened slightly with an inserted insect pin to measure the keel. We report the keel measurement as a percent of the mesotibial keel length (fig. 7).

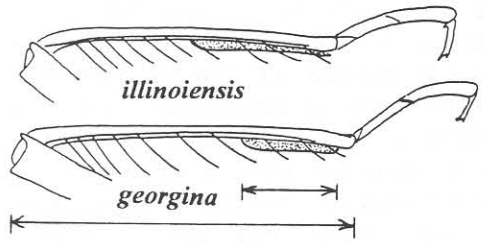

Fig. 7. Sketch of mesotibiae of ***illinoiensis*** and ***georgina***, showing the keel and defining the lengths used for tabulation.

Length of hamule tip. - The hamule tip was measured from the small pointed proximal hook to the tip, along the shaft of the tip, which is commonly slightly inclined to the main shaft (fig. 8). In ***alleghaniensis*** the tip is most commonly tapered, but in ***illinoiensis*** and ***georgina*** the shaft of the tip is generally parallel sided or even narrowed centrally. Many ***illinoiensis*** specimens have a tip which is almost as short as that of ***alleghaniensis***; however, the tip of the latter is generally stouter and more massive than that of ***illinoiensis*** (figs. 9, 10). In many older specimens the tiny proximal hooks, and in several cases the entire hamule tips, were broken off, evidently as a result of mating.

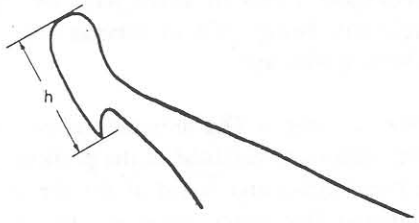

Fig. 8. Sketch of the hamule tip, showing the measured length.

We report the hamule tip as a length in mm. We did not normalize this measurement, as we did for

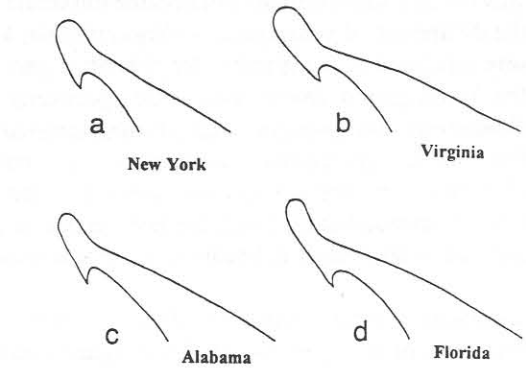

Fig. 9. Sketch of hamule tips of four specimens of ***illinoiensis*** sspp., from New York, Florida, Virginia, and Alabama, showing variation.

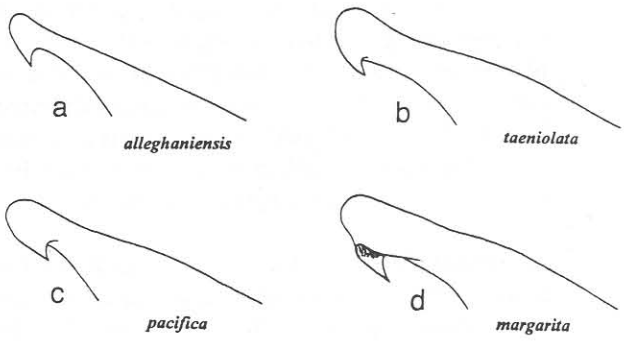

Fig. 10. Sketch of hamule tips of ***alleghaniensis*** (AL), ***taeniolata*** (FL), ***pacifica*** (MO), and ***margarita*** (NC).

the mesotibial keel. Normalization could have been done by dividing the hamule tip length by a general size character, such as length of the abdomen. Many specimens had part of the abdomen missing, and in many more it so curled that the length could not be accurately recorded. Because the hamule tip length varied within the entire population by a factor of 2.43X, and the abdomen lengths varied by a factor of only 1.4X, we feel that normalization would not have changed our result. In local populations (counties), the observed range of hamule tip length was far more variable than the fairly narrow range of abdomen lengths.

The H - K (Hamule - Keel) Index. One of the most obvious results was that the length of the hamule

tip and the relative length of the mesotibial keel were inversely related (fig. 11). In order to have a single numerical value for ranking the specimens, we developed the hamule - keel index, which is a simple numerical expression of this negative correlation. The hamule - keel index (H - K index) is defined as

$$\text{H - K index} = 1 + \left(\frac{0.35 - \text{ham}}{0.25}\right) - \left(\frac{55 - \text{keel}}{40}\right)$$

where **ham** is the length of the hamule tip, in mm; and **keel** is the relative length of the mesotibial keel, measured against the full length of the tibia. The **H - K index** varies in our specimens from 0.22 to 1.59. Specimens with 0.22 to 0.85 are referable to ***georgina***; 1.10 to 1.59 to ***illinoiensis***, and specimens in the intervening range 0.85 - 1.10 are considered intermediate.

Length of abdomen. - This was measured along the ventral surface from the base of segment 1 to the tips of the appendages.

Length of hind wing. - This was measured from the basal membrane to the tip. Doubtless different workers will measure the wing somewhat differently.

RESULTS

The structural part of the analysis was undertaken using two characters: the percentage of the length of the mesotibia occupied by the keel, and the length of the hamule tip. The first of these is independent of overall size, but the latter character will vary with overall size. As discussed above, we feel that the use of a normalized and non-normalized character is valid in this analysis, especially for local (county) populations.

The main result was that for both structural and color-pattern characters, the specimens fell broadly into two groups, which correspond to ***illinoiensis*** and ***georgina***. We summarize this distribution with a plot of hamule tip length vs. the percent length of the mesotibial keel (fig. 11). This figure shows, however, that there is a continuum between the taxa, requiring either a highly refined criterion, or the introduction of a wholly new character, for the separation of the taxa. A further result of this plot is that it unambiguously separates ***alleghaniensis*** from both ***georgina*** and ***illinoiensis***.

Figure 12 shows the same plot, but with the data shown as abundance of specimens, expressed as contours. The continuum between two major popluations is obvious. Superimposed lines show values of the H - K index superimposed along a line of variation of this index roughly bisecting the data set.

Figure 13 is a histogram of the frequency of H - K values, and can be thought of as a cross section of figure 12 along the long diagonal line. In this figure the specimens are further divided into three classes, depending on the length of the antehumeral stripe. The division into marked (***georgina***) and unmarked (***illinoiensis***) specimens is fairly good, but many specimens with no antehumeral stripe appear structurally to belong to ***georgina***.

The definition of ***alleghaniensis*** and its separation from ***illinoiensis*** **and** ***georgina***

According to published keys, ***alleghaniensis*** is separated from ***georgina*** by its lack of an antehumeral stripe and from ***illinoiensis*** by its pale ring around segment 7. Our study shows that ***alleghaniensis*** is defined most meaningfully by the combination of a short hamule tip and short mesotibial keel (Fig. 11), with a characteristic thick, tapered profile (Fig. 10A); a pale ring aroung segment 7, and the pale ring on segment 2 connected laterally and narrowly divided dorsally.

The published statement that ***alleghaniensis*** lacks an antehumeral stripe is clearly negated by our results. Figure 14 shows that relatively few specimens of ***alleghaniensis*** completely lack this stripe, and that many have a stripe up to 3.5 mm long, or even longer. Although most of our specimens of ***alleghaniensis*** are from North Carolina, we have found several specimens from other states with this stripe.

As noted previously, numerous specimens which we examined had been labeled as possible hybrids between ***alleghaniensis*** and ***georgina***. In almost all cases, these specimens were ***alleghaniensis*** specimens with a pale antehumeral stripe. A few ***alleghaniensis*** had longer tibial keels, which might represent merely the end of the range of variation of this character. Less than one percent

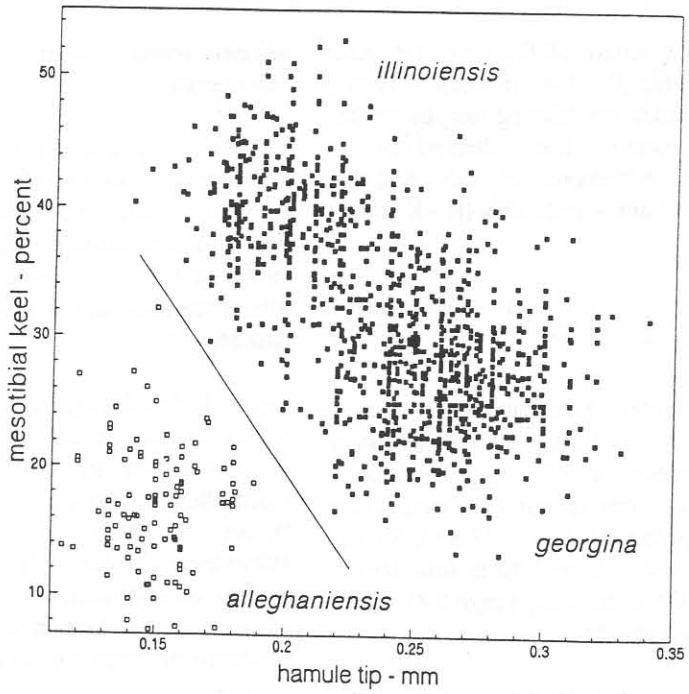

Fig. 11. Graph showing the length of the hamule tip (mm) vs. the length of the mesotibial keel (percent). Note the continuity between ***georgina*** and ***illinoiensis*** and the distinction between these taxa and ***alleghaniensis.*** A very few of the specimens close to this line may be hybrid specimens.

Macromia illinoiensis sspp.

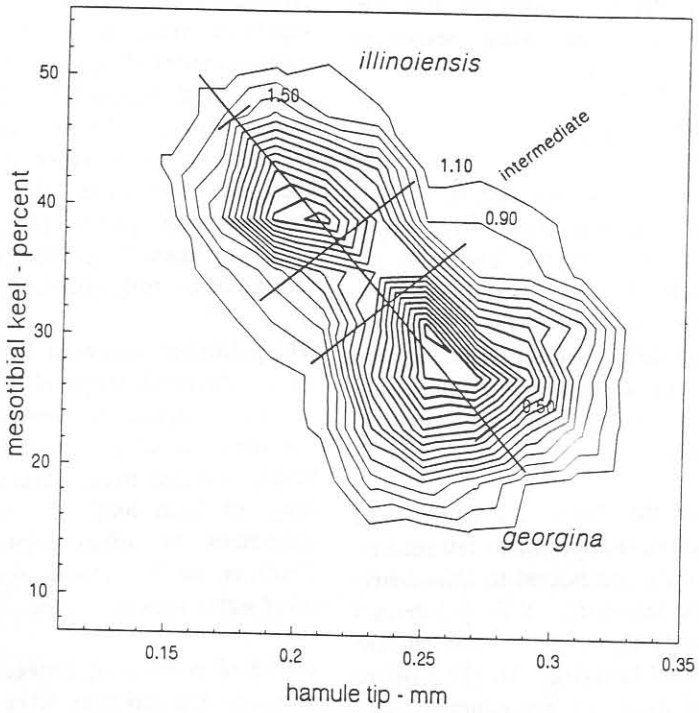

Fig. 12. Graph showing the length of the hamule tip (mm) vs. the length of the mesotibial keel (percent), expressed as abundance of data shown by contours. Data have been gridded into cells measuring 2 per cent keel by .01 mm hamule tip. Lines labeled 0.50, 0.90, 1.10, and 1.50 are values of the H - K index. Contours center on areas of maximum number of specimens, corresponding to typical ***illinoiensis*** and ***georgina***, as defined structurally.

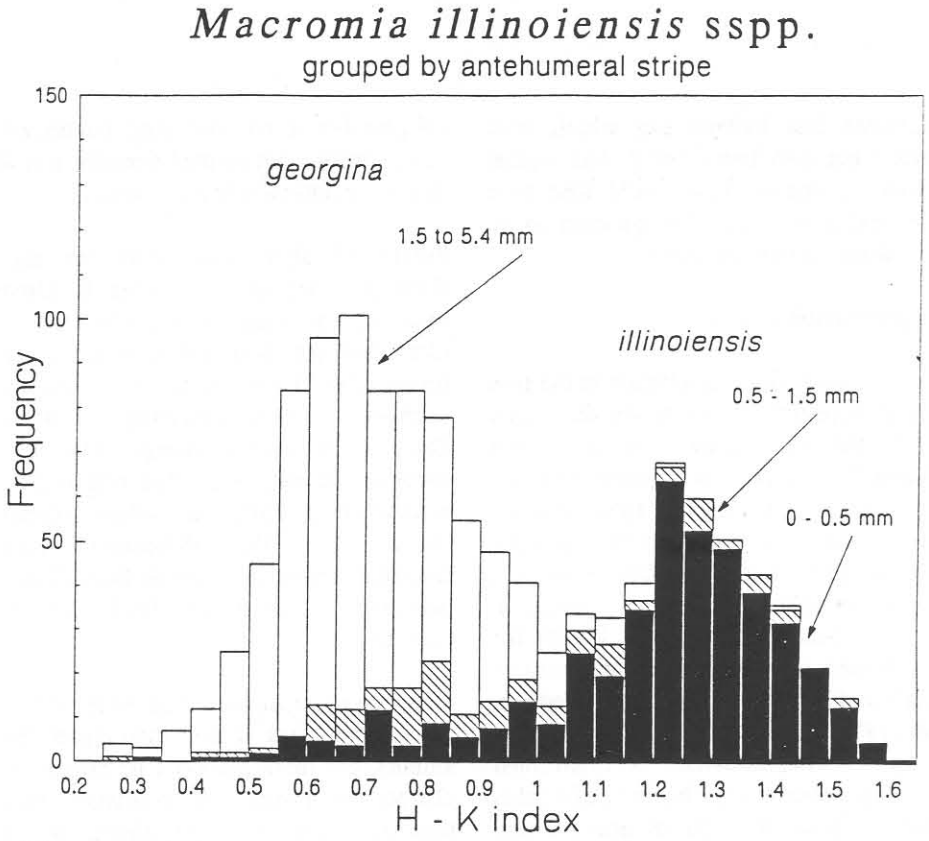

Fig. 13. Histogram of H - K index for the ***georgina*** and ***illinoiensis*** populations, with the specimens grouped into three degrees of development of the antehumeral stripe : (0 to 0.5 mm; 0.5 to 1.5 mm; > 1.5 mm). This histogram shows clearly the bimodal distribution of the structural index and also shows vividly the overlap of specimens lacking an antehumeral stripe to the field of ***georgina.***

