THE NEARCTIC SPECIES OF THE GENUS DOLOMEODES (ARANEAE: PISAU RIDAE)

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ABSTRACT. Of 34 names given in the literature for nearctic species of Dolomedes, only seven have validity: D. tenebrosus Hentz, D. okajunensis Bishop, D. albiceps Hentz, D. scriptus Hentz, D. titidus Walckenaer, D. striatus Giebel, and D. triton (Walckenaer). Two new species are described, D. gerschii and D. holti. Four new synonyms are recognized.

An effort is made to fully characterize each species in terms of habitat, affinities, geographic distribution, behavior, and morphological variation. New taxonomic characters are described, many of which are measurable. A characteristic array of color pattern zones in nearctic Dolomedes is described.

Pleistocene geographical isolation is proposed as the probable cause of evolutionary divergence in three species-pairs.

INTRODUCTION

Approximately forty-nine years ago Sherman Bishop (1924) published his revision of the Pisauridae of the United States which, for its time, stood as a classic among works on the taxonomy of spiders. The genus Dolomedes was given comprehensive treatment and most of the North American species were included. Although it is rather unusual for a particular spider group to be revised twice within the same half-century, the present study was undertaken for three reasons: (1) additional collecting of familiar species since 1924 provides a better knowledge of their ranges; (2) new forms have been found since then; (3) new techniques and concepts in taxonomy, when applied to Dolomedes, bring about interpretations different from those of Bishop.

Thirty-four specific names have been applied to nearctic spiders of the genus Dolomedes. Here only seven of these names are regarded as valid, 14 have been synonymized, either in this paper or previously, and 13 are nomina nuda, inquirenda, or do not apply to species of Dolomedes. Among the major reasons for this proliferation of names is an apparent lack among previous workers of an appreciation or knowledge of variability within the group. Bishop did much to stabilize the nomenclature of well-known species of Dolomedes, but at the same time he introduced some new names which were based merely upon variants of other species. Since Bishop's work, Chamberlin and Ivie introduced new names and revived old ones which were applied to what I consider to be intraspecific variants. The problems of interpretation seem to arise from the variability of color pattern and certain parts of the genitalia which occurs in a number of the species. With this in mind I have attempted to gather

some objective data on the extent of intraspecific variability involved in the species under investigation.

The primary objectives of this revision, however, are to redefine known species and describe new ones, compile information pertaining to their biology, and speculate upon factors of evolution in the genus.

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BIOLOGY OF DOLOMÉDES

Generally speaking, the members of the genus Dolomedes are large, rather robust spiders, with the length of the body in one species ranging to about 35 mm. They are usually encountered near permanent bodies of fresh water, over the surface of which they can run with surprising agility, apparently kept afloat by hairs coated with hydrophobic substances on the ventral surface of the body. These spiders utilize this ability to run on the water's surface to escape predation and to capture prey. In the latter case, they use the surface film as if it were a web, because they sit at the edge of the water and pursue insects that accidentally fall upon the water and are trapped by the surface tension. Thus, these spiders occupy the neuston community.

Prey capture. Detection of prey trapped by surface tension is probably by two means: eyesight and tactile stimuli from the surface of the water. Frequently, the spiders will be encountered resting upon a solid object floating on or emerging from the water with the anterior two pairs of legs resting upon the surface of the water itself. Apparently the ripples caused by an insect provide the stimulus for the predatory response and possibly also provide information as to the location of the prey. No data are available about visual acuity, and there is nothing to indicate that it is any greater or less than in any other member of the Lycosoidae.

Spiders of the genus Dolomedes are rather easy to capture by hand because they rarely give a flight response, even if the slowly moving pursuer is but a few inches away. Whether this is due to poor eyesight or to a peculiar behavioral pattern is not known.
Another unusual behavioral trait of Dolomedes is the ability to dive into the water either to escape predation or to prey upon aquatic organisms. Submergence beneath the surface film is accomplished only with considerable force, such as jumping off a high object or launching from a relatively stationary object at water level. During submergence, an envelope of air surrounds the body with the tips of the longest hairs and spines determining the thickness of the air space. Duration of submergence may be considerable. Bishop (1924) records "... one-half an hour or longer..." for D. triton, an observation which I have confirmed with other species as well. The mechanism must be similar to the plastron breathing of various aquatic insects in which the air bubble functions as an accessory lung to furnish dissolved oxygen and dissipate carbon dioxide. Spraying the spider with alcohol before submergence results in inability to produce an air envelope and subsequently the animal will remain underwater for only a few seconds. Whether this quick return to the surface of the water is due mainly to the influence of the alcohol or to the lack of sufficient oxygen is not known.

Prey taken underwater seems to be limited to fish. Barbour (1921) observed three spiders in southern Florida (which he believed to be D. tenebrosus), each involved in consuming a small fish. Considering the locations, the spiders were probably D. okefinokensis. McCook (1889) fancifully figured a spider riding the back of a relatively huge fish. Davis (1891) stated that while watching one of a number of specimens of D. triton on the surface of a small pond "... it suddenly made a rapid motion and seized a little silvery fish over an inch in length. It held it firmly and remained as stationary as it had been before the capture." Dolomedes triton has been known to cause considerable damage in fish hatcheries (Meehean, 1934). In such cases, these spiders were observed to have a standard method of attack which was with the "... mandibles sunk in the prey at the base of the head and the legs clasping the body in a straddling position."

Several other accounts of fish capture, apparently by Dolomedes, may be found in articles by Spring (1859), Peters (1876), Gudger (1922, 1925, 1931), and Adams (1927). More recently, a striking photograph was published in Turtox News (Mohrhardt, 1963) which showed a specimen of D. scriptus consuming a small fish along a Michigan stream. The only such case I have observed was of a female D. scriptus feeding upon a small darter. It is reasonable to believe that aquatic invertebrates, especially insects, would also fall prey to Dolomedes, but no cases have been reported nor have I observed any. On the basis of present information, it is difficult to say whether or not fish are the preferred underwater prey.

Habitat relationships. Considerable field observation has shown that the species of Dolomedes have fairly well-defined habitats, especially wherever several species are found together in the same stream system. The majority of nearctic species are confined to the eastern United States, approximately east of the one-hundredth parallel, and in almost any stream system in this area a number of species will occupy essentially different microhabitats. Descriptions of the microhabitats must be understood to be rather general and there are frequent invasions of microhabitats by other species. Habitat specificity seems to be related primarily to size and type of the body of water and to the vegetation. It is difficult, in the latter case, to determine whether the type of vegetation or the amount of shade is more important.

Three common species in the midAtlantic states, D. scriptus, D. vittatus and D. triton, have been studied most closely. In this region many stream systems are occupied by all three species. Dolomedes triton is usually found among emergent vegetation
in ponds, lakes, and slow moving streams which are characterized by relatively quiet water. *Dolomedes scriptus* is usually common along large, moderately swift streams where there are rocks, boulders, and entangled rubbish emerging from or bordering the water. These larger streams typically are open to the sun because of the wide separation of tall, woody vegetation on the banks. *Dolomedes vittatus* is most often encountered along smaller, moderately swift streams with most of the sunlight shut out because of a rather continuous cover of tall, woody vegetation overhead. Several streams have been studied, and two examples will demonstrate the habitat relationships of these three species.

The first example is the relatively undisturbed upper parts of the Cullasaja River system near Highlands, North Carolina. Two small, artificial lakes, located near the town at the headwaters of Mill Creek, Lake Ravenel, and Harris Lake, have rather stable vegetation composed of water lilies and sedges. The chief spider occupant of these lakes is *D. triton*. However, the small streams that drain these lakes are well shaded by tall vegetation and are inhabited chiefly by *D. vittatus*. Further downstream, in the Cullasaja River proper, *D. scriptus* is the species most often encountered. The stream here is rather rapid and possesses many emergent boulders but is not shaded by a continuous canopy.

The other example is from the Toxaway River drainage of Transylvania County, North Carolina. The specific area studied is the part of the river near Bearwallow Creek and the creek itself. The river is wide, open and contains many rocks, boulders, and much rubbish, while the creek is small, closed overhead and also contains rubbish and rocks. *D. scriptus* is the main occupant of the river and *D. vittatus* is the chief occupant of the creek. The general area of the creek mouth is a transition zone where some *D. scriptus* are found part way up the creek, and *D. vittatus* is found under clumps of grass and in other dark areas along the banks of the river.

The above-mentioned species are protectively colored for their respective habitats. *Dolomedes triton* usually varies from greenish to light tan in color and blends with the aquatic green herbaceous vegetation, sometimes covered with mud, among which it is typically associated. *Dolomedes scriptus* is gray with distinct light and dark markings which make it blend well with the gray rocks and weathered, sun-bleached rubbish with which it is found. *Dolomedes vittatus* ranges from light to dark brown (in males) to almost entirely dark brown (in females), and approximates the brownish hues of rotting, unbleached, woody rubbish and dead leaves found in and around the water.

Protective coloration suggests predation by visual predators. Pompilid and sphecoid wasps, which hunt primarily by sight, and although more properly called parasites, apparently take their toll of *Dolomedes*. This assumption is based on the collection of a large paralyzed female *D. tenebrosus*. Vertebrate predation is known only from a collection from Florida which contains 32 *D. triton* adults and juveniles taken from the gut of an immature little blue heron, *Florida caerulea caerulea*.

In the southern coastal plain of the United States, there are at least three different species typical of the streams of the region. Observations have been made on parts of the Waccamaw River, in Horry County, and the Santee River, in Georgetown County, South Carolina. In many of these slow-moving streams *Dolomedes* is found on cypress and other trees as well as herbaceous vegetation emerging from the water. *Dolomedes triton* is found among the herbaceous vegetation and occasionally at the waterline on small bushes and trees. *Dolomedes albineus*, a light gray species, is found higher up the trunks of trees, lying flat against the bark about three to six feet above the waterline, while *D. tenebrosus*, another gray species, remains usually within
two feet of the waterline. Both *D. albineus* and *D. tenebrosus* blend well into the gray bark background. A similar relationship among these species has been observed in a small stream in Leon County, Texas.

In the Okefenokee Swamp, Georgia, a similar situation exists. This area is also characterized by a mixture of vegetation such as cypress trees and other woody plants, along with various herbaceous plants. Here the same species as those named above exist, with the exception that *D. tenebrosus* is replaced by its close relative *D. okefenokensis*, which occupies a similar habitat. These three species are found throughout peninsular Florida and probably occupy their respective microhabitats wherever they coexist.

**Sexual biology.** In experiments, Kaston (1936) showed the presence of substances that could elicit a mating response from spiders even in the absence of other spiders. One of the spiders he used was *D. scriptus*. Other experiments by Hegdekar and Dondale (1969) have shown the specific nature of sexual pheromones in interspecific mating in the closely related lycosids. This evidence seems to indicate a major role played by chemotactic stimuli in the mating process.

My observations of the mating of two species of *Dolomedes* suggest that visual stimuli play a relatively minor role. These observations were made upon *D. scriptus* (two complete matings) and upon an unusual case in which an adult male and a penultimate female *D. vittatus* were displaying preliminary mating behavior. In all these observations there was a preliminary period of “palpation,” consisting of leg waving and touching, beginning with contact with the tarsi and proceeding to contact with the tibiae as the pair gradually moved closer together. The contact was primarily between leg pair I and, to some degree, leg pair II. This stage required about thirty minutes, and the majority of the time the animals were unable to see more than each other’s legs waving in the air because they were on opposite sides of small rock ledges or flat pieces of wood. In one case the initial parts of this preliminary period were begun while the female was unable to see its partner at all because the contact was made while her legs were flexed over the edge of the rock. Whenever complete mating occurred, the contact was made between the femora. The male faced the anterior end of the female during the preliminary period, moved about 180° around the stationary female, and then advanced backward over the female, which had, during this time, assumed a posture with the legs I and II extended forward while she stood high off the ground on the tips of the tarsi III and IV, with the femora almost vertical. As the body of the male crossed over the female, he settled down upon her, reached around the body between legs III and IV, and placed the palpal organ against the epigynum, apparently immediately releasing the sperm into a bursa copulatrix. After this first contact with the palpal organ, the female appeared to quickly throw off the male. The male approached a second time, with the preliminary palpation period lasting but a few seconds, and the other palpal organ was then emptied. The male approached a third time and possibly as much as a fourth, but each time the female rejected him and the two subsequently parted. The two observations of complete *D. scriptus* matings were made 29 August 1961, and 3 September 1961, in mountainous streams of southwestern North Carolina. In both cases the females were gravid at the time of mating. These observations of mating in the natural habitat are quite similar to observations made in the laboratory by Kaston (1936).

In other groups of spiders the embolus of the male palpal organ is frequently broken off during mating and remains embedded within the bursa copulatrix of the female. Notable in this sense is the Theridiidae (Levi, 1959) and the Lycosidae (Hegdekar and Dondale, 1969). Some specimens of *D. scriptus*, *D. triton*, and *D. vittatus* in the collections I have studied each had
one embolus still inserted. No palpal organ studied was without an embolus. It appears that breaking of the embolus in Dolomedes is infrequent.

**EVOLUTION IN NEARCTIC DOLOMEDES**

It is with hesitation that I attempt to speculate upon the evolution of a group whose biology and systematics are so poorly known. However, underlying any similar venture in any group, there is at least an unarticulated understanding that what is said is subject to future revision. Such speculations, then, are useful at any stage of knowledge in giving direction and focus to further work.

I wish to comment chiefly upon the recent evolution of three species-pairs of Dolomedes. This effort was prompted by observations upon the known distributional patterns and upon apparent evolutionary relationships that are based upon structure and ecology. But first, consideration must be given to some basic biological factors involved in spider evolution.

*General considerations.* Apparently, the chief event that precedes speciation is geographic isolation. Therefore, an understanding of how a population can be isolated is directly related to knowledge of the dispersal mechanisms of that species. Two known important mechanisms of dispersal in Dolomedes could be classified as passive and active.

The passive means of dispersal is the process referred to as "ballooning." This is the well-known mechanism involving the dispersal of spiders by wind currents. Our knowledge is incomplete, not only about which species balloon, but also which families balloon. Additionally, we have inadequate information about the importance of ballooning in colonization and therefore what part it plays in geographic isolation.

Whether ballooning is a generic characteristic of Dolomedes is unknown, but there is some evidence that certain species are capable of this practice to some degree. The nursery web is typically placed high in weeds, higher than where these animals usually stay at other times in their respective habitats. Perched at this height, the spiderlings at least have an increased opportunity for successful ballooning even though there is no available evidence that the nursery is a specific adaptation to this function. I have not observed ballooning, but Emerton (1908) reported finding evidence of considerable fall ballooning in *D. triton*.

If we conclude that some species of Dolomedes do balloon as a general rule, then we must consider the degree of their capability, and further, the relationship of this capability to the ability to colonize new areas across wide barriers. Some indirect evidence is available to suggest that their ballooning capability is not as great as in many other spiders.

