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REVISION OF THE MILLIPED GENUS *CHEROKIA*
(POLYDESMIDA : XYSTODESMIDAE)

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Introduction

The student of humus fauna who pursues field work in the circum-Appalachian region of southeastern United States cannot help but become impressed with the abundance and variability of millipeds of the genus *Cherokia*. It is a well-marked ensemble of xystodesmids which in many areas is the most conspicuous element of the diplopod fauna. Besides the interest engendered by the broad ecological tolerance and geographic variability of its forms, *Cherokia* has a still more compelling claim upon our attention, for despite the diversity of body form, color pattern, and morphological details which occurs in the genus, the male gonopods remain essentially similar.

Generally, species in xystodesmid genera tend to be remarkably similar in external body form, specific individuality being expressed solely in the gonopods, which often assume bizarre shapes of great specific constancy. *Cherokia* represents an apparent departure from this condition, and in working out the systematics of this genus one faces the problem whether to assume the occurrence of heteromorphic species—with external differentiation in body form at the expense of the normally variable gonopods—or a single highly variable species within the genus.

¹This paper was written while the author was affiliated with the Biology Department, Virginia Polytechnic Institute, Blacksburg, Virginia.

Solution of this difficulty involves more than merely clarifying systematics and phylogeny within the small confines of *Cherokia*, and will provide insight into the problem of coping with related genera composed of heteromorphic "species" held together by a constant gonopod structure. The ultimate challenge in this direction is the large neotropical genus *Rhysodesmus*, already with about 80 named forms despite only desultory collecting in the region it occupies.

The considerable quantity of material of *Cherokia* now at hand from a large number of localities facilitates a fairly thorough examination of speciation and geographic variation in diplopod genera characterized by basically uniform gonopod structure. It is hoped that the following account will be of interest and value to other investigators who find pleasure and reward in unraveling the intricacies inherent in this neglected class of arthropods.

REVIEW OF THE LITERATURE

Apparently the first specimens of this genus to be collected were obtained in Georgia by L. M. Underwood. During the summer of 1887, he secured material at Macon, Lookout Mountain, Indian Springs, and Tallulah, and two years later Charles H. Bollman described from it two species referable to *Cherokia*. These were *Fontaria georgiana*, based on numerous specimens from Piedmont localities, and *Fontaria tallulah*, the types of which are two immature females from Tallulah Falls on the edge of the Blue Ridge province. Bollman recognized the similarity of these two species in most respects and made the separation between them primarily on the basis of differences in the color patterns.

Remarkably enough, no further information on the genus was published for 50 years. In 1939, R. V. Chamberlin described material from Soco Gap, North Carolina, under the name *Mimuloria ducilla*, and followed it a year later with the closely related *Mimuloria furcifer*. These names were considered to be synonyms of *georgiana* by H. F. Loomis (1943), who had seen Bollman's types and felt that only a single form was involved. Under the name *Dynoria parvior*, Chamberlin (1947) described another local population of *Cherokia* from north Georgia and compared it only with *Dynoria icana* although the two species clearly are not congeneric. This fact was pointed out in a subsequent paper by Loomis and Hoffman (1948), who considered *parvior* to be a junior synonym of *georgiana*.

For a decade, specimens belonging to this genus were referred to *Mimuloria* (Chamberlin, 1928) although the type species, *M. missouriensis* Chamberlin, had never been described sufficiently to give any idea of its attributes. Finally in 1949 Chamberlin set up the new genus *Cherokia* and designated *Fontaria georgiana* Bollman as

the type species, but he did not stipulate which other names belonged in *Cherokia*.

During the summer of 1949, I acquired considerable field experience with *Cherokia* in the southern Appalachians. In a paper appearing the following year, I discussed variation and distribution in the genus and concluded that of the five which had been proposed, only a single specific name was valid. This synonymy was based on topotypes of *tallulah* and *ducilla*, specimens from near the type locality of *furcifer*, and Bollman's types of both *tallulah* and *georgiana*. No attempt was made to consider the general problem of geographic variation over the entire range. But in subsequent years, with the acquisition of rich collections made in Georgia, Alabama, and Tennessee by Leslie Hubricht, I found it necessary to review the status of the genus, and the outcome of the investigation is presented in the following paper.

MATERIALS AND ACKNOWLEDGMENTS

The material studied is included in more than 105 lots and totals well over 400 individuals. Probably 95 percent of these are in my personal collection (RLH), thanks to the kindness of many friends who have picked up millipeds incidental to their own line of special interest. Specimens have also been examined in the following collections: American Museum of Natural History (AMNH), New York City, Chicago Natural History Museum (CNHM), Chicago; and U.S. National Museum (USNM), Washington, D.C.

The type specimens of *Fontaria georgiana* and *F. tallulah* of Bollman are in the U.S. National Museum and have been studied. Topotypes of *tallulah*, *Mimuloria ducilla*, and *M. furcifer* have been seen in life and have provided an idea of the basis of those three names. Specimens collected less than 20 miles from the type locality of *Dynoria parvior*, while not strictly topotypical, are nonetheless representative of the population described under that name and make its evaluation possible with considerable confidence.

Methods of study outlined in previous papers have been followed and need no repetition here. Because of the confused state of nomenclature in the genus, all previously published information was rejected as prejudicial. Specific characters and the distribution of populations thus defined were worked out at the beginning; only after this work had been done was the application of available names undertaken.

Particular attention has been paid to the evaluation and comparison of localized populations in order to determine geographic variation. In this respect, likewise, each of the structural variables found useful in diagnosis has been separately plotted cartographically. These precautions have been found useful in light of the remarkably uniform gonopod structure in all of the specimens, a condition which compelled my giving attention to details of body form.

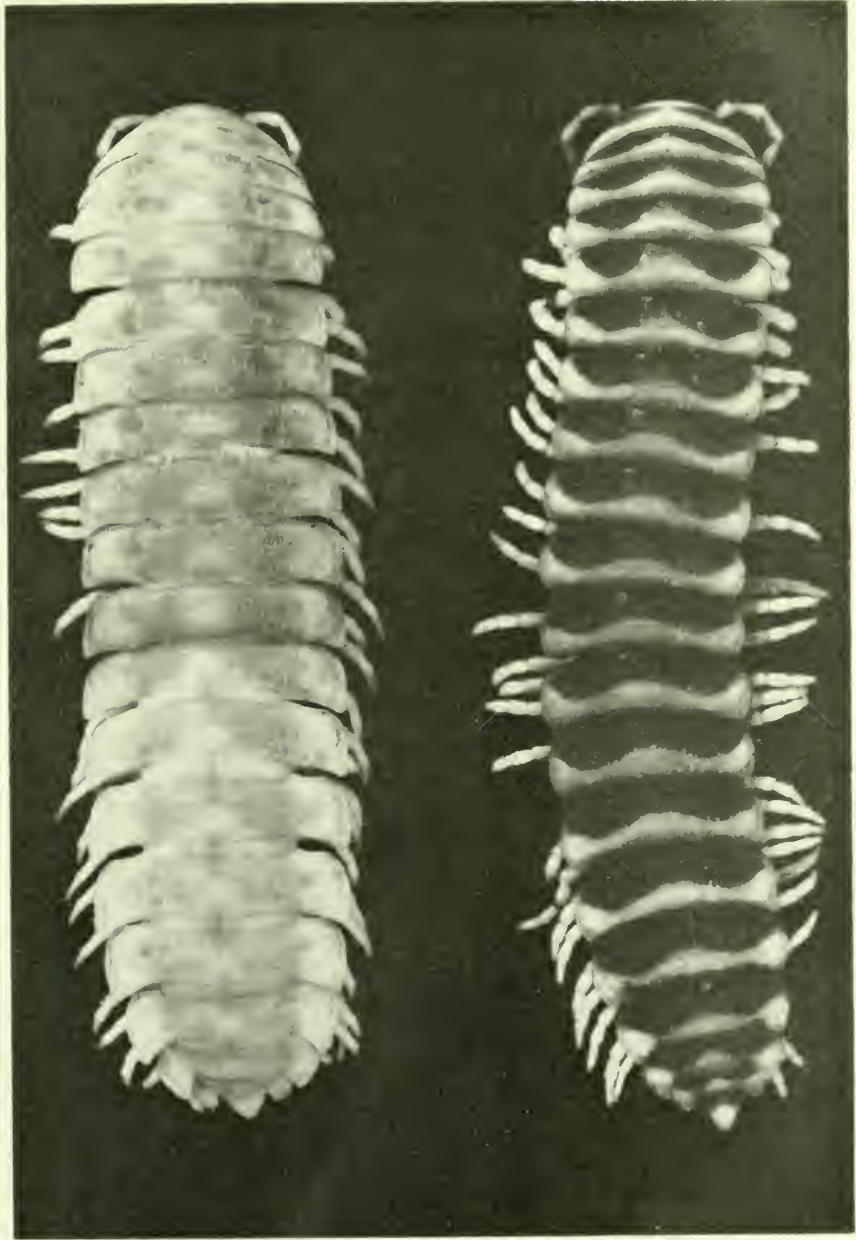
The pronounced geographic variation in color pattern obtaining in *Cherokia* imposes a higher premium on knowledge of the living colors in this genus than in most other. Much of the material of *C. georgiana latassa*—with which I have had little field experience—was sent to me by Leslie Hubricht soon after collection, with the colors still fresh. Of *C. g. georgiana* and *C. g. ducilla*, which intergrade extensively, I have been most fortunate in being able to collect living specimens at more than 30 localities, chiefly through two summers of residence at the Highlands Biological Station. This first-hand knowledge of subtle color details has facilitated numerous inferences about microevolution which could never be made from faded specimens. Most of the work with color characters was done during the summer of 1958 through the aid of a National Science Foundation grant administered by the Highlands Station. Special thanks are due its director, Professor Thelma Howell, for her continued interest and material aid during the past decade of my summer investigations at Highlands.

For the loan of material, I am indebted to Dr. Ralph E. Crabill, Jr. (USNM), Dr. Willis J. Gertsch (AMNH), and Drs. Henry S. Dybas and Rupert L. Wenzel (CNHM). Those who have generously donated specimens are named in the lists of material examined, but special mention must be made of the outstanding contribution of Leslie Hubricht, whose superb collections form the basis of this revision.

TAXONOMIC CHARACTERS

The most casual inspection of *Cherokia* specimens from different parts of the generic range reveals a remarkable amount of geographic variation in body form, shape of the paranota, color pattern, and details of the gonopods. In addition, there is considerable individual or sporadic local variation in tergal sculpture, convexity of the dorsum, shape of the caudalmost paranota, and size of the coxal and prefemoral spines, but these low order variations may for the present be subordinated in favor of those which are correlated to some extent with distribution. Although clear cut and easily defined, such characters are by no means easy to analyze. As will become apparent, only infrequently do we find that two or more characters coincide, a fact which renders their utility in the recognition of taxonomic groups somewhat subjective.

BODY FORM: Perhaps the most striking variation observed in *Cherokia* is in body form—e.g., the ratio of greatest width to length. Specimens from the Great Smokies are so different from lowland animals in this respect that without knowledge of the intermediates which occur, one would naturally assume full specific distinction. The narrow graceful body of a specimen from the Smokies is in strong con-



Two specimens of *Cherokia* photographed in dorsal aspect to show the difference in body proportions between two subspecies. On the left, *Cherokia georgiana georgiana* from Chatooga Ridge, Oconee County, South Carolina; on the right, *C. g. ducilla* from Indian Gap, Sevier County, Tennessee. Despite the differences in form and the probable inability to intermate, these two subspecies are connected by a spectrum of intermediate populations in extreme western North Carolina.



trast to the broad robust form occurring in north Georgia, as can be seen from the accompanying photograph (see plate 1) of two specimens typical of the extremes in this variable character.

Determination of relative body width is by no means a precise operation, yet by uniform measuring techniques the error is held to a minimum. Naturally only well-preserved specimens can be used, with the body lying flat and straight, and not noticeably telescoped. In this position nearly all specimens have the first few segments a little arched (due to the curling reflex) and the collum declined at an angle of about 45 degrees. Efforts to reduce this arching usually result in either breaking the specimen or unduly extending the front end. Measurements have been made with vernier-scale calipers, length to an accuracy of 0.5 mm. and width to 0.1 mm. The greatest width normally occurs at the midbody segments but may be further caudad. The width was in every case checked by moving the calipers along the body until the widest segment was located.