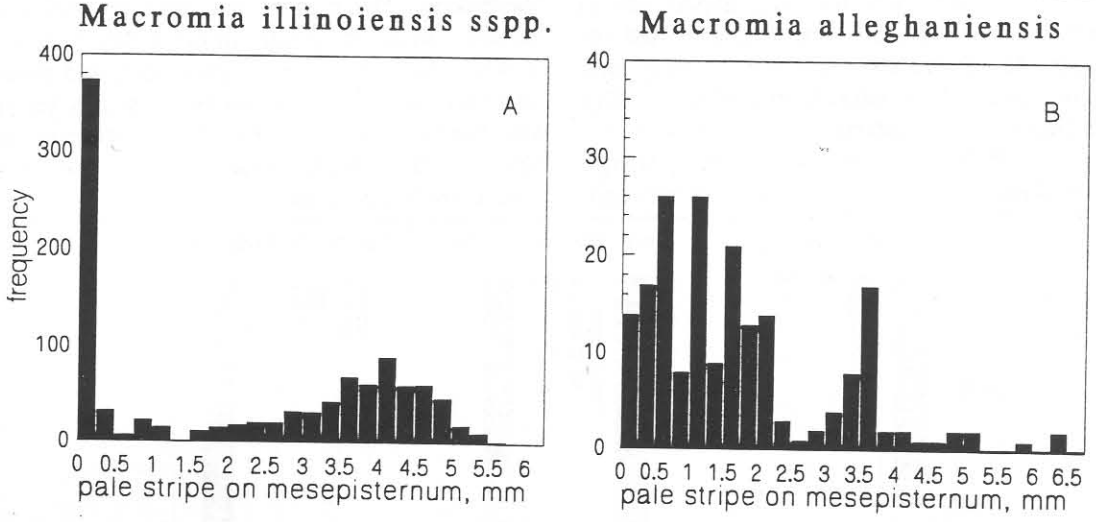

Fig. 14. Histograms showing length of antehumeral stripe for (A) ***illinoiensis*** (*sensu lato*, including ***georgina***) and (B) ***alleghaniensis*** specimens. Note that a substantial proportion of ***alleghaniensis*** specimens have a pale mark or stripe on the mesepisternum and/or katepisternum, and that very few specimens completely lack this pale mark.

of the specimens had hamule tips which were slightly longer, but also less tapered than typical ***alleghaniensis***. Some of these might well have been hybrid specimens, and the question as to genuine hybridization remains open.

Other color pattern differences

Pale rings on the abdomen. In addition to the pale stripe of the mesepisternum, there are diagnostic characters in the pale marks on abdominal segments 2 and 7. The ring on segment 2 is very commonly used to diagnose the three species. According to published keys, the ring on segment 2 is broken dorsally and laterally for ***illinoiensis***, and complete for ***alleghaniensis*** and ***georgina***. According to Needham and Heywood (1929) the ring on 2 is broken for ***illinoiensis*** and entire in ***alleghaniensis*** and ***georgina.*** However, Needham and Westfall (1955) changed this character to note that the ring of ***alleghaniensis*** is interrupted middorsally. Our investigation has amplified this result. Figure 15 shows three bar diagrams which show the percent of specimens with entire or interrupted rings, for three H - K classes of ***illinoiensis*** and ***georgina*** and for ***alleghaniensis***. These show clearly that the ***illinoiensis***-like forms (H - K > 1.10) have the ring almost always interrupted both dorsally and laterally, and the ***georgina***-like forms (H - K < 0.90) usually have the ring entire (80% laterally and 90% dorsally). The specimens with intermediate values of the H - K index (0.90 - 1.10) are correspondingly intermediate in the color character. Interestingly, ***alleghaniensis*** has the ring connected laterally, like ***georgina***, but divided dorsally, like ***illinoiensis*** (but more narrowly in most cases).

Figure 15 also shows data for the ring on abdominal segment 7. This is almost always interrupted in ***illinoiensis***-like forms and ***georgina***-like forms, but connected in more than 10% of the former and 20% of the latter. Williamson (1910), incorrectly stated (referring to a few North Carolina specimens of ***georgina***) that the ring on 7 encircles the abdomen. The ring is almost always connected laterally in ***alleghaniensis***. The character of the abdominal rings clearly discriminates ***alleghaniensis*** from ***illinoiensis*** and ***georgina***, but does not clearly discriminate the latter taxa.

Costa and pterostigma. The color of the costa and pterostigma has been mentioned by various authors, but there has been no attempt to use this character for species discrimination. Walsh (1862) mentions that the pterostigma of ***illinoiensis*** (female) is black, and de Selys (1878) describes that of ***georgina*** as brownish yellow. Both describe the costa as yellow. Williamson (1909) says that the costa of ***illinoiensis*** is dark, ***australensis*** dark colored, and ***georgina*** yellowish brown (narrowing apically in the male). Needham and Heywood (1929) describe the costa and stigma in both species (and ***australensis***) as simply brown, but Needham and Westfall (1955) discriminate between a black pterostigma in mature ***illinoiensis*** and yellow in ***georgina***.

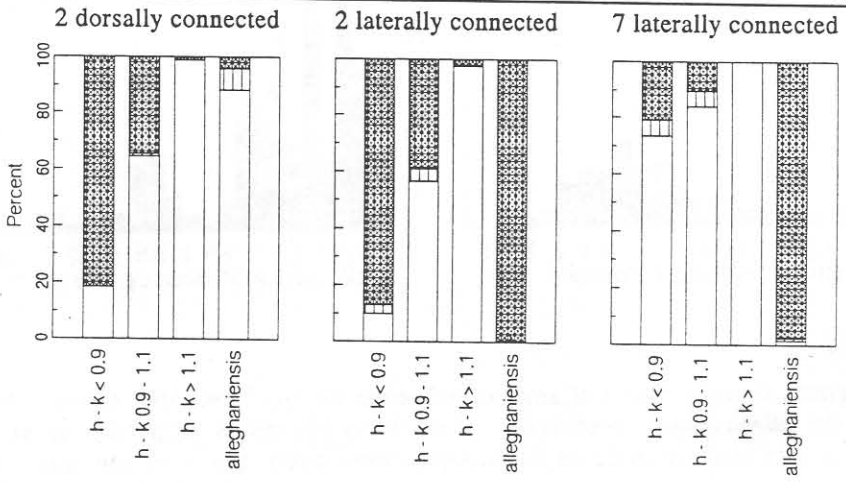

Fig. 15. Three bar graphs showing percentage of specimens with connected (dark pattern), ambiguous (lined pattern) , or broken rings (clear pattern) on abdominal segments 2 (dorsally and laterally) and 7 (laterally). Specimens are grouped into three H - K categories (< 0.9; 0.9 - 1.1 = intermediate and mixed; > 1.1) and also ***alleghaniensis***. Note that all ***alleghaniensis*** specimens have the ring on 2 dorsally broken, and also that a substantial minority of specimens of ***georgina*** have the stripe on 7 laterally connected.

In our experience the costa and stigma are both generally dark in eastern but paler in western ***illinoiensis***. The costa and stigma is paler in ***georgina***. but highly variable through the range. In both core areas, and in intermediate populations, the costa tends to be paler than the pterostigma in the western forms. A further problem is that both the costa and pterostigma appear to darken considerably during the life of the individual, making its almost useless for taxonomic discrimination.

In our specimens the color of the pterostigma seems to be very dark (brown to black) in those forms which are structurally ***illinoiensis*** (Fig. 16).

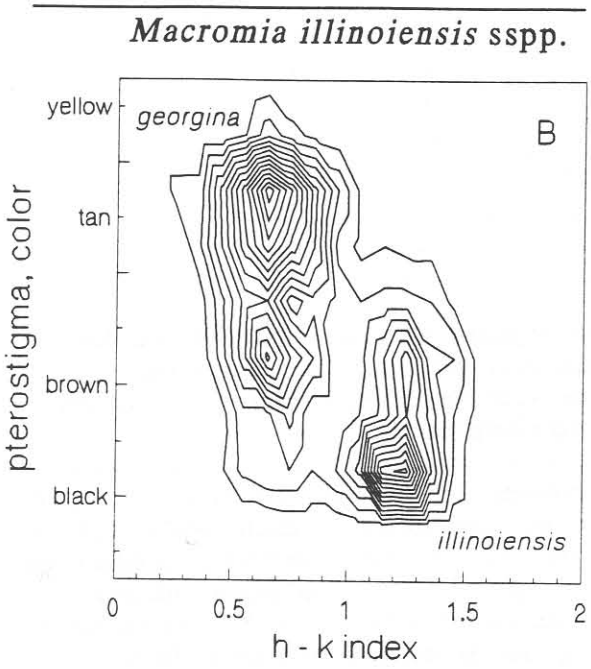

Fig. 16. Graph showing pterostigma color vs. H - K index, showing abundance of data within gridded cells (as for Fig. 12), with a contour interval of 3 specimens per grid cell. Note that structural ***georgina*** specimens generally have a paler pterostigma than ***illinoiensis***, but there is considerable range in the color.

The ***georgina***-like forms tend to have a pale pterostigma, ranging from brown to yellow. Many specimens have a distinct reddish to orange tinge, but we can find no consistency in its distribution.

The costa is variable in color along its length. We examined the portion adjacent to the pterostigma, and generally found that is was pale (brown to yellow) in ***georgina*** and dark in ***illinoiensis***. In ***georgina*** the costa is darker than the pterostigma in more than half the specimens, with the exception of the southwestern forms (Williamson's ***australensis***), in which most specimens have a paler costa. In ***illinoiensis*** the costa is almost always darker, except that northwestern specimens have nearly half the specimens with a paler costa. In the structurally intermediate specimens, the western groups tend to have the costa paler than for the eastern groups. The relative color of the costa and pterostigma seems to correlate with longitude rather than with structural character.

Antehumeral stripe. The original and, in fact, only published criterion for the separation of ***illinoiensis*** and ***georgina*** is the presence or absence of the antehumeral stripe. Our measurements of this stripe show that it is highly variable, but there is an apparent gap in the histogram between 0.5 and 1.5 mm (Fig. 14). Most of the specimens having a stripe longer than 1.5 mm are referable to ***georgina***, but we do not recommend the use of this stripe to discriminate between ***georgina*** and ***illinoiensis***. The problem is that many specimens with no stripe have the structural characteristics of ***georgina***. A much smaller number of specimens with the stripe have the structural characteristics of ***illinoiensis***.

Another serious problem with the antehumeral stripe criterion for the separation of the taxa is that our results indicate that this character is discrete, instead of varying continuously (fig. 17). In a number of county populations, especially those in which the H - K index indicated an intermediate character, the specimens were divided bimodally into those lacking the antehumeral stripe and those possessing it. In this sense the antehumeral stripe varies more or less like eye color in humans rather than skin color.

There is some geographic variation in the length of the antehumeral stripe in ***georgina***, as shown by figure 18. In the northern coastal-plain population (New Jersey to Maryland, Fig. 18A) the stripe is most commonly about 3.5 mm long. Also, and not shown here, the stripe of northern specimens is thin and tends to be discontinuous. In North Carolina (Fig. 18B) to Louisiana (fig. 18C), the mode is closer to 4.5 - 5 mm, and in Texas, Oklahoma, and Arkansas (Fig. 18D), is slightly more than 3 mm. Williamson (1909) compared North Carolina and Oklahoma specimens when he

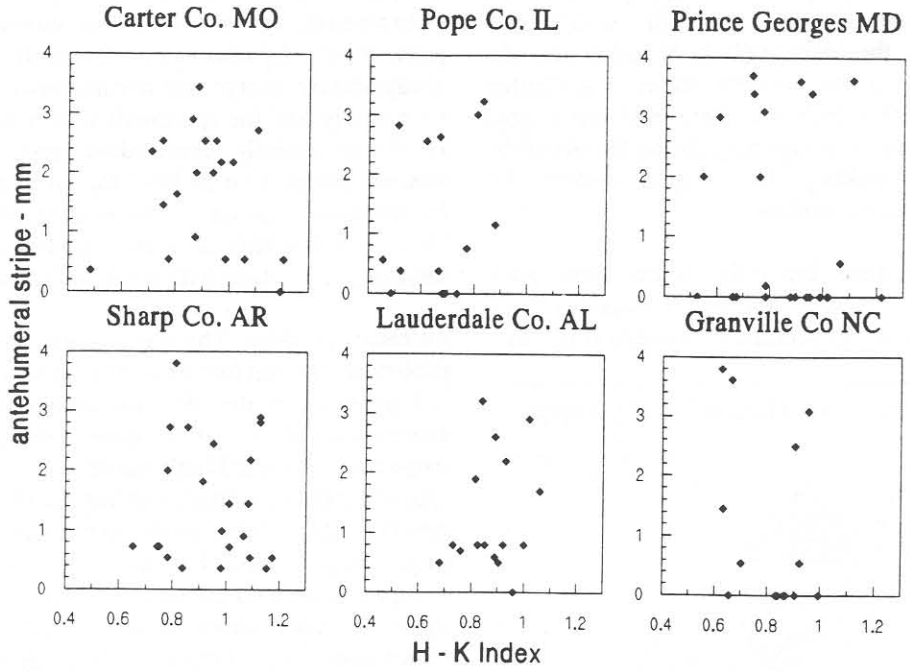

Fig. 17. Graphs plotting the length of the antehumeral stripe against the value of the H-K index for six counties. Although the H - K index is a smoothly continuous variable in these populations, the antehumeral stripe is clearly discontinuous in four of the six counties (Pope, Granville, Prince Georges, and Lauderdale), and somewhat less clearly in two others (Sharp, Carter).

described the latter as ***australensis***. The difference in the length of the stripe is evident, but both populations are part of a larger variable continuum. Specimens from the trans-Mississippi region (Missouri, Kansas, northern Arkansas, and also southern Illinois, figs. 18E, F) tend to be somewhat bimodal overall, but rarely have a stripe longer than 3 mm. As discussed below, the length of the stripe is not correlated with structural criteria. These populations have created considerable difficulty for odonatists, starting with Wiliamson (1932).

Structural Variability Within ***georgina*** and ***illinoiensis*** Populations

The variability of the two taxa in their entire range requires an examination of the homogeneity of local populations. Williamson (1932) had commented on the high degree of individual variation" of his Carter Co., MO, specimens, and this variability must be addressed. For this purpose, we examined specimens from single counties. For 22 counties (tab. 1) there were 11 or more male specimens taken, which was the arbitrarily set minimum number of specimens for testing the homogeneity of local populations. The standard deviations of the H - K index, the hamule tip, and the mesotibial keel are all fairly uniform within single counties. We find that specimens from a single county are fairly homogeneous structurally, contrary to Williamson's (1932) statement, which was evidently heavily influenced by variations in the antehumeral stripe.