First, these spiders are quite dependent upon water. With the exception of *D. tenebrosa*, which may be found in moist basements of houses or woods, they are not found far from bodies of water. Experience with culturing them in the laboratory shows that they are much more susceptible to fatal desiccation than are most other spiders. Their dependency upon water therefore suggests difficulty in surviving long-distance transport in the air. It is unlikely that any but very small immatures would balloon great distances because of the relatively large size of these animals. If only the immatures are able to balloon, then they would be faced with the problems of encountering a suitably moist habitat and surviving there for up to about two years until reaching sexual maturity. If a spider somehow survives to reproductive age then it must encounter a spider of opposite sex, also at the reproductive stage at the same time. These factors of chance tend to raise doubts about the probability of successful long-distance transport and colonization when compared with well-known ballooners.
Another kind of passive dispersal is transportation by flowing water in streams. This would not be of interest in terms of geographic isolation because freshwater connections would potentially provide continuous connections between populations, and similarly between their gene pools. Many changes in streams which affect the distribution of strictly aquatic animals (e.g., stream capture and fishes) would not apply to *Dolomedes*.

*Active* means of dispersal is here meant to include primarily directional movements of the spider by walking. Again, as stated before, water dependency seems to restrict *Dolomedes* to a wet, or at least a moist environment; therefore, species of *Dolomedes* are not found walking in arid areas, and are probably not capable of living in such conditions for very long. Within a drainage system, however, these animals might be expected to move long distances relatively quickly.

Areas of ocean water are also a barrier to dispersal. The apparent absence of *Dolomedes* from most islands off the coast of
southeastern U.S.A. may provide indirect evidence for this, because suitable habitats apparently exist there.

Temperature generally seems not to be a very important limiting factor to dispersal. Some species of *Dolomedes* are distributed over wide geographical areas that include widely diversified and extreme temperature characteristics. Overwintering seems to occur in most, if not all, stages of the life cycle.

**Speciation in certain species pairs.** Below, some particular species of the genus *Dolomedes* are treated in terms of their probable evolution. For the sake of further discussion, it is assumed that the proposed barriers to dispersal are effective against active and passive means.

*Dolomedes scriptus-Dolomedes gertschi.* These two species, which are clearly allopatric, seem to represent a rather closely related monophyletic species-pair. *Dolomedes scriptus* is widely distributed in eastern North America (Map 5), while *D. gertschi* is restricted to the mesic parts of the Gila River drainage in Arizona and New Mexico (Map 6). Invasion of each other's ranges by active means is apparently prevented by the broad xeric barrier separating the two distributions in these southwestern states. There is no indication that there is any invasion by passive means or that this is even very probable (Map 1).

If one assumes that these two species represent evolved fragments of a single ancestral species, then the time of emergence of the dispersal barrier between the fragments may indicate time of gene-pool isolation. That the xeric conditions of the southwest were caused primarily by the emergence of the Rocky Mountains and the Coastal Ranges is well established. It is not certain when the xeric conditions emerged, but they appear to have been at least post-Miocene. Well-documented evidence shows that during the Pleistocene this region experienced fluctuations in climate that caused expansions and contractions of mesic areas. We may postulate then, (1) that the parent species had a continuous distribution from the East into the Gila River drainage, and therefore isolation occurred when xeric conditions between these areas became severe enough to block dispersal and gene flow (perhaps in the Pliocene or early Pleistocene), or alternatively that (2) no populations of the parent species existed in the Gila Basin until they were introduced into the area during a Pleistocene pluvial period (mesic period) followed by disjunction and differentiation in an interglacial (xeric) period. The Pleistocene may be the most likely time of differentiation.

*Dolomedes vittatus-Dolomedes holti.* These two species are probably more closely related than are any other two in North America. *Dolomedes vittatus* is relatively widely distributed in the eastern United States with the range extending westward into eastern Texas (Map 7). *Dolomedes holti* is known only from the drainage of the upper San Juan River, a Mexican tributary of the Rio Grande (Map 8). There is a lack of congenial habitats between the lower reaches of the tributaries of the Rio Grande and the streams of the eastern United States. Therefore, if the geographic range of the parent species included the ranges of the present species, then *D. holti* could have been derived from populations separated by this xeric barrier (Map 1). If, however, the parent species did not originally extend into the Rio Grande before the barrier developed, it is possible that the Mexican species emerged from a population that invaded the Rio Grande drainage during a Pleistocene pluvial stage. Following the invasion, when contraction of mesic conditions occurred, the populations at lower elevations moved into the cooler, wetter canyons in the mountains. The same geological events were apparently involved here as in the first species-pair mentioned.

*Dolomedes tenebrosus-Dolomedes okefinokensis.* Again, these represent a closely related species-pair, but the probable
factors relating to their origin are quite different from those described for the previous pairs. Both are eastern North American species, with *D. tenebrosus* distributed from Canada to western Florida (Map 2) and the apparently allopatric *D. okefino-kensis* chiefly limited to peninsular Florida (Map 3). The most outstanding feature of the southern Coastal Plain that has probable relevance to *Dolomedes* speciation, is the occurrence of islands in peninsular Florida during interglacial periods of the Pleistocene (Map 1). That these islands were formed in the Aftonian, Yarmouth, and Sangamon interglacial periods is well established, and the geological evidence will not be reviewed here (see Flint, 1940; MacNeil, 1950; King, 1965).

The Pleistocene islands of Florida have previously been proposed as important factors in the differentiation of other groups, such as reptiles (Auffenberg and Milstead, 1965). Of greater significance for this discussion is the excellent work of McCrone (1963) in which he gives convincing evidence for Pleistocene speciation in *Geolycosa* owing to isolation on these islands during Pleistocene interglacial times. If one assumes that these islands (1) had a hospitable environment, (2) existed long enough for speciation to occur, and (3) were inhabited by a disjunct population of the parent species, then one might be able to date with some accuracy from geological data the origin of *D. okefino-kensis*.

The present distribution of these species can be explained on the basis of interaction between them. *Dolomedes okefino-kensis* apparently became better adapted to relatively warmer climatic conditions, and eventually a zone of demarcation between their respective ranges became established. There is no obvious difference in other aspects of the habitats, so the allopatry may be now maintained by competition.

In each of the foregoing species-pairs, there is one representative that has a wide eastern distribution and another that has a restricted and allopatric one. All three of the former species are largely sympatric in the East.

Taking an overview of the species ranges under consideration, in reference to geological events, it seems that the large, eastern ranges are found in relatively undisturbed portions of North America, while the smaller allopatric distributions are isolated in areas that are known to have had more Pleistocene climatic (at least in terms of arid-versus-mesic considerations) and geographical disruption. It seems reasonable, then, to conclude that Pleistocene events were the major causes of speciation owing to geographic isolation in these areas.

Not enough evidence is available to arrive at any conclusions about the evolution of the three remaining nearctic species: *D. albinus*, *D. striatus*, and *D. triton*. It is worthwhile, however, to note the geographic distributions of these species which would undoubtedly play a significant part in any conclusions about their evolution. *Dolomedes albinus* (Map 4) is primarily found in the eastern Coastal Plain and geologic events in this region may have influenced the origin of this species. *Dolomedes striatus* (Map 9) is almost entirely limited to the glaciated region of eastern North America. *Dolomedes triton* (Map 10) is very widespread in the Nearctic Region, more so than any other species of *Dolomedes*, and one might expect some differentiation to be evident in the various populations represented in the collections. Most of the collections from outside the eastern United States contained immatures and the few adults available showed no clear evidence of differentiation. Further collecting in these areas may eventually lead to the discovery of new forms.

A summary of probable evolutionary relationships is diagrammed in Table 1. The basis for the construction of this dendrogram of nearctic *Dolomedes* is the structure of the male palpus. Features such as the fundamental configuration of the median apophysis and tibial apophysis
Table 1. Dendrogram of the Nearctic species of Dolomedes. The "degrees" of relationship do not represent any exact point in time, and the distance between each "degree" on the dendrogram is therefore not drawn to any chronological scale.

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appear to be rather sensitive indicators of degree of relationship. Also helpful are configuration of the tegulum and the relative lengths of the cymbium and tibia.

METHODS

All drawings of genitalia were made to the same size to emphasize form rather than size because of extreme variation in the latter. Dorsal color patterns were photographed and drawings made from the photographs.

For purposes of illustration the right male palpus was dismembered at the joint between patella and tibia. The female genitalia were removed and dissected according to the methods described by Carico and Holt (1964).

A zoom stereomicroscope was used in the measuring of all characters. An ocular micrometer was employed in a $10 \times$ wide-field ocular and the system was calibrated by a stage micrometer. The two magnifications used were approximately $10 \times$ and $50 \times$; the latter was obtained with $2 \times$ accessory lens. All measurements were made by myself.

A large number of characters were measured on small samples and only those that appeared to be of practical diagnostic value were utilized on all specimens. Many measurements, ratios, and characters used herein are unique to this study, and an explanation of abbreviations used in the text and illustrations is found in the following list, except that ratios are indicated in the form of a fraction (e.g., EW/EL).

A—atrium; AB—accessory bulb; AE—the four eyes of the anterior row; BC—bursa copulatrix; C—cymbium; CL—length of the carapace; CON—conductor; CW—carapace width; CYL—length of the cymbium as measured from the prolateral side (Fig. 39); E—epigynum; EF—epigastric furrow; EL—maximum length of the epigynum (Figs. 49–50); EMB—embolus; EW—maximum width of the epigynum (Figs. 49–50); FT—fertilization tube; FUL—fulcrum; GP—gonopore; LE—lateral elevation; MA—median apophysis; MAT—muscle attachments (found on all mature female specimens but illustrated only when of diagnostic value); MB—medial borders of lateral elevations; MC—median concavity; ME—median elevation; MEW—width of the middle elevation of the epigynum as measured by the maximum distance between the medial edges of the lateral lobes, used only in fimbrarius group (Fig. 50); OV—oviduct; PAP—point on the proximal end of male palpal tibia that articulates directly with the patella (Fig. 38); PE—the four eyes of the posterior row; PEL—length of the posterior part of the epigynum as measured from the narrowest point of the median elevation to the most posterior margin, used only in tenebrosus group (Fig. 49); PL—post-valvar ligaments; PTL—length of the posterior part of the tibia between the proximal articulation point (PAP and the axilla of the tibial apophysis base (Fig. 38); S—spermatheca; SV—seminal valve; SVH—
maximum height of the seminal valve as measured between the apical tip of the seminal valve and the posterior extreme of the epigynum (Fig. 59); SW—maximum width of the spermathecae (Fig. 59); T—tibia; TA—tibial apophysis; TEG—tegulum; TL—length of the male palpal tibia between proximal articulation point (PAP) and distal apex (Fig. 38).

The length of the carapace is used as an index to the length of the animal instead of total length because the softer abdomen is subject to wider variation as a result of sex, gravidity, feeding, and age. The abdomen is about equal to the length of the carapace in males and about 1.3 the length of the carapace in females.

All statistical data were computed with an IBM 1401 computer through the Fortran IV language. The computations are compiled into modified Dice-Leraas diagrams (Diag. 1).

Specimens were collected during the day or night by hand or net. Because of the vagabond nature of these spiders, sweeping is not effective and it is necessary to find each individual animal by sight alone. Some animals were collected in 3 percent formalin and 80 percent ethanol, which tend to maintain the color patterns more distinctly. Storage of all collections is in 80 percent ethanol.

Some locality data for each species are included in the thesis (Carico, 1970) from which this paper has been taken. A list of additional locality records obtained since the writing of the thesis is deposited in the author's files.

**TAXONOMIC CHARACTERS**

Since early names were given to specimens because of differences in color patterns, attention is given herein to this character. Emphasis is placed upon the relative intensity of coloration of a particular specimen and no attempt is made to describe precise hue because of the less permanent nature of the latter.

During a study of the color patterns of species of Dolomedes the existence of a definable common array of pattern components distinctive of Dolomedes was found. Not all species share the same assortment of variations of components, but all species have some assortment which is usually species specific. This situation, I believe, is further proof of the close phylogenetic relationship of the species. Furthermore, one may derive a common pattern "motif" from the species of a genus and speculate upon its value as a generic character by comparing it with the "motifs" of related genera.

In Table 2 I have indicated diagrammatically those "zones" of the color pattern "motif" which lend themselves to analysis because of their relative distinctness and therefore ease of interpretation. There are several other less distinct features that are not analyzed. The zones analyzed are subject to some intraspecific and intrasexual variation as is indicated in the descriptions, but only the most significant variations are treated. The table is intended primarily for comparative purposes, but it might be used as a supplement to the species descriptions and as an aid to the identification of immatures.

Certain zones may be considered as being "primitive." Specifically, zones 6, 9, and 10 appear to be present in all species, at least at some period of development (with the exception of D. striatus, of which I have not seen older spiderlings). Additionally, very similar markings are seen in some species of lycosids, an indication that these markings are not confined to Dolomedes. They coincide with the hypothesized primitive segmentation of the body, especially those on the carapace, and therefore may be related directly to this segmentation ontogenetically.

The male palpal organ is remarkably similar among the species within a species group and there is no attempt to give full descriptions of it in each species. Instead, references are made to species-group de-
<table>
<thead>
<tr>
<th>Table 2: Variation of standard color zones in Nearctic species of Dolomedes.</th>
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<tbody>
<tr>
<td><strong>Nearctic Dolomedes Spiders</strong></td>
<td></td>
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<tr>
<td>Carico</td>
<td></td>
</tr>
<tr>
<td>1 TRANSVERSE LIGHT BAND</td>
<td></td>
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<tr>
<td>Median or Absent</td>
<td>Present or Indistinct</td>
</tr>
<tr>
<td>2 TANGENTIAL LIGHT BAND</td>
<td></td>
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<tr>
<td>Median or Absent</td>
<td>Present or Indistinct</td>
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<tr>
<td>3 TANGENTIAL LIGHT BAND</td>
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<td>Median or Absent</td>
<td>Present or Indistinct</td>
</tr>
<tr>
<td>4 DARK BANDS</td>
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<td>Present or Indistinct</td>
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<td>Median or Absent</td>
<td>Present or Indistinct</td>
</tr>
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<td>6 DARK BANDS</td>
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<td>Median or Absent</td>
<td>Present or Indistinct</td>
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<td>7 LIGHT BANDS</td>
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<td>Median or Absent</td>
<td>Present or Indistinct</td>
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<tr>
<td>8 LIGHT SPOTS</td>
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<tr>
<td>Median or Absent</td>
<td>Present or Indistinct</td>
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<td>9 LIGHT SPOTS</td>
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<td>10 DARK BANDS</td>
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<td>Median or Absent</td>
<td>Present or Indistinct</td>
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<tr>
<td>11 LIGHT BAND</td>
<td></td>
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<tr>
<td>Median or Absent</td>
<td>Present or Indistinct</td>
</tr>
<tr>
<td>12 DARK BANDS</td>
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</tr>
<tr>
<td>Median or Absent</td>
<td>Present or Indistinct</td>
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</table>
criptions, and only significant distinctions are noted when present. A detailed description of the anatomy of the male palpus may be found in Comstock (1940) and Bishop (1924). Refer to Figures 28 and 38–39 for a review of the anatomy. The basic shape of the tibial apophysis in many cases proved to be diagnostic. Ratios of various parts of the male pedipalp were very helpful in distinguishing species, and these data are presented in Dice-Leraas diagrams. Refer to the list of abbreviations for an explanation of the characters that were measured.

Female genitalia also are basically very similar within a species-group, but any important diagnostic differences that do exist are noted with the use of the terminology of Carico and Holt (1964). A detailed account of the anatomy of the genitalia is found in Carico and Holt and no description is given herein except for a brief review in Figures 2 and 16. Ratios of various parts of the female genitalia also proved to be helpful in distinguishing species, and these data are also presented in Dice-Leraas diagrams. Refer to the list of abbreviations for an explanation of the characters that were measured.

