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## The Taxonomic Status and Distribution of *Thyanta custator* (Fabricius) and *Thyanta pallido-virens* (Stål) (Heteroptera, Pentatomidae)

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A number of species of *Thyanta* are found in the United States. They may be roughly divided into two categories: those up to 7 mm. in length and those from 8 mm. to 12 mm. or more in length. In the latter group are found *Thyanta pseudocasta* Blatchley, *T. perditor* (Fabricius), *T. custator* (Fabricius), *T. pallido-virens* (Stål), *T. calceata* (Say), and *T. bimini* Ruckes. As *T. pseudocasta* and *T. bimini* occur only in the southern tip of Florida and are unrelated to the others, they do not concern us at the moment. The remaining four, however, are quite closely related to one another. Of these, *T. custator* and *T. pallido-virens* form the major subject of the present paper, but for the effective use of keys, here included, *T. perditor* and *T. calceata* are incidentally considered.

*Thyanta custator* was described by Fabricius in 1803 under the generic name of *Cimex* as follows:

"*Thorace obtuse spinoso virescens thorace punctis duobus fasciaque media brunneis, abdomine lineis duabus punctorum nigris.*

"*Habitat in Carolina.*

"*Statura et magnitudo omnino praecedentis (sp. perditor). Antennae basi virescentes in media rufae, apice fuscae. Caput virescens. Thorace obtuse spinosus, virescens fascia media brunnea punctisque duobus nigris*

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*fasciae contiguas. Scutellum et elytra punctata, virescentia, immaculata. Abdomen virescens utrinque duabus punctis atris. Pedes virescentes."*

Translated, this description reads:

"Thorax obtusely spinose, green, the thorax with a pair of spots as well as a median reddish brown band, abdomen with two rows of black spots.

"Habitat in Carolina.

"Form and size like the preceding (sp. *perditor*). Base of the antenna greenish, middle rufous, apex fuscous. Head green. Thorax obtusely spinose, green with a reddish brown band in the middle and two adjacent black points. Scutellum and elytra punctured, greenish, immaculate. Abdomen green with two rows of black points on each side. Feet [legs] greenish."

It is important to note in this description that Fabricius emphasized the presence of two black points on the thorax (pronotum), the two rows of black spots on each side of the abdomen (venter), and the immaculate nature of the elytra and scutellum.

Additional features, not mentioned by Fabricius but characteristic of the species and important in its diagnosis, are as follows: (1) a band of color, similar to that of the transhumeral band, is usually present on the anterolateral margin of the pronotum, with a piceous external edge to this margin; (2) pronounced pilosity on the legs is absent, although seta-like hairs are present which are not longer than the lateral diameter of the tibia; (3) the apical end of the corium is truncated, and at least the basal area of the elytral membrane is spotted with brown or tan dots; (4) the "tongue" or apical portion of the scutellum is proportionately short, and its lateral margins tend to converge; the apex may or may not (usually not) be colored; (5) the outer of the two lateral rows of black spots on the abdominal venter is composed of the succession of piceous apical angles of the abdominal segments; and (6) the green mentioned in the original description is usually on the darker rather than on the yellowish green side, although this is not a very reliable character, as specimens tend to change color after death and prolonged storage.

In 1859 Stål described another pentatomid from California under the name of *Pentatoma pallido-virens* as follows:

"*Obovata, pallide virescens, dense obscurius punctata, callis minutissimis albidis parce sparsa; antennis articulis tribus ultimis apicem versus testaceis; thoracis marginibus antico-lateralibus pallide flavis; scutello apice imo rufescente; membrana subvitrea; subtus pallide flavescens, lateral versus rude virescente-punctata. Long. 10, lat. 5½ millim. Patria: California (San Francisco).*

