PROCEEDINGS OF THE UNITED STATES NATIONAL MUSEUM

issued by the

SMITHSONIAN INSTITUTION
U. S. NATIONAL MUSEUM

Vol. 106 Washington : 1956 No. 3362

REVISION OF THE MILLIPED GENUS DIXIORIA (POLYDESMIDA: XYSTODESMIDAE)

By Richard L. Hoffman

Generally speaking, most of the published work on the classification of the diplopods has been either fragmentary or carelessly superficial, often both. This is particularly true in the United States where, except for the valuable work of O. F. Cook and H. F. Loomis, there is only a welter of short papers on millipeds that contain brief and in many cases meaningless descriptions of miscellaneous new forms.

The prevailing method of treatment apparently has discouraged a number of interested students who have found the confusion too great to overcome. I feel that the time is long overdue for some attempt to assemble and evaluate our present knowledge, and to present it in a form that will be useful to others.

I have undertaken the preparation of formal taxonomic revisions of certain North American milliped groups, to be published as available material permits in the form of revisions of genera. Each paper is intended to be as thorough as possible with the material at hand, and in some cases the results compare favorably with published studies of many vertebrate groups. The family Xystodesmidae is selected as a starting point because it is rich in genera and species as well as

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in individuals; because of the localization of most species which enhances their value in evolutionary studies; and because of the relative ease of obtaining specimens for study. This last factor is particularly true in the case of those genera confined to the Southern Appalachians.

The present study is devoted to *Dixioria*, a small genus of attractively colored diplopods which is restricted to the Southern Appalachians in western North Carolina, eastern Tennessee, and southwestern Virginia. Occurring in a very deeply dissected mountain region, the forms of *Dixioria* are quite localized and afford interesting material for the study of distribution and phylogeny.

My original plan to revise all of the xystodesmid genera in a single publication has been abandoned, as it became obvious that such an endeavor would necessarily be postponed for many years. It seemed best to reserve a general treatment of generic relationships and evolution to serve as a culmination, rather than initiation, of the series.

Materials and Methods

For this study I have examined approximately 100 specimens, representing all of the seven recognized forms of *Dixioria* and including the type specimens of the two previously named species. Five additional names are proposed herein. I have personally collected material of all of the forms except *Dixioria pela brooksi* and *D. dactylifera*, and this field experience has been particularly useful in providing first-hand knowledge of the physiographic factors influencing distribution.

Most of the specimens have been collected by me or by friends, but additional material has been examined from the collections of several museums. Abbreviations used in the text to designate the sources of preserved study specimens are as follows:

AMNH, American Museum of Natural History, New York, N. Y.
CM, Carnegie Museum, Pittsburgh, Pa.
MCZ, Museum of Comparative Zoology, Cambridge, Mass.
RLH, Private collection of R. L. Hoffman, Blacksburg, Va.
USNM, United States National Museum, Washington, D. C.

The drawings were made from gonopods immersed in alcohol, using a binocular microscope equipped with an ocular grid. This attachment facilitated very accurate transfer of the image to coordinate paper, and also made possible careful comparison of gonopods with previous illustrations.

Extreme care was taken to orient the gonopods into a uniform position for drawing, so that fictitious differences in appearance arising from different aspects might be kept to a minimum. Failure to take

such an elementary precaution has been one of the outstanding defects of American diplopod taxonomy.

For the privilege of studying the collections under their care, I am indebted to Dr. E. A. Chapin, formerly of the U. S. National Museum, Dr. Willis J. Gertsch of the American Museum of Natural History, and Dr. P. J. Darlington of the Museum of Comparative Zoology. Gordon K. MacMillan kindly loaned all of the Appalachian millipeds in the Carnegie Museum, including several interesting series of different forms.

Most of my field work was done with the aid of grants from the Virginia Academy of Sciences and the Highlands (North Carolina) Biological Station. James A. Fowler, Hubert I. Kleinpeter, and William T. Keeton have been helpful companions in the field.

More than to anyone else, this study of *Dixioria* owes its existence to my good friend Leslie Hubricht, an outstanding student of American gastropods and an unexcelled collector, who has provided perhaps the largest part of the material in my collection.

Review of the Literature

A certain amount of confusion presently attends usage of the generic names *Deltotaria* and *Dixioria*. I have personally contributed to this misunderstanding, and am glad to take the opportunity to review the status of the two groups with the hope of correcting previous mistakes.

The genus *Deltotaria* was proposed by Causey in 1942 for the reception of a new species (*brimleii*) collected at Swannanoa, N. C. The primary diagnostic character cited for the genus was the presence of a projection on the coxal joint of the gonopod. Somewhat later, two additional species were described, *D. nigrimontis* (Chamberlin, 1947) and *D. coronata* (Hoffman, 1949). Apparently both Chamberlin and I were impressed by the fact that the distal end of the gonopod in our species was similar to that figured for *brimleii* (furcate), and we overlooked the complete absence of a coxal projection in our new forms. With the initiation of intensive studies on the genera of the Xystodesmidae, it became apparent that members of two considerably different genera had been described under the name *Deltotaria*. More recently, Dr. Causey published the descriptions of two additional species, both of which agree with the generotype, thus emphasizing the misplacement of *coronata* and *nigrimontis*.

At first it appeared that a new generic name was needed to embrace these two orphaned species, which seemed to fit into none of the currently recognized genera. Soon, however, I discovered that *Dixioria* of Chamberlin (1947) was available for one of them because its type species is subjectively congeneric with *coronata*, and that the other is

referable to the genus *Sigmoria*, as will be shown in a later paper of this series.