The simple ratio of width divided by length yields a value which ranges from 19 to 28 percent. At any given locality from which a series of measurements is available, the range of variation in this ratio is not over 3 percent, and this magnitude is almost certainly due to the errors inherent in measuring the length of preserved specimens. Nonetheless, the mean value of the w/L ratio, plotted cartographically from as many samples as possible, produces an interesting sort of distributional pattern. Figure 1 is a map reflecting geographic variation in body form, the isophenes inclosing populations the mean w/L ratio of which falls within the specified limits.

From this map, it is seen that broad specimens with a ratio of 26 percent or more occur over most of the generic range, chiefly but not exclusively in low country. In the high ranges of the Great Smoky-Unaka Mountains the ratio is less than 24 percent, while populations with intermediate values (24 to 26 percent) occupy a large part of southwestern North Carolina in the Cowee, Nantahala, and Balsam ranges.

It has been found desirable to rely largely upon ratios derived from male specimens, these generally being in greater supply and usually easier to flatten and measure. A large number of females were studied, however, and these show a certain amount of sexual dimorphism in being slightly wider at any given locality than the males, the w/L ratio of the females being about 1 percent higher.

SHAPE OF PARANOTA: Close examination of the lateral projections of the metazonites shows the occurrence of two rather distinct forms. In one of these forms (fig. 3,a), the paranotal scapuloar (new term, from the Latin "scapula," a shoulder, and "ora," the rim of a shield) as seen in dorsal aspect are strictly marginal; that is, they form the

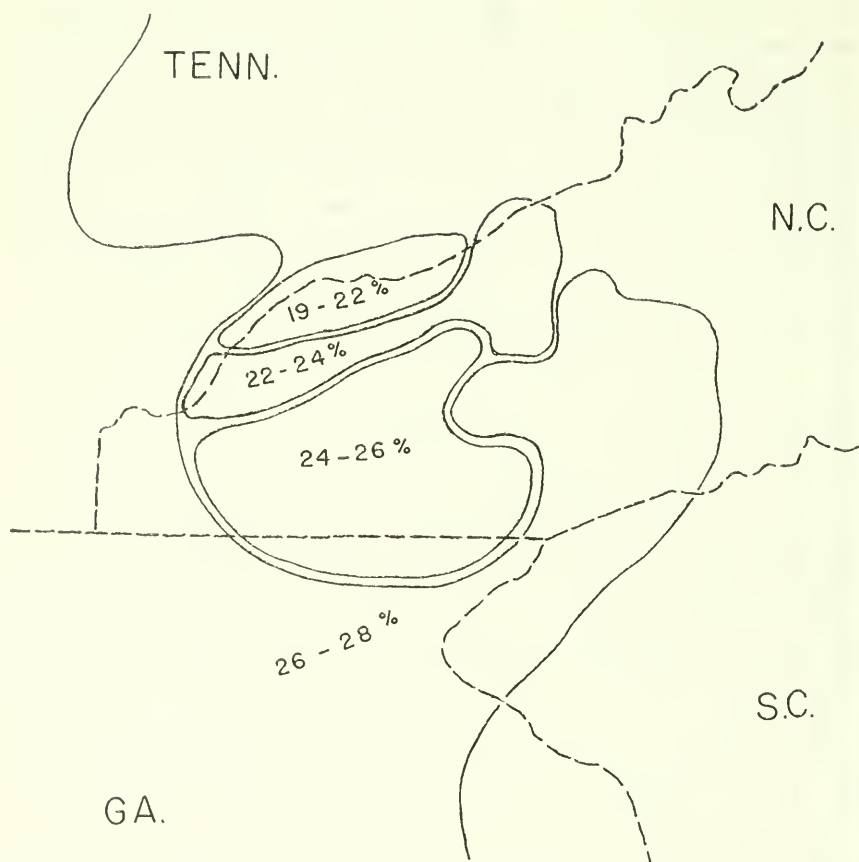


FIGURE 1.—Extreme western North Carolina and adjacent parts of Tennessee, Georgia, and South Carolina, showing the distribution of body proportion in *Cheroikia* in the southern Blue Ridge. The isophenes enclosing the 26–28 percent interval extend south, west, and north to encompass the remaining majority of the range of the genus (see also fig. 7).

anterior rim of the paranota on all segments. The other form (fig. 3, *b*) differs in that the scapularae turn rather abruptly mesiad at the paranotal shoulder and are submarginal in position, with a considerable portion of the cephalic face of the paranota visible below and in front of them as seen in dorsal aspect. The map (fig. 2) shows the distribution of these two structural variants, which are apparently largely complementary.

In the occurrence of two discrete paranotal types we find a situation not hitherto observed in the xystodesmid genera studied in detail, although a similar relationship may occur in the related genera *Rhyso-desmus* and *Boraria*, both of which are known to be highly variable in general body form.

SHAPE OF SOLENERITE OF GONOPODS: In *Cherokia* the male gonopod (fig. 4,a) is superficially bifid distally. This impression is created by a subtriangular, retrorse solenomerite (SLM) and a normally smaller subapical spur. Examination of the gonopods under considerable magnification reveals that in the mountains of North Carolina there is a tendency for the solenomerite to become elongated with evenly converging sides (fig. 4,f), while over most of the remainder of the generic range, the solenomerite is much shorter and frequently somewhat curved, with one margin convex and the other concave (fig. 4,e). Unfortunately this variation is not as constant as might be wished; its distribution is fraught with exceptions and intermediate forms.

OCCURRENCE OF TIBIOTARSAL MARGINAL SPUR: In most specimens of *Cherokia* the coxal margin of the tibiotalrusus is provided with a distinct acute spur of varying size (fig. 4,b, TTS). In the Great Smokies, the spur is typically absent in all specimens. Southward, the percentage of absence decreases to 88 at Soco Gap in the Balsams, 68 in the Cowees, 12 in the Nantahalas, 44 around Highlands, North Carolina, and 36 at Brasstown Bald, Georgia. Throughout the remainder of the generic range, the spur is absent in less than 25 percent of the specimens examined.

The inference to be drawn from these phenomena is that the spur is occasionally absent in most of the populations of *Cherokia*, but becomes progressively suppressed in the southern end of the Blue Ridge and totally so in the Smokies.

VARIATION IN COLOR PATTERN: Modifications of color pattern in *Cherokia* are numerous and complex, and full appreciation of such characters can be had only through knowledge of living colors. This information is available at least for the critical region of the western Carolinas and north Georgia, and permits some inferences on evolution and migration routes in the mountainous region where the genus is, structurally least stable. The different patterns may be classified roughly as follows:

- A. Bimaculate, no median row of spots
- B. Trimaculate
 - 1. Small median spots
 - 2. Broad median spots
- C. Banded
 - 1. Red bands superimposed on the trimaculate phase
 - 2. Bands formed by very wide median spots
 - 3. Complete, characteristically wide crossbands.

There is a sort of progression represented by this breakdown, from A through B1, B2, and C2 to C3. Normally, however, each group is isolated geographically.

Bimaculation has been observed only in one sample, a small series from Lee County, Alabama, on the southern periphery of the generic

range. Freshly preserved material showed only the yellow paranotal spots, with no trace of any median spots. However, the probable derivation of this phase from the normal trimaculate pattern can be inferred from a large series (35 specimens) from a single locality in Transylvania County, North Carolina, on the extreme northeastern edge of the range. Here there is a strong tendency for the median spots to diminish in size, especially anteriorly. The characteristics of this series are summarized as follows:

<i>Condition</i>	<i>Males</i>	<i>Females</i>
Collum immaculate	1	0
Collum with anterior spot only	4	0
Collum with large anterior and very small posterior spot . . .	3	7
2nd segment without median spot	3	0
2nd and 3d segments without median spot	2	0
Collum and following segments with small but distinct spots .	7	7

Immature specimens taken at the same time and place are rather typical of last-stadium forms of the genus; that is, they have moderately large and distinct median spots, a fact permitting the inference that departure from the trimaculate condition is an evolutionary specialization.

Broad median spots, usually lunate or crescentic in form, occur at various places in the range but are most characteristic of the populations in the Smokies, Balsams, and Unakas. Here the spots are up to 50 percent of the width of the segments, and in some females nearly or actually touch the paranotal spots. The same general pattern recurs in the Kentucky segment of the *Cherokia* population.

The pattern characteristic of the population in much of the western Carolinas and adjoining states is that of small yellow paranotal spots, with yellow median subtriangular spots of equal size. This pattern has been seen in the Blue Ridge of South Carolina and Georgia, in the Nantahalas and Cowees of North Carolina, and in the ranges west of the Unakas in southeast Tennessee.

An interesting variation in the pattern occurs in a restricted area of the Blue Ridge. In this phase the three yellow spots of each segment are connected by a transverse chestnut or reddish band, the intensity of which increases adjacent to the yellow spots and produces a most attractive effect. In addition, the legs of this form are pink instead of the typical yellow. Such specimens have been found at four localities: on Chatooga Ridge, north of Mountain Rest, South Carolina; the gorge of the Chatooga River south of Cashiers, North Carolina; around Highlands, North Carolina; and at Walnut Creek Gap in the Cowee Range, 8 miles northwest of Highlands. At all of these places, this variation occurs along with the typical form. None has been found beyond this limited range, a condition shown by the

light stipple in figure 6. Altitudinally the variation ranges from about 1,500 feet at Chatooga Ridge to 4,800 feet at Walnut Creek Gap.

Crossbands formed by lateral prolongation of the median spots are characteristic of the majority of the *Cherokia* population over Georgia, Alabama, and a part of Tennessee. In this phase the band is widest at the middorsal line and pinches somewhat at the base of the paranota.

True crossbands, transversely parallel and rather broad, occur at widely separated localities and doubtless represent the end product of local specialization. In the extreme northwest, on the western Highland Rim of Tennessee, occurs a form with bands almost half as wide as the length of the metazonite and deep red in color. This population clearly derives from adjacent forms to the southeast, which are trimaculate with red or chestnut, but a good picture of the situation cannot be gained at the present with the few available collections from northwest Alabama.

Of more immediate interest is the independent recurrence of a yellow-banded form at two isolated places in the southern Blue Ridge. One of these occupies the northwestern end of the Cowee Range in Macon and Jackson counties, North Carolina. In this region, river valleys do not constitute formidable barriers to gene flow, but the intercalated mountain ranges afford by their height something analogous to the effects of insular isolation, local populations normally attaining greatest differentiation and stability at higher elevations. The *Cherokia* occurring on Cowee Bald (elevation 4,800 feet) is a striking animal—glossy black with broad lemon-yellow crossbands and legs—and the population there seems to be a homogeneous one. Cowee Bald is set off from the rest of the range by a rather low gap just northeast of Franklin, North Carolina, but the development of its local form is presaged by the occasional collection of similar appearing individuals as far to the southeast as Highlands, North Carolina.

Should local populations in this genus ever be considered as eligible for subspecific names (a course which is avoided at the present writing), the Cowee population would seem at first to be an outstanding contender for a name. But its claim is challenged by an identical population which has developed in Cades Cove, on the western base of the Smokies in Blount County, Tennessee. In this case the transition from the trimaculate population to the south is seen in a collection from the southern edge of Cades Cove, containing both forms and one intermediate. This banded population is, in a sense, as isolated as its counterpart on Cowee Bald, for although it is geographically contiguous to the northeast with the narrow-bodied form of the Great Smokies, it seems very unlikely that gene flow takes place between them. In addition to the difference in size and pro-

portions of the two, they are separated by a considerable difference in elevation.

Aside from the variation in dorsal coloration, there is some local differentiation in the pigmentation of other parts. Normally the legs and underparts of *Cherokia* are yellow, but in the Smokies the pleural regions and anal valves become nearly black; in the vicinity of Highlands, North Carolina, the legs may be pink instead of yellow. In xystodesmids generally, the legs assume the same color as the paranota and are brightest on the distal joints—those which extend beyond the paranota when the animal is walking, a coloration giving the impression of much greater body width.

EVALUATION OF CHARACTERS: From the preceding accounts, one can draw several inferences. To begin with, five characters have been detected which seem to vary significantly with respect to the spatial distribution of the genus. As a complicating factor, in only a few cases do any of the variational phases coincide in any given region, and at least one character—color pattern—is subject to a great amount of localized regional variation, sometimes three separate color phases occurring together. What significance is to be assigned to these structural variations in the definition of taxonomic categories?