"*Statura Rhaphig. prasini*, dimidio minor. Obovata. Caput latitudine intra-oculari vix dimidio longius, planisculum, ante oculos utrumque leviter sinuatum, apice rotundatum, levissime reflexo-marginatum, pallide virescens dense punctatum. Antennae corporis dimidia fere longitudine, pallide virescentes, articulus tribus apicalibus apicem versus testaceis, secundo tertio nonnihil longiore. Rostrum coxas posticans aequans, pallide virescens, apice fuscum. Thorax longitudine plus duplor latior, antice sinuatus, pone medium utrumque angulatus, angulis vix vel parum productis, rotundatis, postice rectus, pallide virescens, dense punctatus, marginibus antico-lateralibus pallide flavescentibus. Scutellum suboblongo-triangularare, ante apice utrumque sinuatum, dein anguste parallelum, pallide virescens, dense punctatum, apice imo rufescens. Hemelytra pallide virescentia, dense punctata, callis minutissimus albidis parce sparsa; membrana subvitrea. Subtus virescente-flavescens, praesertim latera versus sat rude pallide virescente-punctata, margine abdominis interdum anguste flavo. Pedes pallide virescentes, puberuli."

The direct translation of the above reads as follows:

"Obovate, light green, densely obscurely punctate with minute pale points scattered sparsely about; antennae with the third to the apical segments testaceous; antero-lateral margin of the thorax [pronotum] light yellow; apex of the scutellum reddish; membrane subvitreous; light yellow beneath coarsely punctured with coarse greenish punctures laterally. 10 mm. long,  $5\frac{1}{2}$  mm. wide. Locality: California (San Francisco).

"Form of *Rhaphig[aster] prasini*, half as big. Obovate. Width of the head between the eyes half the length, flattish, weakly sinuate before the eyes, the apex rounded, the margins weakly reflexed, light green, densely punctate. Antennae nearly half the length of the body, light greenish, third to apical segments testaceous, third somewhat longer than the second. Rostrum reaching the posterior coxae, light green, apex fuscous. Thorax more than twice as wide as long, anteriorly sinuate, angulated behind the middle, the angles not or weakly produced, rounded, posterior rectilinear, light green, densely punctate, anterolateral margin light yellowish. Scutellum suboblong-triangular, sinuate before the apex and from there backward narrowly parallel, light green, densely punctate, the apex red. Hemelytra light greenish, densely punctate, minute pale points sparingly scattered about, membrane clear. Greenish yellow below, coarsely punctate with light green, chiefly laterally, abdominal margin sometimes narrowly yellow. Feet [legs] light greenish, hairy."

It will be noted that there is quite a contrast in the two foregoing descriptions. Stål makes no mention of black spotting on either pronotum or abdomen, or the presence of a colored band between the humeri. On the

other hand, he emphasizes the paler green tone of the whole body, the persistence of yellowish borders, the hairy legs, and by implication the longer tongue of the scutellum, with its more parallel sides and red tip, and the vitreous nature of the elytral membrane.

Later, in 1862, Stål created the generic name *Thyanta* and assigned to the new genus Fabricius' species *Cimex custator* and his own *Pentatoma pallido-virens*, with a few other then known pentatomids that properly belong there.

While Fabricius' description of the species *custator* is by no means exhaustive, in terms of later-day authors, it is, nevertheless, quite adequate and satisfactorily fixes the species. Stål's more lengthy and detailed description of *pallido-virens* more adequately fixes that species.

For nearly a century hemipterists, in this country and abroad, have examined many pentatomids and identified them as *Thyanta custator* (Fabricius) regardless of their places of origin or their strict conformity to the original description. It happens that most of these specimens are not at all like the examples that Fabricius must have had before him as he wrote his description but more closely conform to what Stål described as *pallido-virens*.

In the general survey of the various populations of *Thyanta* in the United States, Canada, and Mexico, the present author has become convinced that previous concepts of various species are erroneous.

Van Duzee in his 1917 "Catalogue" recognized *Thyanta pallido-virens* (Stål) as a distinct species but limited its distribution to California.

On the other hand, Blatchley (1926) takes no cognizance of *pallido-virens* as a species but says of *Thyanta custator* (Fabricius): "*T. custator* is one of the most widely distributed of our heteroptera, ranging all the way from Quebec and New England to British Columbia, California, Texas, Arizona and northern Mexico. . . . On account of the great variation in color and the occasional projection of the humeral angles as a spine, *T. custator* has often been recorded as *T. perditor*." Indeed, his figure 24 on page 114 is in reality the spinose form of *Thyanta pallido-virens* and not *perditor* as implied in his text.

Barber in 1911 spoke of *custator* as "a very plastic and variable species."

Torre-Bueno in 1939 made matters worse by giving entirely erroneous characteristics to *custator* and trying to differentiate it from *T. calceata* (Say) merely on the basis of color difference, of which there is none.