Fontaria pela was described by Chamberlin (1918) from material collected at Burbank, Tenn. The original description did not contain drawings of the gonopods, and the species, more or less unidentifiable, dropped into obscurity for the next 30 years. In 1947, Chamberlin described another new species as *Dixioria dentifer*, the type locality of which is Cranberry, N. C. Less than two years later, in February 1949, I examined the type of *Fontaria pela* at the Museum of Comparative Zoology and discovered that *pela* and *dentifer* are names based upon the same species. *Dixioria*, therefore, becomes the proper name for *Fontaria pela* as well as for my *Deltotaria coronata*. Although there are considerable differences between the original drawings of the gonopods of *coronata* and *dentifer*, I believe that the illustrations in this paper will establish that the two are congeneric. The discovery of intermediate forms also serves to corroborate this relationship.

Taxonomic Characters

The structural peculiarities which characterize the genus *Dixioria* are fairly numerous and distinctive. The most obvious is the color pattern, there being no other genera in the eastern United States in which the dorsum is black with the caudolateral half of the paranota, tip of the telson, and anterior edge of the collum bright yellow. Because of this peculiarity, females as well as males can be placed into *Dixioria* with confidence. However, since the pattern is identical in all of the known forms, it is of no utility in separating species.

Another generically diagnostic character is the configuration of the paranota, of which both anterior and posterior corners are broadly rounded on all except the last few segments. Among other xystodesmids of eastern North America, this feature is duplicated only in some forms of *Brachoria*, all of which are considerably wider in proportion to their length than of the relatively slender species of *Dixioria*.

The gonopods of the male sex, while varying considerably in small details, preserve an over-all similarity throughout the genus and are distinctive from those of other known genera. The prefemoral process is always present and conspicuous, in the form of a wedge-shaped, usually slender, upright peg. The telopodite blade is very slender and unmodified except at its distal end, forming an even curve similar to that found in the genus *Apheloria*. Distally the telopodite is enlarged and provided with one or two subterminal processes of variable size but usually thin and laminate in shape. None of these serves as a solenomerite, as the seminal groove continues on to the tip of the telopodite proper.

So little is yet known of the comparative morphology of the cyphopods in most milliped groups that little can be said of their value in the differentiation of genera. It seems, at present, that the cyphopods do not differ markedly from those of *Brachoria* and of the Trimaculata group of *Apheloria*, although more detailed studies may reveal the presence of very distinct features.

Structural differences used in the separation of the forms of *Dixioria* are of two kinds. Most conspicuous, and perhaps most fundamental, are the differences in the shape of the male gonopods, and these are the features customarily utilized by most students of the Diplopoda.

During the course of my studies of polydesmoid millipeds, however, I have found that in most cases where the gonopods are singular enough to indicate specific distinction, a close examination of the material will reveal other correlated structural peculiarities. It is my belief that, generally speaking, if a species is actually a valid one it can be distinguished from its congeners by characters other than those expressed by the male genitalia.

In the present instance, *Dixioria pela* is separable from *D. dactylifera* by several tangible characters aside from the obviously disjunct gonopods. These differences may be described verbally and are mentioned both in the following key to species and in the diagnosis of *D. dactylifera*. They are of interest in several respects.

First, they serve to indicate that perfectly good taxonomic characters may be disregarded in the general preoccupation with male genitalia and color pattern—two variables which seem to have claimed the attention of most American workers. Second, the discovery that coxal spines may be present in one species and absent from another suggests that their utilization in generic diagnosis may have to be somewhat modified as our knowledge of variability of the character improves. Heretofore, the presence or absence of coxal spines has been considered to be constant in a genus.

Despite the six or seven respects in which the two species of *Dixioria* differ superficially, their general similarity in structure, color pattern, size, and appearance is so great as to preclude any doubt of the homogeneity of *Dixioria* as a generic entity.

Taxonomic differences expressed by the gonopods of the male are, to a considerable extent, qualitative and best appreciated by reference to drawings. Nonetheless, it is quite possible to distinguish and describe some of these differences verbally, and, with the development of homologies and a terminology for the parts, to abolish the old ambiguous phrase, "Gonopods as illustrated." In treating the gonopod characters in *Dixioria*, particular attention is here given to the distal end of the telopodite, with its teeth and lobes, and to the shape of the prefemoral process.

An outstanding characteristic of the genus is the presence of a small, very thin, triangular tooth (referred to as process A) near the end of the telopodite. All of the subspecies of *pela* are provided with this feature. In most of them there is also an expansion of the end of the telopodite and a supplementary oblong lobe, or process (referred to as process B). In the case of *dactylifera*, process B has become unusually enlarged, and A has disappeared entirely. In this instance, and also in those subspecies of *pela* where B is enlarged, it is useful to distinguish the true ending of the telopodite with the term solenomerite (S). Possibly the name parsolenomerite might be adopted to replace "process B," but I hesitate to devise a terminology until homologies have been worked out for all the genera of the family.

One may observe some geographic variation in the gonopods of the forms of *Dixiora pela*. There is a trend from south (*pela*) to north (*fowleri*) toward increase in the size of the prefemoral process and a corresponding decrease in the length and arch of the telopodite blade. A similar variation occurs, altitudinally, in a reverse direction in that *coronata* (presumably a montane derivative of *fowleri*) shows tendencies back toward the characters of *pela*.

The average size of series varies considerably and at first suggested itself as a secondary taxonomic difference. However, this varies within subspecies as well as between them, and I conclude that dimension is a character which varies at least with the individual and at most with any given micropopulation. It may be only a reflection of propitious environmental conditions.

Various other characters, such as the shape of the paranota of the caudalmost segments, were considered for their possible utility in separating subspecies. Several variations, which at first appeared to be useful, were found to break down when series of specimens were checked, and in general it seems that such qualitative differences, even if stable, are so slight that they would be negated by the normal amount of error inherent in making drawings under low magnification.