**Dolomedes Latreille**


**Description. Carapace:** rather uniform in shape, longer than broad, moderately high, slightly indented to entire at posterior edge, thoracic groove distinct. **Eyes:** two transverse rows, anterior row much narrower than posterior; anterior eyes subequal, smaller than posterior, in a straight line or slightly procurred; posterior eyes subequal, in a greatly procurred line; median ocular area much wider behind. **Sternum:** lanceolate, truncated anteriorly, acute posteriorly. **Chelicerae:** basal segment robust; retro-marginal teeth of each segment; promargin with three teeth, distal smallest, middle largest, proximal intermediate in size. **Pedipalp:** dorsal surface of tibiae with 7 spines (Fig. 37). **Legs:** typically IV-I-II-III; supplied with large, articulating spines; undersurface of distal segments clothed with long hairs curved at tips. **Abdomen:** robust; group of strong, curved hairs on anterior declivity. **Pedicel:** superior lorum composed of four sclerites, two median and two lateral. **Integument:** clothed in a variety of types of hairs including plumose hairs located primarily in white areas. **MALE:** **Pedipalps:** tibia with a lateral apophysis. **Bull:** external tegulum, embolus distal and pointed ventrad, median apophysis ventral. **FEMALE:** **Epigynum:** three primary elevations, lateral two elevations with darkened medial borders. **Internal copulatory apparatus:** narrow and tapered bursae copulatrix, spermathecae thick-walled and ovoid, accessory bulbs each attached laterally to a spermatheca.

**Discussion.** Latreille (1804) erected the genus *Dolomedes* with only a reference to "Les courrues de Walekenaer." Walckenaer (1805) used this generic name with *Anurus fimбриatus* Clerck, one of the two species he mentioned in a previous work and which Latreille apparently had in mind when he erected the genus. *Dolomedes fimбриatus* (Clerck), a common and well-known species of eastern Europe, is therefore the type of the genus. On the basis of a comparative study of female genitalia, Carico and Holt (1964) considered *D. fimбриatus* to be conspecific with the American taxa referred to *Dolomedes*, and this opinion has been confirmed by subsequent comparison of the palpal structures of the males.

*Dolomedes* is included in the family...
Diagram 1. Dice-Leraas diagrams (modified) of measurements and ratios in the nearctic species of Dolomedes. A–E Males. F–M Females. (Scales: A and H are in millimeters.)

Explanation of diagrams. Vertical line = mean; horizontal line = observed range; open rectangle = standard deviation; black rectangle = 95% confidence interval for the mean; number in parentheses = number of specimens observed. DAL = D. albineus; DGE = D. gerischii; DHO = D. hallii; DOK = D. okefinakensis; DSC = D. scriptus; DST = D. striatus; DTE = D. tenebrasus; DTR = D. triton; DVI = D. vittatus.
Table 3. A comparison of older nomenclatures for Nearctic species of *Dolomedes* (Bishop, 1924; Bishop and Crosby, 1936; Chamberlin and Ivie, 1946) with the nomenclature adopted in this paper.

<table>
<thead>
<tr>
<th>Old Names</th>
<th>Change</th>
<th>Names used herein</th>
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</thead>
<tbody>
<tr>
<td>D. tenebrosus (1924)</td>
<td>no change</td>
<td>D. tenebrosus</td>
</tr>
<tr>
<td>D. okefinokensis (1924)</td>
<td>no change</td>
<td>D. okefinokensis</td>
</tr>
<tr>
<td>D. suspectus (1946)</td>
<td>synonymized</td>
<td>D. suspectus</td>
</tr>
<tr>
<td>D. albineus (1924)</td>
<td>no change</td>
<td>D. albineus</td>
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<tr>
<td>D. pinicola</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. scriptus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. albiclavus (1924)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. triton (1921)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. sesspunctatus (1924)</td>
<td>synonymized</td>
<td>D. sesspunctatus triton</td>
</tr>
<tr>
<td>D. scapularis (1946)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. spotolatus (1946)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. triton (1946)</td>
<td>no change</td>
<td>D. triton</td>
</tr>
<tr>
<td>D. striatus (1921)</td>
<td>synonymized</td>
<td>D. striatus</td>
</tr>
<tr>
<td>D. fulvius-tramatus (1945)</td>
<td>synonymized</td>
<td>D. fulvius-tramatus</td>
</tr>
<tr>
<td>D. vittatus (1921)</td>
<td>synonymized</td>
<td>D. vittatus</td>
</tr>
<tr>
<td>D. urinato (1924)</td>
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<tr>
<td></td>
<td></td>
<td>new species</td>
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<td>perticae</td>
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<td></td>
<td></td>
<td>new species</td>
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<tr>
<td></td>
<td></td>
<td>D. crassus</td>
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</table>

Pisauridae (Simon, 1898), which is a spider family with a moderately large number of species. Bonnet (1956–1959) lists 53 genera and 350 species, while Roewer (1954) lists 64 genera and 535 species. In the New World, *Dolomedes* is primarily found in the Nearctic Region with only three doubtful species described from South America.

The pisaurids are cursorial spiders recorded from all continents. In the Nearctic Region, they are usually found in close relationship with freshwater or moist conditions. Some genera composed of relatively small-sized species such as *Pisaurina*, *Thanalitius*, and *Pelopatis* typically hunt in low herbaceous vegetation growing on the shores of, or emerging from, bodies of water, while the larger-sized species of *Dolomedes* or *Trechalea* characteristically are found among rocks and debris bordering or emerging from a body of water. Members of many of the latter species are quite proficient at walking on the surface of water or submerging beneath it for long periods.

Species-groups of *Dolomedes*. In a comparative study of females, Carico and Holt (1964) observed that there are two distinct types of female genitalia in the nearctic species of *Dolomedes*. This conclusion has been confirmed by females examined in the present study. Further, the taxonomic implications are strengthened by the discovery that there are also corresponding differences in the male genitalia. The conclusion is that there are two distinct divergent species-groups represented. The bases for this grouping of species, other than genitalia, are mainly the comparative sizes of males and females (using the length of the carapace as an index) and relative lengths of segments of the male pedipalp.

**Nomenclature of Nearctic species.** The revision of the Pisauridae of the United States by Bishop (1924) brought considerable stability to the nomenclature of most nearctic species. Only two subsequent publications (Bishop and Crosby, 1936; Chamberlin and Ivie, 1946) have had any notable influence on the names in use since 1924. Since the nomenclature adopted in this paper varies considerably from the nomenclature of these authors, a summary of it has been tabulated (Table 3).

**UNCERTAIN NAMES**

*D. acuminatus* C. L. Koch, 1848, Die Arachniden, pp. 122–123, fig. 1357. Type lost.—I cannot identify this species. Bishop (1924) suggests that this species is not from the U. S. because Koch listed the locality as “Amerika.”

*D. audax* Marx, 1853, in Howard’s List of Invertebrate Fauna of South Carolina, p. 25.—This citation is from Bonnet (1956) who calls it a “nomen nudum.” I cannot find this in Marx 1853 nor in his “Catalogue” (1889).

*D. bisetatus* C. L. Koch, 1848, Die Arachniden, pp. 121–122, fig. 1355. Type lost.—I cannot identify this species.

*D. convexus* Giebel, 1869, Z. gesamm. Natur., 33: 252–253. Type perhaps in Halle, Germany. I cannot identify this species. From Giebel’s description it is clear that this is not a *Dolomedes*.

*D. fusus* Franganillo-Balboa, 1931, Rev. del Col.
de Belen, pp. 48, 286.—Described from Cuba. I cannot identify this species with certainty, but it may be *D. triton* or a similar species as is suggested from reading the sketchy description. *D. hastulatus* Hentz, 1844, J. Boston Natur. Hist. Soc., 4: 395—396, pl. 19, fig. 9. Type destroyed.—I cannot identify this species, but Hentz states "found ... in a web, like that of *Agelena*," an indication that it is not a *Dolomedes*.

*D. lineatus* Walckenaer, 1837, Hist. Natur. Insectes. Aptères, 1: 347.—Walckenaer refers to Abbot's figures 51 ("variété jaune") and 56 ("variété rouge"). Abbot's figures, the types, are probably of lycosids: *Lycosa rabida* Walck. and *L. punctulata* Hentz, respectively (Bishop, 1924, and Chamberlin and Ivie, 1944).

*D. marginatus* Marx, 1883, in Howard's List of Invertebrate Fauna of South Carolina, p. 25.—This citation is from Bonnet (1956), who calls it a "*nomen nudum."* I cannot find this in Marx 1883 nor in his "Catalogue" (1889).

*D. marginellus* C. L. Koch, 1848, Die Arachniden, p. 120, fig. 1535. Type lost.—This species has been replaced by others (Simon, 1898; Mello-Leitão, 1927; and Franganillo-Balboa, 1936) into *Thaumasia*, a conclusion I do not dispute.

*D. minor* Banks, 1898, Proc. California Acad. Sci., 1(7): 205—308, pl. 17, fig. 5. This species is described from Baja California. It is not a species of *Dolomedes* and is probably a junior synonym of *Titus peregrinus* (Bishop, 1924).

*D. minus* Walckenaer, 1837, Hist. Natur. Insectes. Aptères, 1: 357.—The type is Abbot's figure 321. This species has been regarded as the type of the genus *Pisaurina* (= *Dapanus*?), and is not a *Dolomedes*.

*D. oblongus* C. L. Koch, 1848, Die Arachniden, p. 114, fig. 1350.—This species has been transferred to the lycosid genus *Diapontia* by Petrunkevitch (1911). I do not dispute this conclusion.

*D. tenax* Hentz, 1844, J. Boston Natur. Hist. Soc., 4: 395, pl. 19, figs. 7—8. Type destroyed.—From the description and figures, I believe that this was probably an immature form of *D. albicus* Hentz.

*Aranea rufa* DeGeer, 1778, Mem. l'Hist. Insectes, 7: 319, pl. 39, fig. 6. Type lost.—I agree with Bishop (1924), who said that this description is unidentifiable and that the conclusions of Banks (1898) and Petrunkevitch (1911) are incorrect in saying that this species is synonymous with *D. albicus* Hentz, on the grounds that Pennsylvania is outside the range of the latter species.

*Aranea virgatus* Walckenaer, 1837, Hist. Natur. Insectes. Aptères, 1: 358.—The type is Abbot's figure 291. I agree with Bishop (1924) that this is probably a species of *Pisaurina* (*Dapanus*).

**KEY TO THE ADULTS OF THE NEARCTIC SPECIES OF THE GENUS Dolomedes**

**MALES:**

1. Median apophysis distinctly widest in basal half, narrowed and sinuous apically (Figs. 25—26); CYL/TL > 2.7
   
   — *D. tenebrosus* (tenebrosus group) — 2
   
   Median apophysis not distinctly widest in basal half (Figs. 27—33); CYL/TL < 2.7
   
   — *D. tenebrosus* (tenebrosus group) — 3

2. Narrowed apex of median apophysis bent into an acute angle (Fig. 25)
   
   — *D. tenebrosus* Narrowed apex of median apophysis not bent into an acute angle (Fig. 26)

3. Spiny tubercle or group of stiff spines subapically on femur IV
   
   — *D. okefenokensis*
   
   Spiny tubercle or group of stiff spines not present on femur IV

4. Apex of tibial apophysis rounded and extending beyond distal end of tibia (Figs. 33, 48); spiny tubercle subapically on femur IV (Fig. 34)
   
   — *D. triton* Apex of tibial apophysis toothed and not extending beyond distal end of tibia; group of stiff spines subapically on femur IV (Figs. 35—36)

5. CL/CYL usually > 2.2; known only from the United States and Canada
   
   — *D. vittatus* CL/CYL usually < 2.2; known only from Nuevo León, Mexico

6. TL/PTL > 1.5
   
   — *D. scriptus* TL/PTL < 1.5

7. CYL/TL < 1.7
   
   — *D. albicus* CYL/TL > 1.7

8. CL/CW < 1.17; TL/PTL > 1.32
   
   — *D. gertschi* CL/CW > 1.17; TL/PTL < 1.32

   — *D. striatus*

**FEMALES:**

1. Middle lobe at anterior margin of epigynum; median concavity absent (Figs. 54—56)
   
   — *D. tenebrosus* (tenebrosus group) — 2
   
   Middle lobe at posterior margin of epigynum; median concavity present (Fig. 60)

   — *D. tenebrosus* (tenebrosus group) — 3

2. EL_PEL < 4.0; CW/EW < 3.5
   
   — *D. tenebrosus* EL_PEL > 4.0; CW/EW > 3.5

   — *D. okefenokensis*

3. Posterior median edge of epigynum curved dorsally and anteriorly, thus covering most of copulatory apparatus (Fig. 69);
   
   — EL SVH usually < 1.9 — *D. triton*

---

1. To identify immatures see key below.
Posterior median edge of epigynum not curved dorsally and anteriorly, not covering much of copulatory apparatus; EL/SVH usually > 1.9  4

1. Distinct, continuous light submarginal bands on carapace  5

2. Distinct, continuous light submarginal bands not present on carapace  6

3. CL < 8.0; northeastern United States and eastern Canada  7

4. CL > 8.0; Nuevo León, Mexico  8

5. Series of distinct light spots on the otherwise usually uniformly colored abdominal dorsum (Fig. 15)  9

6. Series of distinct light spots not present on abdominal dorsum, which has a complex pattern  10

7. EW/SW > 1.9; known only from the United States and Canada  D. striatus

8. EW/SW < 1.9; known only from Nuevo León, Mexico  D. holti

9. EW/EL > 1.3; EW/MLW > 2.25; ventral loop of fertilization tube visible from dorsal view (Fig. 59); not known from Arizona or New Mexico  D. scriptus

10. EW/EL < 1.3; EW/MLW < 2.25; ventral loop of fertilization tube not visible from dorsal view (Fig. 59); known only from the Gila River drainage basin of Arizona and New Mexico  D. gertschi

 KEY TO THE NEARCTIC SPECIES OF Dolomedes
 Based Chiefly on Color Patterns

1. Distinct, continuous, light submarginal carapace bands with entire margins (Figs. 18–19)  2

2. No submarginal bands present, or when present, margins are not entire  7

3. Distinct, light, longitudinal bands on abdomen continuous with light bands of carapace (Figs. 20–21)  3

4. Distinct, light, longitudinal bands absent from abdomen  5

5. Short, light marks project medially from abdominal light bands (Fig. 14); abdomen without circular light dorsal spots  4

6. Short, light marks as above absent; circular light spots frequently present on dark median band of abdominal dorsum (Figs. 20–21)  D. striatus  10

7. Distinct, circular light spots on abdominal dorsum, each often surrounded by ring of dark marks, no transverse "W-shaped" dark marks (Figs. 18–19)  D. triton

8. Not found in the Gila River drainage basin in Arizona and New Mexico (Fig. 8)  D. gertschi

9. Found in the Gila River drainage basin in Arizona and New Mexico (Fig. 7)  D. albimaculatus

10. Cephalic area distinct and higher than thoracic area of carapace (Fig. 10)  11

11. Light transverse abdominal bands between "W-shaped" dark bands continuous across dorsum (Figs. 8–9)  D. scriptus

12. Light transverse abdominal bands between "W-shaped" dark bands obscure medially, but laterally present as distinct, elongate pairs of light marks  12

13. Found north of Mexico (Fig. 15)  (female)  D. citatus

14. Found south of Texas  D. citatus

15. Found in Gila River drainage basin in Arizona and New Mexico (Figs. 12–13)  D. gertschi

16. Not found in the Gila River drainage basin in Arizona and New Mexico  10

17. Cephalic area less distinct and not higher than thoracic area of carapace (Fig. 10)  11

18. Light transverse abdominal bands between "W-shaped" dark bands continuous across dorsum (Figs. 12–13)  D. tenebrosus

19. Found in peninsular Florida and southeastern Georgia (Figs. 3–4)  D. okefinokensis

Tenebrosus Group

Males much smaller than females, average female CL/average male CL = 2.25 (D. tenebrosus) and 2.75 (D. okefinokensis). MALES: Tibia of pedipalp relatively shorter, CYL TL = 3.15 (D. tene-
Figures 1-11. Color patterns of the dorsum. Figs. 1-2, Dolomedes tenebrasus Hentz. 1, Male. 2, Female. Figs. 3-4, D. okieinoakensis Bishop. 3, Male. 4, Female. Figs. 5-6, D. albineus Hentz. 5, Male. 6, Female. Figs. 8-9, D. scriptus Hentz. 8, Male. 9, Female. Figs. 7, 10, Lateral aspects of carapaces. 7, D. albineus Hentz. 10, D. scriptus Hentz. Fig. 11, Tibial apophyses of the right palpi of a series of male D. triton (Walckenaer) from Kingston, Tennessee.

