

SYSTEMATICS AND NATURAL HISTORY OF *WADOTES* (ARANEAE, AGELENIDAE)¹

Robert G. Bennett²

Department of Biology
Western Carolina University
Cullowhee, North Carolina 28723 USA

ABSTRACT

The coelotine agelenid genus *Wadotes*, exclusive of the single described Palearctic species *W. primus*, is a monophyletic assemblage of species endemic to eastern North America. Diagnoses, descriptions, distributions, natural history notes, a key, and a phylogeny are presented for eleven species, five of which (*W. carinidactylus*, *W. deceptis*, *W. mumai*, *W. saturnus*, and *W. willsi*) are described as new. *W. convolutus* and *W. carolinus* are synonymized with *W. bimucronatus*. The male palpal tarsus and the female epigynum of the Nearctic group is described in detail. Mating behavior of *Wadotes* is described for the first time.

INTRODUCTION

North American spiders of the genus *Wadotes* Chamberlin, 1925 form a monophyletic assemblage occurring east of the Mississippi River from Nova Scotia, New Brunswick, eastern Ontario, and adjacent Quebec south to the central regions of Alabama and Georgia. These medium- to large-sized araneomorph spiders are commonly found in leaf litter or under various objects on forest floors. In parts of the range, some species have been shown to be among the most common spiders of the forest floor and consequently may be of great importance in the dynamics of such ecosystems (see Coyle 1981).

In 1925 Chamberlin named the genus *Wadotes* for three North American coelotine agelenid species originally described in the genus *Coelotes* Blackwall, 1841 (*Coelotes bimucronatus* Simon, 1898a; *C. calcaratus* Keyserling, 1887; and *C. hybridus* Emerton, 1889). He separated these species from both *Coelotes* and the related genus *Coras* Simon, 1898b by the following characters: two teeth on the retromarginal cheliceral fang furrow; "anterior median eyes much smaller than the laterals"; a posteriorly projecting, anteriorly attached scape; and variously developed processes on the proximal margin of the cymbium.

Subsequently *W. tennesseensis* Gertsch, 1936; *W. convolutus* Muma, 1947; and *W. georgiensis* Howell, 1974 from North America were described. Muma (1947)

¹This work was condensed from a thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree Master of Science (November, 1984).

²Present address: Department of Environmental Biology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada.

revised the taxonomy of the North American species of *Wadotes*. *Wadotes primus* Fox, 1937 from east Asia, is the only non-North American species described in the genus.

Eleven Nearctic species are described and figured in this revision, including five new species (*W. carinidactylus*, *W. deceptis*, *W. willsi*, *W. mumai*, and *W. saturnus*). The status of *Wadotes primus*, which may not belong in *Wadotes* (Lehtinen 1967), is discussed.

MATERIALS AND METHODS

This paper is the result of my own field observations and collecting, and the examination of approximately 1,500 specimens generously lent by museums and individuals listed in the Acknowledgments.

All measurements were made from specimens immersed in 80% ethanol and examined under a stereo dissecting microscope with an ocular micrometer mounted in one eyepiece. Measurements are accurate to 0.1 mm for carapace length (CL) and width (CW) (and also sternum length and width in *W. hybridus*, *W. saturnus*, and *W. mumai*) and to 0.025 mm for sternum length (SL) and width (SW) (except as noted above). Statistics are presented in the following fashion; sample range (mean±standard deviation). The ratios DL/DW and EL/LAE, used in the diagnoses of various species and in the key to species, compare respectively the length (DL) and width (DW) of the connecting ducts (Fig. 26) and the total length (EL) and length from the atrial slit to the epigastric furrow (LAE) of the epigynum (Fig. 22).

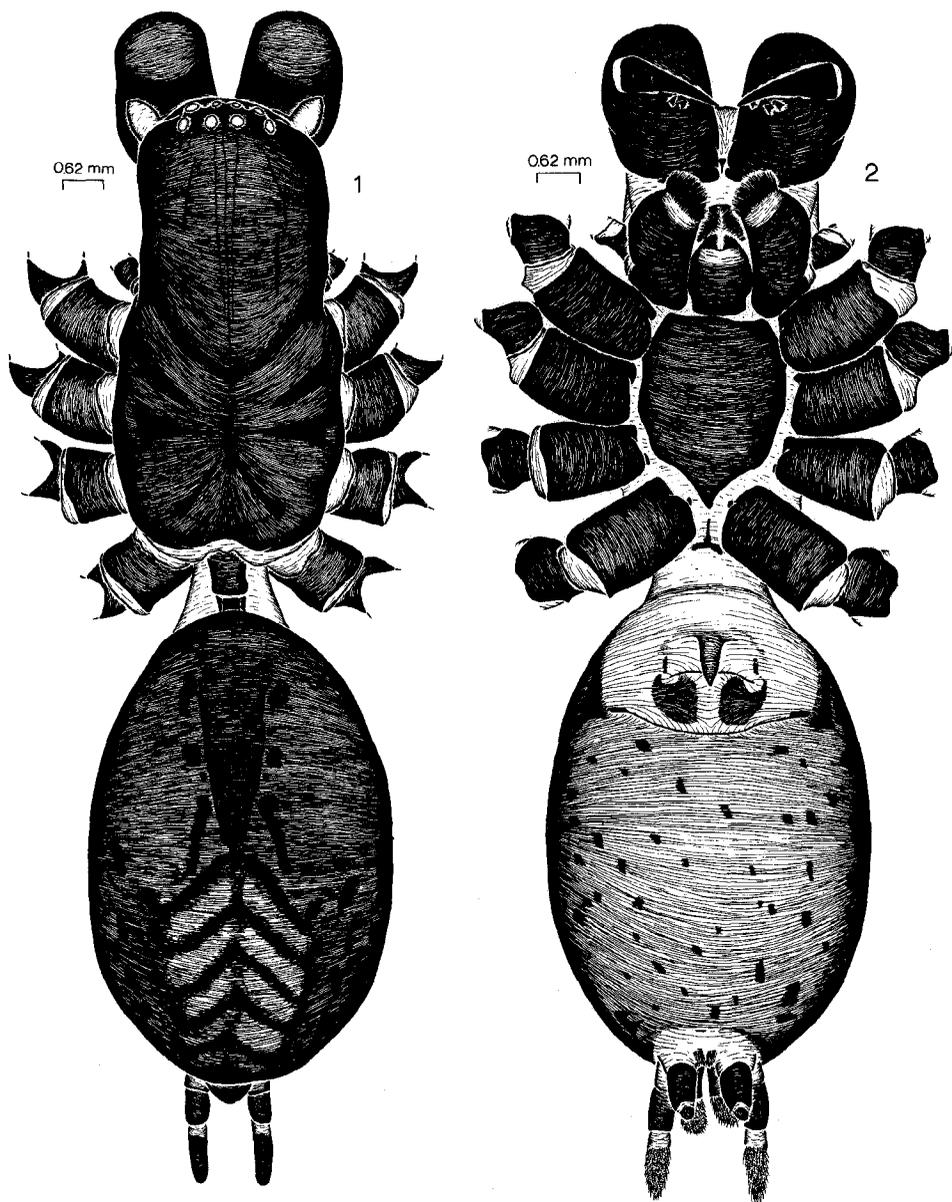
In the genus description, the position and number of macrosetae on a particular face of a leg segment are presented as a series of three numbers (separated by hyphens) which represents the number of macrosetae on the proximal, medial, and distal portions, respectively.

Except where noted, a left palpus was used for drawing male palpal characters. Palpi, or their dissected parts, were drawn while immersed in 80% ethanol. Internal characteristics of epigyna were drawn after being cleared in clove oil. All drawings were executed with the aid of a 10x10 squared grid eyepiece reticle. Figures of morphologically similar species are grouped together to facilitate the identification of specimens.

For simplicity in applying names to the various faces of the species-specific terminal apophysis (ventral, retrolateral, prolateral, and dorsal), the conductor and terminal apophysis have been visualized straightened out to lie along the anterior/posterior axis of the palpus and directly lateral to each other.

Expanded species and genus descriptions and discussions of palpal and epigynal structure are in Bennett (1984). Detailed lists of synonymies and literature records of *Wadotes* spiders can be found in Bennett (1984), Roewer (1954), or especially Bonnet (1959).

Abbreviations and acronyms not explained as they appear in the paper are listed below. Standard postal abbreviations are used for state and province names. Abbreviations used in figures are defined in the legend of the first figure in which they appear. RGB—R.G. Bennett, BRPWY—Blue Ridge Parkway, GSMNP—Great Smoky Mountains National Park, and JKMF—Joyce Kilmer Memorial Forest.



Figs. 1,2.—*Wadotes hybridus*, female, Cullowhee NC: 1, dorsal view; 2, ventral view.

MATING BEHAVIOR

Mating behavior was observed (under low power stereoscopic magnification) in *W. bimucronatus* on one occasion during this study (19.X.1983). A male and female already in some stage of a presumably post-courtship, pre-copulatory embrace were recovered live from a Berlese funnel. The ensuing sequence of events was similar to that described for *Agelenopsis* by Gering (1953).

When first observed, both were immobile with the male above the female and facing in the same direction. Her legs were tightly folded above her carapace and under her sternum (in the manner of a spider "feigning death") such that the male

was able to grip her by the patella/tibia joints securely with his chelicerae. The female was cataleptic at this stage and for most of the proceedings. The male spent several minutes dragging the female about, occasionally releasing his hold of her legs and repositioning himself. Most often the male returned to the superior position, oriented the same way as the female, but periodically he would approach her from either side at various angles. He rolled the female several times from side to side to angles of about 45 degrees. Some pauses in this general activity occurred during which both spiders were motionless for a minute or two, or the male would groom his palps and/or the tarsi and metatarsi of the first two pairs of legs with his chelicerae.

Copulation was initiated when the male approached the female from her left side and grasped her, facing in the opposite direction and in the superior position. He then rolled her onto her right side exposing the ventral surface of her abdomen. This corresponds to a modification of a "Type 2" mating position according to Kaston (1948, see figs. 2006 and 2010) or "Type 3" according to Foelix (1982). The male maneuvered the female's abdomen, contrary to the statement of Foelix (1982:196) that the female adjusts the orientation of her abdomen herself. The male then rapidly rubbed the retrolateral edge of the left cymbium laterally back and forth across the epigynum. This was repeated a few times with the same palpus and was alternated with grooming of both palpi. Following this, the male suddenly inserted the left palpal embolus into the atrial slit.

Insertion was achieved with the dorsal side of the cymbium oriented towards the posterior end of the female and with its proximal dorsal margin pressed against the ventral surface of the female's abdomen in the vicinity of the epigastric groove. The prolateral cymbial process was tightly pushed against the female abdomen at initiation and sank within the epigastric groove as insertion was effected.

Following this rapid sequence of events, inflation of the basal haematodocha was accomplished through a rhythmic and cumulative series of haematodochal pulsations until full expansion of the haematodocha was achieved. Once fully expanded, the basal haematodocha continued to pulsate rhythmically at about 4-second intervals with 1 to 1.5 seconds of maximal expansion followed by 2 or 3 seconds of slight relaxation.

Four consecutive copulatory events involving the left palpus were observed, each separated by short intervals of palpal grooming during which the male retained his basic mating position. Each copulation was preceded by an identical process of rubbing the epigynal surface with the retrolateral edge of the cymbium. The initial event lasted about 45 seconds. Two further events of short duration followed, one about 5 minutes in length and another of 5 to 10 seconds. The fourth event was terminated by the observer after approximately 40 minutes. As this event proceeded, the haematodochal pulsation rate slowed to about once every 5 or 6 seconds. The basal haematodocha remained in a fully expanded state, obliterating all other features of the genital bulb.

While the two were *in copula* the female was always in a cataleptic state lying on her right side with her legs folded over her cephalothorax and the male straddling her. The only obvious point of contact between the two spiders was of the palpal tarsus and the epigynum.

PHYLOGENY

North American *Wadotes* are probably closely related to both North American *Coras* and East Asian *Wadotes* (for the reasons discussed below). Until a better understanding of the latter group (and other coelotines) is achieved this relationship will remain an unresolved trichotomy. The following phylogeny is based upon a cladistic analysis of North American *Wadotes* using *Coras* and east Asian *Wadotes* (*W. primus*) as out-groups to establish character state polarity. Clades are numbered on Figure 119 and discussed below by number.

The presence of a membranous embolus support on the conductor (Figs. 5, 7, 12) is a possible synapomorphy linking *Coras* and North American *Wadotes*. Convoluted, matrix-bound connecting ducts with distinct primary loops (Figs. 24, 110) tie *Coras* and *Wadotes primus* to North American *Wadotes* but both characters may be synapomorphic at the subfamily level (the male of *W. primus* is unknown and I have not examined non-Nearctic coelotines). Three other weak synapomorphies support the monophyly of a group including *Wadotes* and *W. primus*: small anterior median eyes (Fig. 3), two retromarginal cheliceral fang furrow teeth (Fig. 2), and an epigynal scape (Figs. 1, 109, 111). These characters have arisen independently in various araneomorph genera (e.g. a scape occurs, within the Agelenidae, in such divergent agelenid genera as *Ethobuella* and *Calilena*).

Synapomorphies of the Nearctic species of *Wadotes* include the reduced sclerotization of the connecting duct matrices, a single transverse atrial slit (Fig. 21), and the sickle-like form of the conductor sclerite (Figs. 15, 16). Within this group, *W. tennesseensis*, *W. calcaratus*, and *W. willsi* (component 2) are linked by two synapomorphies: a roughened terminal apophysis surface (Figs. 38, 43, 47) and reduced and separate connecting duct matrices (Figs. 50, 58, 62).

Component 3 (*W. calcaratus* and *W. willsi*) is defined by three apomorphies: the large and conspicuous retrolateral cymbial process (Figs. 35, 41), lateral support sclerites (Figs. 49, 58), and the position of the spermathecae ventral to the secondary loops of the connecting ducts (Figs. 50, 58).

All the remaining species (component 4) are united by the following synapomorphies: a furcate terminal apophysis with a conspicuous median retrolateral process (Figs. 15, 97), a bisected prolateral cymbial process (Figs. 13, 93), and a reduced support sclerite not fused with the lateral plates of the superficial epigynal sclerotization (Fig. 23). (In *W. hybridus* the support sclerite has been lost.) Within this clade two monophyletic sub-groupings are evident: one composed of *W. bimucronatus* and *W. georgiensis* (component 5) and the other *W. carinidactylus*, *W. deceptis*, *W. dixiensis*, *W. hybridus*, *W. mumai*, and *W. saturnus* (component 6).

The presence of a reduced prolateral arm of the terminal apophysis (Figs. 15, 19), a deeply and narrowly bisected prolateral cymbial process (Figs. 13, 17), and the anterodorsal orientation of the connecting duct matrices (Figs. 24, 32) are autapomorphies of component 5. Despite the lack of females of *W. carinidactylus*, *W. deceptis*, and *W. mumai* these species are included in component 6 which is defined by the presence of relatively broad connecting duct matrices (Figs. 78, 84, 104). No defensible synapomorphies are known which bind either *W. carinidactylus* or *W. deceptis* to any of the lineages within component 6. They are placed there on the basis of their closer similarity to species of this component

than to those of component 5. A better understanding of the polarity of male character states (particularly the form of the prolateral cymbial process and the relative development of the terminal apophysis arms) will help resolve species relationships within component 6.

Synapomorphies of *W. hybridus*, *W. mumai*, and *W. saturnus* (component 7) are the lack of superficial epigynal sclerotization anterior to the atrial slit (Figs. 70, 76, 82—probably independently evolved in *W. tennesseensis* [Fig. 60]) and the presence of a ridge on the ventral surface of the prolateral arm of the terminal apophysis.

Finally, the reduction of the ventral arm of the prolateral cymbial process (Figs. 68, 85) and the elongation of the dorsal prolateral tibial extension to form an apophysis (Figs. 68, 86) constitute synapomorphies uniting *W. mumai* and *W. saturnus* (component 8). The development of this apophysis may be functionally correlated with the reduction of the prolateral arm of the cymbial process.

The ranges of *W. hybridus*, *W. mumai*, and *W. saturnus* (Fig. 118) are in accordance with the close relationship of these three species. *W. hybridus* and *W. saturnus* almost certainly have parapatric distributions. Possibly *W. hybridus* and the common ancestor of *W. saturnus* and *W. mumai* evolved from an ancient species with a range in the southern Appalachians. Subsequently, perhaps, *W. hybridus* expanded its range northward (after the retreat of the last of the Pleistocene glaciers) and *W. saturnus* and *W. mumai* differentiated from their common ancestor.

TAXONOMY

Genus *Wadotes* Chamberlin, 1925

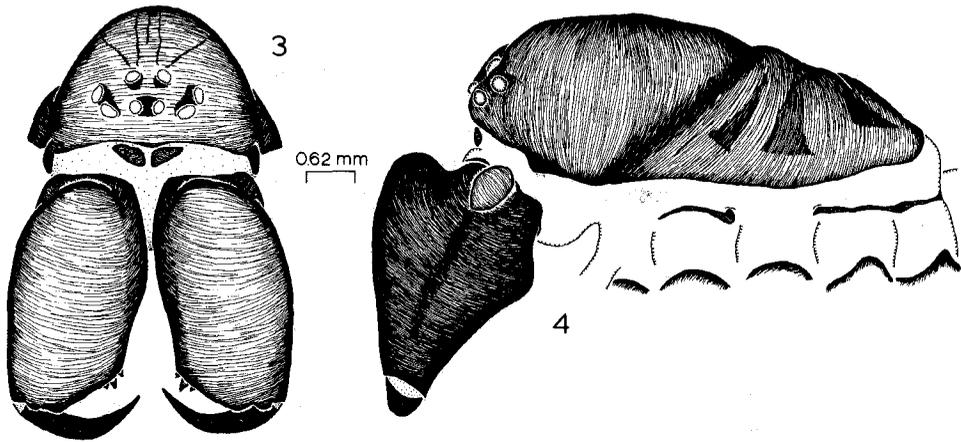
Wadotes Chamberlin, 1925:120. Type species *Wadotes dixiensis* Chamberlin by original designation.