Of the five characters, one is represented by two quite different forms, which are geographically exclusive in their distribution (fig. 2). This character is the structure of the paranotal scapulorae. Most of the specimens seen so far fall readily into one category or the other and make a strong case for full specific value. There is, however, some evidence suggesting that the geographic and morphologic gaps between these two populations are more apparent than real, something to be discussed under a subsequent heading (page 258). There is reason to believe that intergradation between the two populations occurs in extreme western Georgia, an area from which no material was available. Since other structural characters in the genus, such as male gonopods, size, body form, and color pattern, transgress the boundary between the paranotal types, the latter are considered as diagnostic of a wide-ranging western subspecies of *Cherokia georgiana*, rather than of a different species.

Of the various names which have been based upon specimens of *Cherokia*, all apply to the form characterized by submarginal scapulorae. Of them, the oldest available name is Bollman's *Fontaria georgiana*, proposed for specimens from Macon and Tallulah, Georgia. To the best of my knowledge, there is no name available for the population of Tennessee and Alabama with marginal scapulorae, and a new one is herein proposed.

The latter is quite uniform over its range with respect to body form, but the distribution of the more eastern *georgiana* includes specimens

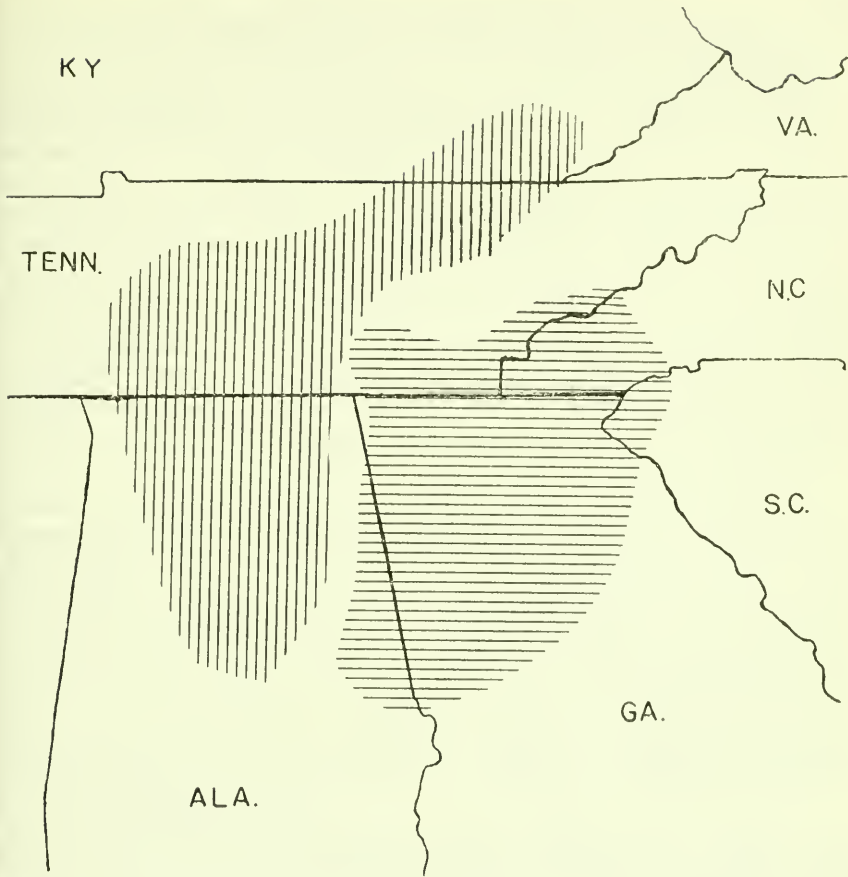


FIGURE 2.—Distribution of the two paranotal forms discussed in the text and illustrated in figure 3, *a-b*. The open area between the two patterns represents merely a gap in the distributional data. Vertical shading represents the extent of marginal scapuloarea, and horizontal that of submarginal.

ranging from 20 to 28 percent in the ratio of body width to length (fig. 1). Over most of this area, comprising the northern half of Georgia and the western part of South Carolina, the ratio is fairly stable at 26–28 percent, but as the species invades the high country of the Blue Ridge, there is a striking tendency toward a narrowed body form with much lower w/L ratios, the trend culminating in the high reaches of the Unicoi and Great Smoky Mountains. Even with this clinal variation, however, one can utilize the fact that the change from the normal broad body to the unusually narrow form occurs over a relatively small area, and that the narrow form maintains itself as a stable unit in a region where several other characters likewise attain their strongest development. Despite the great dissimilarity of the

extremes, there is an area of intermediate types, and body form can be given a value no higher than that of a subspecific character.

Nearly the same summary can be made concerning the distribution of the tibiotarsal spur of the gonopod, which becomes obliterated in a more or less sporadic fashion throughout the range of the species *georgiana*, but which is invariably wanting in the region occupied by the slender-bodied subspecies. From a normal absence of about 25 percent in most of the generic range, the tibiotarsal spur is absent from 36 percent of a sample from Towns County, Georgia, from 44 percent of the population around Highlands, North Carolina, and from 66 percent of specimens collected in the Cowee Mountains. It is missing in 100 percent of the millipeds from the Great Smokies. Here is a case of variational coincidence which certainly reinforces the desirability of recognizing the slender-bodied population as sub-specifically distinct.

The variation of color pattern hardly needs review. The tendency for localized color races is pronounced, and if subspecies were recognized on this basis alone, one could name about eight. Since most such populations would not correlate with groupings made on more fundamental structural bases, it is felt that in *Cherokia*, at least, no practical ends would be served by the wholesale application of names to color forms. This view is particularly true when we recall that one distinctive phase has arisen independently at two different and widely separated localities, and that elsewhere two or more color phases occur together both typically and with various intermediate forms.

At only one place does a color pattern phase coincide with other local structural divergence—again in the Smokies, where, for instance, the typical pale color of the pleurites is replaced by dark burnished brown or dilute black. The combination of at least three distinct localized character variants makes it impossible to discount the importance of evolution in this region, even though all the characters merge into the more typical phases of *C. g. georgiana* by gradual gradations, which however do not progress at the same rates of modification.

In summary, working with geographic variation in paranotal form, body proportions, and coloration, we can divide *Cherokia* into three mutually exclusive populations, a partition which is supported by such other characters such as those of the gonopods and cyphopods (fig. 5). However, either direct or presumptive evidence indicates that all these populations merge where their ranges meet, and should be regarded as geographic races of a single species, *Cherokia georgiana* (Bollman.) One is recognizable by a very distinct modification of the paranota which holds uniform over a rather extensive geographic range. The other two, which share another paranotal form, differ from each other in three or four characters. The lowland population

of Georgia carries the name of the nominate subspecies. That which occurs in the Great Smokies may be recognized as the third subspecies. A name is already available for this form, *ducilla* Chamberlin, based on specimens from Soco Gap, North Carolina.

Genus *Cherokia* Chamberlin

Cherokia Chamberlin, 1949, p. 3.—Hoffman, 1950, p. 23.—Chamberlin and Hoffman, 1958, p. 26.

TYPE SPECIES: *Fontaria georgiana* Bollman 1889, by original designation.

DIAGNOSIS: A genus of moderate-size, compact xystodesmids of variable form and appearance, with the following characters in common:

Head smooth and polished, vertigial groove evident but not terminating in a shallow depression. Facial setae as follows: four supra-antennal, two interantennal, two subantennae, and two frontal setae. Genae almost flat, without median depressions, their ends not surpassing margin of cranium. Antennae long and slender, articles 2-6 subequal in size and shape, with four sensory cones.

Body shape variable, either broad (the width up to 28 percent of length) or very narrow (as little as 19 percent of length), depending upon width of paranota. The latter slightly interrupting slope of dorsum, their dorsal surface coriaceous, the lateral edges smooth and rounded, pores opening dorsally in elongate pyriform peritremata, the pore formula normal.

Sterna smooth and glabrous, forming a gradually inclined podosternum between the legs, this area divided by a transverse groove, and produced into small conicles at the base of each leg; pleural regions smooth and unmodified. Sterna of 4th and 5th segments of males with low rounded knobs between the legs.

Coxae of male gonopods moderate size, cylindrical, attached to a weakly sclerotized but distinct sternite; lacking apical apophyses or other modifications, socket of solenite well removed from the distal margin. Telopodite attached to coxite at a right angle, extending cephalad between legs of 6th segment, the two gonopods parallel with the distal ends usually in contact; prefemora elongate, tapering distad, densely setose mesially, with a short simple acicular prefemoral process. Remainder of telopodite set off from prefemur by a conspicuous, flexible, cingulum but continuing in the same axis, distally with a short falcate process (here provisionally regarded as tibia) projecting mesiad from the mesial margin and with two terminal tarsal processes, a slender parasolenomerite from the upper margin, and a short recurved solenomerite from the lower.

Gonopod aperture very wide, almost diamond-shaped prozonite; of 7th segment reduced to a mere thin transverse vestige in front of the aperture.

Cyphopods (fig. 5) very strongly compressed, the inner valve much smaller than the outer; receptacle completely lost, a detail which separates *Cherokia* from all other xystodesmid genera. Epigynal region not differentiated or modified.

RANGE: Southeastern United States, in the Piedmont, southern section of the Blue Ridge Province, and the Cumberland Plateau. All of western North Carolina south of the French Broad River, extreme western South Carolina, the northern half of Georgia and Alabama, most of the Cumberland Plateau as well as the Valley and Ridge Province south of the French Broad River in Tennessee, and extreme southeastern Kentucky (Harlan, Bell, and Laurel Counties).

SPECIES: One, *Cherokia georgiana* (Bollman), with three subspecies, separable by the contrasts stipulated in the key given below.

Key to Subspecies of *Cherokia georgiana*

1. Scapulae marginal, anterior surface of paranota concealed in dorsal aspect (fig. 3,a); central Alabama north through the Cumberland Plateau to southeastern Kentucky **georgiana latassa**, new subspecies
Scapulae submarginal, in dorsal aspect anterior face of the paranota is exposed (fig. 3,b); distribution not as outlined above 2
2. Width of body 26 to 28 percent of the length; tibiotarsal marginal spur of male gonopods (fig. 4,b, TTS) normally present; color of legs and undersides whitish to yellowish **georgiana georgiana** (Bollman)
Width of body 19 to 24 percent of the length; tibiotarsal marginal spur of gonopods absent from virtually all specimens; color of pleurites and anal valves brown to nearly black; Great Smoky and Unaka Mountains, intergrading widely with the preceding in western North Carolina.
georgiana dueilla (Chamberlin)

Cherokia georgiana georgiana (Bollman)

FIGURES 3,d; 4,e; 5,a; 6; 7

Fontaria georgiana Bollman, 1889, p. 344.

Fontaria tallulah Bollman, 1889, p. 344. Type locality: Tallulah Falls, Habersham County, Georgia; type specimens, USNM 2302, two females.

Mimuloria furcifer Chamberlin, 1940, fig. 3, p. 282. Type locality: Bent Creek Experimental Forest, Buncombe County, North Carolina; type specimen, Chamberlin collection, male.

Mimuloria georgiana Loomis, 1943, p. 402.—Chamberlin, 1946, p. 151.—Loomis and Hoffman, 1948, p. 52 (in part).

Dynoria parvior Chamberlin, 1947, fig. 4, p. 10. Type locality: Neel Gap, Union County, Georgia; type specimen, Chamberlin collection, male.

Cherokia georgiana Chamberlin, 1949, fig. 1, p. 3.—Hoffman, 1950, figs. 9–12, p. 23.—Chamberlin and Hoffman, 1958, p. 26.

TYPE SPECIMENS: Male holotype and female paratype, USNM 750, from Macon, Bibb County, Georgia, collected in 1887 by L. M. Underwood.