In the matter of the plasticity and variability of *custator*, I am sure that any entomologist who examines enough material will be impressed with the fact that the species is rather stable and varies only within the

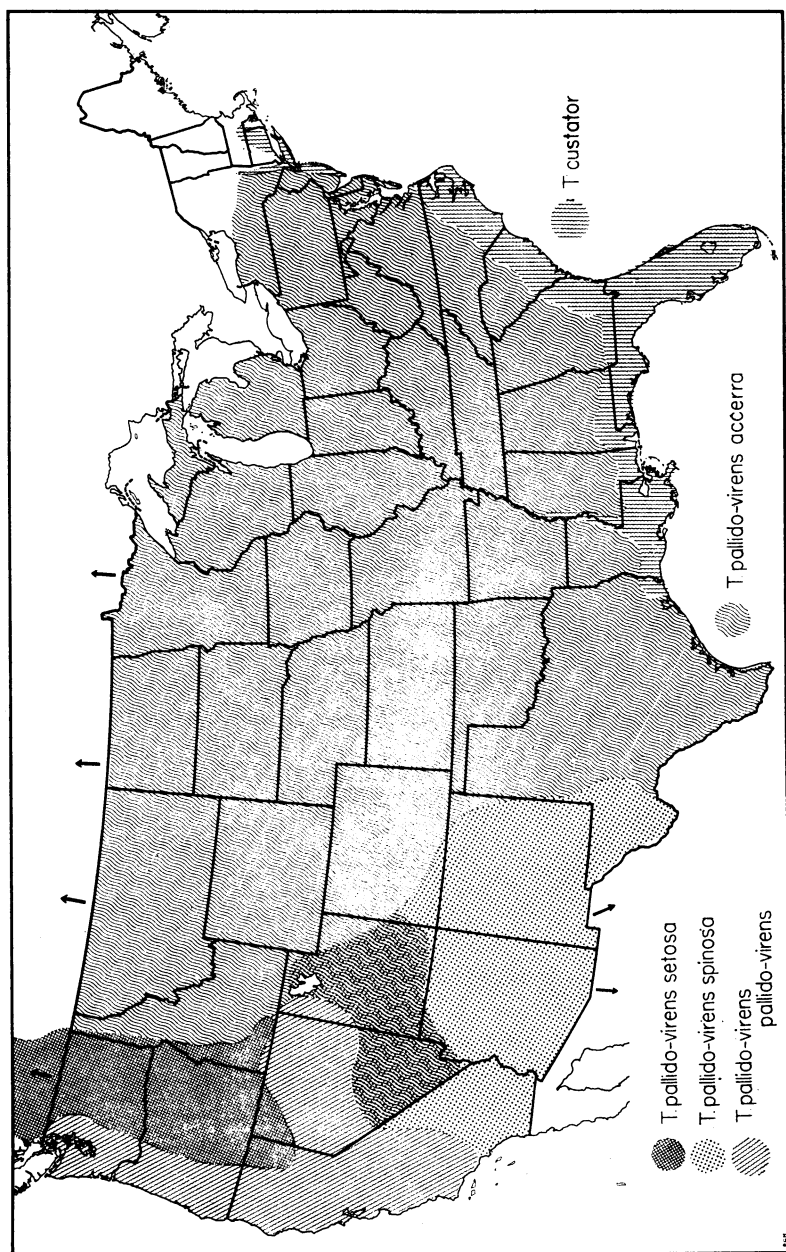


FIG. 1. Distribution of *Thyanta custator* (Fabricius) and the subspecies of *Thyanta pallido-virens* (Stål).

range of its own genetic composition, which apparently is rather limited.

In the matter of its wide distribution, I believe, from all the evidence at hand, that the species is confined to a rather narrow maritime area of the Gulf States and Atlantic seaboard, as indicated on the accompanying map (fig. 1).

In the matter of the restriction of the species *pallido-virens* to the California area from which the types came, I maintain that, while the basic form is limited in its distribution to adjacent areas, the species has, in the course of time, radiated eastward, northward, and southward to become widespread throughout the United States, Canada, and Mexico, occupying that territory not inhabited by *T. custator*, and in the course of that spreading several geographic subspecies have arisen and become established as definite ecological populations.