Scales. Figs. 1-10, 5.0 mm. Fig. 11, 1.0 mm.
Dolomedes tenebrosus) and 3.03 (D. okefinokensis); tibial apophysis broad, flat, wider distally than basally and wider than diameter of tibia, truncated at tip with small teeth; palpal bulb with median apophysis distinctly widest at basal half with distal half narrowed and sinuous; tegulum bulbous with rounded outer curvature which projects from ventral face of bulb (Figs. 25-26). No spiny tubercle or group of spines on femur IV. FEMALES: median elevation of epigynum at anterior border; lateral elevations broadly joined posteriorly at midline, atria large, rounded internally and conspicuously ventrally, no median concavity present (Figs. 54, 56); fertilization tubes about as long as bursae copulatrix and twisted in appearance, seminal valves wider than diameter of fertilization tubes and spatulate in shape (Figs. 53, 55).

**Dolomedes tenebrosus** Hentz

**Figures 3-4, 25, 40, 53-54; Map 2**


**Diagnosis.** Dolomedes tenebrosus (Figs. 1-2) is most closely related to *D. okefinokensis* and together they represent a distinct monophyletic group.

The two species of the *tenebrosus* group are indistinguishable except by means of sexual characters. The males differ primarily in the median apophysis of the palpal organ, which is acutely bent in *D. tenebrosus* (Fig. 25) and not acutely bent in *D. okefinokensis* (Fig. 26). The number of teeth on the distal edge of the male tibial apophysis of the pedipalp, although variable, does not overlap with those of *D. okefinokensis* in the samples examined. *D. tenebrosus* males have more teeth (mean 7) than those of *D. okefinokensis* (mean 4).

The epigynum of *D. tenebrosus* (Fig. 54) has the PEL distinctly longer than that of *D. okefinokensis* (Fig. 56). Internally the bursae copulatrix develop from the atria in different directions, i.e., in *D. tenebrosus* (Fig. 53) they run more nearly anteriorly than in *D. okefinokensis* (Fig. 55).

The color patterns of the largely allopatric *D. scriptus* (Figs. 8-9) and *D. tenebrosus* are similar, but the two species are easily distinguished by the genitalia (Figs. 28, 43, 59, 60).

**Description.** Average female CL average male CL = 2.251.

**Male** (from Colleton County, South Carolina): On the carapace, ocular area, clypeus dark except for medial light spot on anterior edge; central disc dark gray, darkest near edge, with widening dark lines radiating from thoracic groove; irregular submarginal bands lateral to central disc, extend from clypeal dark area almost to posterior edge of carapace; extreme lateral edges dark gray, two pairs of light lines extend posteriorly from posterior eyes. Sternum gray at edges with median lanceolate mark. Labium about as long as wide,
color of central area gray with light area anteriorly, becoming indistinct annular bands. Leg length order IV-(I-II)-III. Abdominal background color gray to brownish. Dorsum anteriorly, with light lanceolate cardiac area with two curved lateral longitudinal lines; posterior two-thirds with 4 transverse “chevron-shaped” dark bands terminated laterally by 4 pairs of elongate light spots; lateral margins of dorsum with reticulated light areas. Sides light anteriorly, each with reticulated lighter area that merges into dark area posteriorly. Venter dark gray to brownish with two irregular, indistinct light lines beginning at transverse groove posterior to book lungs, extending to spinnerets. The epigynum and internal copulatory apparatus is used as the standard for the tenebrosus species-group. PEL relatively long (see Fig. 54). Bursae copulatrix (Fig. 53) develop initially in anterior direction from atra. Internally, atria protrude posteriorly to origin of bursae copulatrix and are close together (Carico and Holt, 1964). For measurements see Diagram 1 for dimensions and ratios of the body and genitalia.

Female (from Horry County, South Carolina): On the carapace ocular area, clypeus dark with inverted “V-shaped” black mark beginning at AME extending to edge of clypeus, enclosing light spot on its anteromedial margin; general background color gray to reddish brown; central disc with widening dark lines radiating from thoracic groove, some terminating in white spots; two triangular dark spots anterior to thoracic groove; lateral submarginal areas marked with irregular reticulated light lines, extreme edges each marked with incomplete dark band; two pairs of light lines posterior to PLE and PME, medial light line extends from between PME to thoracic groove. General color of sternum light gray with median longitudinal area. Labium about as long as wide, dark reddish brown, becoming lighter at anterior edge. Palpal endites dark reddish brown, becoming light at anterior edge. Chelicerae dark reddish brown, clothed anteriorly with long, erect, white hairs. Coxae of legs light with few indistinct maculae; other segments with irregular maculae, some coalescing into indistinct annular bands. Leg length order IV-(I-II)-III. Abdominal background color gray to brownish. Dorsum anteriorly, with light lanceolate cardiac area with two curved lateral longitudinal lines; posterior two-thirds with 4 transverse “chevron-shaped” dark bands terminated laterally by 4 pairs of elongate light spots; lateral margins of dorsum with reticulated light areas. Sides light anteriorly, each with reticulated lighter area that merges into dark area posteriorly. Venter dark gray to brownish with two irregular, indistinct light lines beginning at transverse groove posterior to book lungs, extending to spinnerets. The epigynum and internal copulatory apparatus is used as the standard for the tenebrosus species-group. PEL relatively long (see Fig. 54). Bursae copulatrix (Fig. 53) develop initially in anterior direction from atra. Internally, atria protrude posteriorly to origin of bursae copulatrix and are close together (Carico and Holt, 1964). For measurements see Diagram 1 for dimensions and ratios of the body and genitalia.

The immatures have essentially the same color pattern as do the adults.

Variation. The complex color pattern does not vary greatly through the wide geographic range of D. tenebrosus. Contrasting light and dark areas seem to intensify northward with the northernmost specimens often quite dark. In any part of the range there are differences in the relative extent of light and dark areas in the pattern. Typical of the latter point is the pattern of the submarginal bands which are occasionally solid light bands, frequently a series of disconnected light areas of various sizes and shapes, and occasionally solid gray or brownish similar to the color of the central disc. Also typical is the variation of the pattern of the sternum, which in some specimens is almost entirely gray with a white median longitudinal line

Scales. 5.0 mm.
and in others is almost entirely light with gray edges.

Natural history. The habitat of this species seems to be more variable than that of other members of the genus. Collection notes and personal observations show it to be commonly encountered in the environs of the swamps and ponds in the southern United States coastal plain and the lakes and ponds of the glaciated part of the range. Although little microhabitat data accompanied the northern collections, a large number of collections gave the name of a lake as part of the locality data. In the southern coastal plain I have collected *D. tenebrosus* primarily from the vertical trunks of trees and other objects emerging from slow-moving streams and ponds, a habitat that is shared with *D. okefenokensis*. Unlike other *Dolomedes*, this species was regularly collected a considerable distance from water. Data with specimens collected in Indiana and Pennsylvania state that they were found "on trunk of dead tree in beech maple forest" and on "dead trees in deep woods," respectively. In the mountainous regions of Virginia and North Carolina, I have never taken a mature specimen of *D. tenebrosus* near bodies of water (where I have done considerable collecting), but have encountered it infrequently in woods under logs and more often in association with houses. Although I have collected males and females in basements, most such specimens have been brought to me by excited homeowners who have also found them in basements, kitchens, and, in one case, the bedroom. Comments by Bishop (1924), Kaston (1948), and Gertsch (personal communication) confirm that the relative freedom from the aquatic habitat is a distinct feature of the natural history of this species.

A collection from Ottawa, Canada (11 July 1935) contained the following note: "numerous proctotrupoid [sic?] parasites emerged from egg case."

Eight collections taken from 30 June to 14 August from the northern part of the range (Ontario, Quebec, Nova Scotia, Michigan, and New York) contained egg sacs. The earliest and latest of these dates are from Quebec. Five females from the same general area with swollen abdomens (and presumably gravid) were taken from the first half of June to August. Kaston (1948) reported an egg sac as early as June 22 and stated that the number of eggs or spiderlings in three egg sacs ranged from 858 spiderlings to 1393 eggs. He also observed two females in their nursery webs on July 13 and September 10 respectively. No data are available on the reproduction of southern *D. tenebrosus*. Adult females are present virtually throughout the year but are probably inactive during cold months. Penultimate females hibernate in Connecticut according to Kaston (1948). Adult males are more prevalent in May but may be found earlier in the south and later in the north. Immatures in all sizes are present all year.

Fish-capturing observations were discussed in the section on biology of the genus.

Distribution. *D. tenebrosus* ranges from Newfoundland, southern Quebec, and Manitoba southward to the Florida Panhandle.

Scales. Figs. 25–36, 5.0 mm. Fig. 37, 2.0 mm.
and westward to eastern Texas, eastern Kansas, western Nebraska, and eastern North Dakota (Map 2). The ranges of *D. tenebrosus* and the closely related *D. okefinokensis* do not seem to overlap. Because of the similarity of the color patterns of these two species, no immature figures of the *tenebrosus* group are plotted in southern Mississippi, Alabama, Georgia, and all of Florida.

Bishop (1924) listed *D. tenebrosus* from the Okefinokee Swamp, Georgia, and from Archer, Florida, neither of which I have been able to confirm. He did not designate sex nor maturity, and therefore the observations may have been made upon immatures, a practice of dubious validity. His record from Yuma, Arizona, was apparently based upon erroneous collection data.

**Material examined.** Twenty-five male, 118 female, and 91 immature specimens.

**Dolomedes okefinokensis Bishop**

**Figures 3-4, 26, 41, 55-56; Map 3**

Dolomedes okefinokensis Bishop, 1924. Bull. New York State Mus., 252: 38-10, pls. 17, 18, fig. 1: pl. 19, figs. 1, 2. Female holotype and allotype from Billy’s Island, Okefinokee Swamp, Georgia, deposited in the New York State Museum. I have not been able to confirm the existence of the holotype and allotype, and the paratypes originally deposited at Cornell University were not in the spider collection on loan to the American Museum of Natural History in New York. I have collected adults of this species from the type locality.—Roewer, 1954, Katalog der Araneae, 2(a): 131.—Bonnet, 1956, Bibliographia Araneorum, 2: 1535.—Carico and Holt, 1964, Virginia Agr. Exp. Sta., Tech. Bull., 172: 13, ♀.

**Diagnosis.** *D. okefinokensis* (Figs. 3-4) is quite similar to *D. tenebrosus* in coloration and can be distinguished with confidence only by examination of the genitalia (see above, Figs. 26, 41, 55-56).

**Description.** Average female CL/average male CL = 2.75.

**Male** (from Okefinokee Swamp, Georgia). On carapace, ocular area, clypeus dark except for medial light spot on anterior edge; central disc dark gray, darkest near edge, with widening dark lines radiating from thoracic groove; irregular submarginal bands lateral to central disc extend from clypeal dark area to posterior edge of carapace; extreme lateral edges dark gray, one or two pairs of light lines extend posteriorly from PE. **Sternum** gray at edges with central irregular lanceolate mark. **Labium** about as wide as long, color of central area somewhat gray on light background around edges. Basal segments of chelicerae elongate, each marked with anterior, longitudinal gray band. **Palpal endites** light, without distinct markings. Coxae of legs light ventrally with 2-3 indistinct maculae, other segments with irregular maculae which sometimes coalesce into indistinct annular bands. Leg length order IV-(I-I-I)-III. **Abdominal** background color dark gray to brownish dorsally with light lanceolate cardiac area, two curved anterolateral longitudinal lines, posterior third with 4 transverse “chevron-shaped” bands terminating laterally with 4 pairs of white spots. Sides dark, each with incomplete dorsal band beginning anteriorly, becoming diffuse posteriad. Venter light in color with dark lateral areas nearly converging just anterior to spinnerets. **Palpal organ** (Fig. 26) as for *tenebrosus* group. Median apophysis curved into a “question-mark-shape,” without acute angles, narrowed distally. Distal edge of **tibial apophysis** with 2-6 teeth (mean 4) (Fig. 41). For measurements see Diagram 1 for dimensions and ratios of the body and genitalia.

**Female** (from Okefinokee Swamp, Georgia). On the carapace, ocular area, clypeus dark with inverted “V-shaped” black mark beginning at AME, extending to edge of clypeus, enclosing light spot on its anteromedial margin; general background color gray to reddish brown; central disc with widening dark lines radiating from thoracic groove, some terminating in white spots; two elongate dark spots anterior to thoracic groove; lateral submarginal areas marked
with irregular reticulated light lines, extreme edges each marked with black line; two pairs of light lines posterior to PLE and PME, medial light line extends from between PME to thoracic groove. Edges of sternum light gray, enclosing lighter medial area. Labium about as long as wide, dark reddish brown, becoming lighter at anterior edge. Palpal endites dark reddish brown, becoming light at anterior edge. Chelicerae robust, dark reddish brown, clothed with long, erect white hairs. Coxae of legs light with few indistinct maculae, other segments with irregular maculae, some of which coalesce into indistinct annular bands. Leg length order IV-(I-II)-III. Background color of abdomen dark gray to brownish. Dorsum with light lanceolate cardiac area with two curved lateral longitudinal lines anteriorly, posterior two-thirds with about 5 transverse "chevron-shaped" dark bands terminated laterally with 4 pairs of elongate white spots; lateral margins of dorsum with reticulated light areas. Sides each light anteriorly with reticulated lighter area that merges into dark area posteriorly. Venter dark gray to brownish with two irregular light lines beginning at transverse groove posterior to book lungs, extending to spinnerets. Epignyum, internal copulatory apparatus as for tenebrosus group; PEL relatively short (Fig. 56); bursae copulatrix (Fig. 55) develop initially in anteromedial direction, atria internally do not protrude posteriorly, are well separated (Carico and Holt, 1964). For measurements see Diagram 1 for various dimensions and ratios of the body and genitalia.