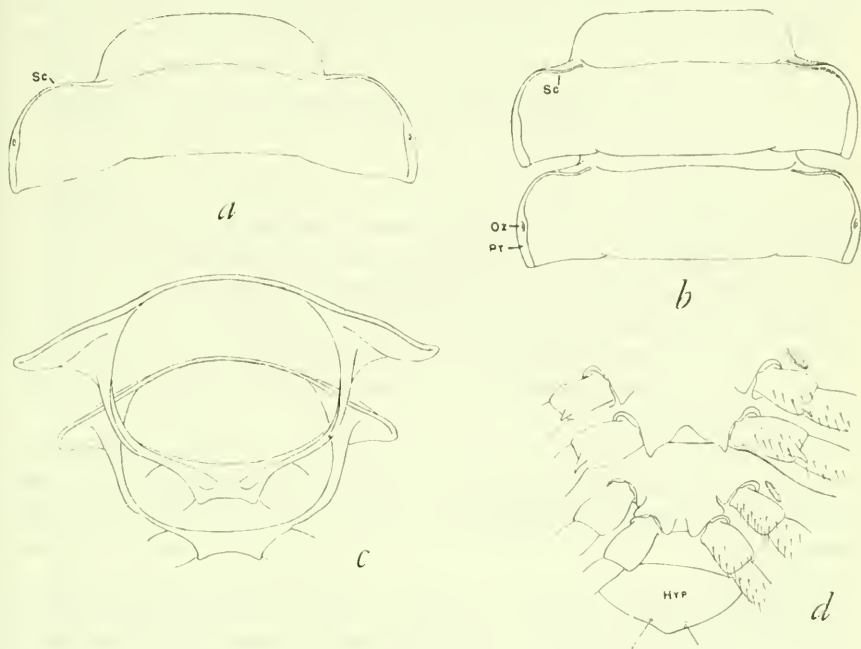


FIGURE 3.—Structural details of *Cherokia*: *a* and upper part of *c*, dorsal and caudal aspects of a midbody segment of *Cherokia georgiana latassa* from Jackson Co., Alabama; *b* and lower part of *c*, the same views of *C. g. ducilla* from Soco Gap, North Carolina; *d*, ventral aspect of caudal end of body of *C. g. georgiana* from Banks Co., Georgia, showing sternal spines, bases of legs, and hypoproct. Abbreviations: Hyp., hypoproct; Oz, ozopore; Pt, peritreme; and Sc, scapulora.

DIAGNOSIS: A broad, flat subspecies (w/L 26–28 percent) of *Cherokia georgiana* of which the scapulorae are submarginal and expose the anterior face of the paranota.

DESCRIPTION: Two male specimens from Banks County, Georgia, were compared with the holotype and are virtually identical with it. A broad, compact, robust form, the width/length ratio from 26 to 28 percent, paranota only slightly depressed from the horizontal and interrupting slope of the slightly convex dorsum. Metazonites of segments 5–16 of essentially full width (8.5–9.5 mm.); width of collum about 7.0 mm.

Head capsule normal in appearance, oval, convex, smooth and polished. Setae of vertex 2–2, forming a strongly procurved row with the innermost seta of each pair set a little lower on the vertex than the outer, the space between the pairs greater than the distance between

the setae of each. Two narrowly separated setae in the isthmus between the antennae, and another pair of more widely separated setae at the level of the lower edge of the sockets. A pair of widely spaced frontal setae, and a submarginal row of three closely set setae on the lower part of each gena. Clypeal setae long and closely set, in a row of 30 or more; labral setae equally long but wider spaced, about 20 in the series. Genae not margined, nearly flat, with only a vague median depression; the ends broadly rounded and not surpassing adjacent margin of cranium.

Antennae long (8-9 mm.) and slender, reaching back to caudal margin of 3d segment. Article 1 broadest, short, cylindrical, glabrous. Articles 2-6 subequal in size and shape, each slightly clavate. Article 7 very short, slightly conical, the distal edge not inturned between the 4 small widely separated sensory cones. Antennae nearly glabrous proximally (the setae of article 2 mostly on the ventral side), becoming increasingly invested distally, the setae of article 6 very numerous, long, and procumbent.

Collum broad, smooth or finely coriaceous, its caudal edge almost transverse. Lateral thirds of the anterior edge strongly curved caudolaterad and strongly margined, forming a bluntly acute angle with the posterior edge. Lateral ends of collum not exceeding width of following segments.

Tergites of body segments smooth medially, becoming increasingly coriaceous on the paranota, especially toward the end of the body. Paranota slightly depressed, inclined cephaloventrad, much longer than median length of the metatergites. Caudal edges of paranota directed caudolaterad on all segments posterior to 4th, becoming increasingly angular caudad; paranota of segment 18 forming almost true isosceles triangles, the apices pointing directly caudad. Paranota of segment 19 forming blunt lobes including only half the length of the epiproct.

Caudal edges of paranota not margined, lateral ends set off as elongate, nearly parallel-sided peritremata (fig. 3, *b*, PT), the pores opening dorsally near cephalic end of swelling, at about the midlength of the paranota. Anterior to the pore, the peritreme is extended forward as a strong, high marginal ridge (the scapulora), its free edge reflexed caudad over the deeply impressed paranotal surface just behind. In dorsal aspect the scapulae extend in an irregular line directly mesiad from the scapular convexity, and reveal the anterior face of the paranotum sloping downward. At juncture with the body cylinder the scapulae are so strongly reflexed caudad as to become appressed and merged with the dorsum.

No distinct interzonal furrow present, the surface of metazonites somewhat lower than that of prozonites, which it meets at a sharply

defined fault line. Dorsolateral rugosity of metazonites not carried over onto prozonites, which are completely smooth. Aside from coriaceous texture, the metazonites are provided with minute setiferous tubercles, most conspicuous posteriorly, which tend to form three irregular transverse rows. The caudalmost of these rows normally consist of about 22 (up to 28 in some cases) tubercles, three widely separated near the caudal paranotal edge, and 14 to 16 set much closer across the dorsum itself. The other two rows are less regular in number and distribution, the widely spaced tubercles ranging from 10 to about 16.

Epiproct evenly conical in dorsal aspect, its surface mostly smooth except for some basal striations and distinct setiferous tubercles, the apex decurved slightly and bearing four terminal compound setae. Peripheral areas of disc of anal valves vertically costate, the median area elevated and smooth, with a single paramedian setiferous socket. Free edges of valves produced into distinct marginal swellings, becoming thicker upwards, the point of greatest breadth including the marginal seta. Hypoproct a broadly oval plate (fig. 3,*d*), the surface smooth and unmodified, paramedian apical setae widely separated from each other and well removed from the caudal margin of plate. Apical projection very small or wanting.

Pleural areas unmodified, surface finely granular except for the caudal edge, which is set off as a depressed, smooth, parallel-sided margin, the edge strongly sigmoidally curved ventrad, ending on dorsal curve of coxal socket. Interzonal furrow more definitely formed down sides and across venter.

Sternal areas smooth and glabrous, tending to form a raised area (podosternum) between the legs but this area sloping gradually cephalad to the interzonal furrow. Each podosternum divided by a vague transverse groove which becomes accentuated laterally where it is preceded by a low conical knob formed by the sternum at the base of the anterior leg pair. Sternum between posterior leg pair projecting shelflike caudad, its margin transverse except for the strongly produced corners, which become increasingly larger and more acute back to the 18th segment (fig. 3,*d*). Sternum of 7th segment flat, without subcoxal spines or very low ones. Midbody legs separated by a distance up to 2.5 mm., equalling or exceeding length of prefemur. Sternum of 4th segment of male produced into two low rounded knobs between the legs, anterior leg pair of 5th segment separated by two larger, more transverse, and cephalically directed processes. Sternum of 6th segment broad, flat, unmodified.

Legs long, those of midbody segments up to 9.0 mm., the joints in decreasing order of length, 3-6-2-5-4-1. The basal two joints glabrous but for a ventral row (coxa) or field (prefemur) of

setae, other joints with setae becoming increasingly larger and denser distally, the four terminal joints each with a distal whorl of large robust setae, tarsal joint with most vestiture on its dorsal (outer) surface. Tarsal claw long and evenly curved except on leg pairs 3-15 of males, where they are bisinuate and compressed, distinctly ellipsoidal in cross-section, the upper edge thin and carinate.

Prozonite of 7th segment reduced to a mere thin vestige mid-ventrally in front of gonopod aperture. The latter broadly transverse, up to 2.4 mm wide, its caudolateral edges elevated and flared laterad,

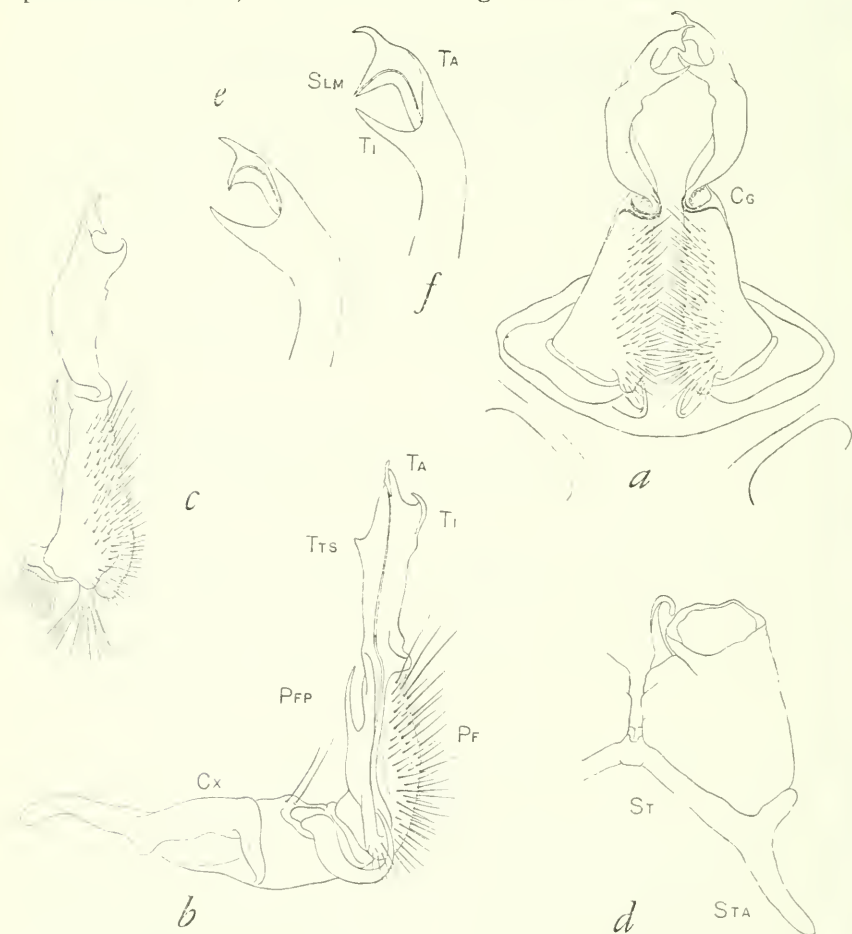


FIGURE 4.—Gonopod structure in *Cherokia georgiana latassa* (a-d), *C. g. georgiana* (e), and *C. g. ducilla* (f): a, ventral aspect of gonopods in situ; b, mesial aspect of left gonopod; c, sublateral aspect of right gonopod; d, cephalic aspect of gonopod sternite, its apodemes, and coxa of right side; e, ventral aspect of tibiotarsal region; f, same, slightly enlarged, of another subspecies. Abbreviations: Cg, cingulum; Cx, coxa; Pf, prefemur; Pfp, prefemoral process; Slm, solenomerite; St, sternite; Sta, sternal apodeme; Ta, tarsus; and Ti, tibia.

caudal rim between 8th leg pair set off by a low marginal ridge, the adjacent sternal area narrow and depressed. Gonopods rather small, the coxae normally retracted into the body, the elongate, nearly straight telopodites exposed, parallel to each other, directed cephalad between the legs of the 6th segment. Prefemur elongate, setose, the setae becoming longer distally, coxal side provided with a short, acicular prefemoral process. Gonopod in mesial aspect almost identical with that of *C. g. latassa* (fig. 4,b), the distal end with a rather short subtriangular solenomerite and nearly straight subapical process (fig. 4,e).

Epigynal region of 3d segment of females without special lobes or other modifications. Cyphopods elongate-reniform in outline, the basal two-thirds with scattered large setae, the operculum with longer and more profuse vestiture. Width of outer valve nearly uniform, not somewhat greater near the base as apparently is the case in the other two subspecies (fig. 5,a).

Dorsum glossy blackish, with the paranotal and broad median series of spots yellowish orange, the underparts whitish gray with the legs becoming yellow distally. The median dorsal spots are sublunate, and extend laterad almost to the paranota.

VARIATION: The body form of the typical subspecies is quite uniform over its range. Some minor geographic variation can be noted, however, for several structural details.

Male specimens from eastern Alabama and most of Georgia are provided with fairly conspicuous subcoxal sternal knobs on the 7th segment. These become reduced in the mountain region and are obliterated in the intergrade population of western North Carolina. The solenomerite of the male gonopod tends to increase in length northward.

The color pattern is somewhat variable. The population of extreme eastern Alabama appears to be bimaculate. In central and northern Georgia the median spots are enlarged and lunate in form and in the males often contact the lateral series of spots and forming transverse bands of yellow. In southeastern Tennessee the three rows of spots are of about the same size, except in the western foothills of the Great Smokies in Blount County, where a local population has developed striking crossbands. It is of some interest to note that in the same region specimens of the normally trimaculate *Apheloria montana* are likewise transversely banded, and we may have a case of mimicry or a very improbable coincidence.