Genus *Dixioria* Chamberlin

Dixoria Chamberlin, Proc. Acad. Nat. Sci. Philadelphia, vol. 99, p. 28, 1947.
Deltotaria (not Causey) Hoffman, Proc. U. S. Nat. Mus., vol. 99, p. 379 (in part), 1949.

Type species: *Dixioria dentifer* Chamberlin 1947 (=*Fontaria pela* Chamberlin 1918), by original designation.

Diagnosis: A fontariid genus characterized as follows: prefemora of legs with a sharp distal spine, coxae with or without small ventral spines; sternites without obvious processes at bases of legs and not produced on caudal margin; tergites smooth, paranota rather small,

with both corners rounded on most segments, pores opening dorsolaterally.

Male gonopod rather simple; no coxal process, prefemoral portion globosely swollen and with an erect, somewhat cuneiform process, remainder of telopodite a slender, unmodified, strongly curved blade, with one or two small subterminal processes and occasional subterminal enlargement. Coxae separate from each other but connected by a strong band of sclerotized tissue.

Size of animals moderate, from 30 to 40 mm. in length, rather slender, width about 20 percent of length. Dorsum black, with caudolateral corners of paranota and anterior margin of collum bright lemon yellow, legs and other ventral surfaces yellowish tan to light brown.

Range: Southern Appalachian Mountains, specifically in and adjacent to the Iron-Unaka mountain chain, from Bland County, Va., south to Grandfather Mountain, N. C., and Roan Mountain, Tenn. In general, the ranges in distribution of each form coincide closely with separate mountains or mountain ranges.

Species: Two, one of which is divided into six subspecies.

Key to the known forms of Dixioria

1. Coxal spines absent or represented only as a faint remnant on some of the caudalmost legs; all sternites with at least 8 setae; gonopod socket extending laterad past outer end of coxal acetabula; process A of gonopods absent, process B greatly enlarged . . . . . **dactylifera**
   Coxal spines present, conspicuous; most of the sternites glabrous, a few with up to 8 or 10 setae; gonopod aperture not extending laterad past coxal acetabula; process A of gonopods present, process B variable 2
2. Distal end of telopodite of male gonopod with only one subterminal process (A) 3
   Distal end of telopodite of male gonopod with two subterminal processes (A and B) 4
3. Telopodite gradually tapering distad; distal end of prefemoral process bent lateral at a right angle or nearly so . . . . . **pela pela**
   Telopodite conspicuously laminately expanded near end; prefemoral process straight or nearly so . . . . . **pela acuminata**
4. Distal end of telopodite noticeably capitate (enlarged on the outer margin), processes A and B more or less coalesced; telopodite rather flattened in cross section . . . . . **pela brooksi**
   Distal end of telopodite not especially capitate, its subterminal processes discrete; femoral portion subterete in cross section 5
5. Process B very large, becoming larger and broadly truncate distally; prefemoral process bent at a right angle distally; solenomerite very long. **pela wrighti**
   Process B small, digitiform, only slightly larger than A; prefemoral process cuneiform, not bent distally 6
6. Prefemoral process broader, with an obtuse lobe on its outer edge . **pela fowleri**
   Prefemoral process narrower, outer edge nearly straight but with a small subterminal indentation . . . . . **pela coronata**

Dixioria pela pela (Chamberlin)

FIGURE 1,*a*

Fontaria pela Chamberlin, Psyche, vol. 25, p. 123, 1918.
Dixioria dentifer Chamberlin, 1947, Proc. Acad. Nat. Sci. Philadelphia, vol. 99, p. 28, fig. 13, 1947, (Cranberry, Avery County, N. C.; type in AMNH).
Apheloria pela Hoffman, *in* D. L. Wray, Insects of North Carolina, Second Supplement, p. 44, 1950.

TYPE SPECIMENS: Male holotype and paratypes of both sexes (MCZ), from Burbank, Carter County, Tenn., collected by Roland Thaxter.

DIAGNOSIS: Prefemoral process of male gonopod slender, upright, only slightly bent distally; telopodite with tip attenuated, very little expanded and modified only by the presence of a subterminal tooth (A); telopodite blade long and slender, somewhat sigmoidally curved distally.

DESCRIPTION: Given in full only for the typical subspecies since the others differ only in gonopod structure.

Length, 35 to 42 mm., width, 5.0 to 9.0 mm. Body relatively slender, parallel-sided, segments 4–16 essentially of full width. Width of body about 20 percent of length, varying from 19 to 22 percent.

Head smooth and shining, vertigial groove distinct and obviously punctate, genae slightly swollen near antennal concavity but not medially impressed. A single paramedian clypeal seta on each side, interantennal frontal setae and supra-antennal occipital setae absent. Antennae separated by a distance equal to length of 3d antennal article, moderately long, extending caudad to caudal margin of second tergite; articles 2–5 subequal in size and shape, approximately 1.2 mm. in length and distinctly clavate; 6th article slightly shorter and somewhat thicker; 7th short but distinct, with four sensory cones. Articles 1–4 sparingly setose, 5th slightly more so, 6th and 7th densely covered with short declivous setae.

Collum slightly wider than following tergite, its caudal margin completely straight across and the lateral ends broadly rounded; anterior margin straight across head, laterad of which it is swept back on each side and set off by a marginal groove. Surface perfectly smooth and shining except for a slightly impressed area near the front margin adjacent to the antennae in some specimens.