Those immatures suspected of being of this species had essentially the same kind of pattern as the adults.

Variation. Color variation was not great in the few cases where more than one specimen was present in a single collection. Other variations may have been due to the differences in collecting date and preservative. The only significant variations were (1) in the intensity of color, (2) the extent of development of the submarginal bands of the carapace of the male and (3) the distinctness of the reticulations and light spots in the submarginal areas of the female carapace.

Natural history. According to data with the museum collections and personal observations at Okefinokee Swamp, Georgia, this species inhabits primarily swampy areas. Typically these spiders were seen flattened against vertical sides of cypress or other emergent trees in pools of water. They were also taken from other objects such as concrete bridges and docks. They are found above the water to about four feet. A female taken in Jacksonville, Florida, was found "under a log in a dried-up cypress swamp." The general habitat preference of D. okefinoakensis does not differ in any obvious way from that of the southern D. tenebrosus.

A female taken 7 October 1949, on Lake Lochloosa, Alachua County, Florida, car-
ried an egg sac that was whitish in color and covered with a fluffy layer of loose threads (which is different from that of other species). The contents of the egg sac included 140 fully developed spiderlings that were probably near emergence and 369 fully developed adult chalcidoid wasps still within the egg membranes.

**Distribution.** Peninsular Florida and southeastern Georgia (Map 3). Because of the difficulty of distinguishing immatures of *D. okefinokensis* and *D. tenebrosus*, only immatures of the *tenebrosus* species-group were plotted in Florida and in the southern portions of the states of Mississippi, Alabama, Georgia, and South Carolina. Although I find little overlap of the geographic ranges of these two species, Bishop (1924) listed two localities for *D. okefinokensis* in Alabama and in Louisiana. I have not located these collections, and it is possible that these data were based upon immatures of *D. tenebrosus*. Further discussion of the distribution of species of the
tenebrosus group may be found above in the section on evolution.

Material examined. Seven male and 23 female specimens. Several immatures were examined from the apparent range of this species, but their identity is uncertain.

Fimbriatus Group

Males smaller than females, but size difference not as much as in tenebrosus group, average female CL: average male CL = 1.38 (range 1.11–1.38) or less. MALES: tibia of pedipalp relatively longer, CYL/TL = 2.20 (range 1.29–2.20) or less, tibial apophysis narrow, width less than diameter of tibia, bearing various types of projections, and usually not truncated; palpal bulb with median apophysis narrowed at basal half and widest at distal half or uniform in width, tegulum not as bulbous and outer curvature not as rounded, protruding less from within concavity of cymbium (Fig. 28). Some species with spiny tubercle or group of spines on femur IV (Figs. 34–36).

FEMALES: median elevation of epigynum at posterior border, lateral elevations narrowly joined (if at all) posteriorly at midline with juncture usually obscured, atria small, flattened internally, inconspicuous ventrally, median concavity present posterior to median elevation (Fig. 60); fertilization tubes looped and/or coiled at least twice length of bursae copulatrix, seminal valves usually not wider than diameter of fertilization tubes, not spatulate in shape (Fig. 59).

Dolomedes albineus Hentz
Figures 5–7, 42, 57–58; Map 4

Nearctic Dolomedes Spiders • Carico


Scales. 1.0 mm.


Thaumasia pinicola, Banks, 1910, Bull. United


**Diagnosis.** The elevated cephalic area of the carapace (Fig. 7) and the color pattern of the abdomen (Figs. 5–6) are the most distinctive characters. In adult males the tibia of the pedipalp is comparatively long, making the CYL TL ratio a distinctive feature when compared with males of sympatric species. The epigynum and internal copulatory apparatus are very similar to *D. scriptus*, but may usually be distinguished from the latter by the lack of complete sclerotization and dark coloration of the anterior edge of the epigynum, which causes the muscle attachments (MAT) to be distinct from the epigynum (Figs. 58, 60).

**Description.** Average female CL, average male CL = 1.29.

**Male** (from Alachua County, Florida): Background color of *carapace* light, covered with white hair; ocular area, clypeus dark with transverse band of white hairs on latter passing about midway between AME, clypeus margin; pair of dark, elongate, median marks anterior to thoracic groove; indistinct dark lines radiate from thoracic groove; marginal dark line present; cephalic area elevated above rest of carapace. **Sternum** light, slightly darker at margins. **Labium** about as long as wide, dark reddish brown laterally, lighter medially, light at anterior margin. Basal segments of *chelicerae* elongate, each with dark background color, darker distally, covered anteriorly with long white hairs, thick patch of short, closely appressed white hairs laterally around boss, which extends subdistally. **Palpal endites** dark on lateral, medial margins, lighter centrally, light distally. All segments of *legs* light ventrally, slightly darker dorsally; femora with indistinct longitudinal dark dorsal marks. Leg length order I-II-IV-III. **Abdominal background color** light dorsally, covered with white hairs, darker lanceolate cardiac area, four transverse dark lines terminated laterally by light areas, indistinct lighter bands between darker ones. Sides light, each with dark band that extends obliquely, ventrally from anterodorsal end. Venter light with very light median longitudinal band, bordered laterally with somewhat darker bands. **Palpal organ** (Fig. 27) as for *fimbriatus* group. **Tibial apophysis** (Fig. 42) with three well-defined teeth, smallest ventral, largest central. For measurements see Diagram 1 for dimensions and ratios of the body and genitalia.

**Female** (from Alachua County, Florida): Background color of *carapace* reddish brown, covered with white hairs; ocular area, clypeus dark with transverse band of white hairs on latter passing about midway between AME, clypeus margin; obscure elongate marks anterior to thoracic groove; indistinct bands radiate from thoracic groove; marginal dark line present; submarginal areas broken into series of light areas; cephalic area elevated above rest of carapace (Fig. 7). **Sternum** medium reddish brown, slightly darker at margins. **Labium** dark reddish brown, light at anterior margin, with distinct transverse, central groove. Basal segments of *chelicerae* each very dark reddish brown, clothed anteriorly with long erect light hairs, thick patch of short white hairs laterally around boss, which extends almost to distal end.
Palpal endites dark reddish brown, light distally. Coxae of legs medium reddish brown ventrally, lighter medially; other segments medium reddish brown ventrally, covered with white hairs, dorsal surfaces with indistinct darker longitudinal areas. Leg length order IV-I-II-III. Abdominal background color light, covered with patches of light hair; dark lanceolate cardiac area; five transverse dark lines preceded by a white line, terminated laterally by light areas, first, third lines longest; pair of
oblique dark lines join cardiac area with first transverse line. Sides each with central, anterior, irregular dark longitudinal band; remainder of area covered with small dark, white spots. Venter with median, light band narrowing from epigynum to tracheal spiracle, bordered laterally by pair of medium brown bands, each bordered in turn by series of dark spots. Epigynum (Fig. 58), internal copulatory apparatus (Fig. 57) as for fimbriatus group. Pair of anterolateral muscle attachments not entirely joined to epigynum, anterior edge of epigynum often appears incompletely sclerotized, indistinct in outline. Fertilization tubes each composed of one coil and two loops, seminal valves located in posterior half of dorsoepigynal area (Carico and Holt, 1964). For measurements see Diagram I for dimensions and ratios of the body and genitalia.

Immatures typically have a lighter background color with the color pattern somewhat more distinct and extensive than the adults. Perhaps the most distinctive feature is the carapace shape, which is depressed except for the noticeably elevated cephalic area.

In some immatures and adults the carapace has a distinctly maroon color in life.

Variation. No significant geographic variation could be ascertained from the limited sample that was examined. In general, the variation of the color pattern is limited to differences of distinctiveness. Some notably light-colored specimens are treated under the discussion of nomenclature below.

Natural history. Collection data with the specimens studied include no information about the biology of this species. Limited personal observations of it suggest that D. albiceps is most common in swamps, ponds, and slow-moving streams, resting upon the vertical trunks of emergent trees with the head in a downward position. Bishop (1924) reported the same observations and also stated that if disturbed “... they rush into the water or dodge with surprising quickness to the opposite side of the tree, after the manner of a squirrel.” The manner of diving into the water is typical of the genus, but their manner of “... dodging...” to the other side of the tree is unique. Whereas Bishop seems to imply that these animals walk around to the opposite side of the tree, I have observed them to spring away from the surface of the tree in such a way as to “swing” quickly around the tree suspended by the dragline. This habit, in conjunction with their relative shyness and superb camouflage, makes them difficult to collect.

In his discussion of the “Habits” of D. okefinoakensis, Bishop stated that members of that species “... were found on herbage and the prostrate trunks of trees and not usually in such close proximity to water as in the case of Dolomedes albiceps...”. On the contrary; where I have collected these two species together, D. albiceps has been higher on the tree than D. okefinoakensis. Walckennaer (1837) cited some biological notes made by Abbot which seem to agree with my observation. Abbot said (after Walckennaer, 1837), “Elle ne fait pas de toile, mais se retire dans le creux des arbres...”. Perhaps the hiding places were merely shallow depressions on the tree surface in which the spider rested, the result being that the outline of the spider came into greater conformity with that of the tree. The latter situation I have observed.

Herring and Dowling (1947) made an observation upon D. albiceps which seemed to be unique, at least for the genus. While collecting at night they discovered numerous adult members of this species assembled in a tree at Payne’s Prairie in Alachua County, Florida. Although other trees were nearby, one particular tree was the only one that contained these spiders in great numbers, some of which were quite high above the water. They suggested, and reasonably so, that this phenomenon may have been related to sexual activity. If this were a spider version of a “mating swarm,” it deserves greater attention because this kind
of behavior does not seem to be common among spiders.

**Distribution.** Typically, *D. albíneus* is associated with slow-moving streams, lakes, and ponds in the southern coastal plain as far north as Virginia and westward to about the 100° longitude in Texas. The range extends northward in the Mississippi River basin, and in some cases into the uplands of northern Alabama, the midsection of Kentucky, the Ozarks of Missouri, and the Appalachians of North Carolina (Map 4).

**Material examined.** Thirteen male, 25 female, and 50 immature specimens.

**Discussion.** The survey of the literature on this species has been of nightmarish complexity and deserves some comment. I agree with Bishop (1924: 11) that *Aranea rufa* DeGeer is probably not *D. albíneus* for at least one of the same reasons, i.e., that the reported locality, Pennsylvania, is far outside the apparent range of this species. Walekenaer (1857), however, believed that four figures of Abbot (numbers 1, 6, 16, and 281) are *Dolomedes rufus* (DeGeer) and described them as four "varieties" that may actually have represented various stages in development. His descriptions were apparently made from specimens, because he mentioned characters that cannot be viewed from the dorsal side, which was the only view that Abbot had figured. The descriptions of color pattern and habitat match fairly well those of *D. albíneus* Hentz, but only figure six can confidently be determined to be this species. DeGeer's name is therefore not retained (see Art. 49 in Rules of Zoological Nomenclature).

Hentz clearly described and figured *D. albíneus* in 1845, but later (1850) he described and figured the synonymous *Microthoma pinicola*, which subsequently resulted in confusion in the literature. Hentz's specimen of *M. pinicola* has been destroyed and no other specimen was referred to this species until Bishop's (1924) revision of the Pisauridae. The species was transferred in the meanwhile to *Dolomedes* by Banks (1904) and Comstock (1912). Bishop (1924) examined an immature from Punta Gorda, Florida, collected by Banks, which resembled Hentz's drawing and description. I have studied this specimen and find that it is a small immature of *Dolomedes albíneus*. It is indeed very light and devoid of many clear markings, but the shape of the carapace and the position of the markings that are present clearly indicate its identity. The series of dots on the venter of the abdomen mentioned in Hentz's description are merely points of muscle attachment which are present in all species, but are only noticeable against a light background. Because Bank's specimen resembles closely the figure of *Microthoma pinicola*, I have concluded that Hentz must have described an immature of *D. albíneus*. One adult female that I examined from Florida (no other locality data) is also very light, but still shows distinct *D. albíneus* sexual structures as well as other structural features.

Later (1936) Bishop and Crosby described and figured a mature male of *D. pinicola* from Edinburg, Texas. Although the coloration is very light as in Banks' specimen, the resemblance ends there. The shape of the carapace and position of the few faint markings do not resemble those of Banks' specimen at all. In fact, the
structure of the palpus and body appear to be almost identical in shape to that of the “typical” *D. scriptus*, the species into which it is here tentatively placed. Bishop, in his key, distinguished the tibial apophysis of this male from *D. scriptus* upon the basis of the presence of a basal tooth. I have found this feature in both his species. This male, however, is distinctly smaller (CL = 5.0 mm) and much lighter than most males.
of *D. scriptus*. It is also noteworthy that it was collected outside the known range of *D. scriptus* and, indeed, this is the only record of *D. scriptus* in all the Rio Grande drainage. I unsuccessfully attempted, in the summer of 1968, to collect specimens of *Dolomedes* in this location. It would be interesting to determine the significance of this unusual specimen, a task obviously requiring additional collecting.

**Dolomedes scriptus** Hentz

Figures 8-10, 22-24, 28, 43, 59-60; Map 5


**Diagnosis.** *Dolomedes scriptus* and *D. gertschi* are apparently closely related. See “Diagnosis” under the latter species.

The females of *D. scriptus* are also very similar in pattern (Fig. 9) to the largely sympatric females of *D. tenebrosus*, but they are easily distinguished by characters of the genitalia (Figs. 28, 43, 59-60), which place them in different related species groups. The relationship with *D. albinus* is discussed under “Diagnosis” of the latter species.

This species can usually be distinguished from other species by its abdominal dorsum, which has distinct “W-shaped” transverse bands.

**Description.** Average female CL average male CL = 1.17.

**Male** (from Transylvania County, North Carolina): On the carapace ocular area dark; clypeus with transverse band of light hairs interrupted by irregular dark mottled area descending from ALE, marginal line interrupted medially with white spot; wide submarginal light bands continuous with clypeal band, extend to posterior edge of carapace, enclosing distinct medium gray central disc; irregular, narrow, dark marginal band widens posteriorly; curved light line extends posteriorly from each PLE, pair of indistinct triangular marks anterior to thoracic groove; narrow, medial, light band extends posteriorly from between thoracic triangular marks, surrounds thoracic groove; several dark lines of varying distinctness radiate from thoracic groove, each ending abruptly at edge of central disc, some widening at this terminus; pair of “Y-shaped” marks posterior to PME. **Sternum** dark gray laterally with irregular medial band extending from labium to posterior apex. **Labium** light, becoming medium reddish brown at laterobasal margins. Basal segments of *chelicerae* elongate, each marked anteriorly with longitudinal mottled gray band, anterior surfaces clothed with long light hairs. **Palpal endites** entirely light. All segments of *legs* light gray ventrally, darker dorsally; dorsal surfaces with indistinct gray longitudinal marks that appear to coalesce in some places into indistinct annular bands. Leg length order IV-I-II-III. **Abdomen** dorsally with medium gray lanceolate cardiac area bordered by pair of lateral narrow sinuous light bands; pair of oblique light marks that project posteriorly from posterior apex of cardiac area; two “W-shaped” transverse light
bands across posterior half of dorsum connected laterally to two narrow longitudinal light bands that extend from basal end; transverse light bands bordered anteriorly by similarly shaped black bands, posteriorly by dark gray areas; posterior apex with three transverse alternating black, dark gray bands. Sides medium gray that becomes lighter ventrally. Venter light with faint mottling that becomes darker towards sides; light spot just anterior to each anterior spinneret. Palpal organ (Fig. 28) as for fimбриatus group. Tibial apophysis (Fig. 43) with two large, broad, subequal teeth on end of truncated distal edge, small tooth at base on ventral margin. For measurements see Diagram 1 for dimensions and ratios of the genitalia and body.