The following diagnosis and description of the genus pertain to the Nearctic species group. The single Palaearctic species, *W. primus*, is discussed following the species descriptions.

Diagnosis.—Spiders of the genus *Wadotes* can be distinguished from all other coelotine agelenids by the presence of two retromarginal cheliceral fang furrow teeth (Fig. 2); variously developed, caudally projecting processes proximally on the prolateral and retrolateral margins of the male palpal cymbium (Figs. 13, 14, 34, 35, 45, 46); a caudally projecting, anteriorly attached scape on the ventral surface of the epigynum (Fig. 2); and a single, transverse, slit-like atrial orifice on the posterior two-thirds of the epigynum (Figs. 48, 82).

Description.—Species with carapaces averaging 3.9 to 6.7 mm in length; longer than wide, widest at coxae II, with well defined longitudinal thoracic groove; sparsely setose; ground color pale yellowish-brown to dark reddish-brown (usually darker anteriorly) (Fig. 1). Pars cephalica slightly elevated (Fig. 4). Eight eyes in two rows, rows straight in dorsal view (Fig. 1), slightly procurved in frontal view (Fig. 3); anterior median eyes smallest, other eyes subequal; median ocular quadrangle wider posteriorly than anteriorly, slightly higher than clypeus.

Chelicerae (Figs. 1-4) dark brown, robust, strongly geniculate; each with conspicuous, proximal, yellowish-brown boss retrolaterally (Fig. 4); two fang furrow teeth retromarginally (Fig. 2); three promarginally (Fig. 3), middle one



Figs. 3,4.—*Wadotes hybridus*, female, Cullowhee NC: 3, face and chelicerae, frontal view; 4, carapace and chelicerae, lateral view.

largest. Endites (Fig. 2) slightly convergent. Labium (Fig. 2) ca 0.7 times as long as endites, constricted basally. Endites and labium dark colored except narrow, lightly pigmented borders distally. Sternum colored as in carapace, longer than wide, widest between coxae II, with short caudal projection extending partly between coxae IV.

Abdomen (Figs. 1, 2) longer than wide, clothed with short setae, base coloration ranging intraspecifically from very light gray to dark gray. Anterodorsal "heart mark," posterodorsal chevrons, and other abdominal markings also of variable coloration and intensity.

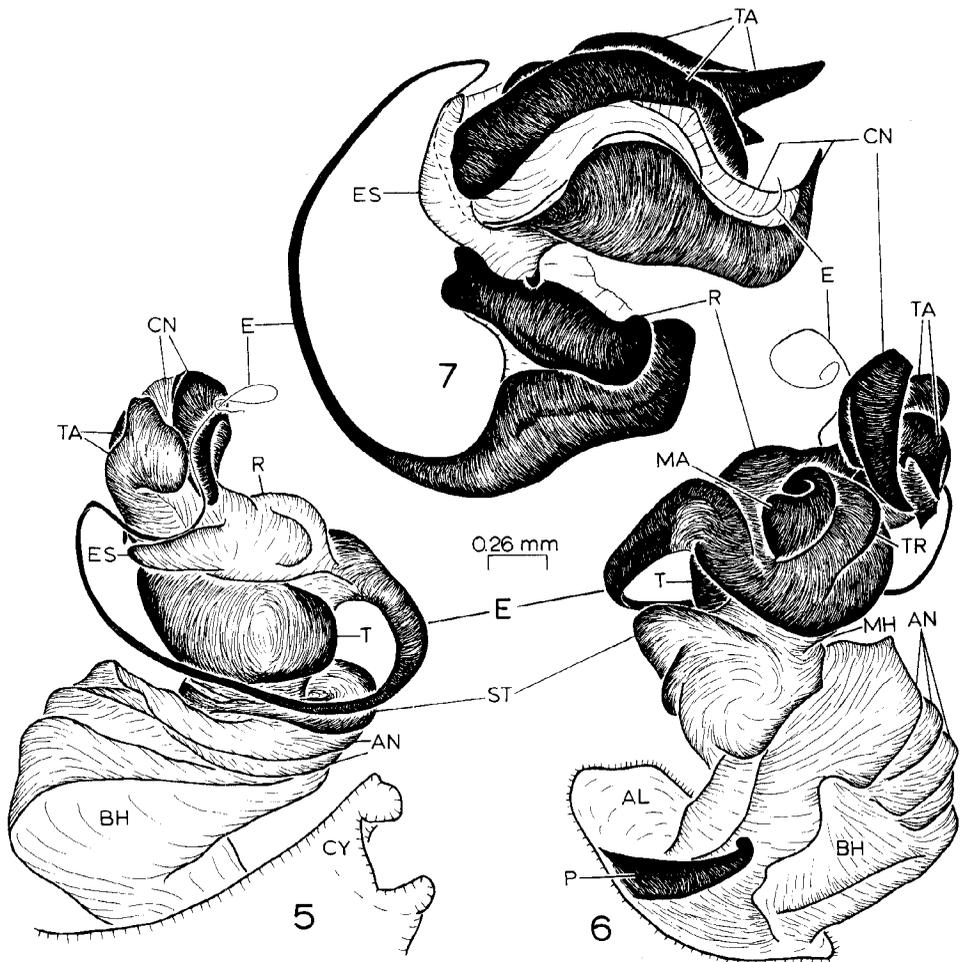
Spiracle minute, located anterior to two groups of less than ten colular setae each. Anterior spinnerets (Fig. 2) slightly separated, median and anterior spinnerets subequal, posterior spinnerets twice as long as others (Figs. 1, 2).

Legs in order of decreasing length, 4123; femora, tibia, and metatarsi with numerous macrosetae. Femur I usually with one (*W. calcaratus* and *W. willsi*) or two prolateral macrosetae distally. Tibiae I, III, and IV usually 2-2-2 ventrally. Tibia II either 2-2-2 or 1-2-2 ventrally with proximal ventral prolateral macroseta absent or reduced. Metatarsi I to IV all 2-2-2 ventrally (*W. tennesseensis*) or metatarsi I and II 2-2-3 and metatarsi III and IV 2-2-2. Tarsi with three claws; six to nine trichobothria dorsally, normally tarsi II and III each with one less trichobothrium than tarsi I and IV.

Male palpal patella distally with well developed retrolateral apophysis (Figs. 36, 37), dorsodistal macroseta arising from short dorsal apophysis (*W. calcaratus*—Fig. 36) or slight prominence. Tibia with three conspicuous prolateral megasetae (Figs. 72, 73, 93, 94); ventral retrolateral carina along length of tibia terminating in dorsoventral ridge distally; dorsal prolateral extension of tibia simple (Figs. 17, 34) or terminating in apophysis (*W. mumai*—Fig. 68).

Structure of the male palpal tarsus.—An understanding of the palpal tarsus is required in order to identify male *Wadotes*. Terminology used here is based on Gering's (1953) discussion of *Agelenopsis* and other agelenid genera.

The tarsus is comprised of the cymbium (CY; Figs. 9, 10) and the various components of the genital bulb or palpal organ which protrude from the alveolus (AL) on the ventral surface of the cymbium (Figs. 9-12).



Figs. 5,6. —*Wadotes saturnus*, expanded left genital bulb, Vogel State Park GA: 5, prolateral view; 6, retrolateral view. Fig. 7. *W. georgiensis*, terminal division of left genital bulb, ventral view, Vogel State Park GA. AL—alveolus, AN—anneli of subtegulum, BH—basal haematodocha, CN—conductor sclerite and/or membrane, CY—cymbium, E—embolus, ES—embolus support of conductor, MA—median apophysis, MH—median haematodocha, P—petiole, R—radix, ST—subtegulum, T—tegulum, TA—terminal apophysis, TR—tegular ridge.

Retrolaterally on the proximal half of the cymbium, there is a well developed, dorsally ridged concavity. The proximal margin of this is notched, and articulates with a dorsoventral retrolateral ridge on the tibia. The dorsal ridge of the concavity terminates proximally on or adjacent to a variously developed retrolateral cymbial process (RC; Fig. 14). This process is conspicuous in *W. calcaratus* and *W. willsi* (Figs. 35, 41), but is only a short knob in all other species. The proximal prolateral margin of the cymbium (PC; Fig. 13) is modified into a caudally oriented process which is obvious in all species except *W. calcaratus* and *W. tennesseensis* (Figs. 13, 93, 98). When present, this process is variously bifurcated, except in *W. willsi* where it is a simple extension of the cymbial margin (Figs. 40, 42).

The genital bulb occupies the alveolar cavity and is attached to its margins by means of the membranous and highly extensible basal haematodocha (BH; Figs.

5, 6, 10). A triangular, flattened sclerite, the petiole (P), is attached to the surface of the haematodocha near its proximal retrolateral boundary with the margin of the alveolus (Figs. 6, 10).

Distally, the basal haematodocha merges with the anelli of the subtegulum (AN, ST; Figs. 5, 6, 9, 10). Gering (1953:32-33) stated that "the subtegulum is virtually wanting as a sclerotized structure" and "the anelli are entirely obliterated" in *Wadotes*. These structures can, however, be readily observed by carefully dissecting an uncleared palpus (Fig. 10) or by drawing the genital bulb out from the alveolus with needles.

The anelli are approximately four long, narrow, lightly sclerotized, parallel bands interconnected by expansible membranes (Fig. 10). They form a nearly complete revolution before merging with the sclerotized ring of the subtegulum. In the unexpanded bulb, part of this ring is usually evident as a band of sclerotization between the proximal prolateral margin of the alveolus and the tegulum (Figs. 8, 9).

Collectively, the basal haematodocha, petiole, and components of the subtegulum comprise the basal division of the genital bulb (Comstock 1912, Gering 1953). Likewise, the middle haematodocha, tegulum, and median apophysis form the middle division in *Wadotes*.

The membranous, inconspicuous middle haematodocha forms a flexible union between the ventral margin of the subtegulum and the dorsal margin of the tegulum (MH; Figs. 6, 10).

The tegulum is a bowl-shaped, heavily sclerotized structure (T; Figs. 5, 6, 9, 11). It is readily obvious in the unexpanded bulb (Figs. 8, 9). All remaining components distal to the tegulum are associated with its ventral surface. Upon its ventral surface it bears a bevelled tegular ridge and the median apophysis (TR, MA; Figs. 6, 11).

The median apophysis, as defined by Gering (1953) for *Agelenopsis*, does not appear to exist in *Wadotes*. Here, Lehtinen (1967) and Roth and Brame (1972) are followed in naming, as the median apophysis, the sclerotized structure located in a ventral retrolateral excavation of the margin of the tegulum and joined to it by a narrow membrane (MA; Figs. 6, 11). This apophysis protrudes ventrally from the surface of the genital bulb and is shaped like one half of a bivalve shell. The ventral anterior margin of the median apophysis is distinctly and deeply notched.

In *Wadotes* the terminal division of the genital bulb is made up of the embolus, radix, conductor, terminal apophysis, and the membranes joining them to each other and to the ventral margins of the tegulum. The radix is an oblong, round-surfaced sclerite between the embolus and the conductor and adjacent to the median apophysis (R; Figs. 5-9). It is not rigidly attached to any sclerite as it is in *Agelenopsis* (Gering 1953).

The embolus, attached directly to the caudal margin of the tegulum, is long, slender, and flexible beyond the broad base (E; Figs. 5-7, 9, 11). Only the proximal third of this distal portion (the truncus) is visible in ventral view of the unexpanded bulb (Figs. 8, 9). Distally the truncus is enclosed by the embolus support (ES) and the conductor membrane joining the ventral surfaces of the terminal apophysis (TA) and conductor sclerite (CN; Fig. 7).

The conductor is the combined hyaline embolus support membrane, the crescent-shaped, pointed conductor sclerite caudal to the terminal apophysis, and

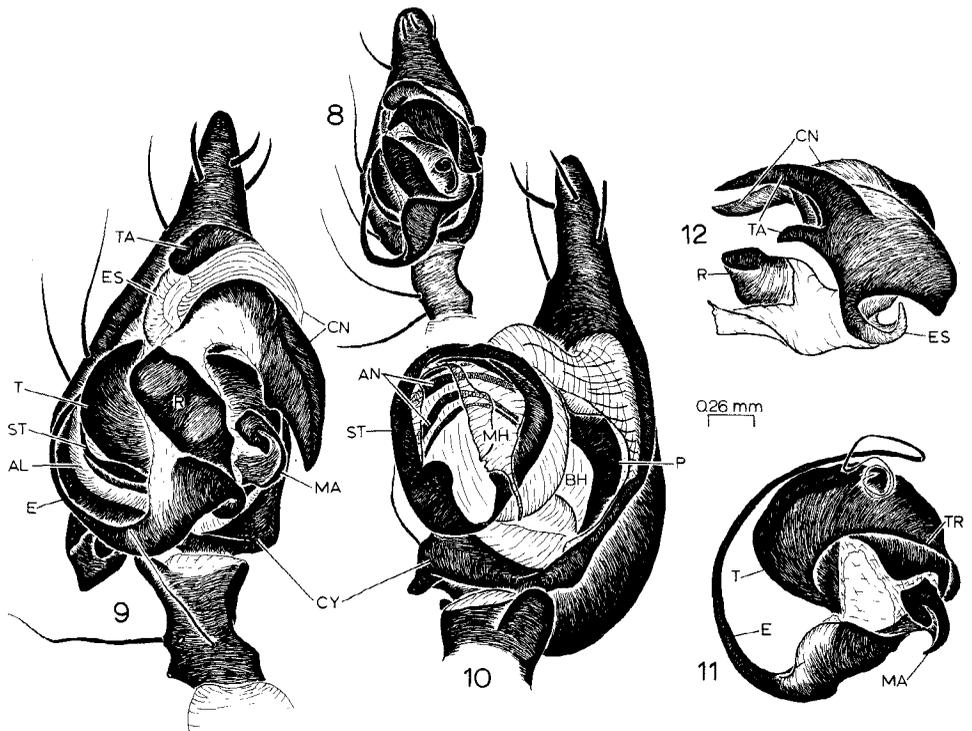


Fig. 8.—*Wadotes tennesseensis*, left palpal tibia and tarsus, ventral view, Newfound Gap (GSMNP) NC/TN. Figs. 9-12. *W. saturnus*, Vogel State Park GA: 9, left palpal tibia and tarsus, ventral view; 10, same, ventral retrolateral view, components of genital bulb distal to subtegulum removed; 11, tegulum, median apophysis, and embolus of left genital bulb, anteroventral view; 12, radix (interior surface), terminal apophysis, and conductor of left genital bulb, prolateral view.

the flexible membrane connecting this sclerite to the terminal apophysis (CN, ES; Figs. 5-7, 9, 12). Many terms have been applied to these components. The conductor sclerite is the embolic conductor of Muma (1947), the secondary terminal apophysis of Howell (1974), and the fulcrum of Lehtinen (1967). Roth and Brame (1972), feeling that a true conductor is lacking in *Wadotes* (and *Coras*), preferred to call the conductor, as here defined, the functional conductor (which, in combination with the terminal apophysis, forms the embolic process). Howell (1974) mistakenly believed that Muma (1947) had not mentioned the conductor sclerite, and that the embolic process of Roth and Brame (1972) included only the terminal apophysis.

The terminal apophysis is the primary conductor of Lehtinen (1967), and the functional conductor of terminal apophysis of Howell (1974). It is the only component of the genital bulb of *Wadotes* that exhibits apparent species-specific variation. Shear (1967) and Lehtinen (1967) incorrectly felt that this structure and the conductor sclerite are fused together (at least in *W. calcaratus*).

The terminal apophysis in its simplest form (*W. calcaratus*, *W. willsi*, and *W. tennesseensis*) (TA; Figs. 38, 39, 43, 44, 47) is truncate distally, laterally compressed, rough surfaced, and, except for a median retrolateral process (MRP; Fig. 38) projecting ventrally in the region of the embolus support and a dorsal extension supporting the latter structure, is unadorned by arms or other apophyses. The males of all other species possess complex terminal apophyses.

The complex type also bears a median retrolateral process (MRP; Fig. 15) and a dorsal extension bracing the embolus support as well as a long, pointed ventral arm (VT; Figs. 15, 19, 95, 100) and less obvious retrolateral (RT; Figs. 15, 19) and prolateral arms (PT). The retrolateral arm is either fused to the ventral retrolateral edge of the ventral arm (Figs. 87, 88, 91, 92) or to the prolateral arm by means of a variously-developed dorsal plate (Figs. 15, 101). The prolateral arm may be distinct (Fig. 12), an integral part of the dorsal plate (Fig. 97), or greatly reduced (Fig. 19).

The ventral, retrolateral, and prolateral arms are the median, basal, and apical apices, respectively, of Muma (1947). Howell (1974), in his description of *W. georgiensis*, mistakenly interpreted the median retrolateral process (discussed below) of that species as Muma's basal apex and the retrolateral arm (basal apex) as the apical apex. As well, he did not mention the very inconspicuous prolateral arm (Fig. 19) which is Muma's apical apex.

Muma (1947) did not discuss the median retrolateral process (MRP) of the terminal apophysis. This prominent feature of the dorsal surface of complex terminal apophyses (Figs. 15, 87) is inconspicuous in simple terminal apophyses (Fig. 38). It is broadly triangular and not attached to any of the nearby membranes as is the adjacent process which strengthens the embolus support.

In ventral view, the terminal apophysis is inconspicuous and overlain by the conductor (Figs. 8, 9) with only the proximal knob and the distal end of the ventral arm (or truncated tip in simple terminal apophyses) visible. These features are the only parts of the genital bulb which may be visible in dorsal view (TA; Figs. 14, 35, 94), other than the proximal loop of the embolus in *W. tennesseensis* (Fig. 46).