In order to emphasize local homogeneity, we illustrate for twelve individual counties the values of the keel and hamule tip. Figure 19 shows three counties with purely ***illinoiensis*** populations: Green Co., KY; Sullivan Co., NY; and Grayson Co., VA. In addition, we show Macon Co., NC, which is the only county which we have found to have a structurally bimodal population, which we discuss below. The colors of the symbols also show the extent of the antehumeral stripe; the structurally typical ***illinoiensis*** specimens

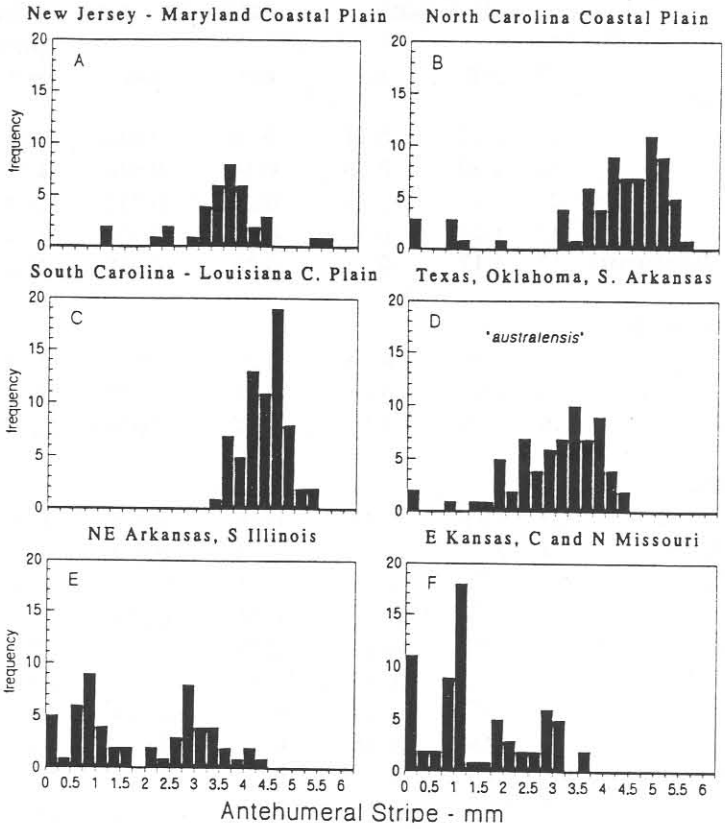

Fig. 18. Histograms showing length of the antehumeral stripe for six geographic areas: (A) northern coastal plain (New Jersey to Maryland (entirely ***georgina***); (B) ***georgina*** from North Carolina coastal plain (entirely ***georgina***); (C) southeastern coastal plain (South Carolina to Louisiana (entirely ***georgina***); and (D) Texas, Oklahoma, and Arkansas (entirely ***georgina***; this group is what Williamson (1909) considered "***australensis***"); (E) northeastern Arkansas, southern Illinois, southeastern Missouri, and western Tennessee (mainly Mississippi River valley) (mainly ***georgina*** with a few structurally intermediate forms); (F) eastern Kansas, and central and northern Missouri (mainly structurally intermediate types and several ***georgina***). Note that the southwestern populations of ***georgina*** have a shorter stripe than populations east of the Mississippi.

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uniformly lack this stripe in the counties shown, and, indeed, in nearly all specimens studied. Note that the three ***illinoiensis*** populations are almost entirely on the high side of the H - K value of 1.1, which we have arbitrarily taken as the higher limit for the structurally intermediate condition.

Figure 20 shows the corresponding hamule and keel values for four counties with purely ***georgina*** populations. Again this diagram emphasizes the relatively few values of H - K greater than 0.9 for typical "end-member" populations. Note that several of the Orange Co. NC, specimens lack a pale antehumeral stripe, and that most Clark Co. MO, specimens have this stripe only poorly developed.

Figure 21 shows the hamule and keel values for four counties with structurally intermediate specimens. Both Lauderdale Co. AL, and Prince Georges Co. MD, have average structural values slightly on the ***georgina*** side of the purely intermediate character, but they overlap strongly with the intermediate field. Note that the development of the antehumeral stripe is not

correlated with structural characters. The values of the two western populations, Sharp Co. AR, and Carter Co. MO, also have their structural average well within the intermediate range, and again have the antehumeral stripe uncorrelated with structural characters. All of these counties presented serious problems to the collectors who originally

		H - K index		hamule tip - mm		mesotibial keel - percent	
	N	avg	std	avg	std	avg	std
M. i. illinoiensis							
VA Grayson	24	1.31	0.11	0.19	0.016	42.1	3.53
NY Sullivan	16	1.30	0.10	0.19	0.016	42.2	3.22
KY Green	23	1.26	0.13	0.20	0.013	40.5	4.48
WI Price	13	1.25	0.12	0.20	0.020	41.4	3.09
NC Macon ***illinoiensis***	51	1.17	0.12	0.20	0.019	38.2	4.19
struct. intermediate							
AR Sharp	23	0.95	0.15	0.23	0.021	33.3	4.58
MO Carter	20	0.91	0.17	0.24	0.020	33.6	5.65
AL Lauderdale	16	0.88	0.10	0.24	0.025	32.7	2.36
M. i. georgina							
MD Prince Georges	25	0.84	0.18	0.26	0.024	33.6	5.94
NC Granville	14	0.81	0.12	0.23	0.015	28.7	4.37
NJ Cumberland	24	0.76	0.13	0.25	0.017	29.4	4.47
MO Clark	24	0.75	0.12	0.24	0.024	28.0	3.16
NC Chatham	11	0.72	0.12	0.25	0.023	27.6	5.90
NC Cumberland	12	0.70	0.15	0.25	0.025	27.3	3.31
IL Pope	14	0.67	0.13	0.28	0.014	30.2	3.98
NC Orange	171	0.66	0.15	0.26	0.023	27.4	4.52
NC Durham	69	0.63	0.16	0.26	0.023	26.4	4.40
NC Pender	27	0.62	0.13	0.26	0.019	25.3	3.82
NC Macon ***georgina***	11	0.62	0.13	0.28	0.026	28.2	3.47
TX McLennan	15	0.62	0.13	0.28	0.022	28.7	3.91
MS Wayne	12	0.61	0.13	0.27	0.023	26.3	4.13
NC Robeson	14	0.59	0.12	0.26	0.022	23.7	3.22
NC Johnston	12	0.55	0.12	0.26	0.019	23.1	4.18

Table 1. Counties with more than 11 or more specimens of ***M. illinoiensis*** sspp., with averages and standard deviations of the H - K index, hamule length, and mesotibial keel percent. The Macon Co. NC, specimens have been divided into two groups, as discussed in the text.

assembled these specimens. This figure makes it evident that the populations are homogeneous but are intermediate in character between the two end-member taxa, and that color pattern variation is no more than an arbitrary criterion in these cases.

It is these structurally intermediate areas which provide the major challenge to the retention of two distinct species. Either one would conclude that the two forms are hybridizing extensively in these areas or that they are not genetically distinct. The major problem with hybridization is that it is a genetic cul-de-sac, in that the progeny are not themselves fertile. Thus, hybrids should be fairly rare in comparison to the parent species. Further, hybrids should be intermediate in their characters, and a population including hybrids should be trimodal, with modes for each of the two parents and for the intermediate hybrid. A taxonomist attempting to name specimens from any of these three areas would be unable to make a clean split into two taxa. Our conclusion is that this is not hybridization, because the intermediate populations form genetic continua and show no tendency to divide into two or three groups.

The Macon CO, NC, (Fig. 19C), forms appear to form a counter example. The bulk of the 62 specimens examined are assignable to one or the other taxon with little ambiguity, suggesting that they do not tend to interbreed (or at least, very much) in this area. A taxonomist studying this population would not hesitate to divide the specimens into two categories based on either structural or color-pattern criteria. Why is this county different from other intermediate areas?

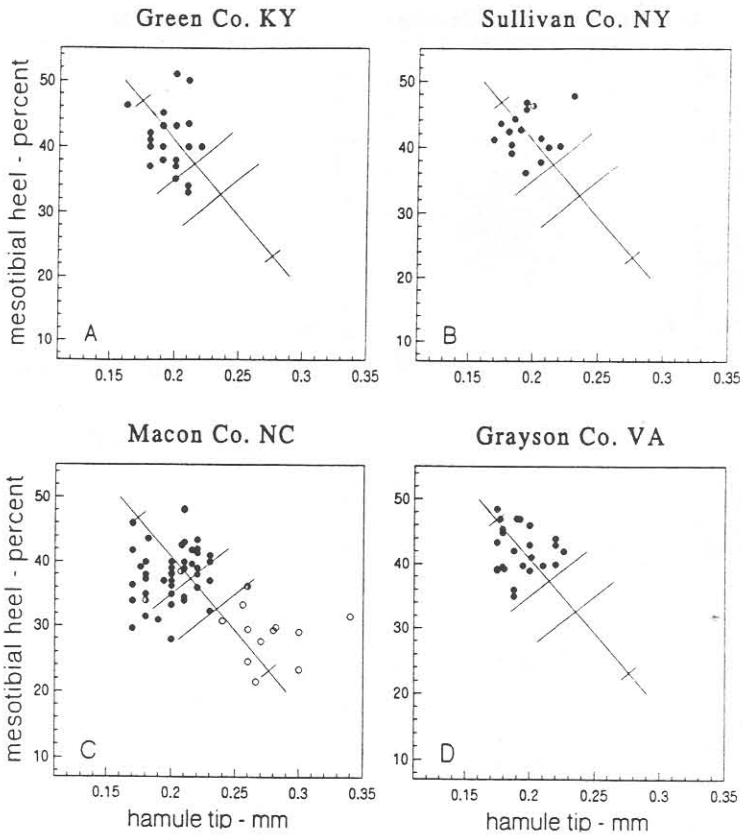

Fig. 19. Graph showing hamule tip (mm) vs mesotibial keel (percent) for four individual county populations. Shown are typical ***illinoiensis*** populations from Green Co. KY, Sullivan Co. NY, and Grayson Co. VA. The population from Macon Co. NC is bimodal. Shown for comparison are the lines from figure 12, with H-K values of 0.5, 0.9, 1.1, and 1.5 shown as cross lines. Filled circles are for antehumeral pale stripe 0 to 0.5 mm; half-filled circles for stripes 0.5 to 1.5 mm and open circles for stripes longer than 1.5 mm.

The answer may lie in the abrupt mountain-front topography of southwestern North Carolina. Whereas other intermediate areas have topography (and lotic habitats) which grade smoothly and gradually from upland to lowland, Macon County has sharply distinct topographic terranes: the relatively large Little Tennessee River at lower elevation (about 2000 feet), and an adjacent nearby mountain area with extensive stream habitats to 3000 feet and even higher. The availability of distinct upland and lowland stream habitats probably diminishes the interbreeding of the two taxa here. However, the area is too small to separate patrolling adults, which evidently range widely enough to fly together.

Variation of Structural Characters Along Geographic Lines: Four Sections

Figure 22 shows the location of four rectangular areas with data which were used to construct cross-sections from the inland (***illinoiensis***) to coastal (***georgina***) areas. For these areas, cross sections parallel to the long axis of the rectangle are plotted. In these sections, values of the H - K index are plotted against the distance along the line, which extend from an inner (***illinoiensis*** zone) to an outer (***georgina*** or intermediate) zone. The data points are symbols indicating the length of the antehumeral stripe, as for figures 19 to 21.

Figure 23 shows the structural variation (H - K index) poltted against geographic position for specimens from eastern Tennessee and adjacent Kentucky across Macon Co., NC and extending to coastal North and South Carolina. Figure 24 shows a similar cross section from south-central Pennsylvania to eastern Maryland. Note again the gradual change of the H - K index with geographic

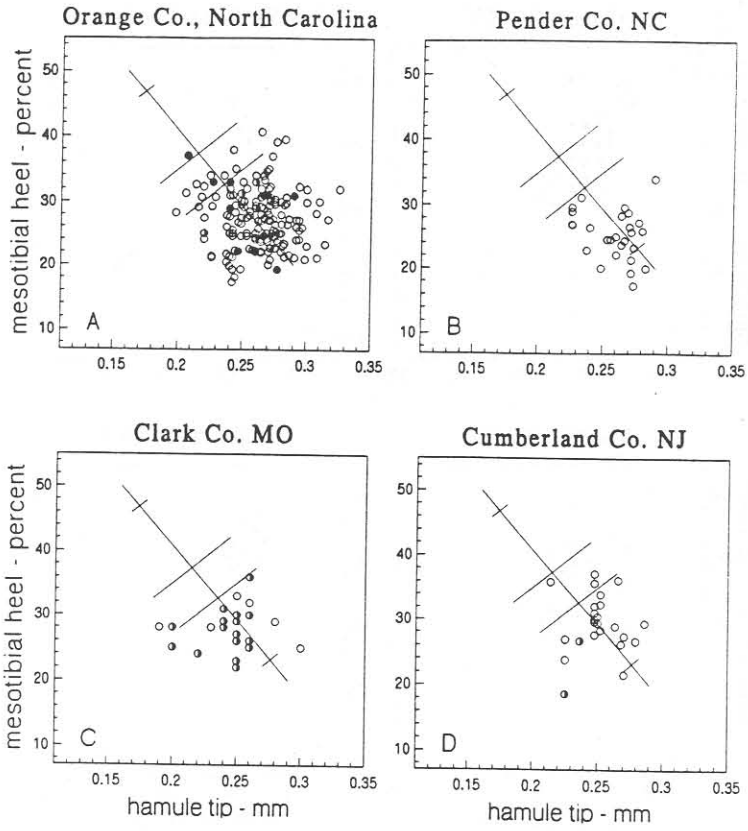

Fig. 20. Graph showing hamule tip (mm) vs. mesotibial keel (percent) for four individual county populations of structurally typical ***georgina***. Shown are populations from Orange Co. NC, Pender Co. NC, Cumberland Co. NJ, and Clark Co. MO. Symbols as for figure 19.

position. As for the preceding figure, a regression for the ***georgina*** area has not been plotted. Figure 25 shows a cross section from central Kentucky to eastern Louisiana. The change of the H - K index with position is evident in the ***illinoiensis*** portion of this section, but less so in the ***georgina*** area.