The largest male specimen of *C. g. georgiana* measured is from Banks County, Georgia: 9.2 mm. wide and 34.5 mm. long. The largest female is from Pickens County, South Carolina: 9.0 mm. by 37.0 mm.

SYNONYMY: Dissatisfied with the full specific status originally accorded the various new names proposed in this genus, subsequent authors have at one time or another considered them all to be strictly junior synonyms of *georgiana*, a feeling tentatively embodied in Chamberlin and Hoffman's "Checklist of the millipeds of North America." With diagnostic characters in *Cherokia* now being drawn from nonsexual modifications, a reappraisal of the names is very much in order.

Fontaria tallulah was based by Bollman upon two female specimens collected by Underwood at Tallulah Falls, Habersham County, Georgia. The name thereupon fell into complete obscurity and was not investigated until 1949, when I had the opportunity to search for topotypes. Despite unfavorable climatic conditions, I was able to obtain in the penultimate instar two female millipeds which matched Bollman's description closely. These specimens were later found, on direct comparison, to be conspecific with the the types of *tallulah*. The name is based upon a population of *Cherokia* which cannot be separated from typical *georgiana*, Bollman apparently not having realized that his types were immature and that the final moult appreciably modifies the color pattern. My

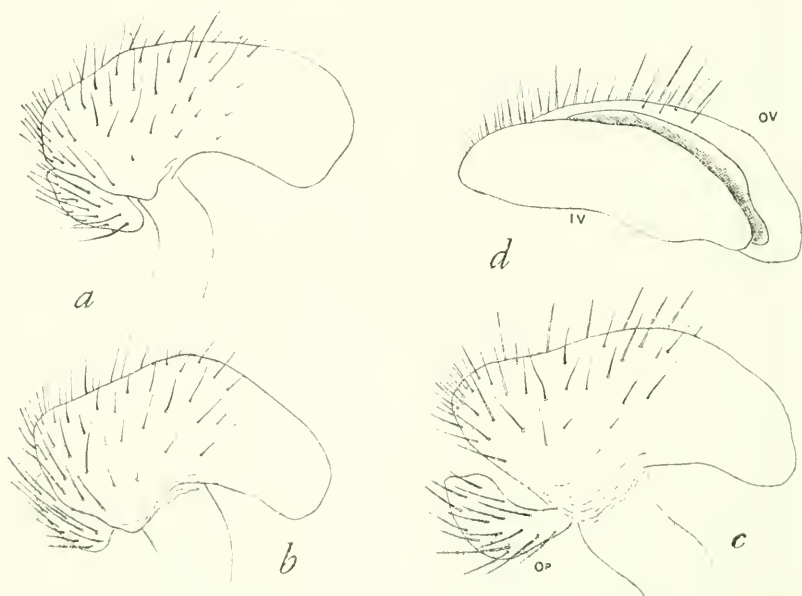


FIGURE 5.—Cyphopods of subspecies of *Cherokia georgiana*: a, *C. g. georgiana*, Stephens County, Georgia, lateral aspect of right cyphopod; b, *C. g. ducilla*, Sevier County, Tennessee, same aspect; c, d, *C. g. latassa*, Jackson County, Alabama, lateral and mesial aspects of right and left cyphopods, respectively. Abbreviations: IV, inner valve; OV, outer valve; and Op, operculum.

paper of 1950 placed *tallulah* into a genus for the first time since the partition of the old name *Fontaria*, and correctly regarded it a junior synonym of *georgiana*, which has a one page priority in Bollman's paper.

Exactly 50 years after the proposal of the name *georgiana*, Chamberlin (1939) described a new xystodesmid under the name *Mimuloria ducilla*, the types coming from Soco Gap, North Carolina. The diagnosis was very brief, but included an accurate illustration of the gonopod. Loomis (1943) subsequently considered *ducilla* to be a synonym of *georgiana*, in which he was followed by my later discussion of the matter, largely because of the gonopod structure. I have now studied two series of topotypes of *ducilla*, both obtained personally, and find that the population at Soco Gap is representative of the narrow-bodied montane subspecies of *georgiana*, to which the name *ducilla* must now be applied.

Mimuloria furcifer was described also by Chamberlin, on the basis of four specimens collected by A. S. Pearse in the Pisgah National Forest near Asheville, North Carolina. The form was contrasted only with *ducilla*, with differences in size, color, and gonopod minutae being noted. These are all differences which are here considered to distinguish *ducilla*, but it was apparently not realized by Chamberlin that *furcifer* might be the same as *georgiana*. After several unsuccessful visits to the type locality, I was finally rewarded in July 1958 by the collection of several immature specimens, which, when reared to maturity, turned out to be representative of the intermediate population between *ducilla* and *georgiana*, and closer to the latter in most respects. These topotypes agree closely with other specimens from the same general region in having the median row of spots conspicuously reduced (see p. 234).

Finally, once again Chamberlin (1947) proposed a new name for a species of *Cherokia*, but unfortunately placed it in the genus *Dynoria*, which probably belongs in a different subfamily. The types of *Dynoria parvior* came from Neel Gap, in the Blue Ridge country of north Georgia, and were very briefly described with respect to color, size, and gonopod structure. The contrasts with *Dynoria icana* are, of course, meaningless. The size range is given as 18–19 mm. in length, with a width of 7 mm. Correction of the length dimension to 28–29 mm. would yield a normal w/L ratio.

I have not seen material from the type locality, but do have a fair series taken less than 20 miles away in the same mountain range. These specimens belong to the widespread trimaculate phase of the intergrade population, to which the name *parvior* (now no longer appropriate) is allocated as a strict junior synonym of the nominate subspecies of *georgiana*. This synonymy is not new; it was first

made by Loomis and Hoffman in 1948 and was repeated by me in 1950.

I hope that the information contained in the present paper will be sufficient to prevent any additions to the list of junior synonyms in this genus.

DISTRIBUTION: From extreme western South Carolina west to south-eastern Tennessee, south through Georgia to central eastern Alabama and western Florida. Material has been examined from the following localities:

SOUTH CAROLINA: OCONEE COUNTY: Chestoogs Ridge, 2 miles north of Mountain Rest, 3 ♀, July 23, also 4 ♂, 2 ♀, July 23, 1958, Hoffman, RLH.

GEORGIA: HARRISHAM COUNTY: Tallulah Falls, 2 ♀, 1887, L. M. Underwood, USNM, types of *Fondoria tallulah*; 6 ♂, 4 ♀, October 10, 1928, O. F. Cook, USNM; 2 ♀, July 17, 1949, Hoffman, RLH. Panther Creek Picnic Area, 4 miles south of Tallulah Falls, 1 ♀, August 2, 1958, Hoffman, RLH. **STEPHENS COUNTY:** Cool Springs Picnic Area, 7 miles northeast of Toccoa, 1 ♂, 2 ♀, July 16, 1958; also 3 ♂, 3 ♀, July 30, 1958, Hoffman, RLH. **BANKS COUNTY:** 7 miles north of Commerce, April 4, 1953, 2 ♂, Leslie Hubricht, RLH. **BIBB COUNTY:** Mason, ♂ and ♀, 1887, Underwood, USNM, types of *Fondoria georgiana*.

TENNESSEE: POLK COUNTY: Benton, 2 ♂, June 20, 1950, 2 miles east of Ocoee, 4 ♂, 4 ♀, May 5, 1951; Oswald Dome on Beans Mountain, 1 ♂, 2 ♀, June 12, 1953; Sugarloaf Mountain near Parksville, 2 ♀, May 10, 1954, all by Hubricht, RLH. **BLOUNT COUNTY:** Townsend, 2 ♂, June 21, 1950, Hubricht, RLH. Cades Cove, 1 mile east of Ranger Station, 3 ♂, 5 ♀, May 4, 1951, Hubricht, RLH. **SEVASTOPOL COUNTY:** 11 miles south of Dunlap, 2 ♀, May 9, 1951, Hubricht, RLH. **HAMILTON COUNTY:** Signal Mountain, 1 ♀, August 18, 1956, Hoffman, RLH.

ALABAMA: LEE COUNTY: Auburn, 6 ♂, 10 ♀, 1897, C. F. Baker, USNM. Bluff on Little Uchee Creek, 17 miles southeast of Opelika, ♂ and ♀, May 6, 1954, Hubricht, RLH.

The species has also been reported from Atlanta, Georgia, by Chamberlin (1946), from Lookout Mountain, Georgia, by Bollman (1939), and from Liberty County, Florida, by Loomis (1943).

INTERGRADATION WITH *C. g. lucilla*: The apparent structural uniformity of *georgiana* over much of its namesake state is subject to considerable disintegration when the species enters the high country of the Blue Ridge province. Thence, both north directly into the mountains or northeast along the eastern flanks of the Blue Ridge, profound modifications of body form and color pattern are imposed upon the species. Some of the variations thus encountered are gradational in nature, such as the decrease in body width and loss of the tibiotarsal spur. Color pattern tends to vary more sporadically, with local modifications superimposed upon vaguely defined geographic progressions. Some of these phases have already been discussed, or mentioned, in a preceding section. It remains to relate them to the taxonomic status of the animals under study.

The accompanying map (fig. 6) indicates the location of the samples which I have examined from western North Carolina and adjoining parts of other states. The symbols reflect the nomenclatorial disposition made of each local population, the decision in most cases being made on the basis of characters taken in combination. Solid triangles represent the northernmost specimens of *C. g. georgiana* seen, solid spots indicate all known localities for *C. g. ducilla*, and open circles represent populations considered intermediate between the two.

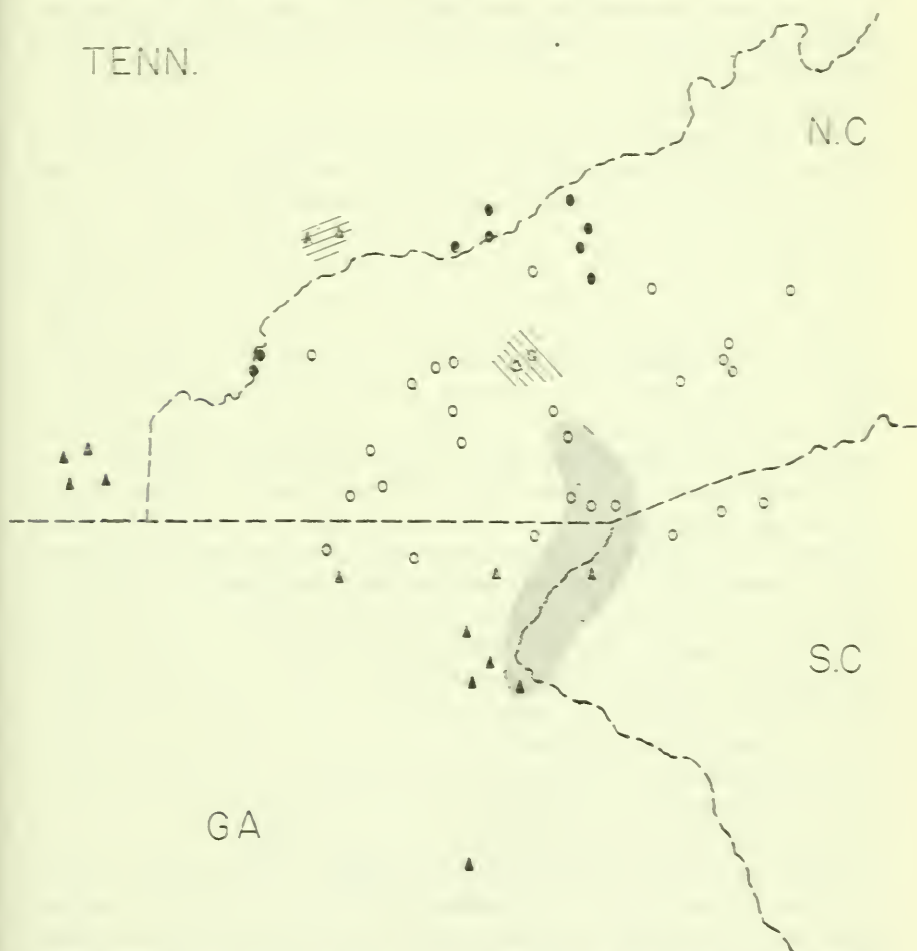


FIGURE 6.—Intergradation and local variation in *Cherokia georgiana* in western North Carolina and adjacent region. Solid triangles, *C. g. georgiana*; solid dots, *C. g. ducilla*; open circles, intergrades. Diagonal right to left shading in Tennessee indicates location of a yellow-banded population of *georgiana*, and left to right shading in North Carolina shows location of an identically marked but narrower-bodied phase of the intergrade population. Fine stipple-shading reflects distribution of the red-banded and pink-legged color phase affecting both typical *georgiana* and intergradient populations.