Among North American agelenids, the tarsal components of *Wadotes* are morphologically most similar to those displayed by the genus *Coras* (see Muma 1946). The genital bulbs of *Wadotes* and *Coras* differ markedly only in the structure of the conductor and terminal apophysis. In *Wadotes* the conductor exhibits a fairly constant morphology and the terminal apophysis is variable. In *Coras* the terminal apophysis is usually blunt and rounded and the conductor sclerite is variable. Muma (1946) used the latter to partially define the species of *Coras*. The embolus support is similar in both *Coras* and *Wadotes*.

Structure of the epigynum.—The epigyna of *Wadotes* are simple organs but are difficult to describe as there are few well pigmented or sclerotized structures and the internal epigynal characters are enveloped by soft tissue.

In *Wadotes* the epigynum is characterized externally by a scape, a transverse atrial slit, and a variable amount of superficial sclerotization (SC, AS, SES; Fig. 21). The scape (atrial guide [Gering 1953], stylus [Chamberlain and Ivie 1941]) projects caudally from the inside medial edge of the anterior epigynal margin across a central unsclerotized area as a dorsoventrally flattened, finger-like cuticular evagination. Scape morphology is highly variable within species (Figs. 53-57). Dorsal to the scape, the central region of the epigynum is unsclerotized.

The caudal end of the scape lies in the vicinity of the atrial slit which is a single, inconspicuous, transverse fissure located in the posterior one-quarter (Fig. 48) to two-thirds (Figs. 76, 77) of the epigynum. Its position is of some importance in species determinations.

Posterior to the atrial slit the median unsclerotized area (MUA), which corresponds to the posterior median sclerite of Gering (1953) and Chamberlin and

Ivie (1941), extends into the epigastric groove (Figs. 22, 23). Posteriorly, on the lateral margins of the median unsclerotized area, a pair of slight longitudinal depressions is present in *W. tennesseensis* (DN; Fig. 60). These are of variable occurrence in other species (Figs. 21, 83).

The superficial epigynal sclerotization is composed of a pair of large (SES; Fig. 22) or small (Fig. 48) sclerotized plates (lateral to the median unsclerotized area) and, connecting them, a band of sclerotization delimiting the lateral and anterior margins of the epigynum (SES; Fig. 21). This band is reduced or absent in some species (Figs. 76, 77).

In most species of *Wadotes* a support sclerite, perhaps a reduction of Gering's (1953) posterior median sclerite, lies within the epigastric groove on the caudal surface of the epigynum (SS; Figs. 23, 61). *Wadotes hybridus* has no support sclerite and in *W. calcaratus* and *W. willsi* it is a pair of narrow lateral bands running from the vicinity of the spermathecae to the posterior margins of the lateral plates (SS; Figs. 49, 50).

Internally the atrial slit becomes an anterodorsally oriented, shallow, flattened atrium (AT; Figs. 24, 27). The atrium terminates as two lightly sclerotized pockets which are inconspicuously connected to the anterior ends of the connecting ducts (Fig. 27).

The long, narrow connecting ducts (CT; Fig. 26) and the matrices (MX; Fig. 24) in which they are imbedded correspond to Gering's (1953) bursa copulatrix. Since the term bursa implies the presence of a pouch or sac it is not used here. The anterior-most 'S'-shaped section comprises the primary loops (PL; Fig. 25) and the remaining length the secondary loops of the connecting duct. The matrices are lightly sclerotized but tough and durable, and contiguous (Figs. 24, 104) or separated (Figs. 50, 78). In *W. bimucronatus* and *W. georgiensis* the matrices are strongly convex dorsally and extend somewhat posterodorsally from the atrium (Figs. 24, 32).

The oblong, lobed spermathecae (SP; Figs. 23, 24) have thick walls and large lumina and are the only heavily sclerotized internal components of the epigynum. In *W. calcaratus*, *W. tennesseensis*, and *W. willsi* the spermathecae are ventral (as opposed to caudal) to the posterior ends of the matrices (Figs. 50, 58, 62). From the posterodorsal margin of each spermatheca emanates a short, curved, and inconspicuous fertilization duct (FD; Fig. 24) which lies very close to the spermathecal surface and is best observed in profile.

Natural History.—*Wadotes* specimens are usually found on the floor of deciduous or coniferous forests but may also be common in clearcut areas within forests (see Coyle 1981). They have been collected from leaf litter, within rotting logs, under bark or moss on logs, on the underside of and underneath rocks and other objects, and through the use of pitfall traps and Berlese funnels.

The web of *Wadotes* is normally flimsy, tubular, several cm in length and often branched with one or more openings. It is always hidden with only the entrance(s) visible.

KEY TO NEARCTIC SPECIES OF *WADOTES*

(Females of *W. carinidactylus*, *W. mumai* and *W. deceptis* unknown.)

- | | | |
|----|--------------|----|
| 1. | Males..... | 2 |
| | Females..... | 12 |

- 2 (1). Prolateral cymbial margin bisected (Figs. 17, 98); terminal apophysis with variously developed arms (Figs. 19, 95).....5
 Prolateral cymbial margin entire (Figs. 40, 45); terminal apophysis blunt (Figs. 39, 47).....3
- 3 (2). Retrolateral cymbial margin strongly developed, produced over tibia (Figs. 35, 41); embolus not visible in dorsal view.....4
 Retrolateral cymbial margin inconspicuous, not produced over tibia (Fig. 46), basal third of embolus visible in dorsal view.....*tennesseensis*
- 4 (3). Prolateral cymbial margin not developed (Fig. 34); species widespread.....*calcaratus*
 Prolateral cymbial margin well developed (Figs. 40-42) species probably restricted to vicinity of Mount Rogers, Virginia.....*willsi*
- 5 (2). Prolateral cymbial margin deeply bisected by narrow cleft (Figs. 13, 17); in dorsal view prolateral usually slightly longer (Fig. 14) to twice as long as retrolateral cymbial margin (Fig. 18). Prolateral arm of terminal apophysis inconspicuous (Fig. 19) or reduced to a short dorsal plate (Fig. 15).....6
 Prolateral cymbial margin bisected other than by deep, narrow cleft (Figs. 68, 72, 89); in dorsal view prolateral and retrolateral cymbial margins subequal or prolateral slightly longer than retrolateral margin. Prolateral arm of terminal apophysis well developed (Figs. 87, 100).....7
- 6 (5). Base of retrolateral arm of terminal apophysis fused to flattened, short, triangular, prolateral arm (Fig. 15); species widespread in southern Appalachians and surrounding Piedmont.....*bimucronatus*
 Base of retrolateral arm of terminal apophysis fused to base of ventral arm; prolateral arm an inconspicuous projection on dorsal base of ventral arm (Fig. 19); range probably restricted to vicinity of Vogel State Park, Union County, Georgia.....*georgiensis*
- 7 (5). Retrolateral arm of terminal apophysis fused to base of ventral arm (Figs. 88, 92).....8
 Retrolateral arm of terminal apophysis otherwise (Figs. 70, 75, 97, 101).....9
- 8 (7). Bisection of prolateral cymbial margin wide in prolateral view (Fig. 85), ventral and dorsal arms well separated.....*saturnus*
 Bisection of prolateral cymbial margin triangular in prolateral view (Figs. 89, 90), ventral and dorsal arms close together.....*deceptis*
- 9 (7). Ventral arm of terminal apophysis with a conspicuous ventral keel (Fig. 95); prolateral and retrolateral arms forming a broad, conspicuous plate with retrolateral keel ventrally...*carinidactylus*
 Ventral arm of terminal apophysis long and slender with no ventral development; prolateral and retrolateral arms otherwise (Figs. 70, 75, 100).....10
- 10 (9). Retrolateral arm of terminal apophysis with a basal flange dorsally which connects it broadly to prolateral arm (Figs. 69, 75).....11
 Retrolateral arm of terminal apophysis broadly connected to prolateral arm from tip to tip forming a smooth crescent-shaped dorsal plate (Figs. 100-101).....*dixiensis*
- 11 (10). Ventral arm of prolateral cymbial margin as large as or larger than dorsal arm in prolateral view (Fig. 72), species widespread.....*hybridus*
 Ventral arm of prolateral cymbial margin greatly reduced (Fig. 68), dorsal arm large and conspicuous (Fig. 66); species apparently restricted to north-central Georgia.....*mumai*
- 12 (1). Superficial epigynal sclerotization present as two well developed plates posterior to the atrial slit, separated by a narrow median unsclerotized area and joined by a sclerotized band passing anterior to the scape (Figs. 21, 102).....13
 Either median unsclerotized area (posterior to atrial slit) wide, greater than one-half width of epigynum (Fig. 48), or anterior sclerotized band lacking (Figs. 76, 82).....14

- 13 (12). Connecting duct matrices wide (Fig. 104), length and width subequal, DL/DW=0.87-1.29, N=20.....*dixiensis*
 Connecting duct matrices narrower (Figs. 24, 32), much longer than wide, DL/DW=1.30-1.89, N=15 (*bimucronatus*), or 1.38-1.67, N=9 (*georgiensis*).....*bimucronatus* or *georgiensis*
- 14 (12). Median unsclerotized area (posterior to atrial slit) wide, > one-half width of epigynum; LAE about one-fifth to one-quarter of EL; anterior sclerotized band present (Fig. 48); caudal support sclerotization inconspicuous, lateral to position of spermathecae (Figs. 49, 50); species widespread (*calcaratus*) or restricted to vicinity of Mt. Rogers, Virginia (*willsi*).....*calcaratus* or *willsi*
 Median unsclerotized area narrow (sclerotization posterior to atrial slit well developed) (Figs. 60, 76, 82); LAE > one-quarter of EL; anterior sclerotized band absent or weakly developed; caudal support sclerotization lacking or located between position of spermathecae (Fig. 83).....15
- 15 (14). Caudal support sclerotization lacking, species widespread.....*hybridus*
 Caudal support sclerotization present between position of spermathecae (Fig. 83).....16
- 16 (15). LAE between one-quarter and one-third of EL (Fig. 60), duct matrices separate, slender (Fig. 62).....*tennesseensis*
 LAE one-half or more of EL (Fig. 82); duct matrices large, wide and contiguous (Fig. 84).....*saturnus*

Wadotes bimucronatus (Simon)

Figs. 13-16, 21-31, 115, 117

Coelotes bimucronatus Simon 1898a:6.

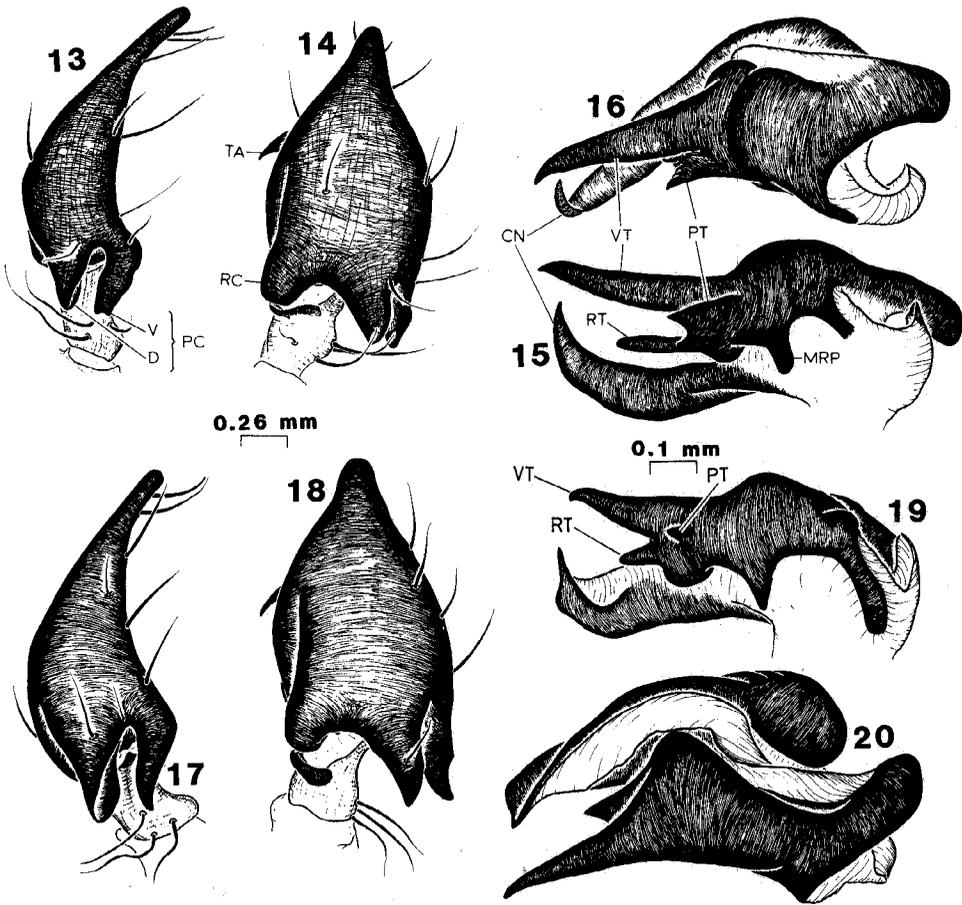
Wadotes bimucronatus: Chamberlin 1925:121.

W. carolinus Chamberlin; 1925:121; Muma 1947:6, figs. 5, 6, 18, 19, 35, 36, NEW SYNONYMY.

W. convolutus Muma 1947:8 (male only), NEW SYNONYMY.

Diagnosis.—Males of *W. bimucronatus* are distinguishable from all other *Wadotes* except *W. georgiensis* by the combined presence of a strongly bifurcate terminal apophysis (Figs. 15, 16) and a proximal prolateral cymbial process laterally divided by a long, narrow cleft (Fig. 13). The prolateral cymbial process of *W. bimucronatus* is shorter in dorsal view (about 1 to 1.5 times as long as the retrolateral process) than that of *W. georgiensis* (compare Figs. 14, 18). The terminal apophysis in *W. bimucronatus* has a conspicuous, somewhat triangular, flattened process dorsally (Fig. 15) which is represented in *W. georgiensis* by only a very slight projection (Fig. 19).

Females of *W. bimucronatus* are distinguishable from all other *Wadotes* except *W. georgiensis* and *W. dixiensis* by the complete superficial epigynal sclerotization, both anterior and posterior to the atrial slit (Figs. 21, 22). *Wadotes bimucronatus* can be separated from *W. dixiensis* by the presence, in the former, of collecting duct matrices which are about 1.5 times as long as their combined width (DL/DW=1.30-1.89, N=15) (Figs. 24-28). No morphological characteristics have been observed which serve to adequately distinguish females of *W. bimucronatus* from *W. georgiensis*. Howell (1974) stated that the relative shape of the boundaries of the median unsclerotized area posterior to the atrial slit distinguishes the two species. This character is highly variable in both species and cannot reliably separate the two.



Figs. 13-16.—*Wadotes bimucronatus*, Cataloochee NC: 13, left palpal tibia and cymbium, prolateral view; 14, same, dorsal view; 15, terminal apophysis and conductor of left genital bulb, dorsal view; 16, same, prolateral view. Figs. 17-20. *W. georgiensis*, Vogel State Park GA: 17, left palpal tibia and cymbium, prolateral view; 18, same, dorsal view; 19, conductor and terminal apophysis of left genital bulb, dorsal view; 20, same, ventral view. D—dorsal arm of PC, MRP—median retrolateral process of TA, PC—prolateral cymbial extension, PT—prolateral arm of TA, RC—retrolateral cymbial extension, RT—retrolateral arm of TA, V—ventral arm of PC, VT—ventral arm of TA.

Description.—*Male*: Figs. 13-16. 40 specimens measured. CL 3.2-4.9(4.2±0.39), CW 2.1-3.2(2.7±0.29), SL 1.63-2.40(2.05±0.18), SW 1.33-1.75(1.58±0.11). Holotype of *C. bimucronatus* CL 5.0, CW 3.3, SL 2.43, SW 1.8. (This specimen was not on hand when the statistics were compiled and, thus, was not included in the sample. Simon's measurement [1898b] of 6.0 mm total length for this specimen is either a mistake or a misprint.)

Female: Figs. 21-31. 40 specimens measured. CL 2.9-5.4(4.0±0.46), CW 1.9-3.3(2.5±0.27), SL 1.55-2.50(1.95±0.19), SW 1.25-1.95(1.56±0.14). LAE about two-fifths of EL, EL/LAE=2.13-2.83(2.54±0.21), $N=16$.

Variation: Considerable variation is found in the form and pattern of the connecting ducts, even among specimens from the same locale. One specimen (from Monroe County, Georgia, on the present southern boundary of the range of this species) has duct matrices wider than average for *W. bimucronatus* (width ca 0.75 times length [Fig. 28]), resembling those of *W. dixiensis*. The matrices

lack the overall squarish, "fat" appearance of those of *W. dixiensis* (Fig. 104), however, so this specimen is tentatively considered to be *W. bimucronatus*.

The tip of the ventral arm of the prolateral cymbial process may be bluntly pointed, rounded, or truncated. The scape (Figs. 21, 23, 29-31) is variously tapered to a blunt, bifid, or pointed tip.

Distribution.—Figs. 115, 117. *Wadotes bimucronatus* is the most common *Wadotes* collected in the southern Appalachians of western North Carolina and northern Georgia, and is found at least as far south as central Georgia as shown by the pitfall trapping of Howell (1976) and a single record from southern Alabama. A population from the north panhandle of West Virginia may be isolated from the southern aggregations as no *W. bimucronatus* have been recorded from the rest of West Virginia except for Mercer County (far to the south on the Virginia border).