Figure 26 shows an east-west cross section from eastern Kansas to centray Kentucky. The Mississippi Valley specimens in this section have been given a contrasting symbol to indicate that they appear to belong to another population. The remainder of the population varies fairly smoothly over a horizontal distance of 1500 km, from a typical ***illinoiensis*** east of the Mississippi to a western structurally intermediate population in Missouri and Kansas.

The decrease in the H - K index among the ***illinoiensis*** populations as the boundary zone is approached is striking in these examples. The ***illinoiensis*** specimens of the first three sections and all specimens of the fourth have H-K indices which vary according to geographic position, showing the gradual change of the typical ***illinoiensis*** gene pool towards the bordering ***georgina*** area. Regressions within the ***georgina*** area are not shown in the first three sections, because the data were too sparse.

These cross sections show dramatically the geographic control of structural characters within these ***Macromia*** and emphasize the futility of attempting to define two species. The main reason that the antehumeral stripe is more dichotomous is that it varies discretely, instead of continuously. It is probably for this reason that this color-pattern character has been historically preferred for the definition of the two taxa.

Nature of Structurally Intermediate Areas

In isolation, any one of the specimens from a structurally intermediate area could be assigned by some criterion to one taxon or the other. In doing so, however, one would be forced to conclude that

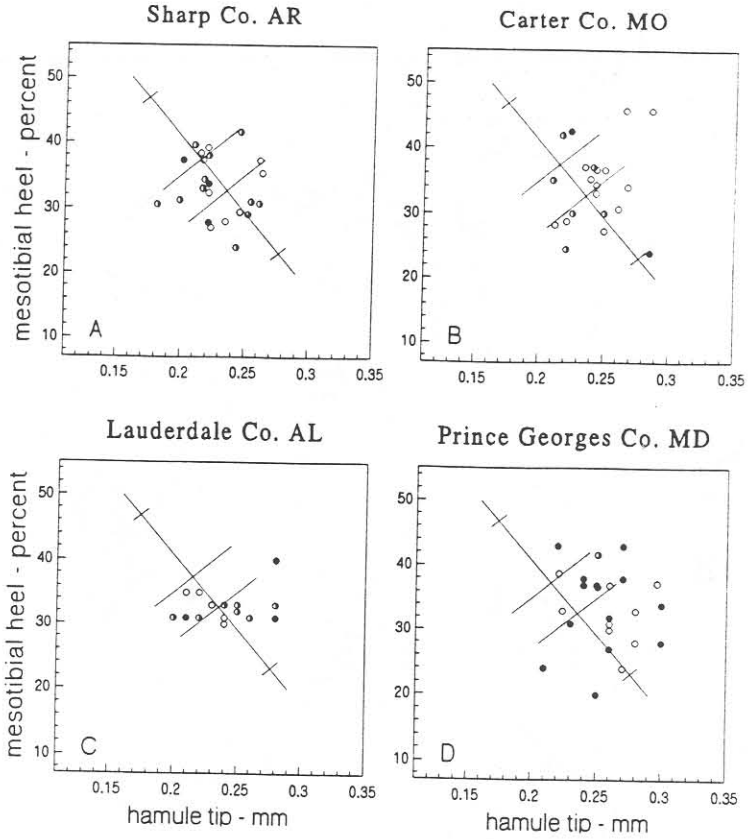

Fig. 21. Graph showing hamule tip (mm) vs. mesotibial keel (percent) for four individual county populations of structurally intermediate specimens. Shown are populations from Sharp Co. AR, Carter Co. MO, Lauderdale Co. AL, and Prince Georges Co. MD. Note both the homogeneity of the populations and the lack of correlation of the antehumeral stripe and the structural characters. Symbols as for figure 19.

the distinction between the two taxa would have to be very small and that the division would be highly artificial. An alternative would be to conclude that the two species hybridize rather freely, and that hybrids actually dominate in some intermediate areas. The main problem with this conclusion is that the very abundance of intermediate ("hybrid") forms is so large that one must conclude that the two forms are not genetically separated and that the "hybrids" are themselves fertile. Broadly fertile hybrids appear to violate the species principal, and we prefer to conclude that the two taxa are *not* genetically separated. They have apparently evolved to adapt to different environments, but they are completely capable of interbreeding. Where contrasting habitats appear within confined regions (as in Macon Co, NC) the two forms tend to interbreed very little.

Regional variations in structure and antehumeral stripe are also shown in maps in which county averages of the data have been gridded and contoured. Figure 27 shows the "core" area with superimposed contours showing the computed predicted value of the H - K index. Contouring is most realistic in areas with a dense county coverage. Note that east of the Mississippi the high H - K (***illinoiensis***) core area has a distinct border zone with the low H - K area (***georgina***). In Missouri there is, however, a broad area of structurally intermediate specimens.

The antehumeral stripe map (figure 28) is similar to the H - K map, and shows east of the Mississippi that the sharp structural boundary corresponds with a sharp antehumeral stripe boundary. West of the Mississippi, the antehumeral stripe sharp boundary is displaced to northern Arkansas. Both of these figures show that the region of the Ozarks and adjacent plateau areas (central and southern Missouri, northern Arkansas, and eastern Kansas) are structurally intermediate and with, on the average, short antehumeral stripes.

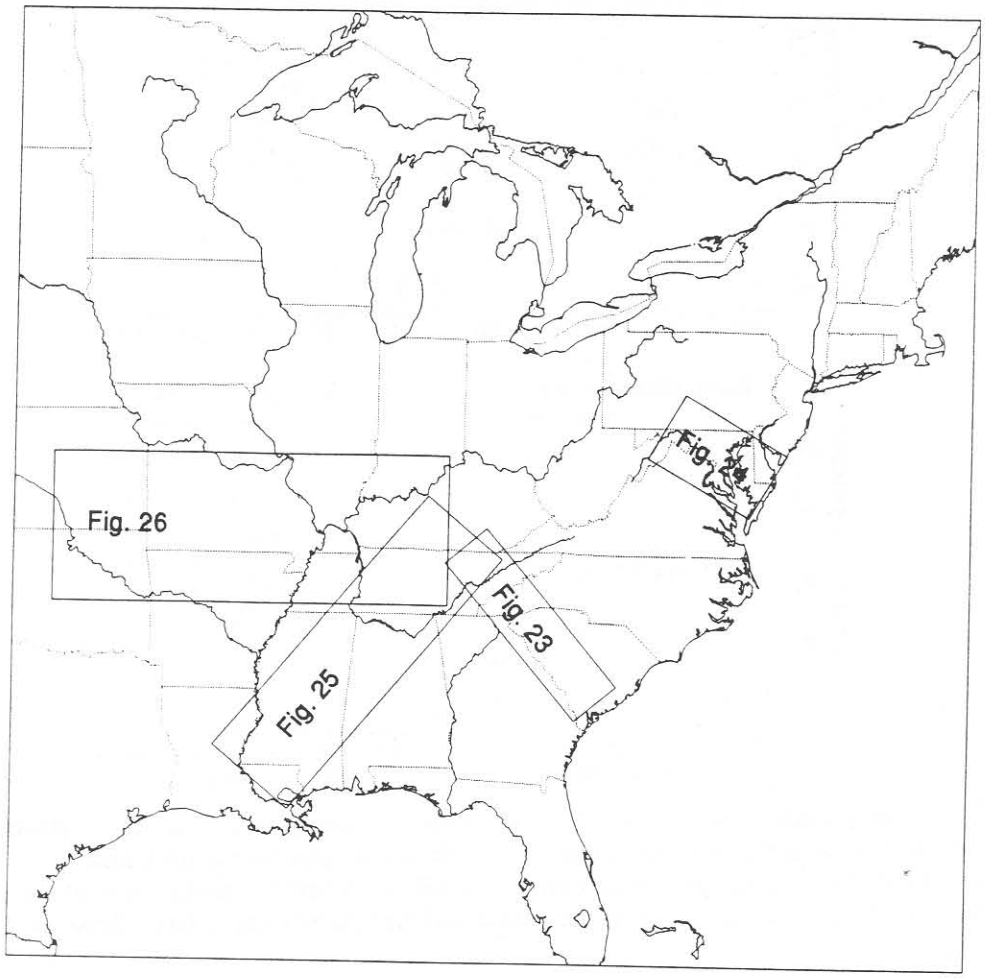

Fig. 22. Map of the eastern United States, showing locations of four lines of section, as rectangular boxes enclosing the data.

Both figures also show clearly the effect of a protrusion of ***georgina*** forms northward along the Mississippi River valley, replacing the upland ***illinoiensis*** and intermediate forms north of Arkansas and Mississippi.

Figure 29 summarizes the distribution of the two taxa. Note that the structurally intermediate area is narrow in the east but very broad in the west. Note also that the antehumeral stripe diminishes in size from east to west.

CONCLUSIONS

We find that the gradation of structural characters towards a boundary between the two taxa, and the occurrence of dominantly intermediate specimens in several boundary-zone populations shows that the two taxa cannot be reproductively isolated. Given the opportunity to interbreed (proximity of two taxa and absence of contrasting habitat types), the two taxa interbreed freely. This negates the conclusion of reproductive isolation which we feel is necessary to define the taxa as species.

On a purely practical level, the student of ***Macromia*** will face a serious problem assigning specific names in the intermediate areas. If separate species continue to be recognized, then we face the unsatisfactory situation that there is no clear distinction between these forms, or that hybrids are suspiciously abundant. It is far clearer to recognize one species, with two end-member subspecies. According to this recommended conclusion, many intermediate specimens will not be assignable to either subspecies, but will have to be named "subspecies indeterminate".

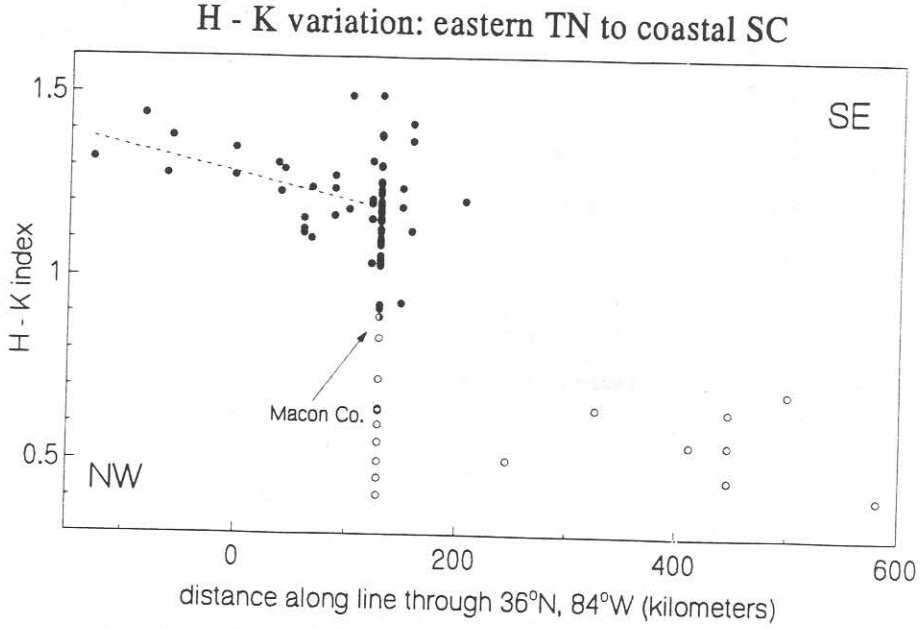

Fig. 23. Graph showing the variation of the H - K value of individual specimens in the Tennessee - South Carolina cross section located on figure 22. The symbols indicate the length of the antehumeral stripe, as for figures 19 to 21. The dashed line is the plotted regression for ***illinoiensis*** specimens in the northwestern portion of the line, but excluding the Macon Co. NC, ***illinoiensis*** specimens. The value of the correlation coefficient of this line is 0.49.

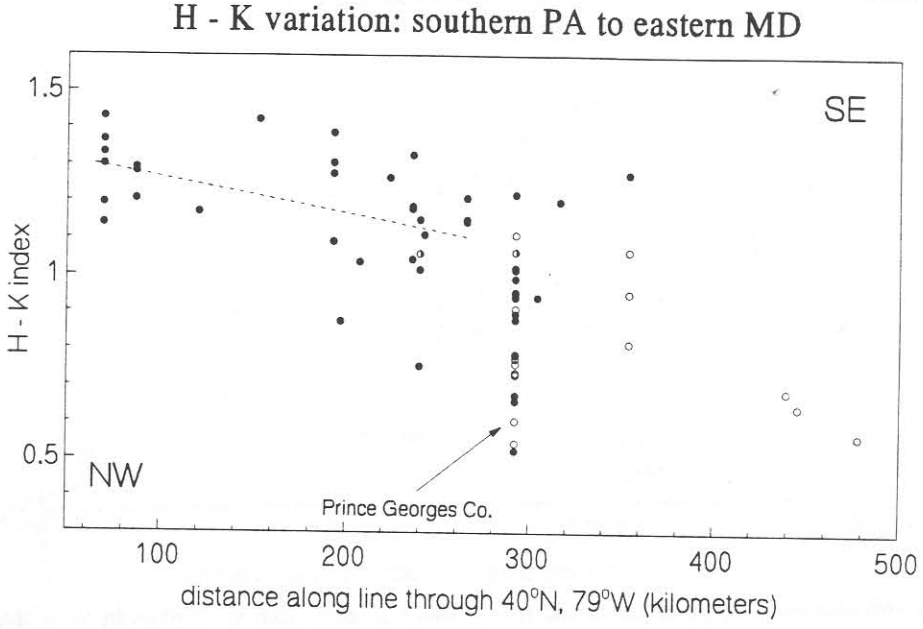

Fig. 24. Graph showing the variation of the H - K value of individual specimens in the Pennsylvania - Maryland cross section located on figure 22. The symbols indicate the length of the antehumeral stripe, as for figures 19 to 21. The dashed line is the plotted regression for ***illinoiensis*** specimens in the northwestern portion of the line, but excluding the Prince Georges Co. MD, structurally intermediate specimens. The value of the correlation coefficient of this line is 0.47.