Tergites of succeeding segments essentially similar to each other, moderately arched and smooth. Paranota rather small, continuing slope of dorsum, their anterior and posterior corners broadly rounded off on all except the last four or five segments; anterior and lateral edges set off by distinct grooves but peritremata not distinct and pores opening almost laterally. Caudal edges of paranota sharp, not mar-

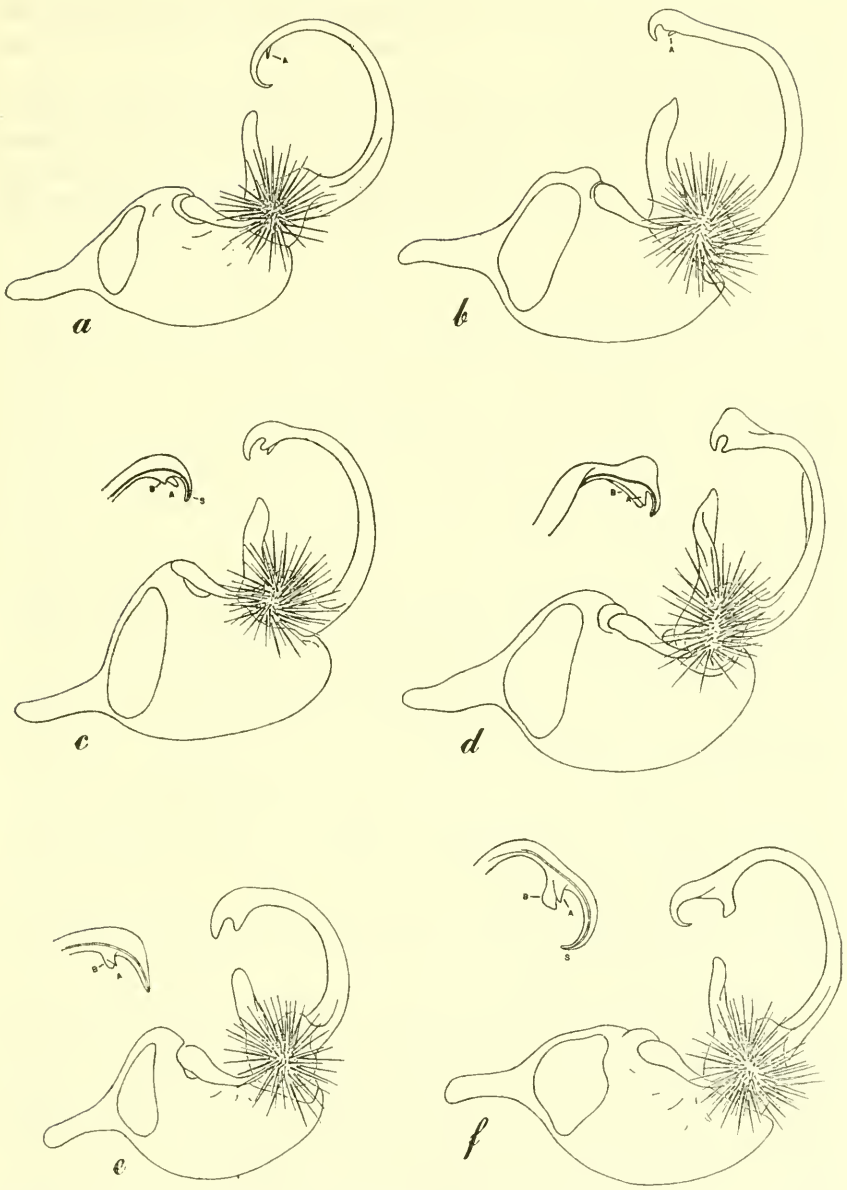

FIGURE 1.—Left male gonopods of the subspecies of *Dixioria pela*, mesial aspect. In most cases the lateral aspect of the end of the telopodite is also shown separately. *a*, *D. p. pela*; *b*, *D. p. acuminata*; *c*, *D. p. coronata*; *d*, *D. p. brooksi*; *e*, *D. p. fowleri*; *f*, *D. p. wrighti*.

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gined; upper surface smooth with extremely faint longitudinal striations. Caudolateral corners of paranota caudal to 14th, becoming increasingly produced.

Median projection of anal segment subtriangular in dorsal aspect, longer than broad, the tip slightly truncate and bearing several long setae. Anal valves glabrous, the mesial margin of each produced into a low ridge but no other obvious sculpture. Preanal scale broadly triangular, wider than long, with a median and two smaller lateral, setiferous, tubercules.

Sternal areas of metazonites essentially flat or slightly concave, not raised above level of prozonite but set off by a broad, shallow, sharply defined interzonal furrow. Sternites slightly produced at base of each leg, becoming subspiniform toward the rear of body. Sternites glabrous or at most with six or eight scattered setae on some of the segments just behind the gonopods. Coxae and prefemora with acute conical distoventral spines, these becoming longer caudad; these leg joints also with numerous long slender setae on the ventral side. Femora nearly glabrous, slightly clavate, shorter than coxae and prefemora combined. Postfemora and tibiae equal in length, the latter of a lesser diameter and about half as long as the moderately setose and subcylindrical tarsi. Tarsal claws of anterior legs of males long, sinuous, with a distinct sharp carina along the dorsal side.

Sternites between 3d legpair produced upward into two slender, digitiform lobes, those between 4th, 5th, and 6th legpairs in the form of low rounded eminences.

Pleurites coriaceous, somewhat obliquely longitudinally striate in some specimens, the caudal margin distinctly set off. No tubercules, granules, or clusters of spines.

Sternal aperture of 7th segment of males large, transversely oval, widest in front of the middle, strongly margined laterally and between the coxae of the 8th legpair.