Natural History Notes.—*Wadotes bimucronatus* is a very common spider of the hardwood forest floor in the southern Appalachians. At high elevations it becomes rare and is probably absent from the spruce/fir community on the high peaks of the region. This spider has been collected syntopically with *W. hybridus*, *W. dixiensis*, *W. mumai*, and *W. carinidactylus*. It may also be syntopic with *W. calcaratus* and *W. saturnus*, but is probably not sympatric with the closely related *W. georgiensis*.

Mature males have been collected from mid-September to late March. Mature females are present all year.

One dipterous pupa (Acroceridae) emerged from the abdomen of a penultimate male *W. bimucronatus* being reared in the laboratory. The spider had been collected sometime previously as a penultimate in Cullowhee, North Carolina. On 3 November 1983 the spider was dead and a small cocoon containing the acrocerid pupa was observed in the spider's webbing. On 5 November the pupa had left the cocoon but was still encased in a puparium. It was removed at this time for examination and then placed in a vial to contain the emergent adult. Shortly thereafter the pupa died, a result that probably illustrates the importance of E. I. Schlinger's advice (pers. comm.) to avoid manipulating or handling acrocerid pupae during attempts to rear them to adulthood.

Types.—*Coelotes bimucronatus* Simon, male holotype, North Carolina, in MNHN, examined. *Wadotes carolinus* Chamberlin, male holotype, North Carolina, Polk Co., Tryon, XI 1913 (W. M. Wheeler), in MCZ, examined. *Wadotes convolutus* Muma, female holotype, Alabama, Marshall Co., Bishop Cave (Ms5), Bishop Mtn., 1.5 mi S. of highway, 12 I 1933 (A. F. Archer), in AMNH, examined.

Discussion.—Muma (1947) misidentified specimens which properly belong in *W. dixiensis* Chamberlin as *W. bimucronatus* Simon.

Wadotes calcaratus (Keyserling)

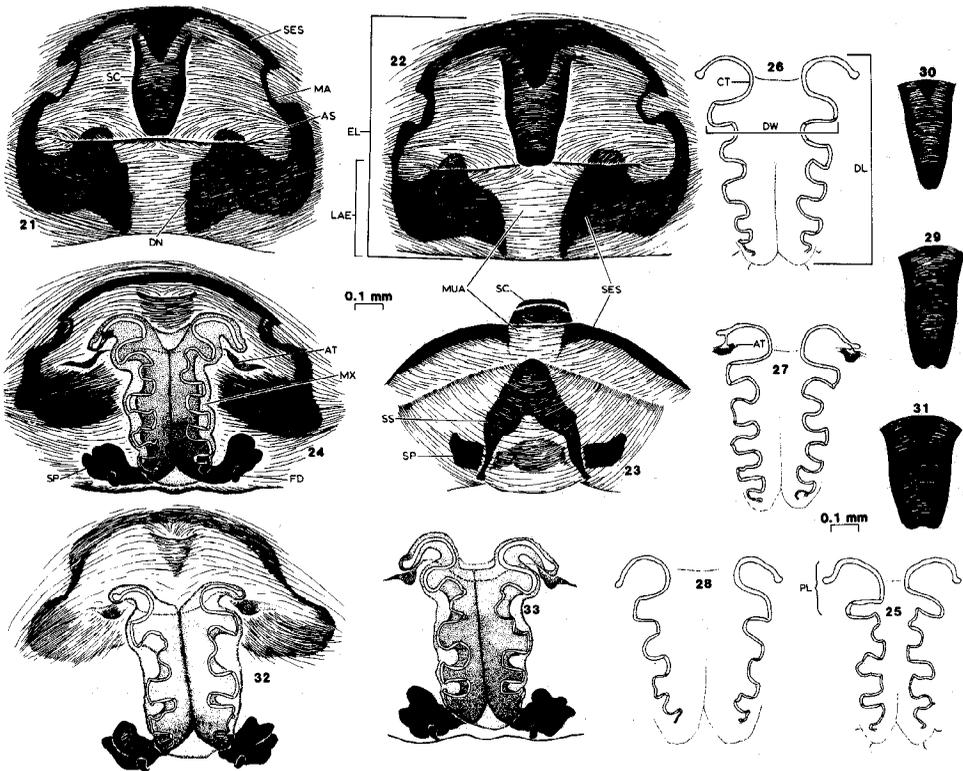
Figs. 34-39, 48-57, 112, 113, 118

Coelotes calcaratus Keyserling 1887:470 (in part), fig. 32 (not fig. 32a [Kaston 1948]).

C. longitarsus Emerton 1889:192 (in part), fig. 2 (not fig. 2a [Kaston 1948]).

C. nigriceps Banks 1895:82.

Wadotes calcaratus: Chamberlin 1925:121; Muma 1947:2, figs. 3, 4, 16, 17, 33, 34; Kaston 1948:282, figs. 903, 904, 916.



Figs. 21-31.—*Wadotes bimucronatus*: 21-22, epigyna, Cullowhee NC, ventral views; 23, same, caudal view; 24, same, anterodorsal view; 25, connecting ducts, anterodorsal view, Bryson City NC; 26, same, Wheeling WV; 27, same, Bryson City NC; 28, same, Monroe County GA; 29, scape, ventral view, Cartersville GA; 30, same, Cullowhee NC; 31, same, Highlands NC. Figs. 32,33. *W. georgiensis*, Vogel State Park GA: 32, epigynum, anterodorsal view; 33, same, ventral superficial features excluded. AS—atrial slit, AT—atrium, CT—connecting duct, DL—length of CT, DN—depression, DW—width of duct matrices, EL—epigynum length, FD—fertilization duct, LAE—EL from AS to epigastric groove, MA—muscle attachment sclerotization, MUA—median unsclerotized area, MX—CT matrix, PL—primary loops of CT, SC—scape, SES—superficial epigynal sclerotization, SP—spermatheca, SS—support sclerite.

Diagnosis.—*Wadotes calcaratus* can be separated from all other *Wadotes* except *W. willsi* by the presence of, in males, a long proximal retrolateral cymbial process (Fig. 35) and a short dorsodistal patellar apophysis (Figs. 36, 37); and in females, EL 4 to 6 times as long as LAE ($EL/LAE=3.70-6.00$, $N=11$) (Fig. 48) and caudally on epigynum a pair of weak support sclerites lateral to spermathecae (Fig. 49). *Wadotes calcaratus* males can be distinguished from *W. willsi* by their lack of a pronounced dorsodistal tibial apophysis and the relatively undeveloped nature of the proximal prolateral cymbial margin (Fig. 34). Females of *W. willsi* and *W. calcaratus* show no apparent structural differences.

Description.—*Male*: Figs. 34-39. 40 specimens measured including lectotype. CL 3.5-4.7(4.1 \pm 0.32), CW 2.3-3.0(2.7 \pm 0.19), SL 1.75-2.33(2.04 \pm 0.13), SW 1.35-1.78(1.57 \pm 0.05). Lectotype CL 4.5, CW 3.1, SL 2.25, SW 1.63. Tibia with a small, proximal, dorsal apophysis (Fig. 37).

Female: Figs. 48-57. 40 specimens measured. CL 3.1-5.2(4.2 \pm 0.43), CW 2.1-3.3(2.6 \pm 0.28), SL 1.55-2.38(2.02 \pm 0.18), SW 1.28-1.88(1.61 \pm 0.13).

Variation: The retrolateral cymbial process varies in length and curvature from slightly shorter than in Figure 35 to slightly longer with an abrupt, truncate, prolaterally bent terminus. The epigynal scape varies widely (Figs. 48, 53-57). The connecting ducts vary considerably in the orientation of the primary loops.

Distribution.—Figs. 112, 113, 118. The range of *W. calcaratus* corresponds fairly closely to a region delimited in the south, south-east, and south-west by the northern boundary of the Gulf and Atlantic Coastal Plains, and in the north by the southern boundary of the boreal forest.

Specimens are reported to have been collected in Nebraska (Worley and Pickwell 1927), Wyoming and Colorado (Keyserling 1887, in Bonnet 1959), and Oklahoma and Arizona (Muma 1947). All these records are old and the Nebraska record is of an immature specimen. Roth and Brame (1972) stated that all western records for this species listed in Muma (1947) are based on mislabelled specimens. This is probably true at least for the Arizona and Colorado collections. Marx, who supplied Keyserling's (1887) type material, is known to have frequently put erroneous locality data with specimens (see Coyle 1971:345).

This species becomes rare south of the North Carolina-Georgia border. One specimen is known from Georgia and one from Alabama.

Natural History Notes.—Although widespread and common throughout much of its range, *W. calcaratus* is not common in pine forests and has not been collected from the isolated spruce/fir forests of the southern Appalachians.

Mature females (and mature males, at least in the northern part of the range) are present year-round.

Specimens of all other species of *Wadotes* have been collected from within the range of *W. calcaratus*, but only *W. tennesseensis* has been shown to exist syntopically with *W. calcaratus*. Specimens of both these species were recovered from a leaf litter sample from Jackson County, North Carolina.

One egg case (from Aylmer, southern Ontario, 21 April 1975) containing 17 eggs was examined.

Types.—*Coelotes calcaratus* Keyserling, two male syntypes, Colorado, Valmont and Minnesota, Olmstead Co., Rochester (G. Marx), in NMNH, examined, here designated paralectotype and lectotype respectively. *Coelotes longitarsus* Emerton, male holotype, New Hampshire, Mt. Carmel, 9 X (J. H. Emerton), in MCZ, examined. *Coelotes nigriceps* Banks, two female syntypes, New York, Roslyn, in MCZ, examined.

Wadotes carinidactylus, new species

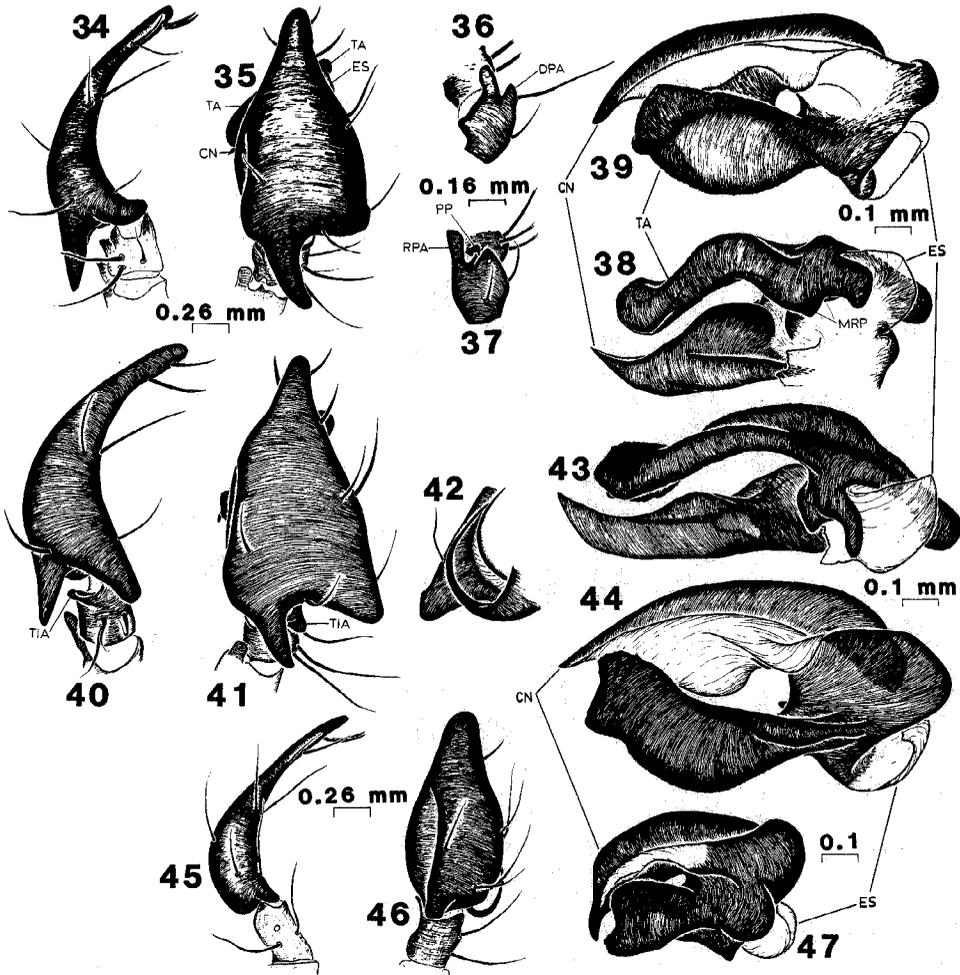
Figs. 93-97, 112, 117

Etymology.—The species name is derived from the Latin adjective *carinatus* meaning "keeled" and the Greek noun *daktylos* meaning "finger" and refers to the diagnostic character described below.

Diagnosis.—This species is readily separated from all other *Wadotes* species by the presence of a conspicuous ventral keel on the ventral arm of the terminal apophysis (Fig. 95).

Description.—Known only from four males.

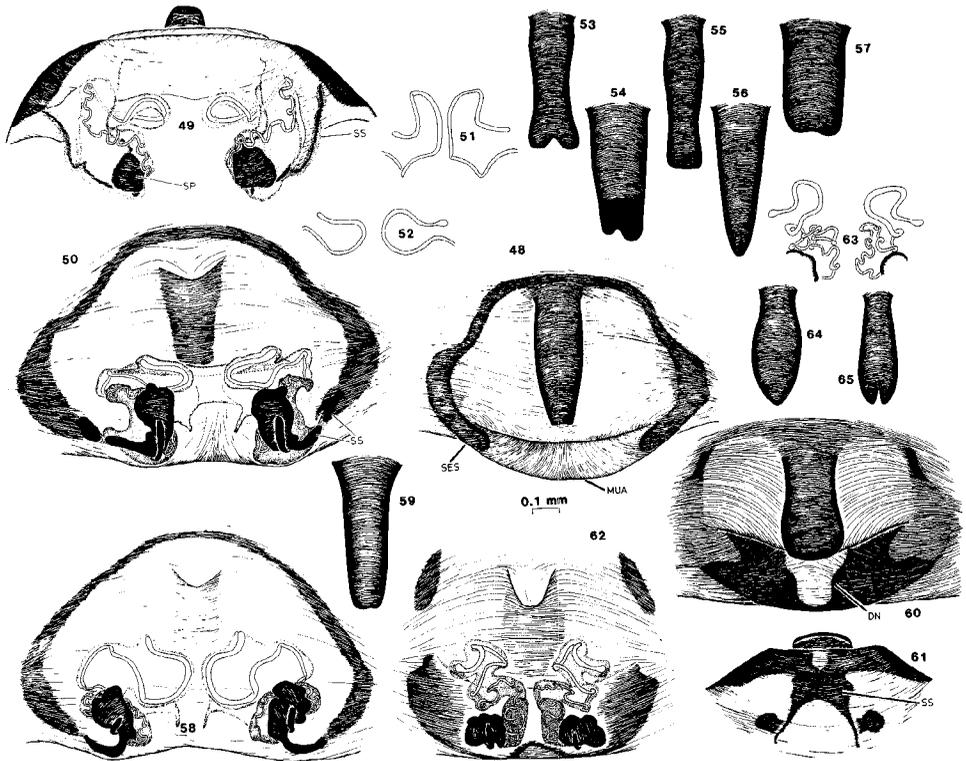
Male: Figs. 93-97. All specimens measured. CL 41.4-4.8(4.4±0.31), CW 2.7-3.1(2.9±0.17), SL 2.05-2.33(2.16±0.13), SW 1.55-1.80(1.63±0.11). Holotype CL 4.1, CW 2.7, SL 2.05, SW 1.58.



Figs. 34-39.—*Wadotes calcaratus*, locality unknown: 34, left palpal tibia and cymbium, prolateral view; 35, same, dorsal view; 36, left palpal patella and base of tibia, retrolateral view; 37, same, dorsal view; 38, conductor and terminal apophysis of left genital bulb, dorsal view; 39, same, ventral prolateral view. Figs. 40-44. *W. willsi*, Mount Rogers VA (holotype): 40, left palpal tibia and cymbium, prolateral view; 41, same, dorsal view; 42, prolateral margin of tarsus including part of embolus and subtegulum, ventral view; 43, conductor and terminal apophysis of left genital bulb, dorsal view; 44, same, ventral prolateral view. Figs. 45-47. *W. tennesseensis*, Newfound Gap (GSMNP) NC/TN: 45, left palpal tibia and cymbium, prolateral view; 46, same dorsal view; 47, conductor and terminal apophysis of left genital bulb, ventral view. DPA—dorsal patellar apophysis, PP—proximal dorsal tibial prominence, RPA—retrolateral patellar apophysis, TIA—dorsal prolateral tibial apophysis.

Retrolateral patellar apophysis short, ca. 0.25 times total patella length. In dorsal view, cymbial processes subequal (Fig. 94). In prolateral view (Fig. 93), prolateral process laterally bisected by somewhat triangular cleft, ventral arm angular ventrally, smoothly and slightly convex dorsally; dorsal arm short and broadly triangular dorsally with shallow ventral cleft.

Ventral arm of terminal apophysis well developed with a high, narrow, longitudinal keel ventrally (Fig. 95); prolateral and retrolateral arms fused into heavy, broad plate (Figs. 96, 97) with strong retrolateral ridge ventrally running



Figs. 48-57.—*Wadotes calcaratus*: 48, epigynum, Pumpkintown NC, ventral view; 49, same, Cataloochee NC, caudal view; 50, same, dorsal view; 51, primary loops of connecting ducts, dorsal view, Washington County VA; 52, same, Pocahontas County WV. Figs. 58, 59. *W. willsi*, Mount Rogers VA: 58, epigynum, dorsal view; 59, scape, ventral view. Figs. 60-65. *W. tennesseensis*: 60, epigynum, Mount Le Conte (GSMNP) TN, ventral view; 61, same, caudal view; 62, same, Rough Butt Bald Trail (BRPWY) NC, dorsal view; 63, connecting ducts, Mount Le Conte TN, dorsal view; 64, scape, ventral view, GSMNP; 65, same, Mount Le Conte (GSMNP) TN.