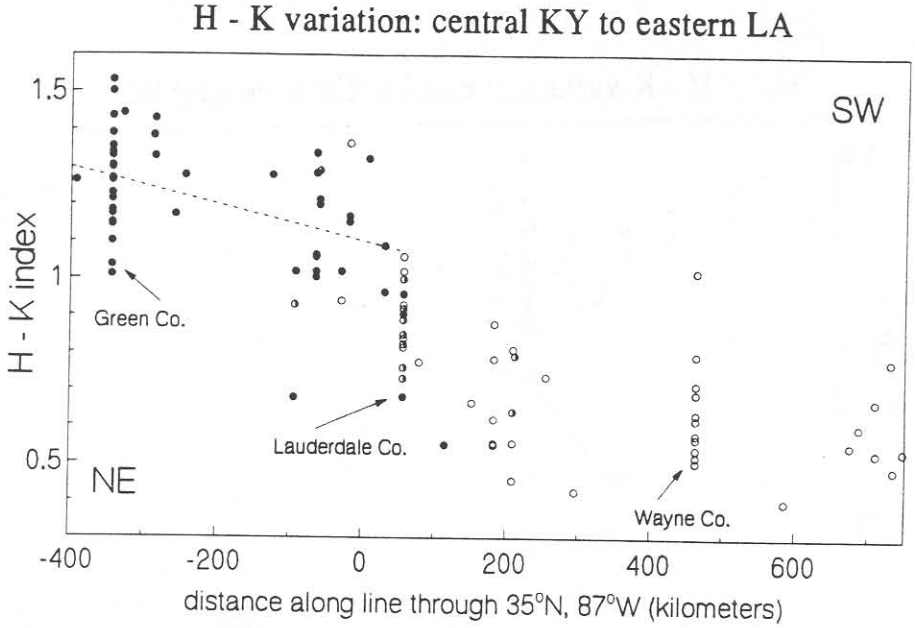

Fig. 25. Graph showing the variation of the H - K value of individual specimens in the Kentucky - Louisiana cross section located on figure 22. The symbols indicate the length of the antehumeral stripe, as for figures 19 to 21. The dashed line is the plotted regression for ***illinoiensis*** specimens in the northern portion of the line, but excluding the Lauderdale Co. AL, structurally intermediate specimens. The value of the correlation coefficient of this line is 0.43. The location of Green Co. KY, and Wayne Co. MS, specimens is also shown.

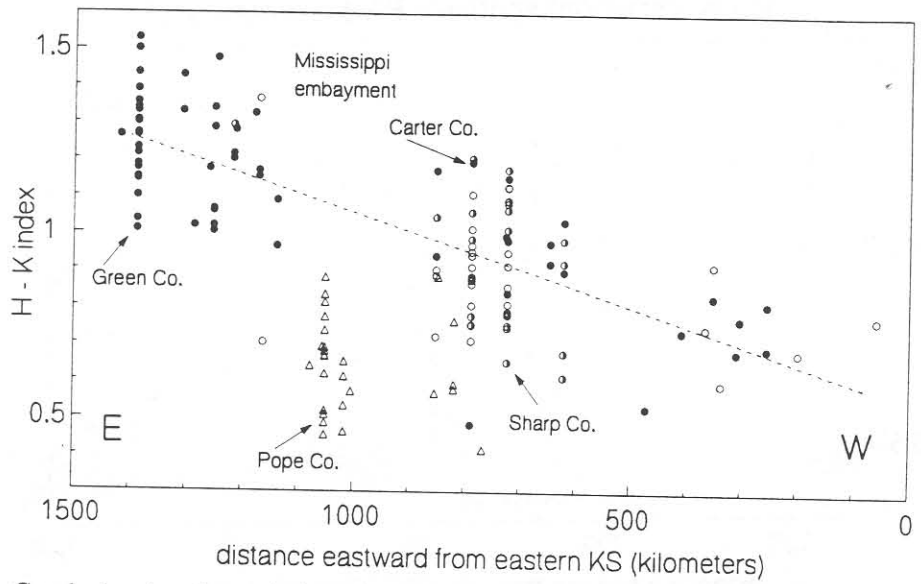

Fig. 26. Graph showing the variation of the H - K value of individual specimens in an east-west cross section from Kentucky to Kansas , as located on figure 22. The symbols indicate the length of the antehumeral stripe, as for figures 19 to 21. Specimens from the Mississippi River valley are shown as triangular symbols, which do not differentiate the extent of the antehumeral stripe. The dashed line is the plotted regression for all specimens excluding the Mississippi Valley population. The value of the correlation coefficient of this line is 0.75. The locations of Carter Co. MO, Sharp Co. AR, Pope Co. IL, and Green Co. KY , are shown. Note that west is at the right side of this diagram to maintain the position of the highest H - K specimens on the left side of the diagram.

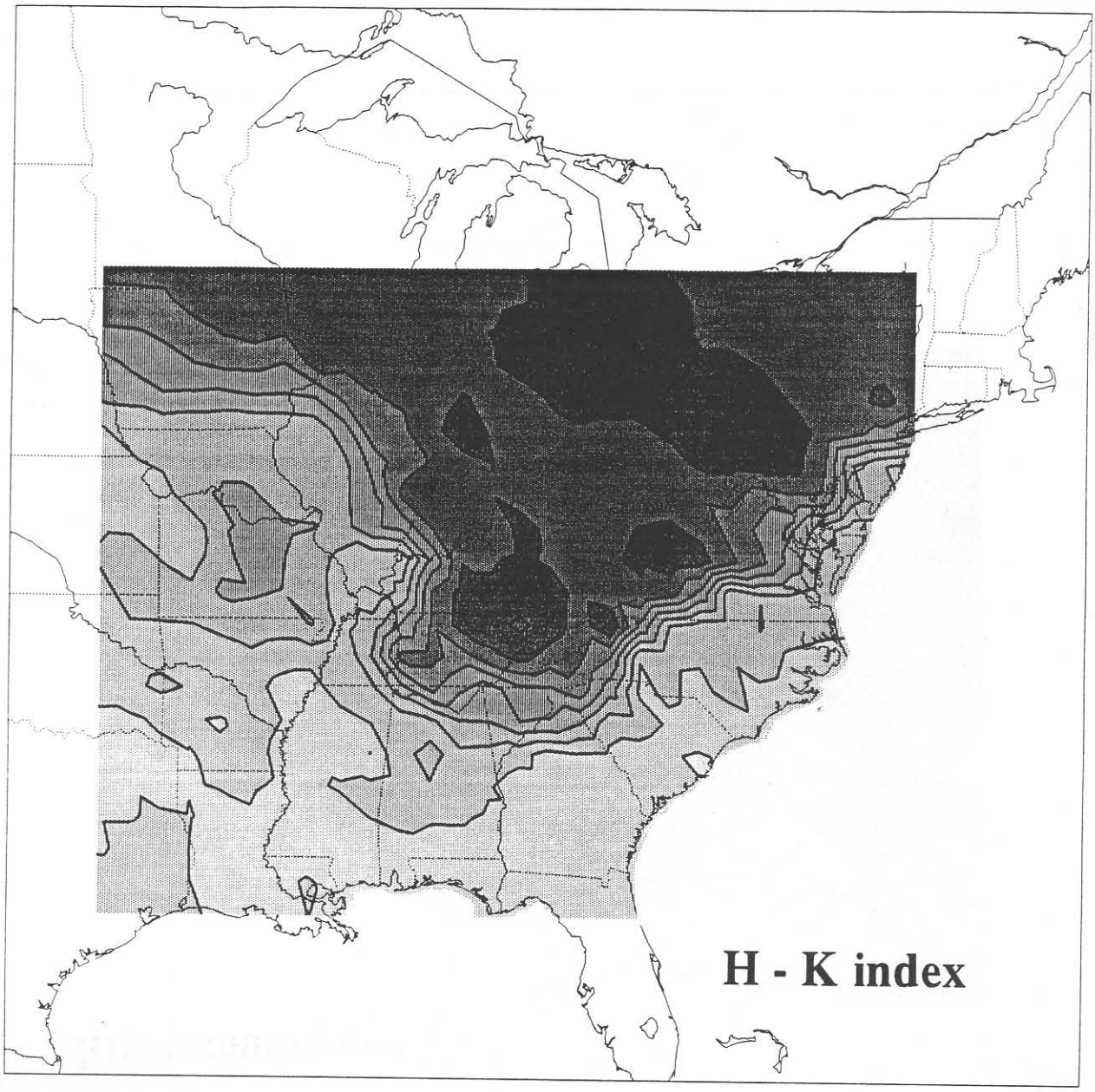

Fig. 27. Contour map showing values of the H - K index, based on county averages for counties (shown in Fig. 1). Dark color corresponds to higher values. Note the relatively sharp boundary between ***illinoiensis*** and ***georgina*** east of the Mississippi, and the broader boundary zone (structurally intermediate forms) west of the river. Also note the protrusion of low H - K forms along the Mississippi River to southern Illinois and adjacent areas.

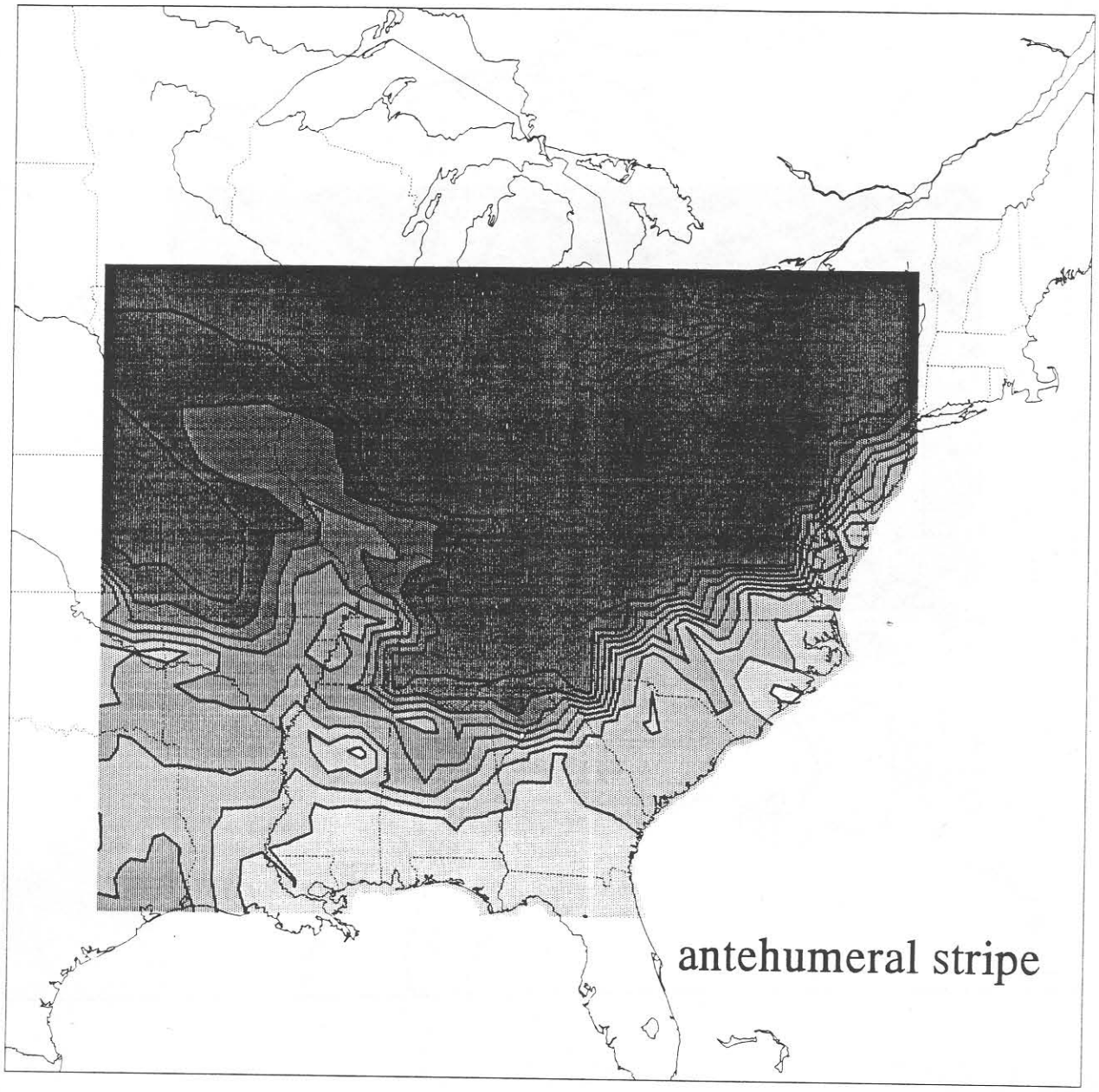

Fig. 28. Contour map as Fig. 27, showing county averages for the length of the antehumeral stripe. Dark color corresponds to shorter stripe. East of the Mississippi River this boundary corresponds closely with the structural boundary shown in Fig. 27. West of the river, however, the boundary is in northern Arkansas, which is south of the structural boundary. Note the protrusion of ***georgina***-like forms up the Mississippi River.

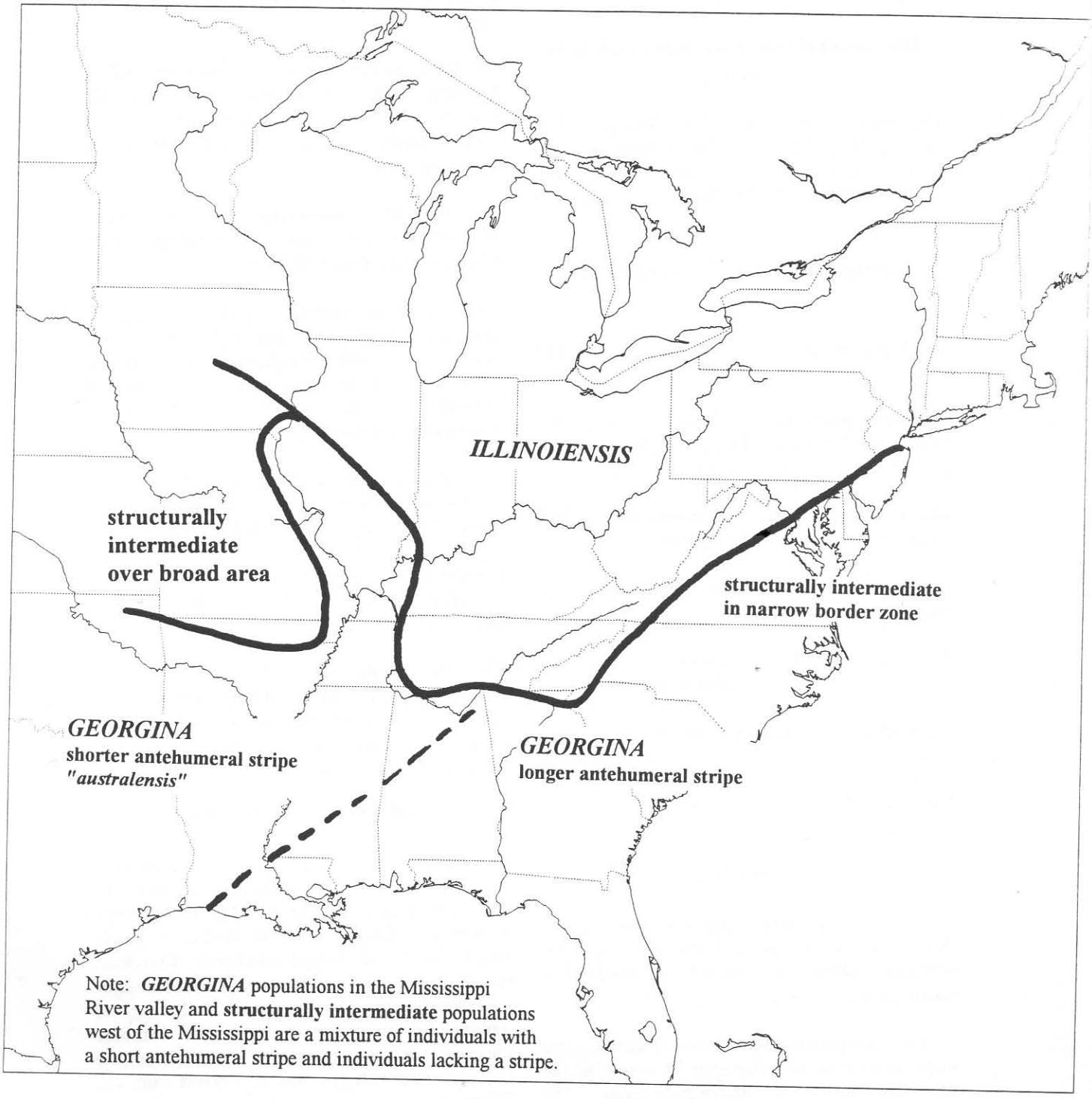

Fig. 29. Summary map showing the distribution of the two subspecies ***illinoiensis*** and ***georgina***, with occurrences of intermediate forms, and showing the decrease in the length of the antehumeral stripe of ***georgina*** to the west. Boundaries are, of course, approximate, especially in the western part of the area.