During the past several years the author has undertaken the difficult task of analyzing this complex of conflicting identities in an attempt to bring some order out of the existing chaos. In the course of this study a total of nearly 8000 specimens of both *Thyanta custator* and *Thyanta pallido-virens* has been examined. These have been collected from all parts of the United States (with the exception of Maine, New Hampshire, and Vermont), from northern Mexico, and from British Columbia. Many specimens examined were lent by state colleges and universities and by interested individuals, to all of whom thanks are extended for their generous cooperation. Many of the collections studied represent populations of local occurrence within restricted geographical limits, while others were of more widespread distribution and afforded an insight into the possibility of geographic subspeciation.

Fabricius described his species *custator* from "Carolina" which might mean any place along the lower Atlantic seaboard. Stål described his species *pallido-virens* from California (specifically San Francisco), which localizes it along the Pacific coast. Between these two extremes, populations of *Thyanta* occur in every state and likewise extend southward and northward into adjacent countries. Unfortunately the Fabrician type no longer exists and therefore is not available for comparative study. Through the courtesy of Dr. René Malaise, of the Riksmuseum in Stockholm, I have been privileged to borrow the types of Stål's *pallido-virens* which I now have for comparative study with our North American material. To him I owe special thanks.

Much of the study of these two species involved the use of micrometric measurements, to wit, the relative lengths of antennal segments, the longitudinal and transverse diameters of the pronotum, the scutellar proportions, and the length of tibial pile. In addition color variation was

studied in terms of the predominance of pattern or absence thereof. The density of puncturation was compared in specimens from all different localities. Body proportions were noted throughout. Unfortunately there is very little difference to be found in the composition of the external male genitalia in these two species. This is an index of close relationship and probably the reason they have been confused so frequently.

As a result of this intensive investigation I have come to the following conclusions :

1. *Thyanta custator* (Fabricius) is a homogeneous species that is confined to the maritime region of the Gulf states and the coastal area of the Atlantic seaboard as far north as Massachusetts, with a break occurring in the continuity between the northernmost eastern counties of North Carolina and the most southern tip of New Jersey, i.e., Cape May. That is to say, the maritime areas of Virginia, Delaware, and Maryland apparently do not have this species now represented. There are records that show that this species was taken in the vicinity more than 50 years ago, but recent collecting has not turned up any new records. It is possible that *T. custator* may extend some distance up the lower part of the Mississippi Valley, following the ordinarily considered Austral Zone. Unfortunately I have not been able to procure specimens from that territory.<sup>1</sup>

2. *Thyanta pallido-virens* (Stål) is a widespread species extending over most of the United States, southern and western Canada, and northern to southern Mexico, ranging from the piedmont area of North and South Carolina, Georgia, and Virginia westward, northward, and southwestward. It is without doubt the most common pentatomid in the entire country and is especially abundant in the Plains states, the Southwest, and California.

3. The species *Thyanta pallido-virens* (Stål) is not a homogeneous one but a complex of several slightly overlapping regional populations representing a number of geographical subspecies (fig. 1). One of these extends from the coastal area of Virginia and Delaware and the piedmont of the Carolinas through the Appalachian Range, thence to the Plains states and westward and northward to Colorado, Wyoming, Montana, North and South Dakota, and southwesterly into west central Texas. Another is typical of the southwestern states, of western Texas, New

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<sup>1</sup> Since submitting the manuscript for this article, the author has found one specimen of the true species *custator* in the collection of the California Academy of Sciences that bears a locality label "Crown City, Gallia County, Ohio." Crown City is on the north bank of the Ohio River in south central Ohio. Thus the range of this species appears to be extended from the Mississippi Valley to the Ohio Valley.

Mexico, Arizona, western Colorado, Utah, northern Mexico, and southern (Baja) California. The third is to be found in northern California, western Idaho, eastern Oregon, eastern Washington, and British Columbia. The fourth and last is the typical *pallido-virens* found in central California, western Nevada, and southwestern Idaho.

4. *Thyanta custator* and some subspecies of *Thyanta pallido-virens* [as well as *Thyanta calceata* (Say), which is not considered here] have what is apparently an autumnal-vernal (overwintering) generation that differs in appearance from the summer broods. This seems to be a case of seasonal dimorphism and was first called attention to by Reece I. Sailer of the United States National Museum. Specimens of such a generation were originally described by McAtee as a color variety of *T. custator* and named by him as *Thyanta custator* var. *accerra*.