Female (from Transylvania County, North Carolina): On the carapace ocular area dark only around each eye; clypeus with homogeneous medium gray area between AME and anterior edge except for median longitudinal white spot that begins at margin; mottled gray bands lateral to clypeal median gray area; lateral submarginal bands divided into series of discontinuous, light, elongate areas that enclose medium gray central disc; irregular, narrow, marginal bands widen posteriorly; curved light line extends posteriorly from each PLE, each of which is bordered laterally by short dark band; pair of triangular dark marks anterior to thoracic groove; light, median longitudinal band begins between PME, extends between triangular marks, widens around thoracic groove, continues to posterior margin of carapace; several lines of varying distinctness radiate from thoracic groove, end abruptly at edge of central disc; some lines become wider and truncated at this terminus, which joins submarginal light areas; “Y-shaped” dark mark posterior to each PME. Sternum medium gray laterally with broad irregular medial band extending from labium to posterior apex. Labium medium reddish brown, darkest laterally, lightest distally. Basal segments of chelicerae robust, medium dark reddish brown in color; anterior surface clothed with long, light and dark hairs. Palpal endites light, becoming light reddish brown at base. Coxae of legs light ventrally; femora with light gray mottling ventrally which coalesces distally into annular bands on light background; other segments light gray with dorsal surfaces with distinct longitudinal gray marks that appear in some places to coalesce into annular bands. Leg length order IV-(II-1)-III. Abdomen dorsally with medium gray lanceolate cardiac area bordered by pair of curved light bands laterally; two pairs of light marks project obliquely, laterally from middle, posterior apex; four “W-shaped” transverse light bands across posterior half of dorsum connected laterally to mottled light areas; transverse light bands bordered anteriorly by similarly shaped black bands, posteriorly by dark gray bands separated by discontinuous narrow light marks. Sides medium gray, somewhat mottled, become homogeneously lighter ventrally. Venter light gray with indistinct longitudinal bands; light spot just anterior to each anterior spinneret. Epigynum (Fig. 60), internal copulatory apparatus (Fig. 59) as for fimбриatus group; pair of skeletal muscle attachments are anterolateral to epigynum, completely joined to it; epigynum completely sclerotized, distinct at anterior margin; fertilization tubes each composed of one coil, two loops; seminal valves found in posterior half of dorsal-epigynal area (Carico and Holt, 1964). For measurements see Diagram 1 for dimensions and ratios of the genitalia and body.

Immatures have dorsal color patterns similar to the adults.

Variation. The rather complex color pattern varies considerably. The male described above possessed a wide, light, submarginal carapacial band. However, in some specimens, this band becomes broken into connected rhomboid light areas, while in others the light areas are reduced to a series of unconnected linear elongate light spots
(Figs. 23–24). Females show a similar type of variation of the carapacial band but they do not have the wide, uniform band of the male, and occasionally the light areas are almost obsolete (Fig. 22). Correlating with the decrease in light areas of the carapacial band is the decrease in light areas of the abdominal dorsum. Especially affected are the lateral light mottled areas of the female which may become a homogeneous medium gray. Likewise, the male shows a decrease in the width of the lateral light bands, but the transverse bands are always in evidence in both sexes. In older specimens the chelicerae, palpal ends, and labium may be quite dark.

In the north, the general color may be darker. The lateral parts of the “W-shaped” transverse abdominal bands are lighter and appear as distinct white marks.

An interesting light male variant from the Rio Grande Valley, previously called *D. pinicola*, was discussed in the “Variation” section of *D. albinus*.

*Natural history.* From personal observation and data from collections made by other collectors, it is clear that this species is most commonly found associated with moderate to fast moving streams. In the Appalachians they are very common among rocks and boulders located at the margins of or in the stream itself. They are also found among piles of dead sticks and leaves washed up along the stream margin. Their general grayish color and complex pattern blend quite well with the gray of rocks and weathered wood. *D. scriptus* is often found associated with *D. vittatus*, and their ecological relationship was discussed above in the section on the biology of the genus.

During the month of August and the first part of September, females with egg sacs are encountered and nurseries are common along stream banks. Occasionally females with egg sacs have been found either earlier (21 July, Pennsylvania) or later (22 October, New Jersey). Among four egg sacs opened, the number of eggs varied from 368 to 769. Gravid females were found more often during July. Two females each had an embolus imbedded in the copulatory apparatus.

*Distribution.* Eastern United States and Canada from Nova Scotia, Southern Quebec, Ontario, and Manitoba southward to Texas, Alabama, Mississippi, Georgia, and east to the Atlantic coast. Westwardly, the range extends to western South Dakota, Nebraska, and Oklahoma (Map 5).

Bishop (1924) listed a locality as Arden, Florida, and another from Ft. Collins, Colorado, neither of which I have been able to confirm. He also referred to *D. scriptus* specimens from Hot Springs, Arizona: most likely these were *D. gertschi*.

*Material examined.* Eighty-two male, 187 female, and 187 immature specimens.

*Holotype.* A female holotype and paratype series from Oak Creek Canyon, Coconino County, Arizona, 22 July 1949, collected by W. J. and J. W. Gertsch, in the American Museum of Natural History.

*Etymology.* It is my honor to name this species for Dr. Willis J. Gertsch for his encouragement and advice, and for calling to my attention that the species was undescribed.
Diagnosis. Dolomedes gertshi seems to be most closely related to D. scriptus, a conclusion based on basic similarities of their color patterns (Figs. 12-13) and shape of the tibial apophyses of the males (Fig. 44). The two species are clearly distinguishable by the CYL TL and TL/PTL ratios of the males and the EW/EL and EW/MEW ratios of the females (see Dice-Leraas diagrams for comparisons). Additionally, the median light band of the carapace is between PME and thoracic groove in D. gertshi (Figs. 12-13), whereas it is between PME and posterior edge of carapace in D. scriptus (Figs. 8-9).

Description. Average female CL average male CL = 1.38.

Male (from the type locality collected 4 July 1953, W. J. and J. W. Gertsch): On the carapace ocular area generally black, black areas around PE contiguous, black areas around AE discrete; clypeus medium gray with medial light spot extending from AME to edge; submarginal light bands extend from clypeal gray area to posterior edge of carapace and enclose distinct medium gray central disc; narrow marginal dark line present; curved light line extends posteriorly from each PLE; pair of indistinct elongate dark marks anterior to thoracic groove; narrow, median, light band extends between PME and elongate dark marks; several dark lines of varying distinctness radiate from thoracic groove, end abruptly at edge of central disc, some widening at this terminus. Sternum medium gray laterally with irregular median band extending from labium to posterior apex. Labium generally light, becoming dark reddish brown at latero-posterior margins. Basal segments of chelicerae elongate, each marked with anterior, longitudinal, indistinct gray band; anterior surface clothed with long light hairs. Palpal endites entirely light. All segments of legs light. Leg length order IV-I-II-III. Abdomen dorsally with light cardiac area bordered by pair of lateral sinuous light bands, pair of oblique light marks that project posteriorly from posterior apex; three “W-shaped” transverse light bands across posterior half of dorsum connected laterally to two light bands that extend full length of dorsum; transverse light bands bordered anteriorly by similarly shaped black bands, posteriorly by dark gray areas; posterior apex with two transverse black bands separated by dark gray. Sides medium gray with dorsolateral longitudinal light bands punctuated by small dark spots. Venter with lighter mottling on light gray background. Palpal organ (Fig. 29) as for fimбриatus group. Tibial apophysis (Fig. 44) with two large broad subequal teeth on distal edge, small tooth at base on ventral margin; dorsal margin has low, broad, rounded projection, basal indentation. For measurements see Diagram 1 for dimensions and ratios of the genitalia and body of this species.

Female (holotype): General color of the carapace reddish brown; ocular area dark principally around each eye; clypeus with dark gray area between AME and anterior edge except for median longitudinal light spot between AME, anterior margin; mottled gray bands lateral to median gray clypeal area; lateral submarginal bands divided into series of discontinuous, light elongate areas that enclose medium reddish brown central disc; narrow, marginal dark bands widen posteriorly; curved light line extends posteriorly from each PLE, bordered laterally by tapered dark band; pair of triangular marks anterior to thoracic groove; light median longitudinal band begins between PME, extends to between triangular marks; several lines of varying distinctness radiate from thoracic groove, end abruptly at edge of central disc; some lines become wider and truncated at this terminus, which adjoins submarginal light areas; angular dark line posterior to each PME. Sternum dark reddish brown laterally with narrow irregular medial band extending from labium to posterior apex.
Labium dark reddish brown, light distally. Basal segments of chelicerae robust, dark reddish brown in color; anterior surface clothed with long light, dark hairs. Palpal endites dark reddish brown, light distally. Coxae of legs light ventrally with indistinct gray mottling; femora with extensive dark gray mottling on light background: other segments medium reddish brown, dorsal surfaces with distinct longitudinal dark marks that appear in some places to coalesce into annular bands. Leg length order IV-II-I-III. Abdomen dorsally with medium gray lanceolate cardiac area bordered by pair of curved light bands laterally, two pairs of light marks which project obliquely, laterad from middle, posterior apex; four "W-shaped" transverse light bands across posterior half of dorsum connected laterally to mottled light areas; transverse light bands bordered anteriorly by very dark bands, posteriorly by dark gray bands. Sides dark gray, becoming lighter ventrally. Venter medium gray. Epigynum (Fig. 60), internal copulatory apparatus (Fig. 59) as for fimbriatus group; fertilization tubes each composed of one coil, one loop not visible from dorsal view; seminal valves in posterior half of dorsoepigynal area. For measurements see Diagram 1 for dimensions and ratios of the genitalia and body.

The few immatures available have a color pattern much like that of the adults.

Variation. Within the limited sample studied, no significant variation was evident in the color pattern.

Natural History. The habitat of Dolomedes gertschi resembles that of Dolomedes scriptus, at least in a superficial way. I was quite impressed with the similarity of Oak Creek (the type locality) to mountain and piedmont streams of equivalent size of the eastern United States. Specifically, the stream has a rather open cover of vegetation and has intermittent riffles and pools among numerous boulders and rocks of various sizes.

Females collected on three dates carried egg sacs: (1) 22 July 1949; 1.7 cm dia. (453 spiderlings), 1.6 cm dia. (approx.); (2) 27 July 1950; 1.8 cm dia. (1003 spiderlings); 1.7 cm dia., 1.6 cm dia.; (3) 8 July; 1.1 cm dia. The egg sacs were typical of the genus and were light brown in color and spherical.

Distribution. The upper Gila River drainage in Arizona and New Mexico (Map 6).

Material Examined. Twelve male, 25 female, and 15 immature specimens from the following localities.

Arizona. Coconino County: Oak Creek Canyon, 25 July 1952, 2 ♀ ♀, (M. Cazier, WJG, R. Schrammel) [AMNH]; 4 July 1953, 7 ♀ ♀ + 8 ♂ ♂ (W. J. & J. W. Gertsch) [AMNH]; 22 July 1949, 6 ♀ ♀ + 4 ♂ ♂, (W. J. & J. W. Gertsch) [AMNH]; 27 July 1950, 2 ♀ ♀ + 5 ♀ ♀, (Mont A. Cazier) [AMNH]; (5128), 18 June 1935, ♀, (E. Saunders) [MCZ]; 17 m. NE White River, 8 July, ♀, [AMNH]; 19 June 1966, ♀ + 3 ♀ ♀ (JEC) [JEC]. New Mexico. Whitewater Canyon, NE Glenwood, 4800', W105.54; N33.23, 18-19 August 1965, 2 ♀ ♀, (H. S. Fitch) [AMNH].
Dolomedes vittatus Walckenaer
Figures 14–15, 30, 45, 63–64; Map 7


Diagnosis. Dolomedes vittatus and D. holti are the most closely related species pair in the Nearctic Region. See the diagnosis section under the latter species for further discussion. Dolomedes vittatus differs from other species by its deep chocolate brown background color and the distinctive pattern of light areas on the dorsum as in Figures 14–15.

The male is distinguished by the shape of the tibial apophysis, which is longer than wide and bears two teeth at the apical margin (Fig. 45), and by the presence of a patch of stiff spines on each femur IV (Fig. 36). In the female the EW/SW and EW/EL ratios are usually distinctive but there is some overlap with other species (see Diag. 1).

Description. Average female CL: average male CL = 1.23.

Male (from Transylvania County, North Carolina): On the carapace ocular area dark; chelae with wide transverse white band continuous laterally with submarginal white bands, and an anterior black margin; wide submarginal white bands continuous with clypeal band extend to posterior edge of carapace to enclose medium brown central disc; black marginal band present; indistinct curved light line extends posteriorly from each PLE; pair of very distinct black triangular marks anterior to thoracic groove; several dark lines of varying distinctness radiate from thoracic groove, end abruptly at edge of central disc, some widening at this terminus. Sternum light gray with indistinct, irregular median band of lighter color. Labium medium reddish brown, light at apical margin. Basal segments of chelicerae elongate, medium brown, each marked anteriorly with five longitudinal dark gray lines; anterior surfaces clothed with long, light hairs. Palpal endites medium reddish brown, light at apical margins. All femurs, coxae of legs light ventrally with indistinct light gray mottingling, dorsal surfaces light with indistinct light brown longitudinal marks; other segments medium brown. Leg length order IV–I–II–III; femurs IV each have subapical patch of stiff spines retrolaterally on ventral side (Fig. 36). Abdomen dorsally with background color dark brown with distinct lateral, longitudinal light bands that extend from base, narrow towards apex; two pairs of alternating posterior light, dark, transverse lines extend medially from lateral light bands; pair of short, oblique basal light lines laterad from distinct cardiac area. Sides mottled with medium brown below longitudinal light bands becoming lighter ventrally. Venter light
brown, distinct from mottled brown areas of sides. Palpal organ (Fig. 30) as for fimбриatus group. Tibial apophysis (Fig. 45) about twice as long as wide, apical margin with two teeth, ventral one largest and curved; two other teeth located basally at anterior, posterior margins. For measurements see Diagram 1 for dimensions and ratios of the body and genitalia.

Female (from Transylvania County, North Carolina): General background color of the carapace dark brown with ocular area, clypeus dark; curved light line extends posteriorly from each PE; pair of triangular black marks anterior to thoracic groove; several lines of varying distinctiveness radiate from thoracic groove, and end abruptly at edge of indistinct central disc; some lines become wider and truncated at this terminus. Sternum dark brown. Labium dark reddish brown, becoming light at apical margin. Chelicerae dark reddish brown, with anterior surface clothed with mixture of long, light, dark hairs. Palpal endites dark reddish brown, becoming light at apical margins. General color of legs dark brown; ventral surfaces with indistinct gray mottling, dorsal surfaces with longitudinal gray marks that appear in some places to coalesce into annular bands. Leg length order IV-(II-I)-III. Abdomen dorsally dark brown in general background color; two pairs of small white spots in basal half with three pairs of larger white spots in apical half joined by indistinct transverse dark lines; indistinct lighter lanceolate cardiac area present. Sides dark brown. Venter dark brown, distinct from sides. Epigynum (Fig. 64), internal copulatory apparatus (Fig. 63) as for fimбриatus group; posterolateral edges of epigynum turned somewhat dorsally and anteriorly; fertilization tubes composed of one coil, two loops, seminal valves located in posterior half of dorsoepigynal area (Carico and Holt, 1964). For measurements see Diagram 1 for dimension and ratios of the genitalia and body.