The distribution of the samples does not, in some cases, coincide exactly with that of certain key characters stipulated in the key and diagnoses. For instance, specimens with a w/L ratio of 26 percent or more occur across the western edge of South Carolina and into North Carolina as far as Pisgah Ridge. This segment of the species is regarded as intergradient rather than as *georgiana* because both color pattern and gonopod details reflect the characters of *ducilla*. It does seem probable, however, that migration to the northeast has carried the wide body form more successfully than the invasion of the mountains directly north of Georgia, although the typical lowland color patterns have been lost in both cases (a matter discussed at greater length on p. 251).

The reader may be curious concerning the arbitrary selection of value upon which the isophenes of figure 1 are based. For the most part, the higher values (26-28 percent) occur throughout most of the generic range with little or no geographic variation. The narrow body form, however, coincides closely with the loss of tibiotarsal marginal spurs and the appearance of dark pleurites, and the ratio values were selected deliberately to include the population so characterized. The subspecies diagnosed by the stipulated aggregate features is thus seen to be restricted to the Great Smokies and the adjacent Unicoi ranges. The mutual development of characters within this area reflects the natural integrity of the population.

It is anticipated that some critics of the subspecific category might assume the decreasing body form to be a function of elevation. This relationship is partly true, but is not the entire answer. Specimens with a ratio of 25 percent or more are available from the vicinity of Highlands, 3,800-4,000 feet; from Walnut Creek Gap, 4,800 feet; and from Cowee Bald, 5,000 feet—all in the Cowee Range. Specimens of *ducilla* with a ratio of 23 percent and less, are from Soco Gap, 3,800 feet; from Mount Sterling, 4,000 feet; and from Chimneys Campground on the north side of Newfound Gap at less than 3,000 feet elevation. The specimens from the last-named locality are the narrowest of the genus, their ratio being 19 percent, and I think these figures prove that the distribution is more horizontal than vertical.

There can be no doubt that the extensive high country of the Smokies has contributed to the ultimate differentiation of the localized segment of the species. I contend, however, that these mountains have received merely the culmination of the gradual northward progression of several variable tendencies which can be traced for more than a hundred miles from the upper Piedmont of Georgia. Specimens from the Tallulah River drainage in northeastern Georgia and those from the basin of the Ocoee River in southeastern Tennessee agree well

both in body form and color pattern with typical *georgiana* from farther south.

Intermediate specimens from the Nantahala Range, at Wayah Bald, for instance, are the narrowest outside the range of *ducilla*, the average w/L being 24.3 percent. Millipeds from Smokemont, at a low elevation (about 2,000 feet) at the very base of the Smokies and less than 10 miles from Newfound Gap, are closer in every respect to the Nantahala population than to *ducilla*. Specimens from the type locality of *ducilla* are the broadest of the subspecies, five measurable males averaging 23.4 percent. These topotypes agree with narrower specimens from the high Smokies in color pattern and gonopod structure, however even though certainly not structurally typical of the population here called *ducilla*. Soco Gap is located in the Plott Balsam Mountains, a southeasterly trending satellite of the Great Smoky massif, which forms the boundary between Jackson and Haywood Counties, North Carolina, for about 30 miles. At its southeastern end, perhaps 20 miles below Soco Gap, the local *Cherokia* population bears little close resemblance to typical *ducilla*.

The local picture with reference to color pattern is somewhat more complicated. *C. g. georgiana* of the lowlands is either transversely banded or trimaculate with very broad median spots (these absent, however, from a single local population in southeastern Alabama). In the Blue Ridge foothills of north Georgia the median spots tend to become smaller, and this reduction produces the trimaculate *Cherokia*, which is characteristic of the intermediate population as shown by hollow circles on the map. To the northeast, along the South Carolina border and into Pisgah Ridge, however, the median spots tend to become even smaller and create a local variant (discussed on page 234), in which they are obviously being lost.

The basic color pattern in *Cherokia* (and many other xystodesmid genera) appears to be trimaculation. This inference is drawn both from its prevalence and from the fact that the penult instars of cross-banded adults are trimaculate. In some genera, as well, support is drawn from the geographic location of bimaculate or banded populations on the periphery, or at extremes, of the range of vicarious trimaculate populations. With so little known of the main *georgiana* lowland population, it would be premature to speculate on the independent recurrence of bands and spots in the range, but it is certainly noteworthy to disclose microevolutionary developments within the intergrade population.

Aside from the tendency toward reduction of the median spots, there are two local phenomena. First, in a very localized region shown by fine stipple on the map, many of the specimens (perhaps a third or

half of the population sampled) have the basic yellow trimaculation, but additionally the spots are connected by a narrow chestnut-red band on the caudal edge of the tergites. This red does not merge with the yellow, but becomes more intense at the point of contact. In this form, the distal joints of the legs are pinkish or reddish instead of yellow. Specimens of this variety have been taken at the southern

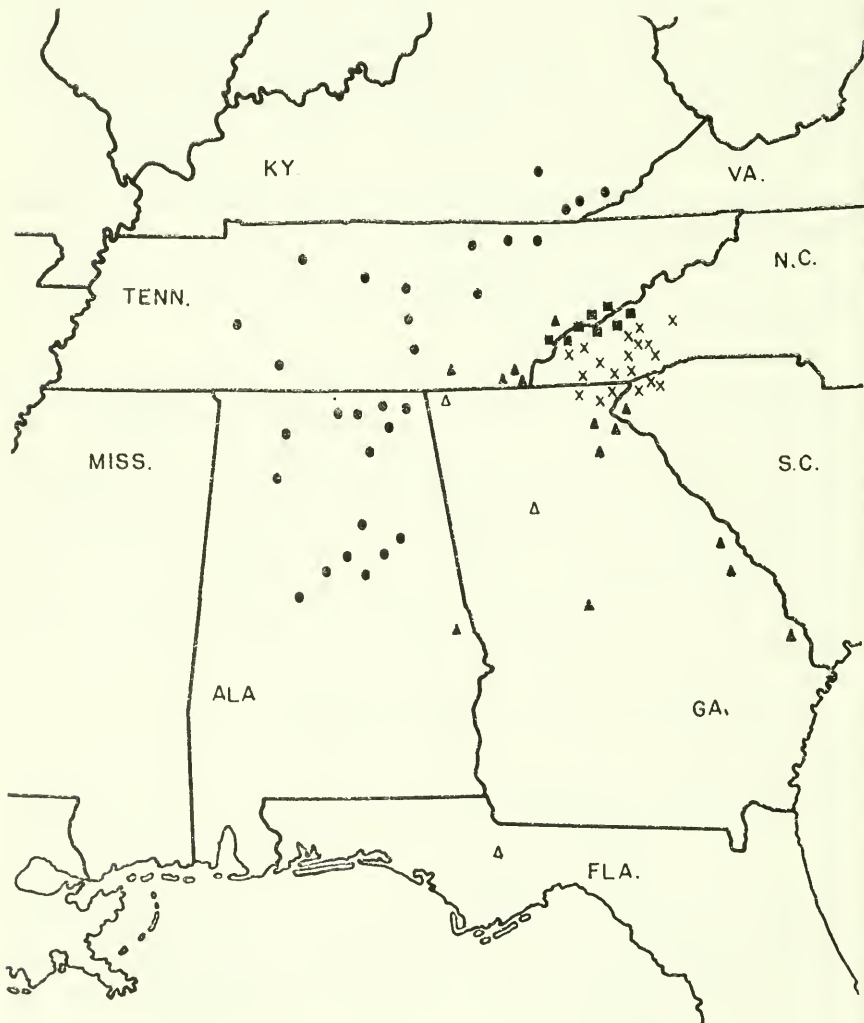


FIGURE 7.—Known localities for the subspecies of *Cherokia georgiana* based upon specimens examined and literature records. Localities: \blacktriangle *C. g. georgiana*, \bullet *C. g. latassa*; \blacksquare *C. g. ducilla*; X, specimens intermediate between *C. g. georgiana* and *C. g. ducilla*.

end of the Cowee Range, in the vicinity of Highlands, North Carolina, and at several localities in the Chatooga River drainage shared by the two Carolinas and Georgia.

At two places, Chatooga Ridge north of Mountain Rest, South Carolina, and Cool Springs, northeast of Toocoa, Georgia, specimens of the red-banded phase occur with fairly typical *georgiana*. At the latter locality, in addition to these, I found a male specimen with broad lemon yellow crossbands, all of which suggests considerable genetic instability at least as far as color is concerned.

The second of the color variants occurs in the vicinity of Highlands, North Carolina. The median spots of many specimens of the normal trimaculate form tend to be quite wide, especially in females, and occasionally may touch those of the paranotal series. Occasional specimens will show a neat narrow yellow band on each tergite. In going northwest along the Cowee Mountains the red-banded form drops out at Walnut Creek Gap, 8 miles north of Highlands. Only 7 miles farther, at Cullowhee Gap, I found no specimens so marked. The extreme end of the Cowee Range, however, is taken over by a very attractive color form occurring in and around Cowee Bald, north of Franklin, North Carolina, as shown on the map (fig. 6) by the diagonal shading. In this form the tergites have a straight transverse yellow bar, which does not widen anteriorly on the paranota, nor middorsally except in a few females. As this phase seems to occur to the exclusion of all others at the isolated end of the Cowees (perhaps isolated by a rather low gap northeast of Franklin), this phase might form the subject of future work on genetics in xystodesmids, work I hope will soon be undertaken.

From the occasional capture of similar individuals in the very heterogeneous population around Highlands, one might postulate that the gene for this color pattern has been carried along the Cowees by a branch of what I think must have been a general northward migration of *georgiana* into the mountains.

As can be appreciated from a glance at the map, the Highlands region is one of great importance in the distribution of color patterns in *C. georgiana*. This region shares one color phase with lowland *C. g. georgiana*, has the normal trimaculate pattern, is located adjacent to the area where the median spots are being suppressed, and, possibly, is the point of origin of a distinctive yellow-banded form. Further than this statement I cannot go, and commend investigation to someone with the time and knowledge to perform controlled studies on pattern inheritance with the Highlands population.

Concerning one other key character stipulated for *duvilla*—the complete absence of the tibiotarsal marginal spur—there is less to say. In

the Smokies the spur is uniformly absent; in the Cowee Range, it is absent in about 66 percent of the male specimens; further south at Highlands it is missing in about half. Eight males from western South Carolina have the spur well developed in each gonopod. In north Georgia in the Blue Ridge and Nantahalas, the spur is absent in about 36 percent. For the rest of the species' range, there are no adequate series for comparison.

Specimens considered to be intergrades between *Cherokia g. georgiana* and *C. g. ducilla* have been examined from the localities given below. In some cases assignation to this intermediate category rather than to one of the subspecies has necessarily been a little arbitrary, particularly in the northern portion of Georgia. The specimens examined are as follows (all collections in RLH and by RLH unless otherwise stated):

GEORGIA: RABUN COUNTY: Glade Mountain, about 5 miles south of Highlands, North Carolina, 1 ♂, 2 ♀, July 27, 1949. Rabun Bald, 1 ♂, June 23, 1954, J. T. Darlington; Clayton, 4 ♂, July, 1910, W. T. Davis, AMNH. Rabun Beach, 5 miles west of Lakemont, 2 ♂, 2 ♀, July 11, 1958. Enota Glade Picnic Area, east of Brasstown Bald, 11 ♂, June 7, 1953, Hubricht. Brasstown Bald, 1 ♀, June 23, 1954, Darlington. TOWNS COUNTY: Unicoi Gap, 2,950 feet, south of Presley, 1 ♂, June 6, 1953, Hubricht. West side of Dicks Creek Gap, 1 ♂, 3 ♀, July 11, 1958.

SOUTH CAROLINA: OCONEE COUNTY: Jocassee, 3 ♂, 3 ♀, July 15, 1949, R. E. Gordon and R. L. Hoffman. PICKENS COUNTY: Rocky Bottom, 2 ♀, July 16, 1949, Gordon and Hoffman. Table Rock State Park, 1 ♂, July 16, 1958.