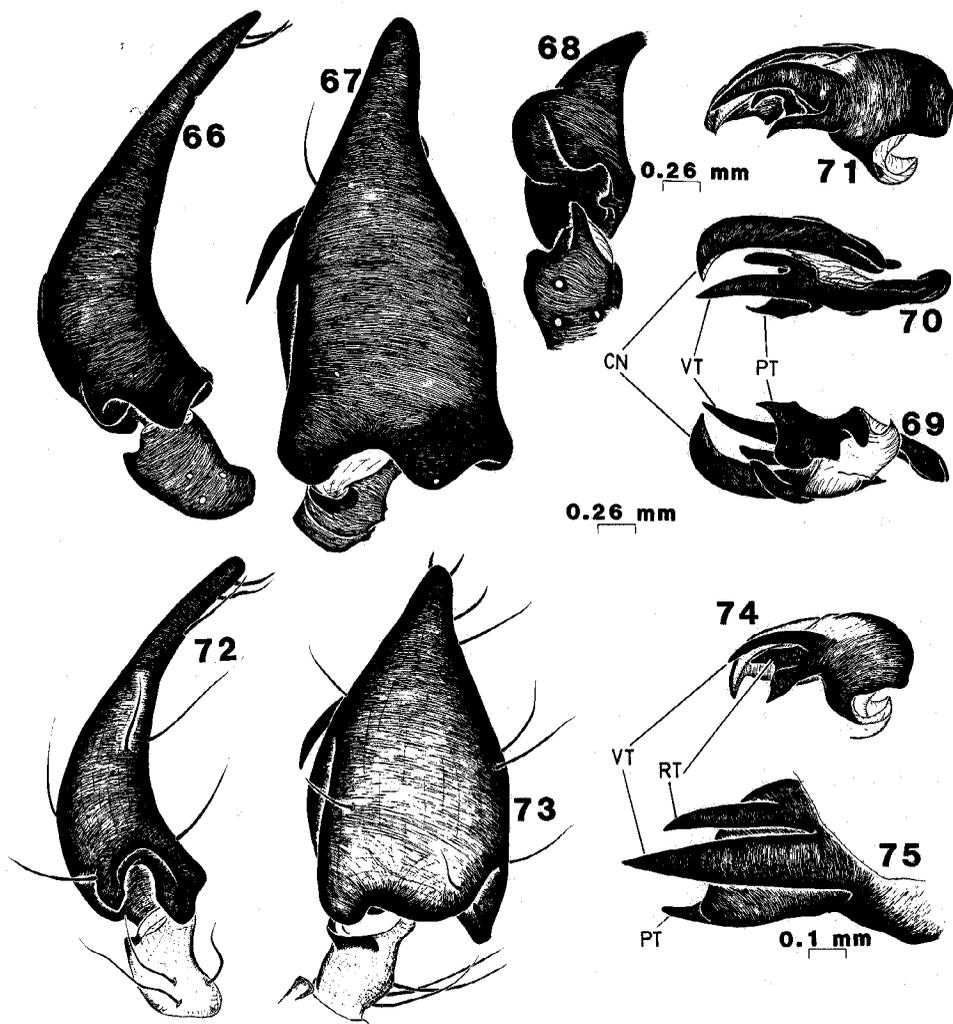
longitudinally and curving prolaterally proximal to base of ventral arm. Median retrolateral process pronounced, bluntly pointed, triangular (Fig. 96).

Distributions.—Figs. 112, 117. *Wadotes carinidactylus* is known only from the type locality in the southern ridges of the southern Appalachians in Georgia and from the Piedmont in the Atlanta, Georgia area.

Natural History Notes.—The holotype and paratype males were collected from within a well rotted pine log on a westerly facing slope of a shallow ravine in the east face of Taylor Ridge. The surrounding forest was composed of mixed pines and hardwoods with pines dominating on the immediate ridges. A female, identical to those of *W. bimucronatus*, was captured from the same log. Given the possibility that this specimen could be the female of *W. carinidactylus* it has been left in the vial containing the paratype male of *W. carinidactylus*.

Type Series.—Male holotype and paratype, Georgia, Chattooga Co., Mack-white Gap, Taylor Ridge, 3 mi E Summerville (1200'), 13 I 1984 (R. G. Bennett) in MCZ.

Collection Data.—U.S.A.: GEORGIA; *Fulton Co.*, Atlanta, 20 I 1944 (P. W. Fattig), 1 male (AMNH), 12 I 1946 (1 XII 1946?) (P. W. Fattig), 1 male (AMNH).



Figs. 66-71.—*Wadotes mumai*, Blue Ridge Mountains GA (holotype): 66, left palpal tibia and cymbium, prolateral view; 67, same, dorsal view; 68, same, posterior prolateral view; 69, conductor and terminal apophysis of left genital bulb, dorsal view; 70, same, ventral view; 71, same, prolateral view. Note: left palpal cymbium of holotype damaged. Figs. 66-68 are of right palpus drawn as mirror images to simulate appearance of left palpus. Figs. 72-75. *W. hybridus*: 72, left palpal tibia and cymbium, Cullowhee NC, prolateral view; 73, same, dorsal view; 74, conductor and terminal apophysis of left genital bulb, Cataloochee NC, prolateral view; 75, distal section of terminal apophysis, Cullowhee NC, ventral view.

Wadotes deceptis, new species

Figs. 89-92, 114, 118

Etymology.—The specific name is a Latin adjective meaning “deceptive.”

Diagnosis.—The bisection of the prolateral cymbial process by a wedge-shaped cleft (Figs. 89, 90) combined with the fusion of the retrolateral arm of the terminal apophysis to the base of the ventral arm (Figs. 91, 92) serve to distinguish this species from all other *Wadotes*.

Description.—Known only from seven males.

Male: Figs. 89-92. Five specimens measured including holotype. CL 4.0-4.8(4.4±0.35), CW 2.7-3.3(3.0±0.26), SL 2.0-2.4(2.2±0.16), SW 1.6-1.8(1.7±0.1). Holotype CL 4.7, CW 3.1, SL 2.3, SW 1.7.

Retrolateral patellar apophysis short, stout, about one-quarter of total patella length. Distal prolateral tibial extension not produced as an apophysis. Cymbial processes subequal in dorsal view. Prolateral cymbial process similar to *W. dixiensis*, laterally bisected by a wedge-shaped cleft (Figs. 89, 90), ventral arm rounded terminally with smoothly curving margins, dorsal arm broadly triangular to somewhat rectangular with shallow ventral cleft.

Terminal apophysis (Figs. 91, 92) similar to *W. saturnus*; long ventral arm tapering to fine point; retrolateral arm fused to retrolateral base of ventral arm; prolateral arm pointed, broadly triangular, connecting with dorsal base of retrolateral arm by means of a narrow flange (Fig. 91); longitudinal ridge on prolateral arm very reduced and more prolateral than ventral. Median retrolateral process well developed, triangular (Fig. 91).

In the GSMNP a male of this species was collected with two females that are morphologically indistinguishable from *W. dixiensis*. These may be *W. deceptis* females.

Variation: The prolateral cymbial process varies as diagrammed (Figs. 89, 90); the JKMF specimens differ from the Little River (GSMNP) specimens in the width of the cleft and the relative shape of the arms. The fused retrolateral arm of the terminal apophysis is shorter in the Little River specimens than in those from the JKMF. Distally on femur I there may be one or two prolateral macrosetae.

Distribution.—Figs. 114, 118. This species is known only from southwestern North Carolina (JKMF) and from adjacent eastern Tennessee (southwestern GSMNP).

Natural History Notes.—Three males, including the holotype, were collected by sifting leaf litter in a hardwood forest. Two more came from underneath rotting logs in a mixed forest of pine, hemlock, and hardwoods.

Holotype.—Male, North Carolina, Graham Co., Poplar Cove, JKMF, 30 X 1971 (F. A. Coyle) in MCZ.

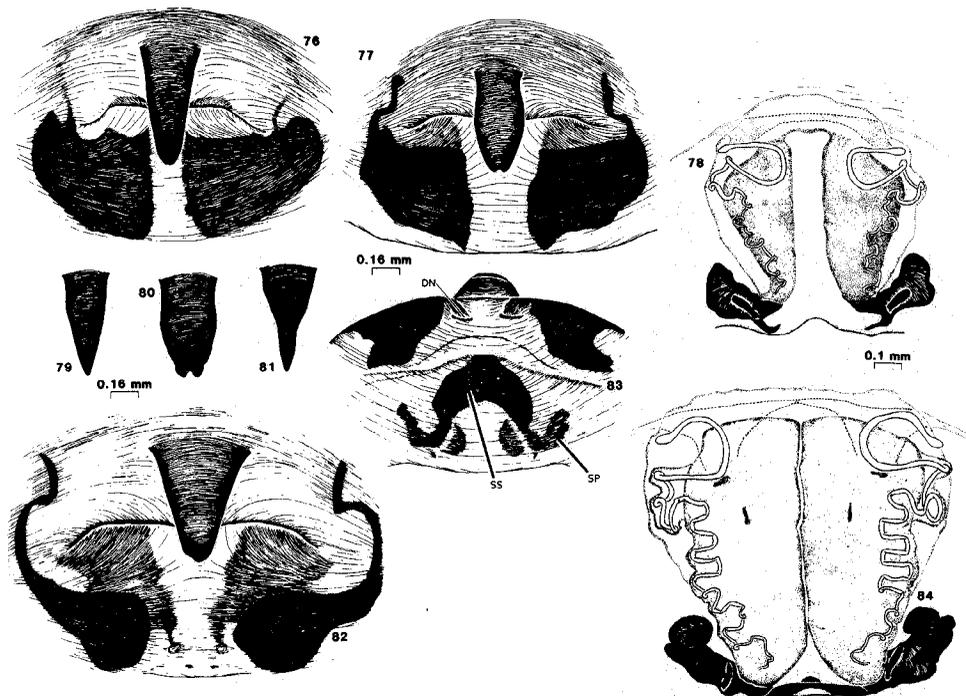
Collection Data.—U.S.A.: TENNESSEE; *Blount Co.*, Parson's Branch Road at Sam's Gap, GSMNP, 7 XI 1984 (R. G. Bennett), 1 male (RGB), Parson's Branch Rd., 2 mi E of Sam's Gap, GSMNP, 7 XI 1984 (R. G. Bennett), 1 male (RGB); *Sevier Co.*, Little River, GSMNP, 3 IX 1936 (W.M.B.), 2 males (AMNH). NORTH CAROLINA; *Graham Co.*, Poplar Cove, JKMF, 25 IX 1971 (F. A. Coyle), 2 males (MCZ).

Wadotes dixiensis Chamberlin

Figs. 98-108, 116, 117

Wadotes dixiensis Chamberlin 1925:120, (not *Wadotes dixiensis*: Muma, 1947 or subsequent authors). *W. bimucronatus*: Muma 1947:5, figs. 8, 9, 20, 21, 39, 40, (misidentification).

Diagnosis.—*Wadotes dixiensis* can be distinguished from all other species of *Wadotes* by the presence of an elongate ventral arm underlying a pronounced, smooth, crescent-shaped dorsal plate on the terminal apophysis of the male palpus (Figs. 100, 101) and, in the female, by the combined presence of complete superficial epigynal sclerotization (Figs. 102, 103) and relatively stout, contiguous duct matrices (Fig. 104) which are, together, nearly as wide as long (DL/DW=0.87-1.29, N=20).



Figs. 76-81.—*Wadotes hybridus*: 76, epigynum, ventral view, Ithaca NY (*Coelotes altilis* syntype); 77, same, Randolph NH; 78, same, dorsal view, ventral superficial features excluded, Straight Fork Creek (GSMNP) NC; 79, scape, ventral view, Straight Fork Creek NC; 80, same, Cullowhee NC; 81, same, Highlands NC. Figs. 82-84. *W. saturnus*, Gainesville GA: 82, epigynum, ventral view; 83, same, caudal view; 84, same, dorsal view, ventral superficial features excluded.

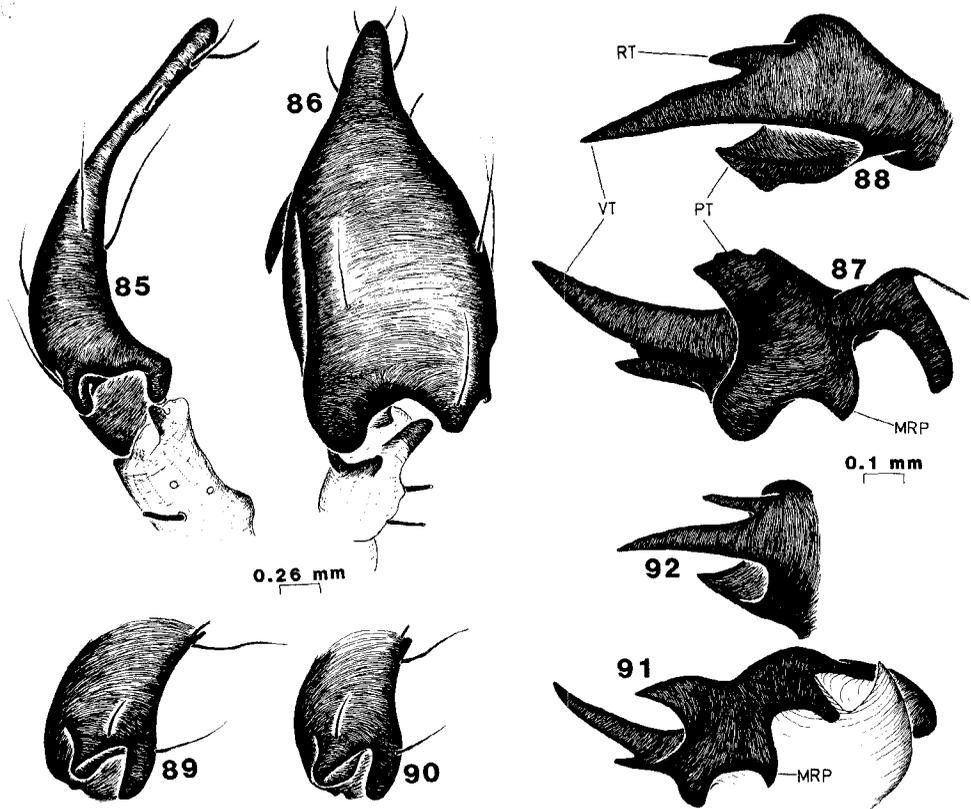
Description.—*Male*: Figs. 98-101. 11 specimens measured including holotype. CL 3.8-5.5(4.7±0.6), CW 2.5-3.7(3.1±0.39), SL 1.88-2.70(2.32±0.26), SW 1.43-2.00(1.78±0.19). Holotype CL 4.7, CW 3.2, SL 2.33, SW 1.80.

Female: Figs. 102-108. 22 specimens measured. CL 3.2-5.7(4.2±0.69), CW 2.0-3.7(2.6±0.48), SL 1.53-2.73(2.03±0.32), SW 1.25-2.08(1.64±0.25). LAE about one-half of EL (Figs. 102, 103) EL/LAE=1.36-2.43(2.05±0.27), $N=18$.

Variation: The scape varies widely in form (Figs. 102, 103, 105-108). The connecting ducts converge rapidly or gradually posteriorly.

There is considerable size variation in both sexes which appears to be related to geographic distribution. The females can be divided arbitrarily into two groups, one (from the northern part of the range in southwestern North Carolina) with carapace lengths < 4.0 mm (3.2-3.9[3.5±0.27], $N=8$) and the other (found primarily in the southern region and to some extent in the north, > 4.0 mm (4.1-5.7[4.7±0.41], $N=14$). There is, however, a continuum of less commonly collected intermediate sizes. At Wayah Bald, Macon County, North Carolina (the northern range boundary in that region), four females which have a continuous range of carapace lengths from 3.2 to 4.7 mm were collected together. Insufficient males are available for analysis.

The specimens here included in *W. dixiensis* may comprise two species. Because of the difficulty of assigning intermediate-sized specimens to one size class or the other, the wide and continuous size range in the Wayah Bald sample, and the absence of any other character with a concordant variation pattern, I conclude that all these *W. dixiensis* specimens are conspecific.



Figs. 85-88.—*Wadotes saturnus*: 85, left palpal tibia and cymbium, Vogel State Park GA, prolateral view; 86, same, dorsal view; 87, terminal apophysis, dorsal view, Indian Springs State Park GA; 88, same, distal section, ventral view, Vogel State Park GA. Figs. 89-92. *W. deceptis*: 89, proximal portion of left palpal cymbium, prolateral view, Graham County (JKMF) NC; 90, same, Little River (GSMNP) TN; 91, terminal apophysis and embolus support of left genital bulb, dorsal view, Little River TN; 92, distal section of terminal apophysis of left genital bulb, ventral view, Graham County (JKMF) NC.