Our proposed synonymy is as follows:

Macromia illinoiensis illinoiensis new status

Macromia illinoiensis, Walsh, 1862, p. 397; de Selys, 1871, p. 342, repr. 109; Williamson, 1909, p. 377; Needham & Heywood, 1929, p. 166; Walker, 1937, p. 12; Needham & Westfall, 1955, p. 339

Macromia illinoiensis georgina new comb.

Epophthalmia georgina, de Selys 1878, p. 197, repr. 19.

Macromia georgina, Williamson, 1909, p. 383; Needham & Heywood, 1929, p. 169; Walker, 1937, p. 12; Needham & Westfall, 1955, p. 338

Macromia australensis, Williamson, 1909, p. 381; Needham & Heywood, 1929, p. 169

The separation between the subspecies is as follows:

Value of H - K index (defined above) greater than 1.10 . . . . . ***illinoiensis illinoiensis***

Value of H - K index (defined above) less than 0.85 . . . . . ***illinoiensis georgina***

Value of H - K index (defined above) 0.85 - 1.10 . . . . . ***illinoiensis*** subsp. indet.

SUMMARY

(1) The taxa formerly considered two species (***Macromia illinoiensis*** and ***georgina***) are not genetically distinct and should be considered a single species.

(2) The color pattern (development of antehumeral stripe) is not a reliable character for separating the taxa, especially in the intermediate zones. The antehumeral stripe is evidently a discrete rather than a continuous variable, and local (county) populations in the intermediate zones commonly have bimodal populations of specimens. We find that structural characters (the combination of the length of the hamule tip and the percent length of the mesotibial keel) provide homogeneous, unimodal groupings of specimens in these local areas.

(3) In the eastern part of their range (east of the Mississipi Valley) the two taxa are subspecifically separable over most of their range. Only in a fairly narrow border zone do abundant intermediate specimens occur.

(4) West of the Mississippi River and north of Missouri, we have seen only three specimens, which are fairly typical ***illinoiensis***.

(5) East of the Mississippi River the ***georgina*** have longer antehumeral stripes than west of the river. In Texas, Oklahoma, and southern Arkansas, the form corresponds to Williamson's "***australensis***", but we do not recommend resurrecting this taxon.

(6) Central and southern Missouri, eastern Kansas, and northern Arkansas (approximately the Ozark Plateau and adjacent upland areas) has a structurally intermediate population which can be considered the western end of a cline which begins east of the Mississippi River but is interrupted by Mississippi Valley populations .

(7) The Mississippi River valley contains a population of ***georgina*** which may have invaded a previously continuous population (varying from ***illinoiensis*** to structurally intermediate) north of Arkansas and Mississippi.

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these. Rosser Garrison provided helpful comments on a draft of this paper.

At the conclusion of this study we realize how much of a debt we owe to the late E.B. Williamson. He was the first American odonatist to conduct major field studies, and his insights have molded the subsequent course of study of this group for the entire New World. He was fully aware of the major problems in this genus and never ceased pursuing his study of these insects. We have examined several specimens taken in late 1932, only five months before his death.

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Appendix I. Summary of original literature (Structural terms modified in places, with original in brackets. Some summary material also in brackets. Bold face usage added for emphasis.)

1) **Walsh, B.D. (1862) List of the Pseudoneuroptera of Illinois contained in the cabinet of the writer, with descriptions of over forty new species, with notes on their structural affinities. Proc. Acad. Nat. Sciences Philadelphia 14: 361- 402**

Macromia illinoiensis Walsh (1862) (some terminology changed)

Female brown. Head with the vertex [vertical vesicle] bilobed, the lobes divaricate, each forming an equilateral triangle. Antennae black. Frons [front] prominent, laterally contracted towards its summit, deeply excavated above, the angulation of the superior with the anterior surface much rounded off at the sides, above black with violet reflections with four basal, obtrigonate yellow spots, two outside the excavation, two inside the anterior surface, with its upper half brown and its lower half yellow, the latter enclosing the usual two transverse striae, which are widely and deeply impressed, but not acute; Clypeus [epistoma] and labrum of a paler semi-transparent brown, the latter with a wide obtuse longitudinal carina, and obscurely yellow towards its tip in the middle, its anterior edge brown; tips of the mandibles black, glabrous; the rest of the mouth pale semi-transparent brown; back part of the head black, polished, without any hair next the eyes. Thorax covered with dense, long, pale, brown hair; the space included in the double edge of each posterior bifurcation of the dorsal carina, bright yellow; **no indications of any stripes on the dorsum;** pleura with a distinct yellow stripe enclosing the spiracle; sternum pale brown. Abdomen inflated at base to the middle of joint three, thence much compressed and carinate above, pubescent, black, except joint one and the basal half of two, which are pale brown; two with a marginal yellow spot on each side underneath at its base and a yellow medial transverse line, interrupted slightly above, beneath much abbreviated; 3 - 6 each with an elongate, semi-oval yellow spot on each side of the dorsum, the straight side of the spot covering two-thirds the distance from the suture to the base of the joint; seven with a dorsal semicircular basal spot extending to the medial suture, and confluent at its extreme tip, with a similar but very much smaller yellow spot immediately behind the suture; laterally three has a lanceolate basal and marginal yellow spot extending two-thirds of its length, and four and eight have a small, obscure, basal triangular yellow spot; venter black so far as visible. Abdominal appendage a little longer than the tenth abdominal joint, black, rather slender, depressed, directed downwards, suddenly curving on their inner edge to an acute point, each surmounting a semicircular, black anal process as long as itself. Vulvar lamina black, very small, composed of two very small, approximate, roundish tubercules, from which proceed two robust, widely divaricate, medially inflated branches, convex in front, concave behind, and with a blunt, subbasal tooth on their posterior edge. Legs black, coxae and trochanters pale brown, except the anterior trochanters, which are distinctly yellow on their anterior surface. Wings hyaline, strongly flavescent at their extreme costal base, and moderately so on their terminal third, the flavescence in the fore [anterior] wing extending inwardly along the costa beyond the nodus; a distinct ferruginous stripe between the costal and subcostal veins, extending from the base of each wing nearly to the first cross-vein; veins and cross-veins black, except the upper of the two veins which coalesce to form the **costal, which in the hind [lower] wing, from a little inside the nodus to the tip of the pterostigma is yellowish anteriorly**; membranule white, cinerous at tip; **pterostigma trapezoidal, black. Triangles with one cross-vein, in the hind [posterior] wing with two**. Antenodals [antecubitals] 18, postnodals [postcubitals] 9-10. Two cells rows in the discoidal field [discoidal areolets], commencing with three, except one fore [anterior] wing where it commences with two.

Length 64 mm, wing [alar] expanse 100 mm. Hind femur 12 mm. hind tibia 11 mm. Pterostigma 3 mm. One female, male unknown. Abdominal segments [joints] 4-6 are equal, 7 is about a fifth shorter than 6, and 8-10 each about a third shorter than the segment [joint] immediately preceding it, 10 being about 1.5 mm long. The hind legs extend to the middle of the 5th abdominal segment [joint]. Very distinct in its ornamentation from all the described North American species, except ***pacifica***, Hagen, of which only a fragmentary specimen exists, and sufficiently distinct from that by the greater number of its antenodals [antecubitals] (eighteen instead of sixteen) but especially by the coloration of the wings.

2) Selys-Longchamps, E.M. de (1878) Secondes additions aux synopsis des Cordulines. Bull. Acad. Roy. Belg. (2) 45: 183-222

Epophthalmia georgina Selys (1878) (p. 197; reprint 19; translation)

Female abdomen 53 mm; hind wing 49 mm. Male unknown. Female: wings hyaline with a very short vestige of a brown mark at the extreme base between the costal and subcostal crossveins. **Venation black, but the costa yellow below. Pterostigma brownish yellow,** covering two cells (2.5 mm long). Membranule white. 18-19 antenodals; 11-12 postnodals; 2-3 supra triangle cells; 4-5 cells in median space; 3 followed by 2 post-triangular cell rows in the front wings; **triangle crossed in all four wings**; sub-triangle crossed in front wing, uncrossed in hind wing. Color shining black with bright yellow except for labrum, which below is yellowish brown and above has a transverse brown spot divided into two; anteclypeus and lower part of frons brown; postclypeus with two small spots below the frons and small spots on the sides; occiput not prominent, the medial prolongation of the eyes projecting. Thorax dark shining bronze in front, with yellow as follows: an antealar sinus, a short antehumeral band, and laterally a median band traversing the thorax between the wings narrowly separated from the wings. Abdomen cylindrical and slightly widened at the base, thereafter slightly flattened, black. **At the 2nd segment a median band passing through the auricle,** on 3 to 6, a semi-band joined at the median suture and slightly divided in two by the dorsal suture; on 7, the dorsal spot begins at the base and occupies half the segment, narrowing caudally; 9 and 10 black. Anal appendages cylindrical, thick, pointed, as long as the 10th segment. Vulvar lamina short, deeply hollowed out. Legs black, except for the fore femora which are dark brown. The hind femora are 13 mm long. Country: Georgia (U.S.) a unique female, collected by Mr. Morrison. (Selys collection).

N.B. It resembles ***taeniolata*** very much, from which it can be distinguished by its smaller size, by having four well marked yellow spots on the lower part of the frons, by having less acute triangles in the front wing, and less elongated triangles [*discoïdal*] in the hind wings. This character approaches true ***Macromia***, in the hind wings of which, however, all triangles are free.

Setting aside the triangles, ***georgina*** is very similar to the European ***Macromia splendens*** in stature and color pattern. It can be distinguished in addition by the front and sides of the frons dark brown and by other details of the color pattern. In ***amphigena*** from Japan the frons is steel black, without spots.

3) Williamson, E.B. (1909) The North American Dragonflies (Odonata) of the genus *Macromia*. Proc. U.S. Nat. Museum, 37:369-398; Pls 35-36.

All the North American dragonflies referred in the past to ***Macromia*** and ***Epophthalmia*** are congeneric and should be referred to ***Macromia***. [W. goes on to discuss structural characters, and venational characters other than the triangles, which separate Asian ***Epophthalmia*** from ***Macromia***.]

Macromia illinoiensis Walsh

Length of abdomen: Male, 47-52 mm; average, 48.8; female, 47-51 mm; average, 49. Length of front wing: Male, 42-45.5 mm; average, 44.1; female, 46-50 mm; average, 48.2. Length of hind wind: Male, 40-45 mm; average, 42.4; female, 45-49 mm; average, 47. Length of first tibia, male, 7 mm; hind femur, male, 10.7 mm. Length of tibial keel in length of tibia: Male: first tibia, 1/2; middle tibia 1/2- to 1/2. (very rarely shorter; I have examined 2 specimens in which it is 2/5.

Without trace of antehumeral thoracic stripe. Latero-ventral metathoracic carina brown. **Yellow ring on abdominal segment 2 narrow and interrupted at the auricles and dorsum to form 4 spots. Costa dark.**

Male. - Postclypeus distinctly paler, clearer in color than the labrum; dorsal spots on the frons variable in size, always small, about 0.5 mm in diameter, and about half as large as the lateral spots; in one specimen dorsal spots are entirely wanting. (There is considerable variation in the coloring of the labrum, especially in the extent of marginal and central black or dark brown, but this seems independent of locality.)

Abdominal spots on 3-6 never meeting in the median line, growing smaller posteriorly, present in only 2 cases on 6, and frequently absent on 4-6; present on 7 as a large dorsal basal spot, posteriorly reaching the transverse carina on either side, produced briefly posteriorly in the mid-dorsal line, not encircling the segment, but limited beneath on the sides by black; segment 8 with a small, narrow, triangular basal spot on either side, the bases of the triangles narrowly separated by the middorsal black line, variable in size and often reduced to mere traces; 8 and 9 (rarely 7) ventrally each with a basal yellowish spot on either side.

Wings hyaline, venation black, in teneral specimens more or less tinged with yellowish; basal costal and subcostal brown spots often present, in their maximum development reaching the first antenodal; wings sometimes fumose beyond the pterostigma [stigma] especially along the anterior margin; **pterostigma [stigma] yellowish brown to black, apparently depending on age.** [In a separate venational table, Williamson tabulates triangles of front wing, free 18, crossed 2; triangles of hind wing, free 18, crossed 2.]

Abdominal appendages seen in profile: the upper edge of the superiors nearly flat, a slight postero-dorsal elevation at the extreme apex; lower edge beyond the enlarged base nearly parallel to the upper edge, very slightly converging posteriorly, the apex truncate; seen from above the superiors are lyre-shaped, a short basal lateral external carina terminating in a small tooth near the middle of each appendage; this tooth or projection is variable in size, always small, and sometimes not apparent; on the ventral surface distal to this tooth the appendage is denticulated; inferior appendage triangular, curved, and equaling or slightly exceeding the superiors.