NORTH CAROLINA: BUNCOMBE COUNTY: Bent Creek Experimental Forest, about 7 miles southwest of Asheville, 1 ♂, 1 ♀, July 14, 1958. CLAY COUNTY: White Oak, Bottom, 1 ♀, June 18, 1954, 1 ♀, August 21, 1955, J. T. Darlington. Tuni Gap, July 20, 1952, 1 ♂, 2 ♀, Thelma Howell. Buck Creek, 6 ♂, June 5, 1952, C. E. Wood, Jr., and C. L. Rodgers. Glade Gap, 3,673 feet, 1 ♀, July 20, 1954, Thelma Howell. GRAHAM COUNTY: Santeetla Creek Road, 3,600 feet, 3 ♀, July 25, 1955, Arnold Van Pelt. HAYWOOD COUNTY: Waynesville, 1 ♂, August 18, 1953, M. J. Westfall. Wagon Road Gap, south of Cruso, 2 ♂, July 14, 1958. JACKSON COUNTY: Below Jones Knob, Plott Balsam Mountains, 5,000 feet, 1 ♀, May 26, 1958, L. Hubricht, perhaps referable to *ducilla*. Whiteside Cove, 4 miles south of Cashiers, 2 ♂, 3 ♀, July 9, 1958. Walnut Creek Gap, south of Glenville, 4 ♂, 4 ♀, July 17, 1958. MACON COUNTY: Highlands, 3,800-4,000 feet, about 30 ♂, 30 ♀, July, 1949, 1953, 1958. Horse Cove, 2 miles east of Highlands, 3 ♂, July 8, 1958. Chatooga River gorge, about 6 miles southeast of Highlands, 2 ♂, August 1, 1958. Cullowhee Gap road, north of Cullasaja, 3 ♂, 2 ♀, July 9, 1958. Wayah Bald, 4 ♂, 1 ♀, June 13, 1953, Hubricht. Wesser Bald, 3 ♂, July 28, 1949. Cowee Bald, north of Franklin, 5,000 feet, 2 ♀, July 1952, Thelma Howell, 4 ♂, 1 ♀, July 17, 1958. SWAIN COUNTY: 8 miles southwest of Bryson City, 2 ♂; base of Cliff Ridge at Nantahala 1 ♂, 2 ♀; near Blowing Spring, 3 miles north of Nantahala 3 ♂, May 6, 1951, L. Hubricht. Smokemont Camp Ground, 6 miles north of Cherokee, 2 ♂, June 22, 1950, Hubricht. TRANSYLVANIA COUNTY: Pink Beds Recreation Area, 20 ♂, 14 ♀, July 28-30, 1958; Looking Glass Creek, 6 ♂, June 13, 1953, T. Howell M. J. Westfall, Hoffman.

Cherokia georgiana ducilla (Chamberlin), new status

FIGURES 3,b-c; 4,f; 5,b; 6; 7

Mimuloria ducilla Chamberlin, 1939, fig. 12, p. 7.*Mimuloria georgiana* Loomis, 1943, p. 402 (in part).—Causey, 1950, p. 6.*Cherokia georgiana* Hoffman, 1950, p. 23 (in part).

TYPE SPECIMENS: Male holotype and female paratype, Chamberlin collection, from Soco Falls, east of Cherokee, Jackson County, North Carolina, collected on April 29, 1939, by Nell B. Causey.

DIAGNOSIS: A small, narrow-bodied subspecies of *Cherokia georgiana*, the width less than 24 percent of the length, in which the tibio-tarsal spur is absent from the male gonopod and the sides of the segments are brown or black instead of yellow. The solenomerite of the gonopod is generally more elongate than in the other two subspecies; the cyphopod a little more highly arched as seen in lateral aspect.

VARIATION: Within the small geographic range occupied by this subspecies, there is an appreciable amount of variation in minor details, probably a reflection of evolutionary recency as well as of the rugged terrain inhabited by *ducilla*.

The smallest specimen examined is a male from Indian Gap in the Smokies, measuring 27.5 mm. in length and 6.1 mm. in width; the largest, a female from Soco Gap, 36.5 mm by 8.7 mm. The average of several dozen male specimens is 30.5 mm. long and 6.5 mm. wide. The w/L ratio ranges from 19 percent, in a male from Chimneys Campground, near Gatlinburg, Tennessee, to 24.5 percent in a male from Soco Falls, North Carolina. Two other males from that locality, however, are much more slender, with ratios of 22.8 and 22.9 percent. The Soco Gap population, typical in the nomenclatorial sense, is not typical of the subspecies in most structural characters, but is representative enough to impose its name upon the population at large. The w/L ratio averages about 22 percent in males from various localities in the Great Smokies.

There is likewise some variability in color pattern, with the median dorsal row of spots chiefly affected. These spots may be either rather broad or smaller than the lateral series, apparently without respect to elevation or locality. The most typical coloration is that described in the following notes made from life at Indian Gap, Tennessee, on August 4, 1958:

Dorsum and head rich glossy black; legs, paranota, and median dorsal spots creamy white. Antennae brownish; sternites brown, pleurites tan in females, dark brown in males, anal valves nearly black in both sexes. Median spots lenticular in females, nearly complete transverse bands in males, anterior collum spot wider than posterior, but collum almost completely ringed in some males.

Subsequent measurements show the median spots of the males from Indian Gap to be as much as 70 percent as wide as the metatergite; at Soco Gap the spots merge with those of the paranota forming complete bands. Smaller median spots prevail both north and south away from the central part of the Smokies, their width only 30 percent of the metatergite width in the vicinity of Mount Sterling, at Chimneys Campground, and in the Unicoi range south of the Little Tennessee River.

Specimens from the Unicois are not entirely typical of *ducilla*; they have lighter colored pleurites (the anal valves quite dark, however), and the tibiotarsal spur is variously developed in 4 of 8 males examined. The body form remains narrow, however; it averages 21.7 percent in 6 males from Little Haw Knob and 22.2 percent in 2 males from Stratton Gap. Whether this segment of *ducilla* has been isolated from that of the Great Smokies by the gorge of the Little Tennessee or has evolved independently from a common ancestral stock in the Nantahala region remains to be established. There would seem to be little chance for genetic exchange between the two isolated populations at the present time.

REMARKS: One of the most interesting aspects of the taxonomy of *ducilla* lies in the fact that to the east and southeast it grades almost imperceptibly into *georgiana* in all its diagnostic characters. To the west, fairly typical *georgiana* occurs in Cades Cove at the base of the Smokies, and *ducilla* in the same region attains its smallest and slenderest body form. No intergradation has been detected here, and I doubt that it occurs, the two forms being so radically different in size and shape.

I hope that someone having the opportunity for extensive studies in the Great Smokies will be able to work out the relationships of the two local forms of *Cherokia* there, particularly in the region between Newfound Gap and Cades Cove, and along the main ridge between Clingman's Dome and Gregory Bald.

Despite having collected *ducilla* at several places and different times, I have learned very little of its life history and activity. The mating season is somewhat later than that of *georgiana*; no mated pairs were collected until August 4, 1958, when some were taken at Indian Gap. Here specimens taken singly paired up while being carried in my hand, and remained clasped in a jar of humus overnight. No doubt the brevity of the warm season at such high elevations influences the maturation of individuals and postpones the mating activities.

Confinement of energetic males from Indian Gap with females of *georgiana* taken near Toccoa, Georgia, resulted in nothing. The males were about 2 mm. narrower, and probably would have been unable to secure a suitable grip even had pairing been attempted.

DISTRIBUTION: The Great Smokies and perhaps also the Unicois along the boundary of North Carolina and Tennessee, generally above an elevation of 3,000 feet. The northern known locality is Mount Sterling; the easternmost, Soco Gap. Whether *ducilla* occurs north of the Pigeon River remains to be determined. Approximately 72 preserved specimens, representing 14 collections, have been studied, as well as several dozen observed in the field but not retained. All of the material listed is in my collection.

NORTH CAROLINA: GRAHAM COUNTY: Stratton Gap, 4,300 feet, Unicoi Mountains, 3 ♂, 2 ♀, May 27, 1958, Leslie Hubricht. Little Haw Knob, 5,000 feet, 6 ♂, 1 ♀, May 27, 1958, Hubricht. HAYWOOD COUNTY: Mount Sterling, 4,800 feet, 3 ♂, July 20, and Cove Creek Gap, 4,000 feet, 2 ♂, 1 ♀, July 21, 1955, Richard Highton. JACKSON COUNTY: Soco Gap Falls, 10 miles east of Cherokee, 6 ♂, 2 ♀, July 28, 1949, Hoffman; also 5 ♂, 4 ♀, May 20, 1956, W. T. Keeton, W. C. Lund, and R. L. Hoffman. SWAIN COUNTY: Heintooga Ridge, 8 miles northeast of Smoke-mount, 8 ♂, 6 ♀, June 13, 1952, Thelma Howell, M. J. Westfall, and R. L. Hoffman; also 3 ♂, July 22, 1955, Arnold Van Pelt. Balsam Mountain Campground, 5,600 feet, 1 ♀, Van Pelt.

TENNESSEE: SEVIER COUNTY: Clingman's Dome, 6,600 feet, 1 ♂, June 14, 1954, Howard E. Evans; also July 24, 1955, 1 ♀, Arnold Van Pelt. West side of Indian Gap, 5,000 feet, 4 ♂, July 14, 1958, John F. Hanson; also 4 ♂, 4 ♀, August 4, 1958, Hoffman. Chimneys Campground, 5 miles southeast of Gatlinburg, 4 ♂, July 28, 1949, Hoffman.

This subspecies has also been reported from several localities in the Great Smoky Mountains National Park by Loomis (1943) and Causey (1950), all within Sevier County, Tennessee.

Cherokia georgiana latassa, new subspecies

FIGURES 3,a,c; 4,a-e; 5,c-d; 7

Mimuloria georgiana Loomis, 1943, p. 412 (in part); 1944, p. 173 (in part).—Loomis and Hoffman, 1948, p. 52 (in part).

Cherokia georgiana Chamberlin and Hoffman, 1958, p. 26 (in part).

TYPE SPECIMENS: Male holotype and two paratypes, USNM Myriapod type No. 2532, (Diplopod No. D-512), from a bluff on the Caney Fork River, one mile northeast of Rock Island, Warren County, Tennessee, collected on May 9, 1951, by Leslie Hubricht.

DIAGNOSIS: A subspecies of *Cherokia georgiana* in which the scapulo-larac are completely marginal, concealing the anterior surface of the paranota when seen in dorsal aspect (fig. 3, a). In details of structure agreeing almost completely with the detailed description given for the nominate subspecies.

VARIATION: The material examined shows very little structural variation. The size is remarkably uniform, the length ranging from 32 to 35 mm. in most of the specimens and the width from 8.0 to 9.5 mm. The largest male seen is from Campbell County, Tennessee: 37.5 mm.

long and 9.5 mm. wide. The largest female is from Talladega County, Alabama: 35.0 by 10.0 mm.

The coloration is somewhat variable, the specimens from Kentucky and Tennessee generally trimaculate with broad median spots. A tendency for crossbanding increases southward, where the collum also develops an anterior yellow border. In northern Alabama (e.g., Jackson County), the transition from trimaculate to banded patterns may often be noted on a single specimen, the bands being on the anterior half of the body and lunate spots being on the posterior half. Two females from Cheatham County, Tennessee, seem to have been cross-banded with chestnut in life; a male from directly south in Perry County, Tennessee, is typically trimaculate with yellow.

Alabama specimens likewise tend toward development of somewhat more acute sternal spines, and in many males the 7th segment is provided with two small conical sternal lobes at the base of the 8th legs. This occurrence can be traced as far north as Mountain View, Grundy County, Tennessee. With the available material, this structural variation cannot be regarded other than as clinal, and even so is of a very low order of magnitude.

The solenomerite of the male gonopod becomes, on the average, slightly more elongated from north to south, but without sufficient constancy to indicate more than a gradual trend. All the variants noted for the species proceed in a north to south direction, but there seems to be no point where an abrupt change occurs in any of them.