The immatures have a color pattern very similar to that of the adults and therefore are relatively distinctive. Sexual dimorphism is evident, making sexual differentiation of the young easy. Frequently, a more complex pattern is apparent in very young or light specimens similar to the pattern of D. scriptus.

Variation. Generally, D. vittatus does not show any significant variation in the color pattern. The principal differences encountered in both sexes in most populations is the degree of darkness in the brown background color. When the background color is relatively light, a more complex pattern of dark lines and bands emerges which roughly resembles that of D. scriptus. A single male collected in Lynchburg, Virginia, has an atypical pattern that resembles the typical female pattern more than that of males.

Natural history. The range of D. vittatus overlaps that of D. scriptus for the most part, as do their habitats. Although they are frequently found together, D. vittatus is more prevalent in small, well-covered streams, whereas D. scriptus is more common in larger, open streams. The dark brown color may be protective because they inhabit shaded areas of streams among piles of woody debris, around rocks and boulders, and on trunks of trees.

I have seen two nurseries of this species and they are of typical Dolomedes construction. Egg sacs occur from late summer (26 July, Virginia) to early fall (11 September, N. Carolina). The number of eggs or spiderlings per sac is among the largest of the genus. Bishop (1924) and Kaston (1948) reported as many as 1457 and 1480 respectively. The maximum is 1134 among the material I have examined. One female collected in Whitfield County, Georgia, had the embolus embedded in the right side of the copulatory apparatus. A mature male and a penultimate female were observed to engage in preliminary mating
behavior for several hours in the laboratory but did not mate.

Distribution. Eastern United States and Canada from Ontario and New Hampshire southward to northern Florida and westward to Arkansas and the eastern parts of Oklahoma and Texas (Map 7). Bishop (1924) reported a male and female from Olney, Illinois.

Material examined. Fourteen male, 65 female, and 100 immature specimens.

Discussion. The striking sexual dimorphism in the color pattern of this species has resulted in considerable nomenclatural confusion, with males having been known generally as D. vittatus or D. lanceolatus, while the females have been known as D. urinata. Banks (1891), Montgomery (1904), and Comstock (1912) considered both sexes to be of the same species, though under different names. However, Bishop (1924: 49) "... found several [female] specimens which agree in size, color and markings to such an extent [with the male of D. vittatus] that it is impossible to reach any other conclusion than that Dolomedes urinata is distinct and known only from the female." Additionally, he says (p. 50) of females of D. vittatus, "I have recently (June, 1923) found the fe-

males to be fairly common in a tamarack swamp near Voorheesville, N. Y." I have not collected nor seen a female with the "male" pattern. This diversity of female patterns is not unlikely. I have observed similar pattern diversity in other species, notably the closely related D. holti.

No reference has been made to a male with the female pattern except that by Kaston (1948), who collected a penultimate specimen at Gainesville, Georgia. I have collected a mature male with the female pattern, as stated before, but the genitalia and tibial characters were typical of D. vittatus. This is not surprising, since the males are also variable in other species.

Dolomedes holti new species
Figures 16–17, 31, 33, 46, 65–66; Map 8

Holotype. A female holotype and paratype series from San Juan River west of Horsetail Falls, Nuevo León, Mexico, 1 August 1968, collected by James E. Carico, in the Museum of Comparative Zoology, Harvard University. One male and one female paratype are deposited in the American Museum of Natural History.

Etymology. This species is named for Dr. Perry C. Holt, who has encouraged and advised me in this project from its inception.

Diagnosis. Dolomedes holti and D. vittatus are the most closely related species-pair in the Nearctic Region. While the color patterns (Figs. 16–17) and genitalia (Figs. 65–66) of these two species show basic similarities, there are, however, certain characters that, at the same time, clearly indicate the distinctiveness of their gene pools.

As stated above in the section on variation, D. holti has a very variable color pattern. Some of the variations are very similar to the color patterns of D. vittatus; however, other variations are unknown for the latter species.

In males the CL/CYL ratio is a reliable
character with the CYL TL (see Diag. 1) being a useful ratio but with some overlap between the two species. Females are clearly distinguished by the EW SW (see Diag. 1) ratio while the EW MEW ratio is generally a good character but having some overlap.

**Description.** Average female CL: average male CL = 1.24.

**Male (paratype):** Ocular area of *carapace* dark; clypeus with wide transverse white band continuous laterally with submarginal white bands, anterior black margin; wide submarginal white bands continuous with clypeal band extend to posterior edge of carapace to enclose a medium brown central disc; black marginal band present; distinct curved light line extends posteriorly from each PLE; pair of dark triangular marks anterior to thoracic groove; several dark lines of varying distinctness radiate from thoracic groove, end abruptly at edge of central disc; some widening at this terminus. **Sternum** entirely light. Labium medium reddish brown, darker at basolateral margins, light apically. Basal segments of chelicerae elongate, medium brown, each marked anteriorly by reddish brown mottling; anterior surfaces clothed with long, light hairs. **Palpal endites** medium reddish brown, light at apical margins. All femurs, coxae of legs light ventrally, dorsal surfaces light with indistinct light brown longitudinal marks; other segments medium brown. Leg length order IV-I-II-III; femurs IV each with subapical patch of stiff spines retrolaterally on ventral side (Fig. 35). **Abdomen** dorsally with background color dark to medium brown with distinct lateral, longitudinal light bands that extend from base, narrow towards apex; three pairs of posterior light transverse lines extend medially from lateral light bands with dark transverse lines just posterior to each transverse light line; pair of obscure, short, oblique basal light lines present; cardiac area indistinct. Sides mot-

tled medium brown below longitudinal light bands that become lighter, obsolete ventrally. Venter light brown, not distinctly set off from mottled brown areas of sides. **Palpal organ** (Fig. 31) as for *fimbriatus* group. **Tibial apophysis** (Fig. 46) about twice as long as wide, apical margin with two teeth, the curved ventral one largest; two other teeth located basally at dorsal, ventral margins, with dorsal one much larger. For measurements see Diagram 1 for dimensions and ratios of the body and genitalia.

**Female (holotype):** General background color of *carapace* dark brown with ocular area darker; clypeus with wide transverse white band continuous laterally with submarginal white bands, black band at anterior margin; wide submarginal white bands continuous with clypeal band, extend to posterior edge of carapace, thus enclosing medium brown central disc; black irregular marginal band present; distinct curved light line extends posteriorly from each PLE; pair of black triangular marks anterior to thoracic groove; several dark lines of varying distinctness radiate from thoracic groove, end abruptly at edge of central disc; some widening at this terminus. **Sternum** medium brown. Labium dark reddish brown, light at apical margin. Chelicerae dark reddish brown, with anterior surface clothed with long mixed light, dark hairs. **Palpal endites** dark reddish brown, light at apical margins. **Leg** color of *legs* medium to dark brown; coxae medium brown, femurs with dark gray mottling that appears to coalesce into annular bands; other segments dark brown with indistinct annular dark bands. Leg length order IV-I-II-III. **Abdomen** dorsally with general background color dark brown with distinct lateral, longitudinal light bands that extend from base, narrow towards apex; two pairs of posterior light transverse lines separated by dark extend medially from lateral light bands; margins
of lateral light bands undulated posterior to origin of transverse lines; two pairs of obscure light basal marks lateral to indistinct cardiac area. Sides mottled dark brown below longitudinal light bands, cuticle folded into several longitudinal grooves and ridges. Venter dark brown, not easily distinguished from sides. *Epigynum* (Fig. 66), *internal copulatory apparatus* (Fig. 65) as for *fimbriatus* group: fertilization tubes composed of one coil, two loops; seminal valves located in posterior half of dorsoepigynal area. For *measurements* see Diagram 1 for dimensions and ratios of the genitalia and body.

Immatures in the paratype series number thirteen and are in various stages of development. Generally they are lighter in color than the adults and are quite varied in pattern.

**Variation.** In the paratype series the males showed little significant variation among themselves, but one of the two males in another series from nearby Horsetail Falls is unusual in that it is very light and the longitudinal bands are obsolete.

Females of the paratype series were unusual in that there were two different color patterns represented. One variant is chocolate brown with white areas limited to white spots on the dorsum as in *D. vittatus* females. The other has very distinct longitudinal white bands on the carapace and abdomen (five of the 13 females in the type series), therefore showing a close resemblance to males of the same species and to the male of *D. vittatus*. In the Horsetail Falls series, the two females showed a complex pattern similar to *D. scriptus* because of the generally lighter background color.

**Natural history.** The paratype series was taken from the San Juan River, which is a generally shallow stream (approximately 25 ft. in width), with intermittent pools and riffles in an open, high-walled canyon. The spiders were found during the day under and around the bases of large boulders at the edges of, or emerging from, the stream. They were usually positioned on vertical faces with head down in typical *Dolomedes* fashion. Many of the females had distended abdomens and were apparently gravid.

**Distribution.** San Juan River drainage in the vicinity of Horsetail Falls, Nuevo León, Mexico (Map 8).

**Material examined.** Seven male, 16 female, and 19 immature specimens from the following localities.

**MEXICO, Nuevo León.** Horsetail Falls, 31 July 1968, 2♂♂ 1♀ (JEC) [JEC]; 27 Nov. 1937, ♀ (L. Irby David & Bruce Brown) [AMNH]; at San Juan R. Canyon, 1 August 1965, 4♂♂ 13♀ [♀ + 13 imm. (type series) (JEC) [JEC]; Villa De Santiago, 16, 18 June 1938, 6imm. (H. Hoogstraal) [MCZ].
Dolomedes striatus Giebel
Figures 20–21, 32, 47, 67–68; Map 9


_Dolomedes fulcricratoratus_ Bishop, 1924, Bull. New York State Mus., 252: 59–60, pl. 19, fig. 3: pl. 34, fig. 1. Female holotype from Pistakee, Illinois, in the Museum of Comparative Zoology, examined.—Roewer, 1951, Katalog der Araneae, 2(a): 134.—Bonnet, 1956, Bibliographia Araneorum, 2: 1532. NEW SYNONYMY.

**Diagnosis.** _Dolomedes striatus_ is often confused with _D. tritou_ because of similarity of pattern. Both possess white bands on the carapace and abdomen, white spots on the abdomen, and dark spots on the sternum. The white abdominal bands of typical _D. striatus_ are more dorsal, more distinct, and are solid colored, and the median dark band is darker at the edge adjacent to the white bands (Figs. 20–21).

The adults are easily distinguished by characteristics of the genitalia. Males of _D. striatus_ have a very distinct earlike tibial apophysis (Fig. 47) that is obviously dissimilar to the long spatulate tibial apophysis of _D. tritou_ (Fig. 48). Also, _D. striatus_ males have no spinous hump on femur IV. The epigynum of _D. striatus_ has a wider middle lobe and wider medial border of the lateral lobes; also, the position of the seminal valve is located more posteriorly in the dorsoepigynal area (Fig. 67).

**Description.** Average female CL/average male CL = 1.11.

**Male** (from Ramsey, New Jersey): General background color of _carapace_ medium brown, with ocular area dark only around each individual eye; clypeus with median light spot between two obscure gray areas; rather straight submarginal white band extends from each anterolateral clypeal angle to posterior edge of carapace and encloses medium brown central disc; dark marginal bands present, several obscure lines of varying distinctness radiate from thoracic groove, end at edge of central disc. **Sternum** light with median, indistinct, longitudinal dark band; four pairs of coalesced dark spots laterally. **Labium** medium reddish brown, darker basolaterally, light distally. **Chelicerae** medium brown, anterior surface with indistinct gray lines, long, dark, light hairs. **Palpal endites** medium brown. **Legs** medium brown with obscure motting on ventral sides of coxae, femurs; obscure longitudinal marks on dorsal surface of femurs. **Leg length order** (IV-I)-11-III. **Abdominal** background color medium to dark brown; dorsally two distinct, narrow, lateral, longitudinal white bands extending from base to apex enclosing wide brown median area that darkens apically, darkens laterally towards edge adjacent to white bands; three pairs of obscure light spots in apical half of median dark band. Sides with numerous parallel dark brown lines. **Venter** light brown with narrow dark brown lines laterally; median medium brown area widest at epigastric groove, narrows to spinnerets. **Palpal organ** (Fig. 32) as for _fimbriatus_ group. **Tibial apophysis** (Fig. 47) closely appressed to tibia, earlike in shape with one or two small teeth. For **measurements** see **Diagram 1** for dimensions and ratios of the body and genitalia.

**Female** (from Ramsey, New Jersey): General background color of _carapace_ medium brown, ocular area dark only around each individual eye; clypeus with median light spot between two obscure gray areas; rather straight submarginal white band extends from each anterolateral clypeal angle to posterior edge of carapace, encloses medium brown central disc; dark marginal bands present, several obscure lines of varying distinctness radiate from tho-
racic groove, end at edge of central disc. Sternum light with median, indistinct, longitudinal dark band; four pairs of triangular distinct dark spots laterally. Labium medium reddish brown, darker basolaterally, light distally. Chelicerae medium brown; anterior surface with indistinct gray lines, long, mixed, light, dark hairs. Palpal endites medium brown. Legs medium brown, obscure mottling on ventral sides of coxae, femurs; obscure longitudinal marks on dorsal surfaces of femurs. Leg length order IV-(I-II)-III. Abdominal background color medium to dark brown; dorsally, two distinct, narrow, lateral longitudinal white bands extend from base to apex, enclose wide, brown, median area that darkens apically, darkens laterally towards edge adjacent to white bands, five pairs of small light spots in median dark band. Sides with numerous parallel dark brown lines. Venter light brown with narrow medium brown lines laterally, medium medium brown area widest at epigastric groove, narrows to spinnerets. Epigynum (Fig. 68), internal copulatory apparatus (Fig. 67) as for fimбриatus group; fertilization tubes composed of one coil, two loops; seminal valves in posterior half of dorsoepigynal area (Carico and Holt, 1964). For measurements see Diagram 1 for dimensions and ratios of the genitalia and body.

The pattern of the immatures is like that of the adults, and may be distinguished from D. triton by the dark edge of the abdominal median band, which is adjacent to the distinct white bands.

Variation. There seem to be two rather different color patterns, one of which is much more common than the other. Most common is the pattern of the specimens herein described and figured, and there seems to be little significant variation within this form.

The least common variation is here referred to as the “fulviatronotatus” color pattern because it was described as a new species under that specific name. It is distinguished by a pattern that is greatly diffused into a rather irregular and scattered array of dark spots and “blotches” over the body. Four adult female and two immature specimens with this pattern were examined and they all showed different degrees of diffusion of the pattern. Refer to Bishop’s (1924) plate 34, figure 2 for an illustration of this variety.

Natural history. This is the only known North American species that I have not collected, even though such an effort was made in Illinois (and the type locality of D. fulviatronotatus Bishop), Michigan, and Ontario the summer of 1968. Therefore, I can only cite from literature, museum labels, and personal correspondence on the subject of natural history.