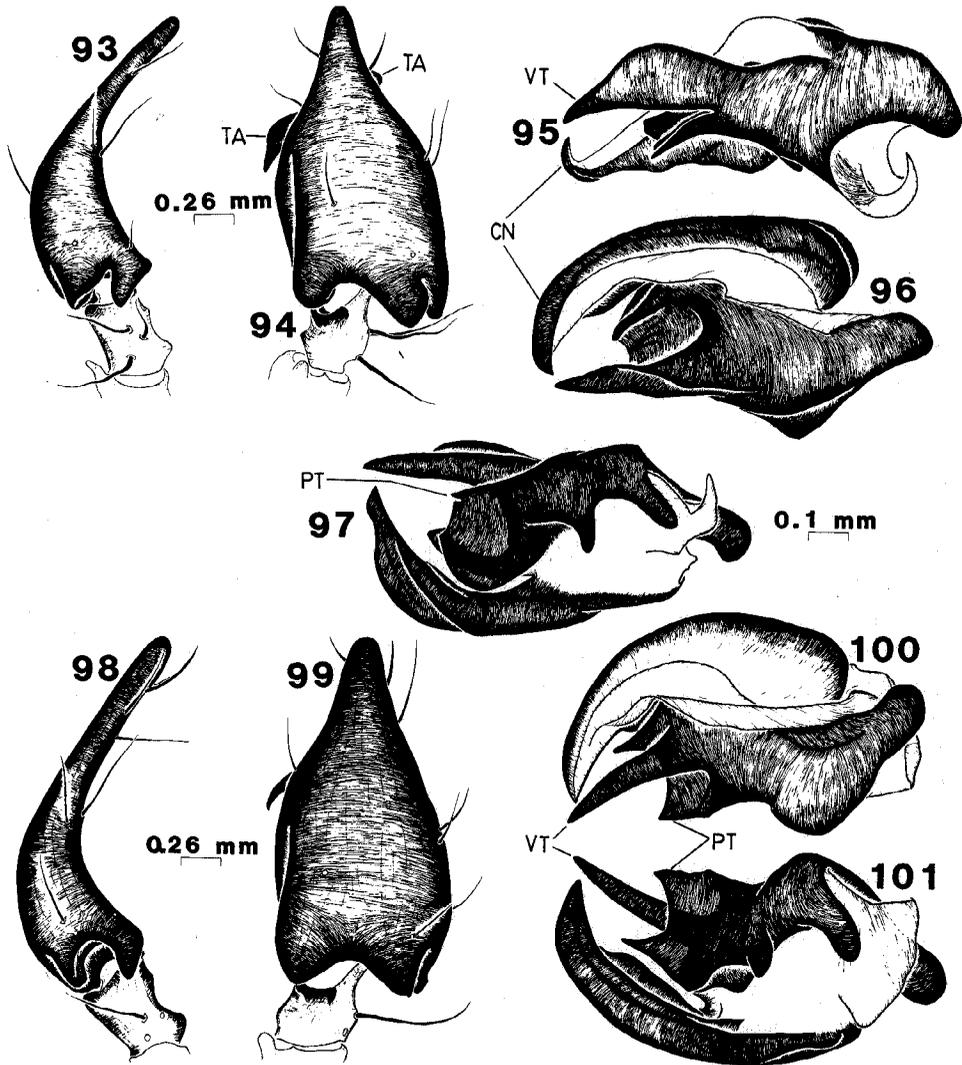
Distribution.—Figs. 116, 117. *Wadotes dixiensis* has been collected from scattered locales through much of the northern half of Alabama into the highlands of southwestern North Carolina and southeastern Tennessee. No specimens are known from northern Georgia.

Natural History Notes.—Within its rather restricted range, this species exploits a variety of habitats from the low oak/pine forests of the northern Gulf Coastal Plain to the high elevation hardwood forests of the southern Appalachians.

Along the Bartram Trail at Wayah Bald, Macon County, North Carolina, *W. dixiensis* is well established in hardwood forests at elevations around 5200 feet and occurs syntopically with *W. bimucronatus* within and beneath rotted logs. In Alabama, *W. dixiensis* and *W. saturnus* both occur at De Soto State Park (De Kalb County).

Mature males have been collected from late September to early May, and adult females throughout the year.

Holotype.—Male, Alabama, Lee Co., Auburn (N. Banks), in MCZ, examined.



Figs. 93-97.—*Wadotes carinidactylus*, Atlanta GA: 93, left palpal tibia and cymbium, prolateral view; 94, same, dorsal; 95, conductor and terminal apophysis of left genital bulb, prolateral view; 96, same, ventral view; 97, same, dorsal view. Figs. 98-101. *W. dixiensis*, De Soto State Park AL: 98, left palpal tibia and cymbium, prolateral view; 99, same, dorsal view; 100, conductor and terminal apophysis of left genital bulb, ventral view; 101, same, dorsal view.

Wadotes georgiensis Howell
Figs. 7, 17-20, 32, 33, 115, 117

Wadotes georgiensis Howell 1974:728, fig. 1 (a-f).

Diagnosis.—*Wadotes georgiensis* can be distinguished from all congeners except *W. bimucronatus* by a combination of a deeply and narrowly bisected prolateral cymbial process (Fig. 17) and a bifurcate terminal apophysis in the male (Fig. 19), and the complete superficial epigynal sclerotization combined with the narrow collecting duct matrix in the female (Figs. 32, 33), $DL/DW=1.38-1.67$, $N=9$. Females of *W. georgiensis* and *W. bimucronatus* are evidently indistinguishable.

ble on morphological grounds. Males of *W. georgiensis* differ from *W. bimucronatus* in having the prolateral cymbial process much longer than the retrolateral cymbial process in dorsal view (Fig. 18); the prolateral arm of the terminal apophysis reduced to a slight, inconspicuous dorsal projection (Fig. 19) (best observed in profile at magnifications of 40X or greater); and a short retrolateral arm extending from the base of the ventral arm (Figs. 19, 20).

Description.—*Male*: Figs. 7, 17-20. 13 specimens measured including holotype. CL 3.7-4.4(4.0±0.26), CW 2.4-3.0(2.7±0.18), SL 1.80-2.18(1.99±0.13), SW 1.38-1.63(1.52±0.08). Holotype CL 4.1, CW 2.7, SL 2.1, SW 1.55.

Female: Figs. 32, 33. 14 specimens measured. CL 3.4-5.0(3.9±0.44), CW 2.1-3.3(2.5±0.29), SL 1.63-2.30(1.90±0.18), SW 1.33-1.88(1.53±0.14). EL/LAE=2.27-2.82(2.52±0.16), *N*=13. Characteristics as for *W. bimucronatus* except that scape varies only slightly, tending towards a thickening of the terminus.

Distribution.—Figs. 115, 117. *Wadotes georgiensis* is known only from the area of Vogel State Park, Union County, Georgia. Due to my inability to separate females of this species and *W. bimucronatus* and the lack of male specimens from other nearby areas, all *W. bimucronatus/georgiensis*-type females collected from the neighboring areas have been conservatively identified as *W. bimucronatus*.

Natural History Notes.—Adults examined were collected from mid-September to early May. Howell (1974) reported a June collection of one female as well and stated that this species was most often encountered "in thick stands of white pine" but could also be collected from "rhododendron thickets and on the slopes of open hardwoods." Most specimens have been recovered from pitfall traps or by sifting leaf litter.

Type Series.—Male holotype and female allotype, Georgia, Union Co., Vogel St. Pk., 8 mi (13 km) S Blairsville, 9 III 1972 (J. O. Howell), in AMNH, examined.

Collection Data.—U.S.A.: GEORGIA; *Lumpkin/Union Co.* line, 1/2 mi W of Neels Gap on App. Trail (3500'), 13 IX 1975 (J. D. Pittillo), 3 males, 4 females (FAC); *Union Co.*, Vogel St. Pk., 23 III 1972 (J. O. Howell), 3 males, 3 females (AMNH and JOH), 20 IV 1972 (J. O. Howell), 3 males, 2 females (JOH), 4 V 1972 (J. O. Howell), 3 males, 2 females (JOH), Vogel St. Pk. (2300'), 12 I 1984 (R. G. Bennett), 1 male, 2 females (RGB).

Wadotes hybridus (Emerton)

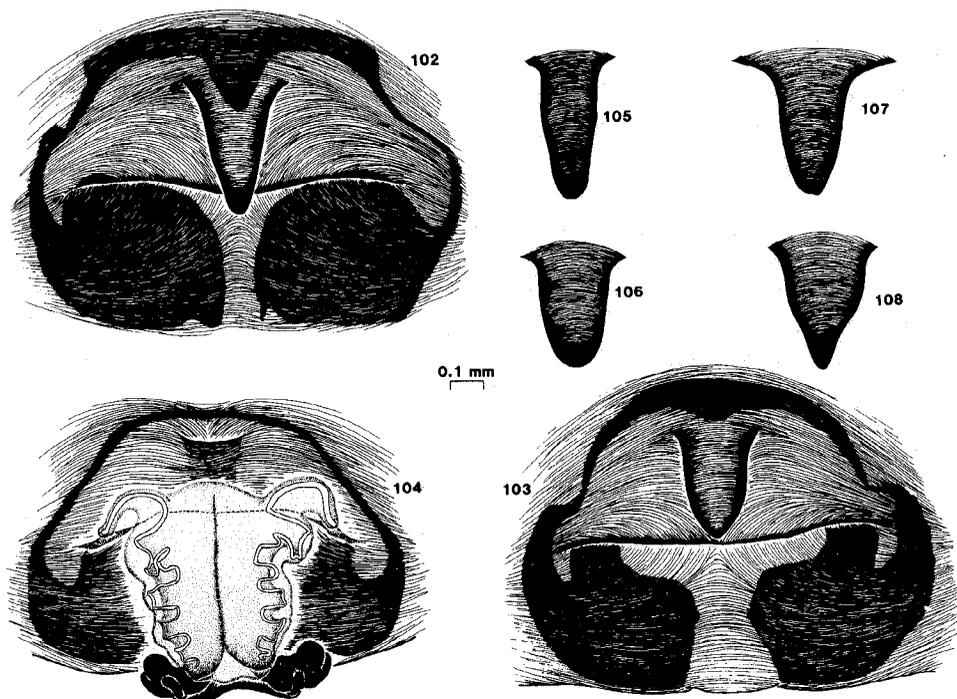
Figs. 1-4, 72-81, 114, 118

Coelotes hybridus Emerton 1889:193, figs. 4, 4a (in Bonnet 1959 and Banks 1910 as Emerton 1890).

C. altilis Banks 1892:25, figs. 74, 74a.

Wadotes hybridus: Chamberlin 1925:122; Muma 1947:7, figs. 10, 11, 24, 25, 41, 42; Kaston 1948:283, figs. 917-919.

Diagnosis.—Males of *W. hybridus* can be distinguished from all male *Wadotes* except *W. mumai* by the combined presence of three distinct arms on the terminal apophysis (Fig. 75), the free ventral arm, and the retrolateral arm joined from its base dorsally to the prolateral arm by a broad plate (Figs. 74, 75). From *W. mumai*, male *W. hybridus* differ in the presence of a strongly developed ventral arm of the prolateral cymbial process (Fig. 72). Female *W. hybridus* are distinguishable from all *Wadotes* females except *W. saturnus* by a combination of the restriction of superficial epigynal sclerotization to two broad plates posterior to the atrial slit and EL about 1.5 to 2 times as long as LAE (EL/LAE=1.55-2.06,



Figs. 102-108.—*Wadotes dixiensis*: 102, epigynum, ventral view, The Sinks (GSMNP) TN; 103, same, Maud AL; 104, same, dorsal view, Clay County NC; 105, scape, ventral view, Graham County (JKMF) NC; 106, same, Clay County NC; 107, same, Acton AL; 108, same, Alberta City AL.

$N=12$) (Figs. 76, 77). From female *W. saturnus*, *W. hybridus* is readily separated by its lack of support sclerotization on the caudal surface of the epigynum within the epigastric groove.

Description.—*Male*: Figs. 72-75. 40 specimens measured including holotype. CL 4.6-6.2(5.6 ± 0.40), CW 3.0-4.3(3.6 ± 0.30), SL 2.3-3.1(2.7 ± 0.20), SW 1.7-2.3(2.0 ± 0.13). Holotype CL 5.1, CW 3.5, SL 2.45, SW 1.88.

Female: Figs. 1-4, 76-81. 40 specimens measured. CL 4.1-6.9(5.7 ± 0.72), CW 2.9-4.6(3.6 ± 0.46), SL 2.2-3.3(2.7 ± 0.30), SW 1.8-2.5(2.1 ± 0.21).

Variation: Aside from scape variability (Figs. 79-81) and a wide range of size (especially in the females), *W. hybridus* exhibits fairly constant morphological characteristics throughout its range.

Distribution.—Figs. 114, 118. Next to *W. calcaratus*, *W. hybridus* has the largest range of all *Wadotes* species and is the most commonly collected species. South of Long Island, *W. hybridus* is absent from the Coastal Plain and Piedmont regions. Specimens from the west central part of the range are rare and thus the western boundary cannot be determined with any accuracy.

The extreme southern boundary of the range of *W. hybridus* passes through Sevier County, Tennessee and Swain and Jackson Counties, North Carolina. Immediately north of this boundary, *W. hybridus* is very common, but it disappears abruptly to the south of this area, where it is replaced by its rarely collected sister species, *W. saturnus* and *W. mumai*.

Natural History Notes.—*Wadotes hybridus* shares its range with *W. calcaratus*, *W. willsi*, *W. dixiensis*, and *W. bimucronatus* but only is known to be syntopic

with the latter species. It is absent from the high elevation spruce/fir forests of the southern Appalachians within its range.

Mature males have been collected from early August until late November. They apparently do not overwinter. Mature females can be collected throughout the year. Twelve egg cases, collected (with females) between mid-April and early July, contained 17 to 151 eggs or spiderlings.

One case from Summers County, West Virginia contained 125 eggs and more than 20 dipterous egg predators in an early instar larval stage. H. J. Teskey (CNC) identified these as acalyprate diptera, probably chloropids.

At "The Sinks" (GSMNP), Sevier/Blount County line, Tennessee, on one occasion several mature females, with egg cases, were collected from underneath large flat rocks. Each female and her egg case were in a small depression in the ground at the end of a short silk tube extending to the edge of the rock. The females, normally relatively shy and retiring, vigorously defended their egg cases by repeatedly attacking and biting at fingers and forceps. Similar behavior was noted for another female collected with an egg case from underneath rotting bark on a log in Jackson County, North Carolina.

Types.—*Coelotes hybridus* Emerton, male holotype, New York, Chateaugay Lk., Adirondacks (F. A. Bowditch), in MCZ, examined. *Coelotes atilis* Banks, three female syntypes, New York, Ithaca (N. Banks), in MCZ, examined.

Wadotes mumai, new species

Figs. 66-71, 112, 118

Wadotes convolutus Muma 1947:8 (in part, not female holotype of *W. convolutus* Muma [= *W. bimucronatus* Simon]), figs. 26, 27, 43, 44.

Etymology.—The specific name is a patronym in honor of Martin H. Muma who first described this specimen.

Diagnosis.—*Wadotes mumai* can be distinguished from the males of all other species of *Wadotes* by the greatly reduced ventral arm of the prolateral cymbial process (Fig. 68).

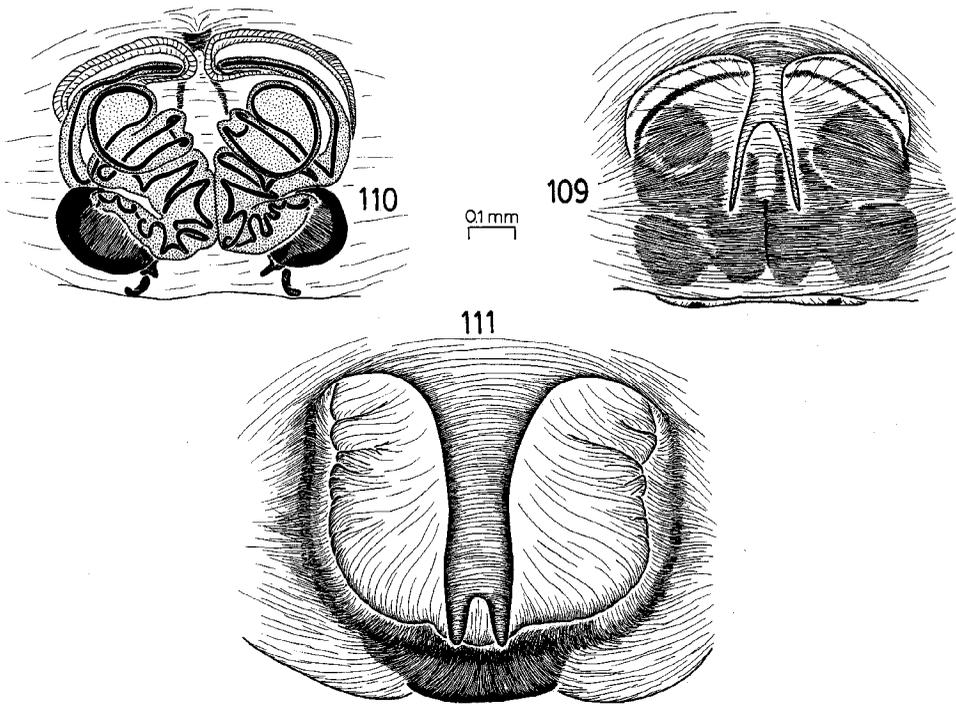
Description.—Known from a single male.

Male: Figs. 66-71. CL 6.2, CW 4.1, SL 3.1, SW 2.2.

Retrolateral patellar apophysis ca 0.2-0.3 times total patella length. Distal prolateral edge of tibia extended into short, thin apophysis (Fig. 68). In dorsal view (Fig. 67) cymbial processes subequal. Retrolateral process short. Prolateral process greatly bisected laterally such that ventral arm is reduced to short, inconspicuous projection (Fig. 68) on proximal margin of cymbium; dorsal arm large, conspicuous; broadly convex dorsally with deep, wide, longitudinal ventral cleft.

Terminal apophysis (Figs. 69-71) with three conspicuous arms; ventral arm long, thin, pointed; retrolateral arm laterally flattened, twisted slightly, with a basal flange dorsally connecting by way of a broad, curving plate with prolateral arm (Fig. 69); prolateral arm in dorsal view triangular and pointed (Fig. 70), with a low longitudinal ridge ventrally (Fig. 71). Median retrolateral process (Fig. 70) pronounced, broadly triangular (broken on left terminal apophysis).