Female. - Postclypeus more obscured than in the male, especially at either extremity; spots on frons larger.

Abdominal spots larger than in the male, excepting on 7 and 8; smallest on 5 and 6, where they may be lacking entirely; 7 similar to male; dorsal spots absent on 8, excepting in 2 teneral specimens; inferior lateral basal spots indistinct or absent on 8 and 9.

Wings hyaline, yellowish brown in several teneral specimens, veins black, brown margined in 2 specimens; basal costal and subcostal brown areas reaching beyond the second antenodal as a maximum; apical fumose area sometimes present, variable in extent, in one case extending basally to nodus; as in the male, the darkest winged specimens are teneral pterostigma [stigma] as in male. The wings of 10 females show the following: triangle of front wing, free 6 crossed 14; subtriangle of front wing, free 4, crossed 16; triangle of hind wing, free 7 crossed 13 (compare with same parts of 10 males tabulated; in rows of postrigonal cells, as well as other areas, female ***Macromia***s have a larger number of cross-veins than the males.)

Vulvar lamina about 1/7 - 1/6 length of segment 9, deeply and widely emarginate in semicircle or right angle. Abdominal appendages equal or very slightly shorter than segment 10.

I refer to ***illinoiensis*** two very similar males, one from Great Falls, Maryland (U.S.N.M.) and the other from Pennsylvania (Acad. Nat. Sci. Phila.). These have abdomen 51 mm in length and hind wing 46. The Maryland specimen has tibial keels as usual for

illinoiensis, but **in the Pennsylvania specimen the keels of the first and middle tibiae are 1/3+ and 1/3 in length of the respective tibiae.** The abdominal spots on 3 - 6 are conspicuous, those on 6 in the Maryland specimen being about 1 mm in diameter, and in the Pennsylvania specimen about half as large. It is possible that a larger series would reveal that these specimens are specifically distinct.

[Recorded from Quebec, Ontario, Maine, New Hampshire, Massachusetts, New York, Pennsylvania, Maryland, Virginia, Michigan, Wisconsin, Iowa, Illinois, Indiana, Ohio, Kentucky, Tennessee]

Macromia australensis Williamson 1909

Length of abdomen: Male 50-52.5 mm, average 51.1; female, 50-52; average 50.7. Length of front wing: male, 44.5-48 mm; average 45.6; female, 48-50 mm; average 49. Length of hind wing: male, 43-47 mm; average 44.2; female, 46.5-49 mm; average 47.5 Length of first tibia, male 7.25 mm; hind femur, male, 12 mm. Length of tibial keel in length of tibia, male, first tibia 3/7 to 1/2-; middle tibia 1/3- to 3/8.

A very short antehumeral stripe, 1.5-2 mm long on the mesepisternum. Latero-ventral metathoracic carina yellow. **Yellow ring on abdominal segment 2 not interrupted dorsally or laterally. Costa dark colored.** Male. - Postclypeus and labrum similar to *illinoiensis;* dorsal spots on frons rounded, in size scarcely perceptible to nearly 1 mm in diameter, and always larger than the lateral spots.

Abdominal spots on 3-6 larger than in *illinoiensis*, growing successively smaller posteriorly, the spot on 3 extended ventrally on either side to meet a longitudinal stripe on the ventral edge of the segment (in *illinoiensis* the dorsal spot is widely separated from the ventral longitudinal stripe); on 3-5 the spots on each segment are separated dorsally by the faintest line of black or the black line may be wanting; in two cases the spots on 6 meet dorsally; the greatest variation in size of spots is on 6, where the spots may be widely separated and about 0.5 mm long, or joined dorsally and 1.5 mm in length; spots never wanting on 3-6; 7 similar to *illinoiensis*; spot on 8 1/2 to 3/4 as long as on 7, divided dorsally in only one case, and then by the merest line of black.

One male from Wister, Oklahoma, is very dark and may not belong here; the tibial keels are like *australensis*, but the coloration is more like *illinoiensis*. However, the head is like a very dark *illinoiensis*, while the abdomen has an unusual amount of yellow for *illinoiensis*; the antehumeral stripe seems to be wanting and the yellow ring on 2 is narrowly interrupted dorsally and laterally; well developed spots are present on 6 and 8. **In *australensis* 7 may be yellow or not on the ventral basal edge of the segment**; in any case the yellow is less distinct than on 8 and 9.

Wing hyaline, without trace of color anywhere even in teneral specimens; **pterostigma [stigma] black.**

Abdominal appendages indistinguishable from *illinoiensis*.

Female. - Head similar to *illinoiensis*, but dorsal spots on frons apparently not larger than in male. Abdomen similar to male, but spots on 3-6 more nearly uniform in size, slightly smaller on 6, 1.5-2 mm long on 3 - 5; dorsal spots present on 7; inferior lateral basal spots present on 7 - 9.

Wings hyaline, short brown basal streaks in the costal or costal and subcostal areas; apex of wings slightly fumose in two specimens; **pterostigma [stigma] yellowish brown to black.** The wings of three females show the following: triangle of front wing, free 1, crossed 5; subtriangle of front wing, free 1, crossed 5, triangle of hind wing, crossed 6.

I cannot be sure of the shape of the vulvar lamina; it seems to be a very short, scarcely emarginate plate; appendages similar to *illinoiensis*.

Types. - Male and female, author's collection taken at Wister, Oklahoma, Poteau River, Frank Collins, August 3, 1907.

Material examined. - Wister, Oklahoma, Poteau River, August 3, 5, and 6, 7 males, 2 females, Frank Collins. Dallas, Texas, male and female, Ball (M.C.Z.). Total, 8 males, 3 females.

Under this name I have included 3 males, which future material and study may reveal are specifically distinct.

Length of abdomen, 50.5-54 mm. Length of front wing 46.5-48 mm. Length of hind wing 44-47 mm. Length of first tibia 7-7.5 mm; hind femur 11-12 mm. Length of tibial keel in length of tibia: first tibia 1/2- to 1/2; middle tibia 2/5.

The yellow ring on 8 is narrowed laterally, widened dorsally and ventrally, and encircles the segment; in all the other material of *australensis* the dorsal and ventral areas of 8 are separated by black , excepting in one individual where the abdominal spots are very large with the yellow spot on 6 not divided in the median dorsal line by black; in the three males under discussion the spots on 6 vary from 0.5-1 mm in diameter and are distinctly to widely separated in the middorsal line. **The pterostigma [stigma] is yellow brown to black.**

Material examined. - Hyattsville, Maryland, July 4, 1899, male, J.S. Hine. Gynn's Button Mill, Maryland, September 20, male (M.C.Z.), Blount Springs, Alabama, July 18, 1890, Charles C. Deam. Total 3 males.

Macromia georgina de Selys

Length of abdomen: male, 50.5-54 mm; average, 51.8; female, 54 mm. Length of front wing: male, 47.5-50 mm; average 48.8; female 53 mm. Length of hind wing: male, 46-48 mm; average, 47; female, 51 mm. Length of first tibia: male, 8 mm; hind femur, male 12 mm. Length of keel in length of tibia, male: first tibia, 2/5; middle tibia, 1/4 to 2/7.

Humeral stripes present , about 3 mm long on the mesepisternum; otherwise similar to *australensis*.

Male. - Very close to *australensis*; the abdominal spots on 3 - 6 decreasing in size very slightly posteriorly; **spots on 7 and 8 encircling the segments.** Abdominal appendages similar to *australensis* and *illinoiensis*, but the superiors have a small, distinct, basal, dorsal yellowish area, and the inferior appendage is distinctly paler than the superior appendages.

Female. - Separated from *australensis* by the longer antehumeral thoracic stripe and the larger abdominal spots, especially on 3 - 5 (1-2 mm long in *australensis*; 1.5-2.5 in *georgina*). The vulvar lamina is a very short plate with converging sides, broadly and shallowly emarginate.

This is the only species in the material before me to which, I believe, *Epophthalmia georgina* de Selys can be referred. In the female the **pterostigma [stigma] is yellow-brown, the costa obscure yellowish brown (in the male the costa has the basal median area yellow, but this yellow disappears with the narrowing of the costa which beyond this point is dull brown).** The is nothing in de Selys's description and Martin's recent figure which conflicts with the specimen before me unless it be the form

of the vulvar lamina. The triangles in all four wings and the subtriangles of the front wings are all crossed.

To this specimen I refer a badly faded female in the Museum of Comparative Zoology labeled "Texas", though in this specimen all triangles and subtriangles are free.

Material examined. - Raleigh, North Carolina, July 31 and August 30, 1902, August 9, 1904, June 30, 1905, and September 12, 1907, 4 males, 1 female, C.S. Brimley (C.S.B.); 1 male with the last five [5] abdominal segments gone. Texas, female (M.C.Z.). Total, 4 males, 2 females.

Macromia alleghaniensis, new species

(excerpts)

Length of tibial keel in length of tibia, male: first tibia, 3/7; middle tibia, 1/7 to 1/5.

Without trace of antehumeral thoracic stripe. Latero-ventral metathoracic carina very narrowly yellow posteriorly. **Yellow ring on abdominal segment 2 interrupted dorsally, not interrupted at the auricles. Costa dark colored**.

Male. - Postclypeus paler than the labrum, usually divided by brown into a central and two extremital pale areas; dorsal spots on frons small or wanting.

Abdominal spots similar to ***illinoiensis***, with the striking difference that **the yellow on 7 encircles the segment,** so that segments 7 - 9 have the inferior basal margin of each segment yellow; small spots are present on 5 in 5 of 7 specimens and are absent on 6 in 6 of 7 specimens.

Wings hyaline, without trace of color; **pterostigma [stigma] very dark brown or black**.

Abdominal appendages seen in profile similar to ***illinoiensis***, but the superiors are constricted ventrally beyond the base and are slightly widened near the apex; in dorsal view the median lateral tooth is present, but minute in every case.

Female. - Dorsal spots on frons larger than in male, about 1 mm in diameter; postclypeus slightly paler than labrum, both obscured with dark brown or black.

Abdominal spots present on 3 - 6, smaller posteriorly and scarcely evident on 6; large spot on 7 not encircling the segment as it does in the male; inferior lateral basal spots on 7 - 9 indistinct or wanting, excepting on 8 in 1 female, where they are conspicuous; dorsally 8 - 10 are uniform black.

Wing in one specimen hyaline; in the other slightly tinged with brown and with veins brown edged, and with a basal trace of brown in the costal space of front wings and in the costal and subcostal spaces of hind wing; **pterostigma [stigma] black**. Two specimens show: triangle of front wing, free 1, crossed 3; subtriangle, free 1, crossed 3; triangle of hind wing, crossed, 4.

Vulvar lamina similar to ***illinoiensis*** but apparently smaller, shorter, and with the emargination narrower and deeper. Abdominal appendages similar to those of ***illinoiensis***.

This species has been confused with ***illinoiensis***. The length of the first tibia in the female is about 9, as compared with 7 in ***illinoiensis***. The male may at once be recognized by characters of the tibial keel of middle tibia and abdominal appendages mentioned above. I have collected all the specimens I have seen but two. Until this study was begun I confused this species with ***illinoiensis***, and I recall nothing striking about its habits in life.

Types. - Male and female in author's collection, taken at Ohiopyle, Pennsylvania, June 24 and June 25, 1900, respectively.

Material examined. - Dunbrooke, Virginia, July 31, 1899, male, R.P. Currie (U.S.N.M.). Ohiopyle, Pennsylvania, June 24, 1900, 2 males, E.B. Williamson. June 25, 1900, 2 males, 1 female, E.B. Williamson (1 male P.P.C.). June 26, 1900, male, E.B. Williamson (U.S.N.M. - Insect Book, pl. 42, fig. 7 [Note: This is Howard, L.O., 1902, The Insect Book, New York, Doubleday, Page & Co., 429 pages. The specimen referred to is labeled ***illinoiensis***.] September 8, 1901, female, J.L. Graf. Livingston, Kentucky, June 23, 1904, male, E.B. Williamson. A damaged female, collected by C.C. Adams, Cleveland, Virginia, August 4, 1899, probably is this species. Total, 7 males, 2 females.

Appendix II. Notes on the Larvae of *illinoiensis* and related species.

We have examined a relatively few larval specimens and exuviae of ***illinoiensis*** and ***georgina***. The larvae of the two taxa in their core areas can be separated fairly reliably; we have not examined larvae from the intermediate areas to see if their larval characters are also intermediate. The abdominal dorsal hooks of ***illinoiensis*** and ***georgina*** are similar when viewed laterally, but the hook of segment 9 is longer in ***georgina*** than in ***illinoiensis*** (Fig. 30).

Needham and Westfall (1955) use the lateral spines of abdominal segments 8 and 9 to differentiate several species from ***illinoiensis*** (axes pointed straight rearward in ***illinoiensis*** vs. incurved in ***alleghaniensis***, ***georgina***, and ***taeniolata***. We find that this character was unreliable in the specimens we studied. We find a difference in the relative lengths of the lateral spines of segment 9, which project further posterior in ***georgina*** than in ***illinoiensis*** (viewed dorsally, tips are further beyond the midlength of the epiproct in ***georgina*** vs. short of the epiproct midlength in ***illinoiensis***. An additional difference between ***georgina*** and ***illinoiensis*** is the ratio of the width to height of the dorsal hook on segment 7 (> 1.0 in ***illinoiensis***; < 1.0 in ***georgina***).