Gonopods freely movable, the coxae separate and connected only by a strong band of connective tissue. In situ, the main axis of the telopodite blade lies at a right angle to that of the body, the gonopods at rest thus have the blades overlapping and often interlocked. Coxal apodeme moderately long, slightly enlarged distally. Coxae without special processes. Prefemur swollen, densely setose, with a prominent, upright, wedge-shaped prefemoral process. Telopodite blade slender, evenly curved into almost a complete circle, without trace of division into femur, tibia, and tarsus. Telopodite distally slightly expanded, with a small thin subtriangular tooth (process A).

Tergites glossy brownish black, with caudolateral two-thirds of the paranota, anterior edge of collum, and tip of anal segment bright lemon yellow. Underparts yellowish tan, somewhat burnished in

appearance. Head dark brown except for the lighter labral area; antennae light brown with distal portion of each article white. Tarsal claws brown, sternites darker than the legs. A faint dark spot in the yellow of the paranota just above each repugnatorial pore.

Ecology: The only specimen of *Dixioria pela pela* that I have collected was found beneath a stone near the edge of a grassy field at Cloudland, on Roan Mountain, at an elevation of about 6,000 feet. It was associated with numerous specimens of the xystodesmid *Boraria media* (Chamberlin). I had previously searched at several places on the Tennessee side of Roan Mountain between 3,000 and 5,000 feet without success, but a week later, on June 27, Leslie Hubricht obtained a good series on the North Carolina side during night collecting for land snails.

This subspecies has perhaps the largest areal range of any member of the genus, and its vertical distribution is certainly not surpassed. The records encompass elevations ranging from about 2,000 feet up to 6,000 feet. The lowland material is not recognizably different in the genitalia.

Distribution: *Dixioria p. pela* appears to be confined to the Unaka range in the immediate vicinity of Roan Mountain. The precise limits of its distribution are yet to be established, but I suspect that its southward occurrence is confined by the Nolichucky River, south of which I have collected at several localities without finding any form of *Dixioria*. It will be of interest to determine the area of intergradation between *pela* and *coronata*, which must lie in the eastern part of Johnson County, Tenn.

Distributional records and the specimens upon which they are based are as follows:

North Carolina. Avery County: Cranberry, date and collector not known (AMNH, type of *dentifer* Chamberlin, probably intergrade with *D. p. wrighti*). Mitchell County: East side of Roan Mountain, 1 mile below Carver's Gap, Leslie Hubricht coll., June 27, 1950 (RLH).

Tennessee. Carter County: Burbank, Roland Thaxter, no date (MCZ, type series); 2 miles southeast of Burbank, Hubricht, Sept. 1, 1951 (RLH); Doe River Bluff, near Hampton, Hubricht, May 3, 1951 (RLH, a male with tendencies toward *acuminata*). Unicoi County: Iron Mountain Gap, 4 miles southeast of Limestone Cove, Hubricht, Sept. 2, 1951 (RLH).

***Dixioria pela acuminata*, new subspecies**

Figure 1,*b*

Type specimen: Male holotype (USNM 2011), collected at the top of Holston Mountain 2 miles west of Shady Valley, Johnson County, Tenn., by J. A. Fowler and R. L. Hoffman on June 19, 1950.

Diagnosis: Prefemoral process nearly straight, very slightly expanded distally, with a small terminal acuminate point. Distal

third of telopodite blade straight (not completing the curve of the basal two-thirds), having only process A, but the terminal portion somewhat enlarged with a very small lobe probably homologous to B.

ECOLOGY: The type and only known specimen was found in deep leaf mold in a rather dry oak-hickory woods. Collected at the same time and place were specimens of the millipeds *Ptyoiulus pennsylvanicus* (Brandt) and *Apheloria waccamana* Chamberlin, and the salamander *Plethodon yonahlossee* Dunn.

DISTRIBUTION: Known only from the type locality, and probably restricted to Holston Mountain, between Damascus, Va., and Elizabethton, Tenn.

Dixioria pela brooksi, new subspecies

FIGURE 1,*d*

TYPE SPECIMENS: Male holotype (USNM 2012), male and female topoparatypes (CM), collected on Holston Mountain at Damascus, Washington County, Va., by Dr. and Mrs. Stanley T. Brooks on Aug. 14, 1941.

DIAGNOSIS: Distinguished from the other subspecies by the curious lobelike distal enlargement of the tibiotarsus of the gonopod, producing a somewhat hammerheadlike shape. Notable also is the fact that processes A and B are more or less coalesced to form what appears with low magnification to be simply a notched process. The telopodite is somewhat flattened and is provided with a small lateral flange just distad to its midlength. The prefemoral process is nearly straight and distally acute.

ECOLOGY: I know nothing of the circumstances under which the type series was obtained. *D. brooksi* is doubtless a low-altitude form.

DISTRIBUTION: Known so far only from the type collection. What is most needed at this time is a very intensive study of the relationships of the *Dixioria* forms around Damascus. Within a 10-mile radius three forms, *coronata*, *fowleri*, and *brooksi*, have been obtained. The first two doubtless intergrade. But whether *brooksi* is really a subspecies of *pela* or a distinct species in itself cannot be guessed at the present.

Dixioria pela coronata (Hoffman)

FIGURE 1,*c*

Deltotaria coronata Hoffman, Proc. U. S. Nat. Mus., vol. 99, p. 380, pl. 26, figs. 7, 8, 1949.

TYPE SPECIMENS: Holotype, allotype, and paratype (USNM 1805); topoparatypes (MCZ); collected at Mount Rogers, Grayson County, Va., by H. I. Kleinpeter and R. L. Hoffman, June 30–July 1, 1947.