Distribution.—Figs. 112, 118. Known only from the type locality in north central Georgia. The original label accompanying this specimen (and the paratype



Figs. 109, 110.—*Wadotes primus*, epigynum, Hong Kong (holotype): 109, ventral view; 110, dorsal view. Fig. 111. "*Wadotes* new species near *primus*," epigynum, ventral view, Nanking China.

female of *W. convolutus*) is apparently missing. A more recent label lists the collection locale as Blue Ridge Mountains, Georgia with no additional data. This is the locality cited by Muma (1947) in his description of *W. convolutus*. It is possible that the original label referred to the small town of Blue Ridge (Fannin County), Georgia.

Holotype.—male (allotype of *W. convolutus* Muma), Georgia, Blue Ridge Mtns., in AMNH.

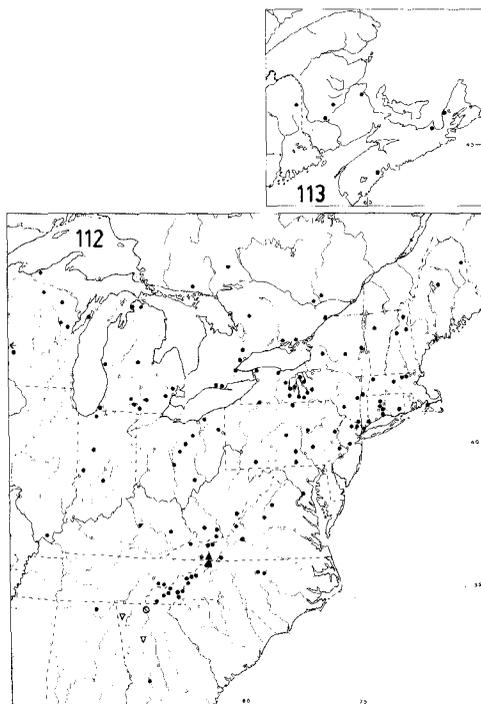
Wadotes saturnus, new species

Figs. 5, 6, 9-12, 82-88, 114, 118

Etymology.—The specific name is a noun in apposition after *Saturnus*, the ancient Italic god of agriculture.

Diagnosis.—Males of *W. saturnus* are distinguished from all congeners by the combined presence, on the terminal apophysis, of a short retrolateral arm fused to the base of the ventral arm (Figs. 87, 88) and, distally on the prolateral edge of the palpal tibia, a short but definite apophysis (as in *W. mumai*, Fig. 68). Females closely resemble females of *W. hybridus* but differ from the latter in the possession of a well defined area of support sclerotization medially on the caudal surface of the epigynum within the epigastric groove (Fig. 83). Female *W. saturnus* are distinguished from all other *Wadotes* females by the restriction of the superficial epigynal sclerotization to two broad plates posterior to the atrial slit and $EL/LAE=1.63-1.97$, $N=5$ (Fig. 82).

Figs. 112, 113.—Distributions of *Wadotes calcaratus*, dark circles; *W. carinidactylus*, open inverted triangles; *W. mumai*, slashed circle; and *W. willsi*, dark triangle: 112, southeastern Canada and eastern United States; 113, southeastern Canadian Maritime provinces. Dark circle with overhead arrow indicates collection locale beyond boundary of map of *W. calcaratus* syntype (Rochester MN).



Description.—*Male*: Figs. 5, 6, 9-12, 85-88. 13 specimens measured including holotype. CL 5.5-6.8(6.2±0.43), CW 3.5-4.4(4.1±0.27), SL 2.7-3.3(3.0±0.18), SW 2.1-2.4(2.2±0.13). Holotype CL 6.4, CW 4.3, SL 3.1, SW 2.4.

Retrolateral patellar apophysis long, about one-third of total patella length. Prolateral tibial extension terminating in short but conspicuous apophysis. Cymbial processes subequal in dorsal view (Fig. 86). Prolateral cymbial process broadly bisected laterally (Fig. 85); ventral arm reduced to a short caudally or prolaterally produced projection; dorsal arm short and broad in dorsal view, concave ventrally.

Terminal apophysis trifurcate (Figs. 87, 88); retrolateral arm short, smoothly fused to middle of retrolateral edge of long, pointed ventral arm; prolateral arm short, with low longitudinal ridge running along entire ventral length (Figs. 12, 88), fused to ventral base of retrolateral arm by a narrow, crescent-shaped, flanged plate (Fig. 87). Median retrolateral process well developed, broadly triangular with dull point (Fig. 87).

Female: Figs. 82-84. 13 specimens measured. CL 5.3-7.4(6.7±0.57), CW 3.5-4.6(4.2±0.32), SL 2.7-3.3(3.1±0.19), SW 2.2-2.8(2.5±0.19).

Posterior plates of superficial epigynal sclerotization usually two-toned (sometimes inconspicuously), with area of lighter sclerotization extending anteriorly into atrial slit (Fig. 82). Internally, duct matrices broad, contiguous; ducts convergent posteriorly and restricted to lateral margins of matrices (Fig. 84).

Variation: Female *W. saturnus* show considerable variation in size. Scape form is also variable: broadly or narrowly triangular with the tip blunt, rounded, or pointed. The superficial epigynal sclerotization is usually confined to the posterior plates but may extend laterally and anteriorly to the muscle attachment

sclerites. The ventral arm of the prolateral cymbial process in males from the Guntersville, Alabama area is bent prolaterally. Males from the rest of the range tend to display a slightly larger and caudally directed ventral arm. Distally on femur I there may be one or three prolateral macrosetae instead of two.

Distribution.—Figs. 114, 118. *Wadotes saturnus* has been collected from locales in northeastern Alabama, northern Georgia and extreme southwestern North Carolina.

Natural History Notes.—Specimens of *W. dixiensis*, *W. georgiensis*, *W. bimucronatus*, and *W. deceptis* have come from the same collecting locales as *W. saturnus*.

One female was collected in early January from a silk lined circular diapause chamber in the earth underneath a log in Unicoi State Park, White County, Georgia. This spider produced a large egg case in the laboratory in late January but consumed the case shortly thereafter.

Mature females are probably present year-round. Mature males have been collected from late fall to early winter.

Type Series.—Male holotype, female allotype, Alabama, Marshall Co., Little Mtn. St. Pk. (now Lk. Guntersville St. Pk.), E of Guntersville, 13 IX 1970 (J. A. Beatty), in MCZ.

Discussion.—Muma (1947) incorrectly associated members of this species with *W. dixiensis* Chamberlin.

Collection Data.—U.S.A.: ALABAMA: *De Kalb Co.*, De Soto St. Pk., X 1937, 4 males (AMNH); *Marshall Co.*, Little Mtn. St. Pk., E of Guntersville, 11 VI 1963 (J. A. Beatty), 1 female, 5 imms (JAB), 13 IX 1970 (J. A. Beatty), 2 males, 3 females (JAB), 13 IX 1970 (T. N. Trudeau) 1 male, 2 females (RGB), 3 VI 1975 (J. A. Beatty), 1 female (JAB). GEORGIA: *Butts Co.*, Indian Springs St. Pk., 2 XI 1972 (J. O. Howell), 2 males, (JOH); *Habersham Co.*, Clarksville, 27 IV 1943 (W. Ivie), 1 female, (AMNH); *Hall Co.*, Gainesville, 23 IV 1939 (B. J. Kaston), 1 female (AMNH); *Union Co.*, Vogel St. Pk., 27 I 1972 (J. O. Howell), 1 male, (JOH), 23 III 1972 (J. O. Howell), 1 female (JOH), 15 XI 1972 (J. O. Howell), 1 male (MCZ); *White Co.*, near Ana Ruby Falls, Unicoi St. Pk. (1800'), 12 I 1984 (R. G. Bennett), 1 female (RGB). NORTH CAROLINA: *Graham Co.*, JKMF, Poplar Cove, 30 X 1971 (F. A. Coyle), 1 female (FAC).

Wadotes tennesseensis Gertsch

Figs. 8, 45-47, 60-65, 116, 117

Wadotes tennesseensis Gertsch 1936:14, fig. 27; Muma 1947:4, figs. 1, 2, 14, 15, 31, 32.

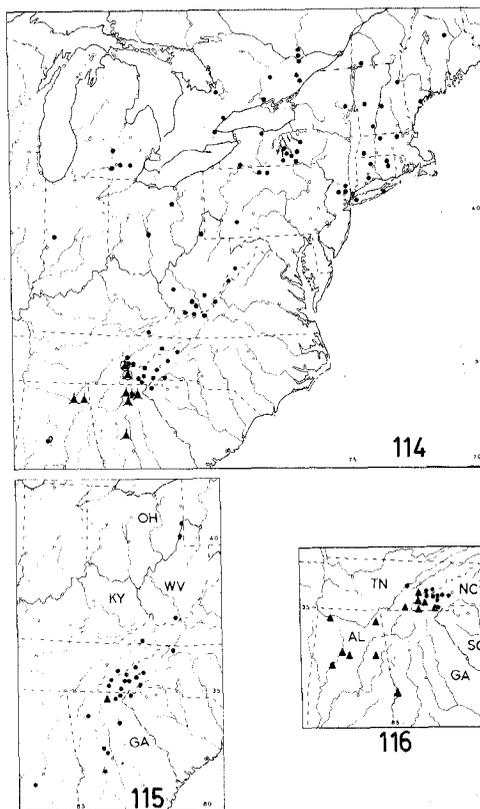
Diagnosis.—*Wadotes tennesseensis* can be distinguished from all other *Wadotes* by its lack of well developed proximal lateral cymbial processes in males (Fig. 46); and in females, by a combination of EL ca three times as long as LAE (EL/LAE=2.70-3.61, $N=19$) and normally a complete lack of sclerotization anterior to the atrial slit (Fig. 60).

Description.—*Male*: Figs. 8, 45-47. 16 specimens measured including holotype. CL 3.4-4.6(4.0±0.35), CW 2.3-3.0(2.6±0.20), SL 1.68-2.20(1.93±0.13), SW 1.43-1.78(1.58±0.10). Holotype CL 4.0, CW 2.6, SL 1.93, SW 1.58.

Female: Figs. 60-65. 20 specimens measured. CL 3.3-4.8(3.9±0.36), CW 2.1-3.1(2.6±0.25), SL 1.58-2.25(1.89±0.16), SW 1.35-1.83(1.55±0.12).

Variation: The scape varies dramatically even among specimens from a single locale (Figs. 60, 65). The superficial epigynal sclerotization is normally restricted to the area posterior to the atrial slit, however, one specimen from Mount Pisgah,

Fig. 114.—Distributions of *Wadotes deceptis*, encircled triangles; *W. hybridus*, dark circles; and *W. saturnus*, triangles with extended apices; in southeastern Canada and eastern United States. Fig. 115. Distributions of *W. bimucronatus*, dark circles; and *W. georgiensis*, triangle; in eastern United States. Fig. 116. Distributions of *W. dixiensis*, triangles; and *W. tennesseensis*, circles; in southeastern United States.



North Carolina has a narrow encircling band of sclerotization passing around the anterior end of the scape and a few other specimens exhibit a very faint band. Males do not exhibit significant variation.

Distribution.—Figs. 116, 117. One specimen of *W. tennesseensis* has been collected at Kingston, Roane County, Tennessee near the confluence of the Clinch and Tennessee Rivers in the lowlands east of the Cumberland Plateau. With this exception, this species appears to be restricted to higher elevations (probably over 900 m) in the Great Smoky Mountains of Tennessee (Sevier and Blount Counties) and North Carolina (Haywood and Swain Counties) and in adjacent areas in the Plott Balsams, Pisgah Range, and the Blue Ridge Mountains of North Carolina from Mount Pisgah (Buncombe County) to Highlands (Macon County).

Natural History Notes.—*Wadotes tennesseensis* is most common in the high elevation oak and spruce/fir forests within its range but is also present in the lower elevation mixed hardwood forests down to about 900 m above sea level.

Overwintering females have been collected from small diapause chambers, not much larger than themselves, which they have constructed in rotting wood under the bark of fir logs. In the spring females construct single egg cases in these cavities and remain with them at least until the young emerge. Two egg cases collected in June contained 19 and 65 eggs.

Adult males appear considerably earlier than do those of other *Wadotes* occurring in the same vicinity and do not appear to overwinter. They have been collected from early July to early September.

Wadotes calcaratus, *W. hybridus*, *W. dixiensis*, and *W. bimucronatus* are all possibly sympatric with *W. tennesseensis*, but *W. dixiensis* and *W. bimucronatus* have been collected only from lower elevations than has *W. tennesseensis*. Specimens of *W. calcaratus* and *W. tennesseensis* were found in the same sample of hardwood leaf litter.

Wadotes tennesseensis may be the sole *Wadotes* found in the southern spruce/fir forest stands within its range. Although both *W. calcaratus* and *W. hybridus* are characteristically northern species, the latter has not been found at the higher elevations of the southern Appalachians and the former, although collected from nearby spruce/fir forests, such as at Mount Mitchell, North Carolina, has not been discovered in this habitat within the range of *W. tennesseensis*.

Populations in the vicinity of Kingston, Tennessee and Highlands, North Carolina (only one specimen is known from each locale) are possibly disjunct from the apparently contiguous populations in the Great Smoky, Plott Balsam and Pisgah Mountains. If the former populations are peripheral isolates, this could indicate that this species has had a larger range in the past. Its range may have been shrinking since the last glacial maximum. The present rapid destruction of spruce/fir habitat throughout the Southern Appalachians may hasten this process and significantly reduce the already restricted range of this species.

Type Series.—Male holotype, female allotype, 6 male and 2 female paratypes, Tennessee, Sevier Co., Mt. Le Conte, GSMNP, 8-9 VII 1933 (W. J. Gertsch), in AMNH, examined.

Collection Data.—U.S.A.: NORTH CAROLINA: *Buncombe Co.*, Mt. Pisgah, 14 X 1926, 1 female (AMNH), no date, 2 females (AMNH); *Haywood Co.*, Waterrock Knob, 30 X 1969 (W. A. Shear), 1 female (MCZ), no locale, 28 V 1934 (A. F. Carr), 1 female, 1 imm (FSCA); *Jackson Co.*, BRPWY, Cherokee Indian Reserve, 3 X 1960 (W. Gertsch, W. Ivie), 1 male (AMNH), BRPWY, Richland Balsam (6000'), 7-20 VIII 1965 (S. Peck), 1 male (AMNH), 25 IX 1982 (R. G. Bennett), 1 female (RGB), BRPWY, Bearpen Gap (5400'), 23 VII 1975 (F. A. Coyle), 2 females (FAC), BRPWY, W slope of Campbell Lick (4700'), 9 VI 1983 (R. G. Bennett), 1 female (RGB), BRPWY, NE slope of Yellow Face (5800'), 9 VI 1983 (R. G. Bennett), 1 female, 19 eggs (RGB), BRPWY, above Grassy Ridge Mine (5200'), 11 IX 1983 (R. G. Bennett), 1 female (RGB), BRPWY, along trail from Haywood Gap to Rough Butt Bald, 27 VI 1984 (R. G. Bennett), 1 female, 65 eggs (RGB); *Macon Co.*, Highlands, 6 IV 1929 (Bishop), 1 female (AMNH); *Swain Co.*, GSMNP, Deep Creek nr. Bryson City, 26 VII 1930 (P. L. Darlington), 1 male (MCZ), GSMNP, Newfound Gap (5200'), 31 VIII 1930 (P. L. Darlington), 4 males, 1 imm (MCZ), GSMNP, Mt. Kephart (6000'), 23 IV 1952, 1 female (MCZ). TENNESSEE: *Blount Co.*, no locale, IX 1931 (W. M. Barrows), 3 females (AMNH); *Roane Co.*, Kingston, 12 VII 1933, 1 female (AMNH); *Sevier Co.*, GSMNP, Mt. Le Conte, 9 IX 1928 (W. M. Barrows), 1 male, 3 females (AMNH), no dates, 11 females, 35 imms (AMNH), GSMNP, Little Pigeon Ck., 9 VII 1933 (W. Ivie), 1 male, 2 females (AMNH), GSMNP, Clingman's Dome, 22 VI 1941 (C. and M. Goodnight), 1 female, 1 imm (AMNH), GSMNP, Elkmont, 8 VIII 1960 (T. C. Barr), 1 female (AMNH), GSMNP, Rt. 441, Buckeye Nature Tr., 8 VIII 1981, (L. N. Sorkin and A.A.S.), 2 males, 3 imms (AMNH), no locale, no date, 1 female (AMNH).

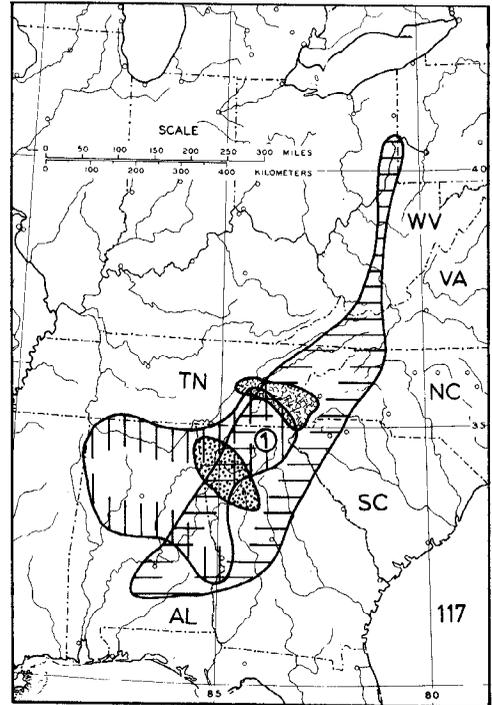
Wadotes willsi, new species

Figs. 40-44, 58, 59, 112, 118

Etymology.—The specific name is a patronym honoring the late band leader Bob Wills.