Kaston (1948) and Joseph A. Beatty (personal communication) both have collected D. striatus around small ponds and marshy areas. H. K. Wallace (personal communication) collected it in marshes and swamps in the E. S. George Reserve, Livingston County, Michigan, by sweeping and sifting, and with the aid of a headlight. Museum specimen labels often indicated the locality as a particular pond, but additional information is lacking except for two Canadian collections, which had comments such as “edge of sandy pool” and “under drift at high water mark.”

Bishop reports observing a nursery in New York on 3 September which resembled the nursery of D. triton and contained an egg sac “about three-eighths inch” in diameter. Egg sacs were in collections from Michigan (26 June) and New Jersey (26 August). Mature males are found in the collections as early as 30 May (Connecticut) and as late as 3 January (Ontario) while mature females are from May (New York) to 24 September (New Jersey).

Distribution. Glaciated regions of the northeastern United States and Canada north of 40° latitude to Labrador, and west to Illinois and western Ontario (Map
9). A mature female from the H. K. Wallace collection found in Giles County, Virginia, extends the apparent range of this species considerably. It might be from a range extension that follows the Appalachian Mountains southward.

**Material examined.** Eleven male, 20 female, and 58 immature specimens were examined.

**Discussion.** Giebel's description has been considered (Bishop, 1924; Bishop and Crosby, 1936) to refer to the species herein described. An examination of his description leaves doubt as to whether he was describing the more common and widely distributed *D. triton*, which is quite similar. The only characters he mentioned are the features of the dorsal abdominal pattern, but the manner of describing some of them is not entirely clear, while other, more clearly described characters are possessed by both species. The holotype, because of its shriveled and colorless condition, is of little help. Measurements of the carapace agree more with those of what is here considered *D. striatus* than those of *D. triton*. I believe that Bishop was therefore justified in resurrecting this name.

Because I have been unable to obtain specimens from the type-locality, Illinois, I have chosen to select specimens for descriptions from a series in good condition from New Jersey which are consistent in taxonomic characters with specimens from other areas of the range.

*Dolomedes triton* (Walckenaer)

**Figures 11, 18-19, 33, 37, 48, 69-70; Map 10**


Dolomedes major Banks, 1898, Proc. California Acad. Sci., 1: 276–277, pl. 17, fig. 5. Male and female syntypes from San José del Cabo and Sierra San Lazaro, Baja California, Territorio del Sur, Mexico, in Museum of Comparative Zoology, examined.—Roewer, 1954, Katalog der Araneae, 2(a): 133—Bonnet, 1956, Bibliographia Araneorum, 2: 1534. NEW SYNONYM.


Dolomedes triton triton.—Bishop, 1924, Bull. New York State Mus., 252: 50–55, pls. 27, 28, 30, figs. 1–4, δ, ♀.


Dolomedes spatulatus Chamberlin and Ivie, 1946, Bull. Univ. Utah, 36(13): 6, fig. 5, δ, ♂.

Male holotype, female allotype from Kingston, Tennessee, in the University of Utah, not examined; paratypes from type locality in American Museum of Natural History, examined. NEW SYNONYM.

Diagnosis. The relationship of D. triton to other species is obscure. It bears a superficial resemblance with D. striatus and is discussed further in the diagnosis section under the latter species. The pattern differs from other species in that it has three pairs of dark sternal spots, light submarginal carapacial bands, and a number of light spots on the abdominal dorsum (Figs. 18–19).

Males are easily distinguished by the shape of the tibial apophysis, which is rounded and expanded apically and extends beyond the apex of the tibia (Fig. 33). The seminal valve of the female copulatory apparatus is located in the anterior half of the dorsoepigynal area, and the fertilization tubes are loosely wound and rather narrow (Fig. 69). The posterior edge of the epigynum is turned dorsally and anteriorly so as to cover part of the dorsoepigynal area (Fig. 69).

Description. Average female CL/average male CL = 1.28.

Male (from Charlton County, Georgia): General background color of carapace greenish gray to medium brown with ocular area dark; clypeus with median, light, submarginal area between two gray areas; submarginal white band extends from each anterolateral clypeal angle to posterior edge of carapace, encloses medium brown central disc; medium dark marginal bands present, curved light line extends posteriorly from each PLE; pair of indistinct, medium dark marks anterior to thoracic groove; narrow, median, light band extends from near PME to posterior edge of carapace; pair of short, medium dark bands encloses anterior end of median light band; several obscure lines of varying distinctness radiate from thoracic groove, end at edge of central disc. Sternum light with three distinct pairs of dark spots laterally. Da-
*Dolomedes furcatius* medium reddish brown, light on apical margin. *Chelicerae* light, each with 2–3 longitudinal dark lines, long light hairs anteriorly. *Palpal endites* light reddish brown. All *leg* segments light ventrally with irregular longitudinal gray lines dorsally; *femur IV* with spiny tubercle apically on ventral side. Leg length order IV-I-II-III. *Abdominal* background color dark reddish brown to light brown. Dark brown color dorsally with a distinct light cardiac area; two pairs of anterior white spots lateral to cardiac area; posteriorly, four pairs of white spots lateral to three pairs of smaller white spots, with obscure transverse dark bands between more posterior pairs of white spots. Sides each with irregular white reticulated band dorsally adjacent to dark area of dorsum; ventrally, sides with irregular dark mottingle. Venter light with longitudinal medium bands, with dark areas of sides nearly in contact just anterior to spinnerets. *Palpal organ* (Fig. 33) as for *fimbriatus* group. *Tibial apophysis* (Fig. 48) length usually more than twice its width at widest point, expanded, rounded, flattened apically; ventral blunt tooth about one-third distance from base. For *measurements* see Diagram 1 for dimensions and ratios of the body and genitalia.

**Female** (from Charlton County, Georgia): General background color of *carapace* greenish gray to medium brown, with ocular area dark only around each individual eye; clypeus with median, light spot between two gray areas; submarginal white band extends from each antero-lateral clypeal angle to posterior edge of carapace, encloses medium brown central disc; dark marginal bands present, curved light line extends posteriorly from each PLE; pair of indistinct medium dark marks anterior to thoracic groove; narrow, median, light band extends from near PME to posterior edge of carapace; pair of short, medium dark bands encloses anterior end of median light band, several obscure lines of varying distinctness radiate from thoracic groove, end at edge of central disc. *Sternum* light, with three distinct pairs of dark spots laterally. *Labium* dark reddish brown, light on apical margin. *Chelicerae* dark reddish brown, with anterior surface clothed with long, mixed light, dark hairs. *Palpal endites* medium reddish brown, lighter apically. All *leg* segments light ventrally with irregular gray lines dorsally. Leg length order IV-(I-II)-III. *Abdominal* background color dark reddish brown to light brown. Dorsally, color dark brown with distinct cardiac area; two pairs of anterior white spots lateral to cardiac area; four posterior pairs of white spots, each encircled by dark ring lateral to four pairs of smaller white spots. Sides each with irregular white reticulated band dorsally adjacent to dark area of dorsum; ventrally, sides have irregular dark mottingle. Venter light with longitudinal obscure dark bands. *Epigynum* (Fig. 70), *internal copulatory apparatus* (Fig. 69) as for *fimbriatus* group; entire posterior edge of epigynum turned dorsally and anteriorly, overlaps much of internal parts of copulatory apparatus, pigmentation may be light, making edges obscure; fertilization tubes relatively slender, loosely looped in dorsoepigynal area, each composed of three loops; seminal valves found in anterior half of dorsoepigynal area (Carico and Holt, 1964). For *measurements* see Diagram 1 for dimensions and ratios of the body and genitalia.

Generally, the color pattern of immatures is very similar to that of the adults. *Dolomedes triton* immatures typically have a lighter and greener background color with the dark rings around the white abdominal spots usually quite distinctive. Very small spiderlings show a more diffuse pattern with some evidence of abdominal transverse markings.

**Variation.** *Dolomedes triton* is probably the most variable of all nearctic species.
The variation is both geographic and intrapopulational.

The populations in the eastern United States show variation in both the distinctiveness and distribution of the color pattern over the body. In females, I have noticed a definite deepening of color in the dark areas of the pattern to be associated with advanced age. While the lighter and younger individuals are greenish tan, the color of older individuals tends towards a deeper brown. On the abdominal dorsum, it seems as if the center for the darkening trend is the dark rings around the larger white spots. These dark rings may vary from narrow rings to broad and coalescing longitudinal dark bands.

Another eastern variation is the width of the carapace bands. The width of the bands may vary (with intermediates) from a narrow submarginal band to a wide band that nearly reaches the lateral margins of the carapace and continues across the elyptus. An attempt was made to measure and therefore quantify these bands because of their supposed taxonomic implications, but their irregularity defied this kind of objective analysis. The wider bands are less common than the narrower ones in any of the populations examined; the wider bands are found in the northeast and southeast, but more often in the latter. As one proceeds westward from the northeastern United States, the narrower carapace bands seem to shift position by becoming more medial and straighter. In the latter case, the carapace bands resemble those of *D. striatus*, which are, in some cases, sympatric with *D. triton* in this region.

Variation of sternal spotting seems to be more geographic. In the southeast these spots are distinct, but in the northeast and throughout the northwest, they usually coalesce to some degree into lateral bands. There appears to be a clinal change from south to north of this variation.

The only feature of the reproductive structures which shows mentionable variation is the male tibial apophysis. As can be seen in Figure 11 the apex of the apophysis varies in the degree to which it is expanded. This expansion seems to be closely related to the overall size, with the greatest expansions present in the largest individuals. In a type of geographic variation, the plane of the expanded apophysis apex is turned so as to lie about 90° relative to the plane of the base. The northeastern and northwestern males generally have this latter variation.

The southern members of this species average larger in size than the northern representatives.

Natural history. *Dolomedes triton* is the species most clearly related to the standing or slow-water habitat. Typically, specimens are collected among the emergent aquatic vegetation at the margins of permanent lakes, ponds, or pools in a stream. They position themselves head-down near the waterline, or have the anterior legs on the water surface while the posterior legs are resting on a leaf or twig. When startled, they quickly dive to the underside of a lily pad or climb down the submerged portion of a vertical leaf. Some individuals have been observed feeding upon adult damselflies as well as other water-related insects. In this still-water habitat, *D. triton* may be found with *D. albinus*, *D. tenebrosus*, or *D. okefenokensis* wherever their respective geographic ranges overlap.

Probably adults of both sexes could be found all year, but in the North they are reported primarily from the warmer seasons. There are numerous collections of adults from Florida during the period December through April.

Egg sacs are found in Florida as early as April, but in the North they appear primarily from June to September. In the College Lake on the Lynchburg College campus, Lynchburg, Virginia, egg sacs annually occur in greatest frequency in nurseries during late August and early September. The nurseries at the latter locality typically occur from one to three feet above
water in thick stands of *Sparganium* where tilted leaves cross each other.

**Distribution.** *Dolomedes triton* evidently has a wider distribution than any other nearctic species of *Dolomedes*. Its range extends from Ontario and Maine to southern Florida and Texas, westward to the southern panhandle of Alaska and southward to Yucatan Peninsula and Chiapas, Mexico (Map 10). The southwestern states seem to be devoid of this species since these areas have been fairly well collected with-
out the occurrence of more than a single record of its being found.

Material examined. Eighty-two males, 219 females, and 287 immatures.

Discussion. The wide variability of this species, as well as its wide geographic range, has contributed to considerable misinterpretation resulting in nomenclatural fragmentation. I will attempt here to review and reinterpret the principal nomenclatural events.

Although Walckenaer clearly had this species in mind under his name *D. triton*, the name was forgotten, and Hentz's junior synonym, *D. sexpunctatus*, generally held sway from the time of its proposal until *D. triton* was revived by Bishop in his 1924 revision. Concerning the distribution of these two subspecies, Bishop said of *D. t. triton* that "... it apparently occurs only in the south"; and of *D. t. sexpunctatus* that it "... is the familiar form in the North [and] also occurs in all the South Atlantic States. ..." Further, he said that he found chiefly the former subspecies "... from various localities in the Okefenokee swamp." Under "Distribution" of the latter subspecies Bishop also listed localities in the Okefenokee Swamp. From the information given in Bishop's revision itself, I am inclined to reject these subspecies a priori. One major element of the modern concept of a subspecies concerns its geographic allopatry with other related subspecies while retaining the apparent potential for interbreeding (Mayr, 1969). Therefore, since Bishop's data suggest sympathy of the two subspecies, I believe that his subspecies division is invalid. Additionally, studies of series from the northern and southern United States, including the Okefenokee Swamp, revealed that the characters used by Bishop were variable and showed intrapopulational intergrades, and that the characters of both subspecies were found in the North. The characters to which Bishop gave especial emphasis were the width of the carapace band and overall size difference of the males.

In the revision, Bishop also described *D. albiclavus* from three widely separated localities, i.e., "Springfield, Mo., Salt Lake, Utah, Billy's Island, Okefenokee Swamp, Ga." Under "remarks" he said: "This large and distinct species is evidently related to *Dolomedes triton* but differs from it in the structure of the epigynum, in its general darker color and lack of paired white spots on the dorsum of the abdomen. The legs are proportionally and actually longer in this species than in *D. triton* and the body more robust." Of the specimens he listed, I have examined only the holotype. This specimen is indeed dark, but can be considered at the extreme end of the range of a highly variable and therefore questionable character. The abdominal spots were indeed absent, but since the dorsum was well rubbed, the white hairs of these spots were removed long ago, and no evidence of their presence was left. The epigynum showed no unusual deviation from the range of variation of the epigynum of *D. triton*. The length of the legs and shape of the body fall within the range of variability of *D. triton*.

Bishop's concept of these various species has generally been followed to the present. Only one later change of Bishop's arrangement has been published. Chamberlin and Ivic, in a short and superficial treatment (1946), proposed recognition of four species in a kind of "triton group." The old and neglected name, *D. scopularis* Koch [sic] was resurrected and applied to males having the apex of the tibial apophysis turned and to those "... *Triton* and *sexpunctatus* north of 40 degrees..." *D. sexpunctatus* Hentz was the only taxon for which a full description was given, but the apparent chief distinguishing character was the narrow apex of the tibial apophysis. *D. triton* (Walckenaer) was distinguished primarily by the intermediate expansion of the tibial apophysis. The only localities indicated for this species are in Georgia. Finally, *D. spatulatus* was described as a new species from Kingston, Tennessee (Cham-
berlin and Ivie, 1946). The very short description emphasized the broad expansion of the tibial apophysis. I have not examined the holotype, but I have examined a large series (AMNH) collected (according to the label) two days later at the same locality which may actually have been the intended paratypes designated by the authors. A study of the tibial apophyses of the fourteen males of this series showed a wide range of apical expansion from the very narrow to the very wide (Fig. 11) which was directly correlated with the overall body size. Indeed, the apophyses of three of Chamberlin and Ivie’s species, D. sexpunctatus (narrow apophysis), D. triton (intermediate apophysis), and D. spatulatus (wide apophysis), were represented along with intergrades among all three. The D. scopularis type of apophysis was not represented in this series, but the species is obviously based on a highly variable and therefore unreliable character. For these reasons, I have concluded that the four species of Dolomedes mentioned above, which were defined by Chamberlin and Ivie (1946), are synonymous.

**LITERATURE CITED**