The reasons for the foregoing conclusions are as follows:

ANTENNAL SEGMENTAL RATIOS: Statistical measurements show that in the true species *Thyanta custator* the fourth and fifth antennal segments are proportionately longer than the homologous parts in examples of *pallido-virens* or any of its subspecies. The following table indicates the differences found in various populations. Because segment I is uniform throughout, it is not included in the table. The numbers recorded represent the lengths of the segments measured by means of a micrometer eyepiece divided into 100 linear units and are not in terms of millimeters. Measurement was made by a binocular microscope, with a 4× objective and a 9× eyepiece. The numbers in parentheses after the species name are of individuals from which measurements were made.

*Thyanta custator* represents the populations found from Mississippi through coastal Alabama, all of Florida, and the coastal areas (within 75 miles of the shoreline) of Georgia, South Carolina, North Carolina, New Jersey, and New York. I have not examined examples of this species from Connecticut and Massachusetts, where it is said to occur rather sparsely.

*Thyanta pallido-virens* represents populations found in the upland regions of the Atlantic and Gulf states, the Plains states, the Rocky Mountain region, the Southwest, the Pacific coastal area, and Mexico, regardless of subspecific differences and geographical variation.

The table on page 9 gives the arithmetical mean of each of the segmental measurements and the total length of the antennae in the two species.

It is patent from these data that the second and third antennal segments are fairly alike in the two species, although in reverse ratio to each other, but that the fourth and fifth ones are at variance, and that the total lengths of the antennae in *custator* are proportionately greater than



	SEGMENTS				TOTAL
	II	III	IV	V	
<i>Thyanta custator</i> (863)	40.03	38.99	49.30	52.69	181.01
<i>Thyanta pallido-virens</i> (900)	39.66	41.81	44.78	46.75	173.00

those of *pallido-virens*, albeit the total body lengths of the two species are just about equal.

**PRONOTAL MARKINGS:** In the inner corner of each of the two pronotal calli (cicatrices) a distinct black pigment spot appears in all examples of *custator*, which accounts for Fabricius' remark "*Thorace . . . punctisque duobus nigris fasciae contiguïs.*" It will be noted that Stål in his description of *pallido-virens* omitted mention of such markings. Rightfully so, as they do not occur in the typical species or any of the subspecies. In *custator* the size of these maculations varies, but the spots never become so small as to be considered obsolete.

**TRANSHUMERAL COLOR BANDING:** In all the eastern coastal examples of the true *custator*, somewhat more than 87 per cent of the individuals possess a band of reddish or purplish pigment extending across the pronotum between the humeri. Of the remaining 13 per cent of the population, there is evidence of irregular blotching which gradually becomes obsolescent and finally disappears in the last 2 per cent of the cases. On the other hand, in the populations of *pallido-virens* throughout the remainder of the country never more than 45 per cent of the individuals (California) show evidence of such a colored band. Indeed in most of the populations the color band occurs in only 10 or 11 per cent of the individuals (Iowa, Kansas, Oklahoma, and eastward), whereas in some regions, particularly the deep southwestern portion of the United States and northern Mexico, fewer than 1 per cent are so marked. Stål's type specimens are devoid of any transhumeral colored band, hence the absence of any reference to such a band in his original description.

Apparently color banding is a fairly common generic character, as it occurs in several other species besides the two considered here. It is found in *calceata* (Say), *perditor* (Fabricius), and in the Neotropical species such as *patruelis* Stål, *antiguensis* (Westwood), *humeralis* Ruckes, and, to some extent, *maculata* (Fabricius).

**VENTRAL ABDOMINAL MACULATION:** In his description of *custator* Fabricius mentioned "*Abdomen virescens utrinque lineis duabus punctis atris.*" Thus, this species has four rows of black spots on the abdomen, two on each side, the inner row consisting of prominent circular dots, one adjacent to each spiracle, the outer row made up of the succession of

piceous apical angles of the abdominal segments. Such pairs of rows are always present and, although the size of the individual spots may vary, they are usually prominent and never disappear.