Diagnosis.—*Wadotes willsi* is only likely to be confused with *W. calcaratus* with which it is closely related. It can be distinguished from all *Wadotes* including *W. calcaratus* by the combination of a dorsodistal prolateral tibial apophysis and

Fig. 117.—Ranges of *Wadotes bimucronatus*, horizontal bars; *W. carinidactylus*, dots; *W. dixiensis*, vertical bars; *W. georgiensis*, encircled 1; and *W. tennesseensis*, flecks; in eastern United States.



a well-developed but unbisected prolateral cymbial process in the male (Figs. 40-42). Females (Figs. 58, 59) are apparently indistinguishable from female *W. calcaratus* but can be separated from all other *Wadotes* by the diagnostic characters of *W. calcaratus*.

Description.—*Male*: Figs. 40-44. Four specimens known. CL 3.8-4.3(4.0 ± 0.22), CW 2.4-2.8(2.6 ± 0.17), SL 1.85-2.13(1.98 ± 0.12), SW 1.45-1.65(1.58 ± 0.09). Holotype CL 4.0, CW 2.5, SL 1.95, SW 1.6.

Retrolateral patellar apophysis long, about one-third of total patella length. Pronounced dorsodistal prolateral tibial apophysis (Figs. 40, 41) extending from dorsal surface of prolateral tibial extension. Retrolateral cymbial process (Fig. 41) long, arched prolaterally, but shorter and less robust than in *W. calcaratus*. Proximal loop of embolus closely associated with ventral surface of prolateral process (Fig. 42). Terminal apophysis (Figs. 43, 44) laterally flattened (Fig. 43) with surface roughened distally.

Female: Figs. 58, 59. Two specimens known. CL 3.8, 4.7; CW 2.3, 2.8; SL 1.85, 2.25; SW 1.48, 1.70. LAE about one-quarter of EL (EL/LAE=4.44). Median unsclerotized area very wide, occupying most of region posterior to atrial slit. Narrow band of superficial epigynal sclerotization extends around anterior end of scape from region posterolateral to atrial slit. Spermathecal support sclerotization (Fig. 58) conspicuous only when specimen is cleared.

These female specimens have been paired with the males of *W. willsi* on the assumption that the population located on and around Mount Rogers is allopatric with and distinct from surrounding *W. calcaratus* populations. This area has been poorly collected. Both species may exist sympatrically on Mount Rogers.

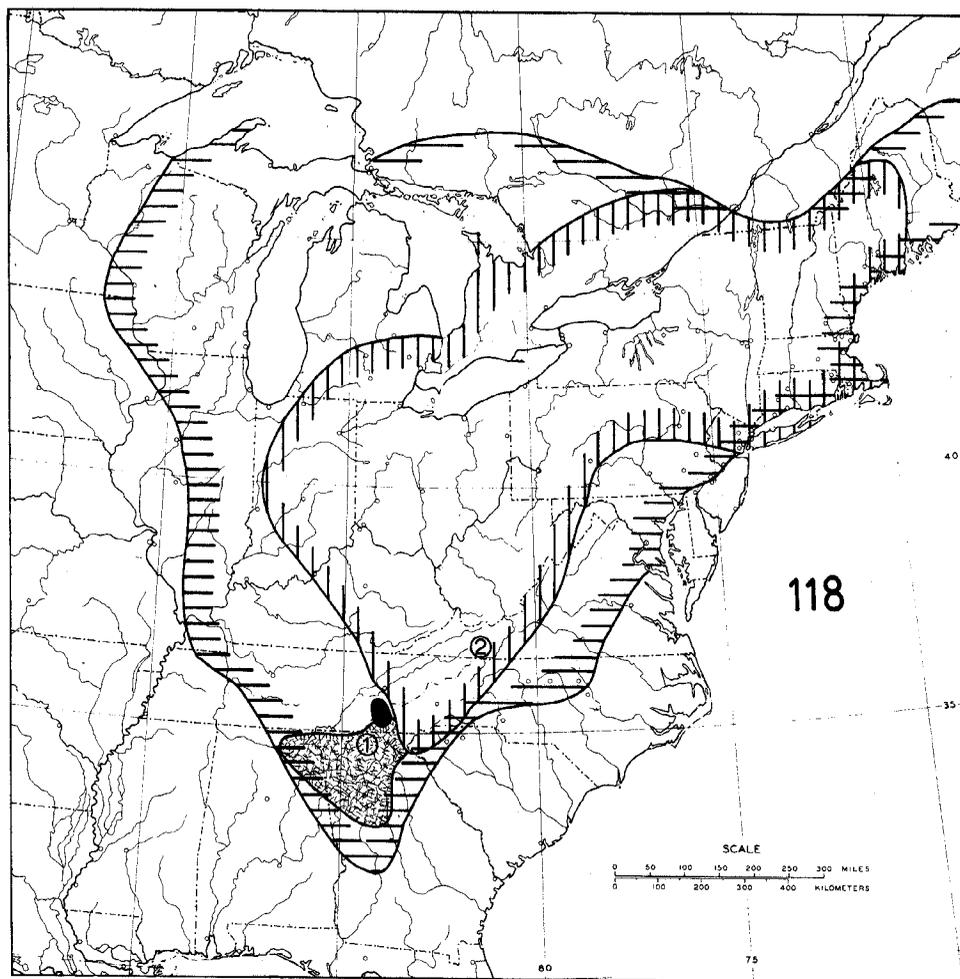


Fig. 118.—Ranges of *Wadotes calcaratus*, horizontal bars; *W. deceptus*, darkened area; *W. hybridus*, vertical bars; *W. mumai*, encircled 1; *W. saturnus*, flecks; and *W. willsi*, encircled 2; in southeastern Canada and eastern United States.

Variation: One female has the primary loops of the connecting ducts oriented nearly at right angles to the main axis of the body such that the anterior terminus of each duct points cephalad (Fig. 58). The ducts of the other specimen exhibit a more *W. calcaratus*-like pattern of looping.

Distribution.—Figs. 112, 118. *Wadotes willsi* is presently known only from the slopes of Mount Rogers in Smyth and Grayson Counties, southwestern Virginia, and from adjacent Ashe County, North Carolina.

Natural History Notes.—Mount Rogers is characterized by a Fraser fir forest and grass and blackberry/hawthorn balds at the higher elevations with northern hardwoods (especially sugar maple, beech, and yellow birch) predominant below (Pittillo 1976). One male was collected from a beech/maple forest near Deep Gap on the west slope of the mountain.

Holotype.—Male, Virginia, Grayson Co., S side Mt. Rogers, 4500', 27 IX 1969, in AMNH.

Collection Data.—U.S.A.: NORTH CAROLINA; *Ashe Co.*, 3 mi NW of Lansing, 13 X 1963 (R. L. Hoffman), 1 male (NMNH). VIRGINIA; *Grayson Co.*, Mt. Rogers (5000'-6000'), 20 VIII 1955

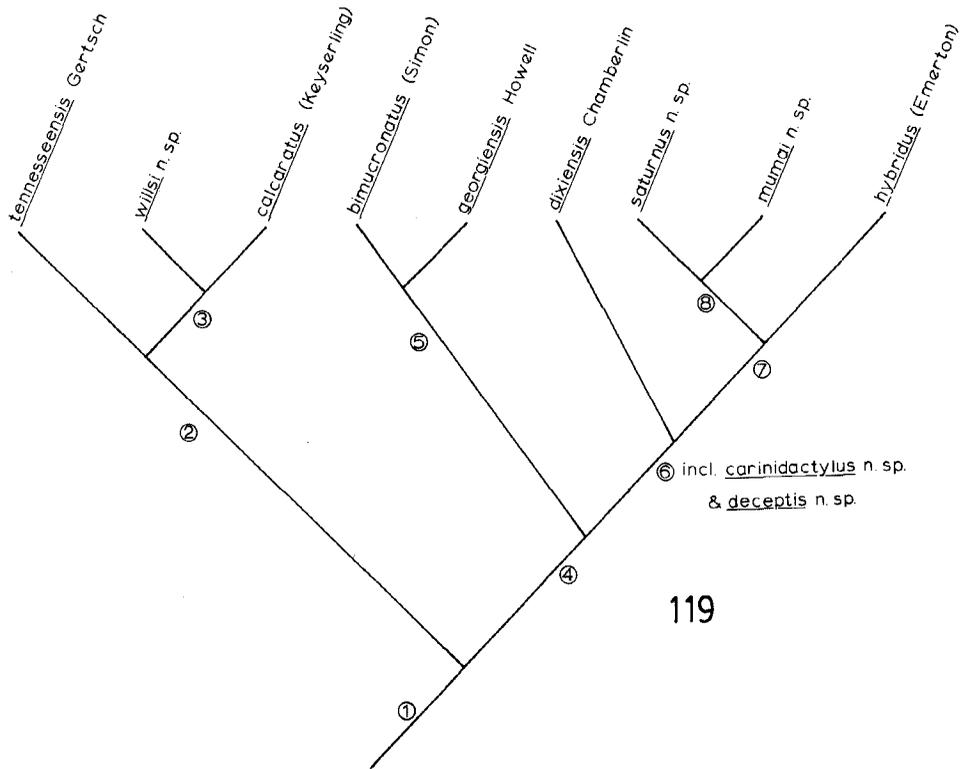


Fig. 119.—Cladogram of hypothesized *Wadotes* species relationships.

(Hanson, Muka, Turner, Hoffman), 1 female (AMNH), Mt. Rogers, 11 XI 1957 (VPI expedition), 1 female (NMNH), Mt. Rogers (4500'), 12 IX 1962 (R. L. Hoffman), 1 male (NMNH); *Smyth Co.*, nr. Deep Gap Shelter on Appalachian Trail (4920'), 2 IX 1975 (F. A. Coyle), 1 male (FAC).

Status of *Wadotes primus* Fox

Wadotes primus Fox 1937 from Hong Kong exhibits several characteristics in common with North American *Wadotes*: two retromarginal cheliceral fang furrow teeth, small anterior median eyes, and an anteriorly attached epigynal scape. The male is unknown. Lehtinen (1967) stated, without discussion, that this species "belongs to an undescribed genus." The female holotype of this species and a female of another species from China (both in AMNH) identified by V. Roth as "*Wadotes* n. sp. near *primus*" have been examined and neither possess any of the putative synapomorphies of the North American species of *Wadotes*.

The following characters of *W. primus* are distinct from those of the North American species of *Wadotes*: epigynum (Fig. 109) with a deeply forked, slender scape; transverse atrial slit near anterior edge of epigynum in region of base of scape, divided such that each half extends from lateral margin of epigynum to edge of scape base; connecting ducts in posteriorly contiguous, heavily sclerotized matrices (Fig. 110), ducts very convoluted, loops traversing entire width of each matrix; anterior terminals of ducts facing each other; spermathecae oval, support sclerotization not apparent on caudal boundary of epigynum.

The female specimen of "*Wadotes* n. sp. near *primus*" (Fig. 111) is superficially similar to *W. primus* (and North American *Wadotes*): scape long and slender, weakly forked posteriorly; atrial slit strongly developed and 'U'-shaped, extending from anterior lateral margins of epigynum to posterior boundary; uncoiled, strongly sclerotized, widely separated connecting ducts extend along dorsal margins of invaginated edge of atrial slit laterally; spermathecae contiguous, located medially at posterior margin of epigynum; (apparent) support sclerite extends from medial posterior lip of atrial slit around posterior boundary of epigynum. This latter species will probably prove to be a member of *Paracoelotes* Brignoli, 1982.

No defensible synapomorphies are known which warrant the continued inclusion of *W. primus* in *Wadotes*, but unless *W. primus* can be shown to belong cladistically to another group, there is no good reason to remove it from that genus. Further decisions as to the generic status of this species must await new data on Palaearctic coelotines, in particular the discovery of Asian *Wadotes* males.

ACKNOWLEDGMENTS

Specimens were loaned by the American Museum of Natural History (AMNH, Dr. N. I. Platnick), the California Academy of Sciences (CAS, Dr. W. S. Pulawski), the Canadian National Collection (CNC, Dr. C. D. Dondale), the Florida State Collection of Arthropods (FSCA, Dr. G. B. Edwards), the Museum of Comparative Zoology (MCZ, Dr. H. W. Levi), le Muséum National d'Histoire Naturelle (MNHN, Dr. J. Heurtault), the National Museum of Natural History (NMNH, Dr. J. Coddington), and by Drs. J. A. Beatty (JAB), F. A. Coyle (FAC), J. O. Howell (JOH), and W. A. Shear (WAS). At various times the following people have given freely of their time to answer questions, give advice, and/or criticize drafts of this work: Drs. R. C. Bruce, J. H. Horton, H. W. Levi, H. R. Mainwaring, J. D. Pittillo, N. I. Platnick, and W. A. Shear, and in particular Drs. F. A. Coyle, C. D. Dondale, and S. A. Marshall. Jennifer and Léa Terpenning did most of the original typing.

Some funding for this project was provided by the Biology Department of Western Carolina University, a Grant-In-Aid from the Highlands Biological Station, and a grant from the Exline-Frizzell Fund for Arachnological Research. Dr. R. Lumb proved adept at hastening bureaucratic process.

LITERATURE CITED

- Banks, N. 1892. The spider fauna of the upper Cayuga Lake Basin. Proc. Acad. Natur. Sci., Philadelphia, 1:11-81.
- Banks, N. 1895. A list of the spiders of Long Island with descriptions of new species. New York Entomol. Soc., 3:76-93.
- Banks, N. 1910. Catalogue of Nearctic spiders. Bull. United States Nat. Mus., 82:1-80.
- Bennett, R. G. 1984. Systematics and natural history of the spider genus *Wadotes* Chamberlin (Araneae, Agelenidae). Unpublished M.Sc. thesis. Library, Western Carolina Univ.
- Blackwall, J. 1841. The difference in the number of eyes with which spiders are provided proposed as the basis of their distribution into tribes; with descriptions of newly discovered species and the characters of a new family and three new genera of spiders. Trans. Linnaean Soc. London, 18:601-670.

- Bonnet, P. 1959. *Bibliographia Araneorum*. Toulouse. Vol. 2(5):4231-5058.
- Brignoli, P. M. 1982. On a few spiders from China. *Bull. British Arachnol. Soc.*, 5:344-351.
- Chamberlin, R. V. 1925. Notes on North American spiders heretofore referred to *Coelotes*. *Proc. Biol. Soc. Washington*, 38:119-124.
- Chamberlin, R. V. and W. Ivie. 1941. North American Agelenidae of the genera *Agelenopsis*, *Calilena*, *Ritalena* and *Tortolena*. *Ann. Entomol. Soc. Amer.*, 34:585-628.
- Comstock, J. H. 1912. *The Spider Book*. New York, Doubleday, Page and Co., 721 pp. in *The New Nature Library*, Vol. 7(2). Garden City, Country Life Press.
- Coyle, F. A. 1971. Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). *Bull. Mus. Comp. Zool.*, 141(6):269-402.
- Coyle, F. A. 1981. Effects of clearcutting on the spider community of a Southern Appalachian forest. *J. Arachnol.*, 9:285-298.
- Emerton, J. H. 1889. New England spiders of the families Drassidae, Agelenidae and Dysderidae. *Trans. Connecticut Acad. Arts Sci.*, 8:166-206.
- Foelix, R. F. 1982. *Biology of Spiders*. Cambridge, Harvard Univ. Press, 306 pp.
- Fox, I. 1937. New species and records of Chinese spiders. *Amer. Mus. Novitates*, No. 907:1-9.
- Gering, R. L. 1953. Structure and function of the genitalia in some American agelenid spiders. *Smithsonian Misc. Coll.*, 121(4):1-84.
- Gertsch, W. J. 1936. Further diagnoses of new American spiders. *Amer. Mus. Novitates*, No. 852:1-27.
- Howell, J. O. 1974. A new species of *Wadotes* (Araneae: Agelenidae) from North Georgia. *Ann. Entomol. Soc. Amer.*, 67(5):728-730.
- Howell, J. O. 1976. New spider records for Georgia. *J. Georgia Entomol. Soc.*, 11(3):240.
- Kaston, B. J. 1948. Spiders of Connecticut. *Connecticut Geol. Natur. Hist. Surv. Bull.*, No. 70:1-874.
- Keyserling, E. 1887. Neue Spinnen aus Amerika. VII. *Verh. Zool.-Bot. Ges. Wien*, 37:421-490.
- Lehtinen, P. T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Ann. Zool. Fennici*, 4:199-468.
- Muma, M. H. 1946. North American Agelenidae of the genus *Coras* Simon. *Amer. Mus. Novitates*, No. 1329:1-20.
- Muma, M. H. 1947. North American Agelenidae of the genus *Wadotes* Chamberlin. *Amer. Mus. Novitates*, No. 1334:1-12.
- Pittillo, J. D. 1976. Potential natural landmarks of the Southern Blue Ridge portion of the Appalachian Ranges Natural Region. Atlanta, National Parks Services, 371 pp.
- Roth, V. D. and P. L. Brame. 1972. Nearctic genera of the spider family Agelenidae (Arachnida, Araneida). *Amer. Mus. Novitates*, No. 2505:1-52.
- Roewer, C. F. 1954. *Katalog der Araneae*. Bruxelles, Vol. 2a:1-923.
- Shear, W. A. 1967. Expanding the palpi of male spiders. *Breviora*, 259:1-27.
- Simon, E. 1898a. Descriptions d'Arachnides nouveaux des familles des Agelenidae, Pisauridae, Lycosidae et Oxyopidae. *Ann. Soc. Entomol. Belgique*, 42:5-34.
- Simon, E. 1898b. *Histoire naturelle des Araignées*. Paris, Vol. 2(2):193-380.
- Worley, L. G. and G. B. Pickwell. 1927. The spiders of Nebraska. *Univ. Stud. Nebraska*, 27(1-4):1-129.

Manuscript received January, 1985, revised June 1986.