DISTRIBUTION: Extreme southeastern Kentucky, west and south through most of the Cumberland Plateau in Tennessee as far as the Western Highland Rim, south through Alabama to the general vicinity of Tuscaloosa; not yet known from the Coastal Plain of this state. In Tennessee it occurs abundantly in the Cumberland Plateau but apparently only west of the Sequatchie Valley, the form occurring on Walden Ridge being *C. g. georgiana*. Specimens have been examined from the following localities (all collections in RLH and by Leslie Hubricht unless otherwise stated):

KENTUCKY: LAUREL COUNTY: 1 mile northwest of Baldrock, 1 ♂, 2 ♀, May 26, 1952. **BELL COUNTY:** Kentucky Ridge State Forest near Pineville, 3 ♂, June 22, 1950. Pine Mountain State Park, 1 ♂, 2 ♀, June 23, 1950, J. A. Fowler and R. L. Hoffman. **HARLAN COUNTY:** Pine Mountain, 1 ♂, June 1946, W. L. Neeker, CNHM.

TENNESSEE: CAMPBELL COUNTY: 1.5 miles southeast of Morley, 1 ♂, April 30, 1954. **FENTRESS COUNTY:** 5 miles north of Jamestown, June 28, 1957. **SCOTT COUNTY:** 1.7 miles northeast of Winfield, 1 ♂, May 30, 1958. Just north of Elgin, 1 ♂, May 30, 1958. **CUMBERLAND COUNTY:** Ozone Falls, 1 ♂, 3 ♀, May 9, 1951. **WARREN COUNTY:** 9 miles southeast of McMinnville, 1 ♂, and 1 mile northeast of Rock Island, 2 ♂, 1 ♀, May 9, 1951. **DEKALB COUNTY:** 0.8 miles southeast of Dowlletown, 1 ♀, July 5, 1958. **PERRY COUNTY:** Near Campbell Cave, 2.5 miles east of Linden, 1 ♂, June 16, 1957. **CHEATHAM COUNTY:** 1.5

miles southeast of Pleasant View, 2 ♀, September 10, 1955. LAWRENCE COUNTY: 3 miles east of Lawrenceburg, 1 ♀, September 25, 1955. GRUNDY COUNTY: 1.5 miles north of Monteagle, 1 ♂, June 21, 1957. Mountain View, 1 ♂, June 20, 1950.

ALABAMA: JACKSON COUNTY: Keel Mountain near Paint Rock, 1 ♂, 3 ♀, June 18, 1957. North side of Poorhouse Mountain, 2 miles west of Scottsboro, 1 ♂, 1 ♀; also near Blowing Cave, 5 miles southeast of Limrock, 2 ♂, 1 ♀, June 19, 1957. Side of Sand Mountain, 1,200 feet, 0.8 miles west of Fabius, 1 ♂, June 20, 1957. MADISON COUNTY: Huntsville Mountain, 800 feet, 4 miles south of Huntsville, 4 ♂, 4 ♀, May 8, 1954. Scott Cave, 5.5 miles northeast of Maysville, 6 ♂, June 18, 1957. LAWRENCE COUNTY: Kings Cove, 1 ♂, June 29, 1950, George E. Ball. MARSHALL COUNTY: 1.5 miles south of Guntersville, 1 ♂, May 6, 1954. ST. CLAIR COUNTY: Steele, 1 ♂, April 4, 1948, Howard E. Evans. SHELBY COUNTY: Oak Mountain, 3 miles east of Acton, 1 ♀, June 10, 1953. BIBB COUNTY: 3.6 miles north of Brent, 1 ♂, June 10, 1953. CLEBURNE COUNTY: top of Cheaha Mountain, 4 ♂, June, 1953. TALLADEGA COUNTY: 6 miles southeast of Sylacauga, 1 ♀, May 7, 1954. 3 miles south of Cheaha State Park, 2 ♀, May 8, 1954. 2.7 miles north of Sylacauga, 2 ♂, May 6, 1954. Renfroe Mountain, east of Renfroe, 1 ♂, May 7, 1954.

In addition, *latassa* has been reported in the literature, under the name *georgiana*, from Monte Sano State Park, Madison County, Alabama, Hubricht, by Loomis (1943, p. 402); from Haleyville, Winston County, Alabama, V. E. Shelford, by Loomis (1944, p. 173); and from Pelham, Shelby County, Alabama, C. J. and M. Goodnight, by Loomis and Hoffman (1948, p. 52).

INTERGRADATION: Throughout its wide range, *Cherokia g. latassa* is remarkably stable as regards its principal diagnostic character. In fact, this structural integrity, coupled with the quality level of its difference from typical *georgiana*, led me to consider *latassa* as a distinct species for some time. This opinion gradually altered as a result of the realization that other equally important taxonomic characters were distributed without regard to the two paranotal types, and with the discovery of several specimens which, while clearly referable to *latassa*, indicate the probability of intergradation with *georgiana*.

A male from Steele, St. Clair County, Alabama (H. E. Evans), is of interest in two respects: First, the scapulae are completely marginal but become somewhat crenulated in outline toward the body; they resemble the form taken in *georgiana*. Second, the sternal spines are much longer than normal for *latassa* and also appear as distinct subcoxal conicles on the 7th segment.

A male from 3.5 miles northeast of Brent, Bibb County, Alabama (L. Hubricht), does not have distinct subcoxal cones on the 7th segment, but the scapulae are almost directly transverse instead of convex anteriorly, and thereby nearly submarginal. While these two specimens alone do not constitute direct evidence of intergradation, they show that the two paranotal types can be joined by intermediate forms.

Phylogenetic Relationships

To the best of my knowledge no one has yet expressed an opinion concerning the systematic position of *Cherokia* or its relationships to other genera, aside from a remark in my 1950 treatment that: "The disparity in sizes of the [cypchopod] valves suggests relationships with *Zinaria*, as does the nature of the sternites and male gonopods." Since then I have found no reason to revise this statement, but have come to recognize other genera as perhaps even more closely related to *Cherokia*. These form a discrete natural group worthy of formal tribal recognition:

Rhysodesmini, new tribe

I propose this tribe for xystodesmid genera in which the coxae of the gonopods are attached to a distinct slender sternite and join the prefemora at a right angle and in which the postcoxal division of the telopodite is typically nearly straight and the prefemur elongate and not globosely enlarged basally. When present, the prefemoral process is simple, slender, and acicular. These genera include polymorphic species of very variable form, in which the general form of the male gonopod is subject to little, if any, specific modifications.

The following genera (the validity of some of which seems not to be beyond challenge) at present constitute the tribe:

<i>Rhysodesmus</i> Cook, 1895	<i>Howellaria</i> Hoffman, 1950
<i>Cruzodesmus</i> Chamberlin, 1943	<i>Cherokia</i> Chamberlin, 1949
<i>Acebronus</i> Chamberlin, 1943	<i>Pleurolooma</i> Rafinesque, 1820 ²
<i>Boraria</i> Chamberlin, 1943	

The first five names of the list represent closely allied species groups, which some authors might prefer to unite in a single genus. The last two are much more strongly differentiated, to the extent that probably no one would question their claim to generic rank. *Rhysodesmus*, in particular, is highly variable and about 80 species have so far been described. The others are less extensive, and their rate of evolution seems to be more moderate.

With the recognition of but a single species in this genus, attention need be paid only to the status of the three geographic races of *C. georgiana*.

That these three groups are conspecific is, I believe, obvious. While remarkably dissimilar in appearance and probably unable to intermate, *C. g. georgiana* and *C. g. ducilla* are nonetheless connected by a broad zone of intermediate populations which bridge by small gradations the gaps in all the diagnostic characters. The two named subspecies are fairly constant over their ranges—as defined by the sum of several characters taken in combination—but it has been sometimes

² Some may prefer to retain the name *Zinaria* Chamberlin, 1939, pending confirmation of the older *Pleurolooma* as the correct one for the genus.

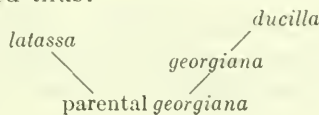
difficult to determine whether a certain local population should be considered as part of a subspecies or of the intergrading series. This fact seems a common and entirely reasonable consequence of geographically induced speciation.

On the other hand, *C. g. georgiana* and *C. g. latassa* differ mainly in but a single character, but in such a profound one that it separates all the material examined into one group or the other. The reasons for considering these two groups as conspecific have already been set forth: The virtual identity in all other structural details; separate distributions; the occurrence of some specimens of *latassa* which presage the appearance of intergradient characters; and the sharing by the two groups of sternal knobs on segment 7, in the region where intergradation is presumed to occur.

The inference I draw from the relationship of *latassa* to *georgiana* is one of a division of the parent population into two parts, with the barrier subsequently withdrawn before specific divergence had been achieved. Judged from present distributions, the Tennessee River seems entirely possible as the isolating mechanism because of the change in course to the southwest through eastern Alabama. That such a diversion occurred is contended by numerous zoologists, although there is by no means complete agreement. Reestablishment of the river in its present course curving westward through northern Alabama would permit an eastward migration of the subspecifically differentiated *latassa* and eventual contact and intergradation with *georgiana* in the region where, today, the evidence suggests it occurs.

The relationship of *ducilla* to *georgiana* seems more intimate and suggests virtually uninterrupted contact between the two, with *ducilla* representing a recent terminal race of the migration northward into the mountains. So far as I know, *georgiana* does not cross the French Broad River, whereas *latassa* ranges much farther north, into Kentucky. From the great variability of *georgiana* in western North Carolina, and its relatively narrow distribution there, I judge that the species' occupation of the mountains is a fairly recent event. Presumably the roughness of the terrain enhances or imposes localized variability; *latassa* varies less over a range thirty times as great.

It therefore seems reasonable to assume that *georgiana* and *latassa* diverged first, and in only one character. The race *ducilla* is a younger offshoot of *georgiana*, and differs in several characters because of the opportunities afforded by the invasion by its parental stock of a strongly dissected country with different climatic conditions. The relationship may be expressed thus:



In recent years several opponents of the subspecies category have, most correctly, pointed out that many workers have erected subspecies on the basis of a single character in a limited region, without consideration of the total variability within the entire species involved. In such cases, whenever another (and perhaps equally important) character is emphasized as the basis for separation, an entirely different pattern of "subspecies" emerges. The present work has been done in complete cognizance and appreciation of such circumstances, but although all the populations in the genus *Cherokia* are held to be conspecific, three of them appear to be so distinctive and so constant throughout their ranges that recognition as subspecies seems to be warranted and actually desirable. Those who wish to discard trinomials may refer to *latassa* as the Cumberland Plateau population, to *georgiana* as the Georgia population, and to *ducilla* as the Great Smokies population, of *Cherokia georgiana*, but I do not see what is to be gained by the substitution of polynomial vernacular names in place of short Latin designations carrying the same implication.

Summary

A number of local populations within the genus *Cherokia* have been given specific names in the past, in many cases the diagnostic characters being more apparent than real. A restudy of the genus, based upon more than 400 specimens and typical material of most of the names, shows that most of these species are merely local populations of one variable species. The gonopods are remarkably similar in all the material examined, and the external body form is equally variable. It is concluded that the most extreme variants in the genus are eventually connected by intergradient populations, and that *Cherokia* is monotypic.

The importance of this conclusion rests in its presumable effect on the definition of species in the family Xystodesmidae. Common practice of the past decade has resulted in the erection of numerous specific names for millipeds from single localities, differing solely in color pattern or other minor features. Such forms have been apparently proposed in a sort of taxonomic vacuum which presupposed that any difference must be of specific value. One paper (Causey, 1951), attempted to justify such an approach with the philosophical suggestion that in some genera, specific differences obtain only in nonsexual features, with the gonopods remaining identical or nearly so in the different forms. Such species were designated by the special term "isogenitive."

It must be obvious that the validity of the idea of "isogenitive species" rests entirely upon what was never proved, that the named forms involved are actually different species. Presumably, as long

as one examined only small samples of specimens, from widely separated localities, such reasoning might have some appeal. It seems more reasonable to me, however, to assume that such local variants are nothing more than populations, perhaps sometimes subspecifically distinct, of widespread polymorphic species. The phenomenon of geographic variability in most species has been recognized and understood for quite a long time.

In disposing of "isogenitive species" as doubtlessly only the results of localized microevolution, which is far from reaching the species level, I note that even the term appears to be incorrectly formed, presumably from the Greek "isos" (equal) and the Latin "genitivus" (possessive case). From the usage of the word, the meaning isogenital was implied—"isos" + "genitalis" (of the sexual organs)—but even this usage is objectionable because of its hybridity.

The present study has shown that populations of one species may be so divergent that, given only specimens of the typical forms, one would be justified in considering them specifically different. This discovery should be of considerable aid in the evaluation of species in large genera such as *Rhysodesmus*, in which the gonopods are remarkably similar, and in which species have been erected on characters such as size and color, and even then only by overlooking previously named species from the same general regions.

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