On the other hand, in all examples of *pallido-virens* the apical angles of the abdominal segments are never piceous or darkly colored, so that there is never more than one row of black spots on each side. These are the ones adjacent to the spiracles and invariably appear somewhat smaller than the homologous spots in *custator*. In many instances, however, especially in examples from the southwestern United States, northern Mexico, and California northward through British Columbia, all abdominal spots are lacking altogether, leaving the venter totally immaculate.

**TIBIAL PILE:** In none of the examples of *custator* that have been examined have I found a case (with the exception of the form referred to as var. *accerra*) where the pile of the tibiae is, in length, greater than the lateral diameter of the leg segment. In other words, the tibial pile is short, stiff, and somewhat sparsely distributed over the length of the shank. Nor does any exceptionally long pile occur on the femora, rostrum, or antennae. On the other hand, in the typical form of Stål's *pallido-virens* the legs are described as being hairy ("*pedes . . . puberuli*"), which obviously implies the presence of at least a few, if not many, longer setae on parts of the legs, and the shorter pile is usually longer than that found in *custator*. All subspecies of *pallido-virens* show evidence of having some long seta-like hairs interspersed between the shorter pile.

**EXTERNAL MALE GENITALIA:** There is little difference in the last abdominal segment of the male in these two species, but such slight differences as there are may be of importance in the separation of one species from the other. In *Thyanta custator* the apical margin of the genital cup is subtended by a shallow rectilinear impression on the posterior surface. This impression is slightly wider than long, and the lateral edges of it tend to bend gradually vertically towards the apical lateral angles. A similar rectilinear impression appears on the segment in *pallido-virens* but is somewhat more squarish in outline, i.e., almost as long as wide, and the lateral edges bend much more abruptly towards the lateral angles. Comparison of the two species is necessary to observe the differences and appreciate these subtle distinctions. Once seen, the dissimilarities of the two are readily recognizable. There seems to be very little difference in the form of the parameres (claspers) except that those in *custator* are slightly smaller than those of *pallido-virens*.

**ELYTRA:** There appear to be two basic differences in the composition of the elytra in the two species. In *pallido-virens* and its subspecies there occur numerous widely spaced, substellate, pale points scattered on the

elytra in about 99 per cent of the cases examined, whereas in *custator* fewer than 1 per cent show such markings, and then only doubtfully. In most cases the elytron of *custator* terminates apically in a transverse or rounded truncation, so that the end of the corium hardly reaches beyond the middle of the fifth connexival segment. In *pallido-virens*, on the other hand, the apical end of the elytron is usually acutely rounded or even angulated and frequently reaches beyond the middle of the fifth segment; indeed, in a few cases it reaches as far as the anterior margin of the sixth.

SCUTELLAR PROPORTIONS: From hundreds of measurements, it is found that the scutellum of *pallido-virens* is proportionately longer than that of *custator*, the basal widths of the shield being almost identical in the two species. The arithmetical means of the measurements are hereby given:

	WIDTH	LENGTH
<i>Thyanta custator</i> (863)	140.16	150.30
<i>Thyanta pallido-virens</i> (900)	140.10	158.58

PRONOTAL PROPORTIONS: Similarly there appears to be a slight difference in the ratios of length and breadth of the pronotum in the two species. The transverse diameter in all instances is measured across the humeri; the longitudinal measurement is the median length of the segment:

	LENGTH	WIDTH
<i>Thyanta custator</i> (863)	82.70	227.73
<i>Thyanta pallido-virens</i> (900)	80.45	230.11

In *pallido-virens* it is obvious that the pronotum is slightly wider, proportionate to its length, than the homologous part is in *custator*, to wit, a difference of 2.85 to 2.75.

ZONAL RESTRICTION: The fact has been mentioned that *Thyanta custator* appears to be a strictly coastal-plain species and that *T. pallido-virens* is widespread over the remaining part of the country. The two species apparently come into contiguity in the piedmont area of Georgia, South Carolina, North Carolina, and Virginia. It is quite important to understand that at that line of contiguity there are no intermediates (naturally occurring) between these two species. On the east and the south of the piedmont region the true species *custator* occurs, and directly in the piedmont a subspecies of *pallido-virens* makes its appearance. The characteristics just set forth for one species do not appear in

the other. In other words, a strictly maritime species (*custator*) is contained within what is ordinarily considered the Austral Zone, whereas the inland species (*pallido-virens* subspecies) occupies what is otherwise known as the Transitional Zone. If these two forms were subspecific, it would be expected that certain intermediate phases, consisting of individuals bearing the traits of both, would appear. There seems to be a very sharp line of demarcation, however, and, as far as the author has been able to discern, admixtures of the two populations do not occur.