DIAGNOSIS: Distal end of telopodite of male gonopod somewhat expanded, with a large curved subterminal tooth (B) and a much smaller and thinner one adjacent to it on the outer side. The prefemoral process is nearly straight along its outer margin, which is subterminally notched or indented.

ECOLOGY: This seems to be an altitudinally restricted form. The altitudes of most places at which it has been taken exceed 3,000 feet. It occurs in hardwood and mixed forests, but not in the spruce-balsam stands which cover the tops of the Iron Mountains. More diurnal in habits than most xystodesmids (perhaps a function of its very moist habitat), *coronata* is often seen abroad during the day. A mated pair was found on July 1.

DISTRIBUTION: The Iron Mountains in Grayson and Washington Counties, Va., and Johnson County, Tenn. Its northern limits are probably reached just north of Mount Rogers, but just how far it goes into Tennessee along the Iron Mountains remains to be determined.

Distributional records and the specimens upon which they are based are as follows:

VIRGINIA. Grayson County: East side of Mount Rogers, 5,000 feet, Kleinpeter and Hoffman, June 30, 1947 (RLH); gap between Bluff Mountain and White Top, Fowler and Hoffman, June 19, 1950 (RLH); Chestnut Mountain, west of Volney, Dr. and Mrs. S. T. Brooks, Aug. 13, 1941 (CM); Elk Garden Ridge, between Mount Rogers and White Top, Dr. L. R. Cleveland, July 15, 1947 (RLH); also by Dr. and Mrs. Brooks, July 29, 1941 (CM). Washington County: Straight Mountain, east of Damascus, Brooks, July 23, 1941 (CM); Coocoo Mountain, near Damascus, Brooks, Aug. 19, 1941 (CM); base of Laurel Mountain, 4 miles southwest of Konnarock, Leslie Hubricht, May 28, 1951 (RLH).

TENNESSEE. Johnson County: Northeast corner, "across line from Taylor's Valley, Va.," Brooks, Aug. 19, 1941 (CM).

***Dixioria pela fowleri*, new subspecies**

FIGURE 1,*e*

TYPE SPECIMENS: Holotype, allotype, and paratype (USNM 2013), topoparatypes (RLH); from Big Walker Mountain, along the west side near the top on U. S. Highway 52, about 10 miles east of Bland, Bland County, Va.; collected by J. A. Fowler and R. L. Hoffman, June 24, 1950.

DIAGNOSIS: Prefemoral process of male gonopod with a strong, somewhat rounded, subterminal shoulder along the outer margin; telopodite distally expanded with both subterminal processes well developed as in *D. p. coronata*, process B somewhat larger than in that form.

ECOLOGY: The following notes were made at the type locality: " . . . the area at which we collected seemed to be a talus slope of large boulders, but the whole area overgrown with a rich mesic woods

consisting chiefly of oak, hickory, and mountain maple. A large number of dead chestnut trees. The herb stratum dominated by *Impatiens biflora* and the ferns *Polystichum acrostichoides* and *Osmunda cinnamonea*. The logs and rocks almost entirely blanketed with moss." Millipeds collected at this place included *Uroblaniulus immaculatus* and *Apheloria kleinpeteri*. East of Marion, Va., *fowleri* was found in a typical *Magnolia-Liriodendron* "cove forest."

DISTRIBUTION: West side of the Iron Mountains and crossing the Great Valley to the folded Appalachians at Big Walker Mountain west of Wytheville. Known from the following localities:

VIRGINIA. Bland County: Big Walker Mountain, 10 miles east of Bland Court House, Fowler and Hoffman, June 24, 1950 (USNM, RLH). Grayson County: Comer's Rock, 3,800–4,000 feet, Leslie Hubricht, June 17, 1950 (RLH). Smyth County: Five miles east of Marion, Hoffman, May 4, 1954, Hoffman and Keeton, Aug. 22, 1954 (RLH). Washington County: Laurel Creek at Damascus, Leslie Hubricht, May 28, 1951 (RLH).

The range of this subspecies is the most interesting to be found for *Dixioria*. It is perhaps as great as that of *pela*, and embraces almost as much altitudinal variation. More pertinent is the fact that Big Walker Mountain is the only known station for a *Dixioria* outside the southern section of the Blue Ridge physiographic province. The situation is quite like that which obtains in the case of the plethodontid salamander *Plethodon jordani metcalfi* Brimley, which is likewise restricted to the Blue Ridge Province except for a single locality (Burke's Garden, Tazewell County, Va.) less than a dozen miles from Walker Mountain. This distribution is strongly suggestive of former continuity in a northwest-southeast direction, which is even today marked by the rugged country forming the divide between the headwaters of the Holston River and tributaries of the Kanawha.

Judging from the distribution of the two races, as well as the evidence available in gonopod structure, it seems likely that *coronata* is to be regarded as a high altitude counterpart of *fowleri*. That the two are subspecifically related is shown both by the quality level of gonopod differences as well as by two male specimens from Comer's Rock, which, although cited under *fowleri*, appear to be intergrades that I am unable to place in either of the two races. The gonopods are like those of *coronata* in the tibiotarsal processes, but similar to *fowleri* in the shape of the prefemoral process. Comer's Rock is also an intermediate locality both horizontally and vertically, as shown by the map.

Five males from Damascus are indistinguishable in every respect from the type series. But intergradation is certainly to be expected in the Damascus area, where future collecting can be profitably carried on.

***Dixioria pela wrighti*, new subspecies**

FIGURE 1,*f*

TYPE SPECIMENS: Holotype, allotype, and paratype (USNM 2014), collected along the east side of Grandfather Mountain about 5 miles northeast of Linville, Avery County, N. C. (U. S. Highway 221), on Aug. 3, 1949, R. L. Hoffman.