Larvae of ***alleghaniensis*** can be distinguished from ***illinoiensis*** and ***georgina*** by having a more slender dorsal hook on abdominal segment 6 (Fig. 30). Also, the lateral spines of segment 9 are shorter, usually not projecting beyond the ventral posterior margin of segment 10 in dorsal view. The length of the hind femur in ***alleghaniensis*** is

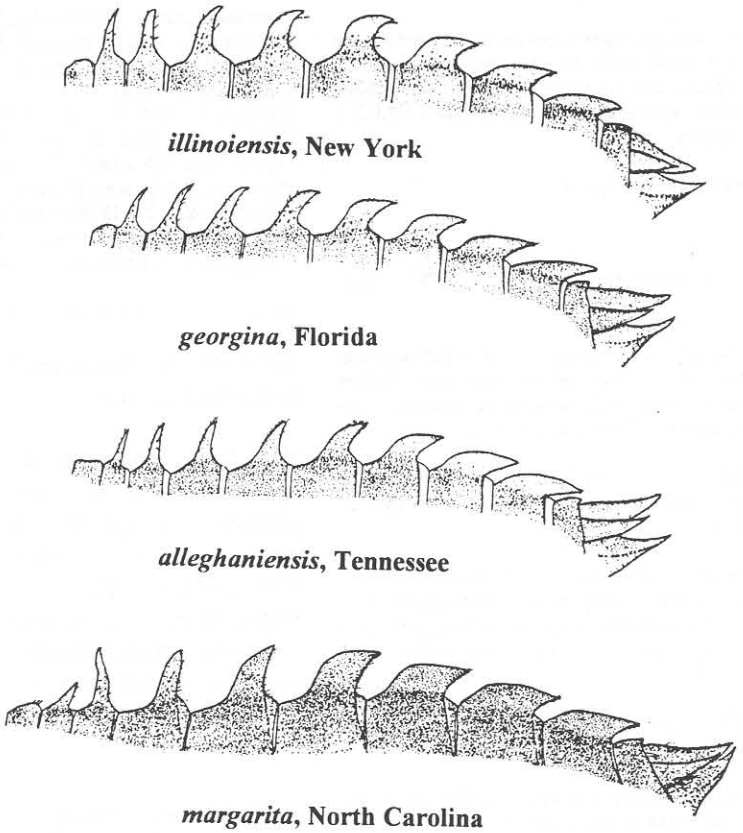

Fig. 30. Lateral ("skyline") views of the dorsa of the abdomens of larvae of ***Macromia i. illinoiensis, i. georgina***, ***alleghaniensis*** and ***margarita.***

typically slightly longer than in ***illinoiensis*** (a range of 11.5 to 14.0 mm vs. 10.4 to 11.5 mm).

The larva of ***M. margarita*** Westfall is undescribed, but two specimens we examined show some distinct differences between it and the remaining species. The dorsal hooks on abdominal segments 4 to 9 are very wide in lateral view (Fig. 30). For the hook on segment 6, the ratio of width to height is 0.83, which is similar to that in ***taeniolata***, but much greater than for ***alleghaniensis*** (0.52) and ***illinoiensis*** (0.62 - 0.64). The corresponding values for the hook on segment 7 are: ***margarita***, 1.29; ***alleghaniensis***, 0.89; ***illinoiensis***, 0.95 - 1.09. The lateral spines of segment 9 do not surpass the posterior margin of segment 10 in ***margarita***, similar to ***alleghaniensis*** and ***taeniolata***. The length of the hind femur was 12.5 and 12.8 mm for the two ***margarita*** specimens studied. ***M. margarita*** differs from ***taeniolata*** in the dorsal hook on segment 2 (0.5 to 0.6 times the height the hook on segment 3 in ***margarita*** vs. 0.8 for ***taeniolata***). The ratio of abdominal length to width is greater in ***taeniolata*** (> 0.8) than in ***margarita*** (< 0.8)

Table 2. Counties with measured ***M. illinoiensis*** sspp. N refers to number of structurally measured specimens, with county averages for H - K and antehumeral stripe.

N	H - K avg.	ante. stripe (avg.)	State, County
1	0.78	0.98	AL Blount
2	0.98	1.10	AL Dekalb
5	0.68	2.20	AL Fayette
4	0.62	2.20	AL Lamar
16	0.88	0.59	AL Lauderdale
5	0.68	2.70	AL Macon
1	0.67	1.50	AL Marion
1	0.73	2.00	AL Pickens
1	0.79	0.54	AL Tuscaloosa
1	0.54	1.75	AR Clark
1	0.88	3.08	AR Clay
1	0.69	1.50	AR Cleveland
3	0.64	2.96	AR Craighead
1	0.42	0.91	AR Lawrence
1	0.75	1.36	AR Montgomery
1	0.57	3.74	AR Sevier
23	0.95	1.47	AR Sharp
4	1.03	2.14	DE New Castle
1	0.68	5.40	DE Sussex
4	0.63	3.50	FL Alachua
12	0.58	3.49	FL Liberty
4	0.52	3.39	FL Okaloosa
2	0.62	2.65	FL Santa Rosa
3	0.55	3.29	GA Burke
2	0.81	0.43	GA Dade
4	0.62	4.20	GA Lee
2	0.50	3.15	GA Meriwether
5	0.54	4.13	GA Pierce
2	1.31	0.18	IA Black Hawk
4	1.02	0.00	IL Coles
1	0.69	0.00	IL Hardin
4	0.57	2.63	IL Johnson
2	1.14	0.00	IL Kankakee
1	1.17	0.09	IL La Salle
3	0.70	1.17	IL McDunough
14	0.67	1.18	IL Pope
1	0.74	0.75	IL Sangamon
5	1.15	0.00	IL Vermilion
1	1.19	0.00	IL Will
2	1.23	0.36	IN Allen
1	1.46	0.00	IN Carroll
1	1.15	0.00	IN Fountain
1	0.70	2.72	IN Gibson
3	1.24	0.30	IN Huntingdon
6	1.27	0.24	IN Lagrange
1	1.48	0.00	IN Martin
1	1.23	0.00	IN Monroe
2	1.24	0.27	IN Putnam
3	1.19	0.00	IN Tippecanoe
6	1.24	0.15	IN Wells
1	0.68	1.80	KS Chautaqua
2	0.88	0.80	KS Cherokee
1	0.81	0.00	KS Coffee
1	0.68	0.00	KS Douglas
1	0.77	0.00	KS Labette
1	0.69	0.00	KS Osage
1	0.77	1.40	KS Sumner
1	1.18	0.00	KY Butler
2	1.38	0.00	KY Edmonson
23	1.26	0.00	KY Green
1	1.32	0.00	KY Laurel
1	1.27	0.00	KY Marion
1	0.54	2.90	LA East Baton Rouge
1	0.53	3.20	LA East Feliciana
1	0.67	2.10	LA La Salle
1	0.78	2.90	LA Livingston
1	0.60	2.50	LA St. Helena
1	0.55	3.36	LA St. Tammany
1	0.48	3.40	LA W. Feliciana
4	1.26	0.00	MA Barnstable
3	1.17	0.00	MD Baltimore
1	1.20	0.00	MD Cecil
1	0.94	0.00	MD Charles
4	1.27	0.00	MD Frederick
		0.00	MD Howard
4	1.19	0.00	MD Montgomery
25	0.84	1.26	MD Prince Georges
1	0.64	3.06	MD Wicomico
1	0.57	3.06	MD Worcester
1	1.26	0.00	ME Cumberland
3	1.28	0.00	ME Piscataquis
1	1.26	0.00	MI Charlevoix
2	1.29	0.00	MI Clare
1	1.26	0.00	MI Delta
3	1.17	0.60	MI Emmet
5	1.26	0.00	MI Gogebic
1	1.31	0.54	MI Huron
1	1.38	0.00	MI Iron
3	1.13	0.18	MI Lake
1	1.34	0.00	MI Mackinac
1	1.31	0.54	MI Midland
2	1.36	0.00	MI Washtenaw
2	1.09	0.00	MN St. Louis
1	0.57	2.63	MO Bollinger
20	0.90	1.69	MO Carter
24	0.75	0.35	MO Clark
		0.00	MO Douglas
6	0.95	1.09	MO Madison
6	0.85	0.54	MO Miller

1	0.99	0.00	MO	Montgomery
1	0.74	0.00	MO	Newton
1	0.57	2.82	MO	Pike
2	0.95	0.09	MO	Pulaski
1	0.95	0.00	MO	Ralls
1	0.53	0.00	MO	St Clair
1	0.61	3.36	MS	George
1	0.42	3.50	MS	Oktibbeha
1	0.40	3.36	MS	Stone
1	0.55	0.00	MS	Tishomingo
12	0.65	3.32	MS	Wayne
4	0.67	4.09	NC	Alamance
11	1.33	0.06	NC	Ashe
1	0.68	3.80	NC	Bladen
3	1.12	0.00	NC	Buncombe
5	0.63	3.73	NC	Cabarrus
1	0.72	3.98	NC	Caldwell
11	0.74	2.34	NC	Caswell
11	0.72	3.02	NC	Chatham
3	1.23	0.00	NC	Cherokee
1	0.50	3.80	NC	Cleveland
3	0.51	3.05	NC	Columbus
12	0.70	2.21	NC	Cumberland
2	0.59	2.27	NC	Davidson
2	0.46	3.62	NC	Davie
1	0.58	4.98	NC	Duplin
69	0.63	3.67	NC	Durham
4	0.53	4.55	NC	Edgecombe
1	0.86	4.16	NC	Forsyth
5	0.74	4.05	NC	Franklin
14	0.81	1.11	NC	Granville
2	0.46	3.17	NC	Greene
1	0.79	3.62	NC	Guilford
6	0.67	3.92	NC	Harnett
5	1.19	0.00	NC	Haywood
2	0.59	3.53	NC	Hoke
1	0.60	4.53	NC	Hyde
12	0.55	4.06	NC	Johnston
2	0.59	4.52	NC	Lee
2	0.54	4.37	NC	Lenoir
6	0.59	4.32	NC	Lincoln
14	0.68	3.05	NC	Macon-G *
48	1.19	0.05	NC	Macon-I *
11	0.66	4.00	NC	Moore
1	0.66	3.62	NC	Nash
2	0.71	4.03	NC	Northampton
171	0.66	3.53	NC	Orange
27	0.62	4.19	NC	Pender
2	0.42	2.55	NC	Person
2	0.57	2.88	NC	Randolph
1	0.55	3.98	NC	Richmond
14	0.60	4.19	NC	Robeson
2	0.67	3.35	NC	Rockingham
1	0.71	3.24	NC	Rowan
5	0.62	2.98	NC	Scotland
1	0.56	3.40	NC	Stanly
2	0.68	4.21	NC	Union
1	0.64	3.24	NC	Vance
7	0.63	4.10	NC	Wake
3	0.76	4.10	NC	Warren
2	0.62	4.54	NC	Wayne
8	0.69	2.85	NC	Wilkes
1	0.81	3.40	NC	Wilson
2	0.66	3.32	NC	Yadkin
3	1.30	0.00	NC	Yancey
1	1.36	0.00	NH	Merrimack
4	0.69	2.77	NJ	Burlington
24	0.76	3.20	NJ	Cumberland
1	0.62	3.23	NJ	Gloucester
3	0.70	2.77	NJ	Mercer
1	0.75	5.10	NJ	Middlesex
1	1.52	0.01	NJ	Morris
4	1.21	0.01	NJ	Somerset
1	1.12	0.00	NY	Broome
4	1.26	0.14	NY	Otsego
1	1.29	0.00	NY	St Lawrence
1	1.29	0.45	NY	Steuben
16	1.30	0.03	NY	Sullivan
3	1.24	0.18	OH	Erie
5	1.30	0.14	OH	Franklin
1	1.16	0.00	OH	Hocking
5	1.38	0.29	OH	Ottawa
6	1.27	0.00	OH	Vinton
6	0.57	1.64	OK	Bryan
1	0.59	2.10	OK	Cherokee
6	0.59	2.02	OK	Johnston
5	0.78	2.10	OK	Le Flore
3	0.70	2.37	OK	Marshall
2	0.56	2.60	OK	Murray
1	0.74	2.86	OK	Sequoyah
2	1.28	0.00	PA	Bucks
2	1.37	0.00	PA	Centre
1	1.42	0.00	PA	Cumberland
6	1.30	0.01	PA	Huntingdon
1	1.08	0.00	PA	Luzerne
6	1.32	0.02	PA	Perry
2	1.29	0.06	PA	Susquehanna
2	1.30	0.00	PA	Union
1	1.27	0.00	PA	York
1	0.69	3.40	SC	Allendale
1	0.41	2.86	SC	Berkeley
1	0.65	3.19	SC	Greenwood
1	0.55	3.10	SC	Lexington
1	1.21	0.00	SC	Pickens
1	1.19	0.00	SD	Spink
1	1.02	0.00	TN	Bedford

* for Macon Co. NC refers to separate populations of ***illinoiensis*** and ***georgina***

1	1.31	0.00	TN	Blount
1	1.49	0.00	TN	Carter
1	1.28	0.00	TN	Cheatham
1	1.28	0.00	TN	Cumberland
2	1.18	0.00	TN	Greene
2	1.32	0.00	TN	Hancock
1	0.57	3.80	TN	Hardeman
1	0.64	2.30	TN	Henry
1	1.33	0.00	TN	Lawrence
3	1.23	0.30	TN	Lewis
6	1.13	0.00	TN	Marshall
3	1.24	0.18	TN	Maury
1	1.30	0.00	TN	Monroe
1	1.39	0.36	TN	Morgan
1	1.44	0.00	TN	Scott
3	1.14	0.24	TN	Sevier
1	1.23	0.00	TN	Sullivan
1	1.19	0.00	TN	Unicoi
2	1.03	0.00	TN	Wayne
1	0.58	2.70	TX	Falls
1	0.69	2.21	TX	Goliad
6	0.65	2.80	TX	Gonzalez
1	0.73	2.35	TX	Grimes
3	0.59	1.72	TX	Hardin
15	0.62	2.24	TX	McLennan
1	0.57	2.40	TX	Robertson
9	0.70	1.98	TX	San Jacinto
2	0.65	1.87	TX	Wilson
2	1.40	0.00	VA	Bath
1	1.04	0.00	VA	Culpepper
1	1.11	0.00	VA	Fairfax
1	1.28	0.00	VA	Floyd
24	1.31	0.00	VA	Grayson
1	0.87	0.00	VA	Loudoun
4	1.00	0.17	VA	Prince William
1	1.16	0.00	VA	Russell
1	1.17	0.00	VA	Shenandoah
2	1.30	0.00	VA	Wythe
6	1.11	0.00	WI	Burnett
1	1.22	0.00	WI	Oneida
13	1.25	0.00	WI	Price
3	1.26	0.00	WV	Hampshire
1	1.28	0.00	WV	Randolph
		Canada		
3	1.11	0.18	ONT	Manitoulin
2	1.26	0.00	QUE	Verendrye

Table 3
Specimens of *Macromia alleghaniensis* with structural measurments

2	AR	Garland
1	AR	Montgomery
1	IL	Pope
2	MD	Montgomery
2	NC	Caldwell
2	NC	Caswell
3	NC	Durham
73	NC	Orange
3	NC	Pender
1	NC	Polk
1	NC	Richmond
1	NC	Scotland
1	NC	Wake
2	NC	Yancey
1	NJ	Burlington
1	NJ	Cape May
3	NJ	Cumberland
1	SC	Chesterfield
2	TN	Cumberland
1	TN	Lewis
3	TN	Maury
1	TN	Scott