DIAGNOSIS: This is one of the most distinct members of the genus. Prefemoral process of gonopod elongate, slender, and distally bent at a right angle; femur very slender, bent at two places rather than evenly arcuate; process B of tibiotarsus very large, becoming broader distally and abruptly truncate, and widely separated from the recurved end of the solenomerite.

ECOLOGY: The specimens taken by me were collected from beneath slabs of bark and under logs residual to a roadside lumbering operation. The elevation was about 3,200 feet, and the locality had been well-drained mesic forest. A large number of immature specimens of the salamander *Plethodon yonahlossee* Dunn was found.

DISTRIBUTION: On and adjacent to the Blue Ridge proper in the vicinity of the Grandfather Mountain massif in Avery and Watauga Counties, N. C., and probably in adjacent counties as well. Geographically as well as morphologically, *wrighti* is intermediate between *pela* and *coronata*. Collections made in the area north of Grandfather Mountain, particularly in Ashe County, N. C., and Johnson County, Tenn., are needed to close the present gap between the known ranges of the two. Known from the following localities:

NORTH CAROLINA. Avery County: On U. S. Highway 221, about 1 mile north of its intersection with the Blue Ridge Parkway, Hoffman, Aug. 3, 1949 (RLH); west side of Grandfather Mountain, between Banner Elk and Newland, Hoffman, May 30, 1953 (RLH); "Blowing Rock to Linville," 3,000 to 4,000 feet, collector not stated, Sept. 7, 1930 (MCZ). Watauga County: Howard's Creek, at Boone, Mike Wright, Aug. 25, 1948 (RLH).

The specimen from Boone appears to be an intergrade, being like *wrighti* in the shape of the prefemoral process and like *coronate* as regards the tibiotarsal processes. Much collecting still needs be done in the western part of Avery County, where *pela* and *wrighti* appear to intergrade.

***Dixioria dactylifera*, new species**

FIGURE 2

TYPE SPECIMENS: Male holotype and topoparatypes of both sexes (AMNH), collected at Mill Hill, Ashe County, N. C., by C. M. and R. D. Breder in August 1910. Male paratype (USNM).

DIAGNOSIS: Similar in general to *Dixioria pela* as described in detail above, but differing from that species in the following respects: vertigial groove of head distinct but not obviously punctate; caudal margin of collum swept forward laterally and its ends somewhat more acute, marginal groove of anterior-lateral edge more distinct; upper surface of paranota with a more pronounced vermiculate sculpture which extends slightly farther onto the dorsum than the very faint rugae of *pela;* all sternites with at least eight setae, some of those near the gonopods with as many as 16–20; coxal spines greatly reduced, apparent only as low remnants on a few of the caudalmost legs; sternal aperture of gonopods much larger and wider than in *pela,*

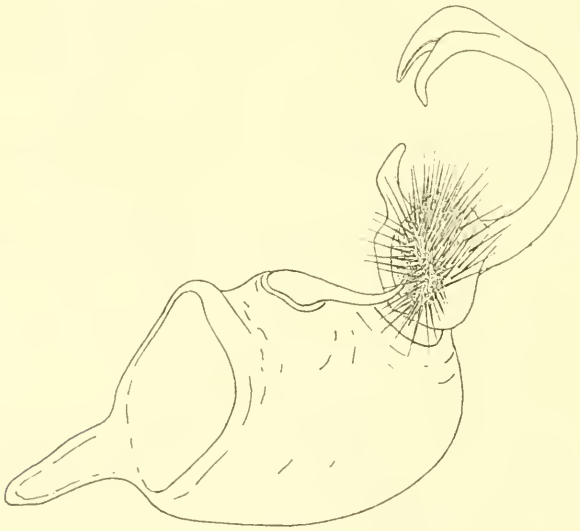

FIGURE 2.—Left male gonopod of male paratype of *Dixioria dactylifera.*

extending laterad at least 0.5 mm. beyond outer ends of coxal sockets of 8th legpair; process A of male gonopod absent, process B much enlarged, digitiform, larger than the solenomerite; and prefemoral process much shorter and bulkier.

ECOLOGY: I know nothing of the circumstances under which the type series was collected. The localities at which the Breders collected during the summer of 1910 are in the hilly country of central and western Ashe County, mostly at an elevation of less than 4,500 feet.

DISTRIBUTION: Known only from the type locality and immediate vicinity, in the central western part of Ashe County, N. C.

Relationships

Generic: *Dixioria* is a member of the group of genera in which the sternites are not strongly spined or lobed, the repugnatorial pores open dorsolaterally through a distinct peritreme, the coxae of the gonopods are without a long process, the prefemora are globosely swollen and densely setose, and the telopodite is long, slender, and unbranched, forming nearly a complete circle. This group also includes the genera *Apheloria* and *Brachoria*, of which the former is obviously the closer relative. Both of these genera contain forms which are distinctly broader in proportion to their length than are the forms of *Dixioria*. *Brachoria* contains several species in which

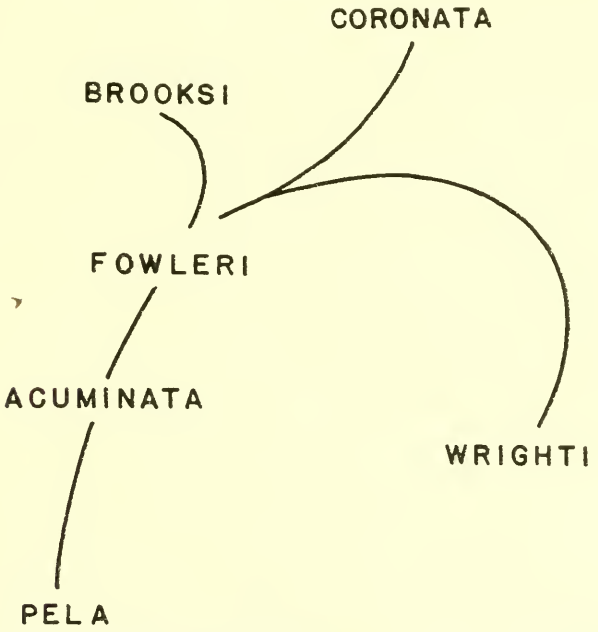

Figure 3.—Diagram of the probable relationships of the subspecies of *Dixioria pela*.

the paranota are broadly rounded caudally as in *Dixioria*, and the cyphopods of the two genera are similar. The males of *Brachoria*, however, are singular in that the telopodite is interrupted at about its midlength by a distinct constriction or flexible articulation. The gonopod of *Apheloria* differs chiefly in lacking subterminal processes on the telopodite, here again the cyphopods are quite similar. In none of the *Aphelorias*, however, are the caudal corners of the midbody paranota rounded off.

Subgeneric: As here conceived, *Dixioria* is composed of two species, one of which is divisible into six geographic races. Both of

these species seem to have had a common ancestor; in fact, it is entirely probable that *dactylifera* is little more than an extreme development of the trend in the *pela*-group toward increase in the size of process B and reduction in the length and arch of the telopodite blade. It has also largely lost the small but acute coxal spines found in *pela*.

The subspecies of *pela* constitute a distinct *Rassenkreis* pattern,

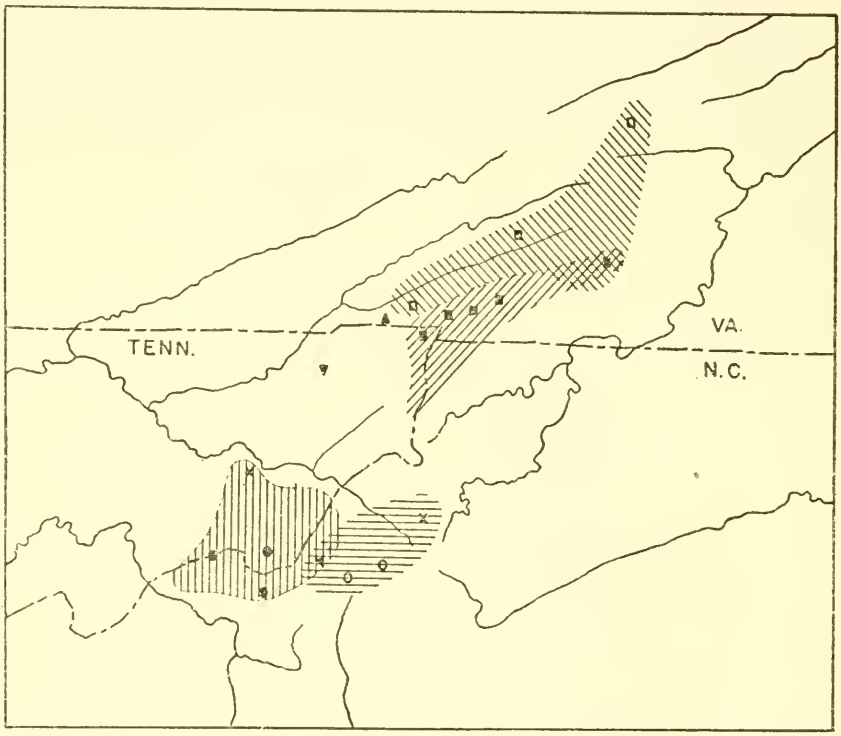

FIGURE 4.—Distribution of the subspecies of *Dixioria pela* in western North Carolina, northeastern Tennessee, and southwestern Virginia. The area is included by the headwaters of the Holston River on the upper left, of the New River on the lower right, and the Nolichucky River on the lower left. *Dixioria pela pela* is represented by solid circles, *D. p. acuminata* by a solid inverted triangle, *D. p. brooksi* by a solid upright triangle, *D. p. fowleri* by open squares, *D. p. coronata* by solid squares, and *D. p. wrighti* by open circles. Intermediate samples are indicated by an X, and are discussed in the text under one form or the other of the two involved.

forming nearly a closed circle, and involving modification from a simple gonopod to a more complicated one (or vice versa) in three major succeeding forms. That systematically different forms rather than a single geographically variable one are involved is borne out by the fact that each of the groups is homogeneous within itself, even though its range may extend almost a hundred miles. Intergradation

between these large, relatively stable, populations, in the few known instances, occurs in narrow belts between them.

A diagram (fig. 3) indicates the relationships of the subspecies of *pela*, of which lines of affinity are obvious from both geographical and structural considerations. I have omitted only an indication of the *direction* of evolution. That it has been linear is indicated by the progressive nature of the changes and by the fact that the most modified form (*wrighti*) finds itself juxtaposed geographically with the simplest (*pela*). I believe that this militates effectively against the possibility of simultaneous, in situ evolution from a widespread parent stock.

The geographical evidence suggests a northward spread through the Iron Mountains, the encounter of a physiographic barrier (the reduction of the uplands by the New River and Tennessee River headwaters) and subsequent exploration back to the south on a subparallel but isolated mountain range. The presence of *Dixioria pela fowleri* on Big Walker Mountain in Bland County, Va., indicates that its isolation from the bulk of the *Dixioria* population to the southeast must have been relatively recent, perhaps by acceleration of base-leveling by a local uplifting during the Quarternary.

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U. S. GOVERNMENT PRINTING OFFICE: 1953