In summation, there seem to be sufficient differences between the two forms to declare them distinct species rather than subspecies of one another. Some 10 features of either structure or distribution have been given wherein the two forms differ and in which distinctions can be established. The probability that 10 morphological and physiological characteristics would mutate at once, so that one type is changed to the other, seems rather remote. Yet we find no cases where, in natural surroundings, one characteristic at a time has changed, and there are no gradual transitions but rather abrupt segregation of the two types.

#### RE-EVALUATION OF SPECIES AND ESTABLISHMENT OF SUBSPECIES

##### *Thyanta custator* (Fabricius)

The characteristics enumerated by Fabricius in his original description suffice to identify this species and differentiate it from other North American forms. In addition there should be mentioned the facts that the general texture of the body is matte, rather than glossy, a character quite common in many Neotropical species of this genus, and that the shape of the body is elongate oval, measuring about 11 mm. by 5 mm. to 5.5 mm.; that the surfaces of the pronotum and scutellum are finely rugose owing to the irregular disposition of the punctures which leaves delicate wavy impunctate lines between them; that the frenum extends no more than two-thirds of the length of the scutellum, leaving about one-third of the scutellum in the form of a "tongue," the margins of which, in general, converge to an evenly and narrowly rounded apex which surpasses the inner angles of the coria; that the lateral margins of the pronotum are vertically rugose and fuscous to piceous in color; that in most cases the membranes of the elytra are provided with small tan or light fuscous dashes along the inconspicuous veins; and that the male genital segment is provided with a minute median notch on its apical margin, below which there is a rectangular impression on the surface of the genital cup.

Unfortunately Blatchley (1926) entirely misconstrued the meaning of

Fabricius' original description. He inadvertently applied to the true species *custator* the characteristics of the subspecies hereinafter referred to as *pallido-virens accerra*. Torre-Bueno (1939) emphasized the fact that the anterolateral margins of the pronotum are neither vertically rugose nor dark colored in *custator*. I have yet to see a specimen of this species that does not have these two combined characters. The use of the keys in either one of these two works leads to improper identification of both *custator* and *pallido-virens*.

*Thyanta pallido-virens* (Stål)

In 1872 Stål questions whether or not his previously described species *pallido-virens* is a variety of *Thyanta custator*. The evidence shows that the two are closely related: there seems to be very little difference in the composition of the male genitalia (a criterion usually used to differentiate species); the general size is alike and the color is not too much at variance; there is a similar matte rugose aspect to the pronotum and scutellum; the head shapes are about the same; and there is no difference in the proportions of the parts of the legs and rostrum. Yet there are so many other somatic characteristics that are not common to the two forms that it is unlikely that they are genetically the same, even to the degree of being subspecific.

The piceous markings so constant and critical in *custator* are entirely lacking in *pallido-virens* (except in part in the subspecies *accerra*); the antennal segmental ratios are not the same; the inconspicuous short pile on the tibiae of *custator* becomes somewhat more noticeable in *pallido-virens* and is frequently interspersed with numerous longer hairs; in *pallido-virens* the anterolateral margins of the pronotum are distinctly pale, usually creamy in color, and the connexivum is provided with bright yellowish or orange markings which are sometimes very conspicuous but are lacking altogether in *custator*; the lateral margins of the tongue of the scutellum tend to be somewhat more parallel rather than convergent, in general the tongue looks slightly longer, and its apex is frequently red; about 99 per cent of the population of *pallido-virens* shows the presence of scattered pale stellate points on the elytra and the scutellum, a character exceedingly rarely seen (less than 1% of the population) in *custator*.

There are four subspecies of *Thyanta pallido-virens*.

When Stål described his species *pallido-virens*, he had before him only two specimens of a vast population that extends from the Pacific coast to the Atlantic states. His description fits exactly those individuals that occur in the limited territory of central California, western Nevada, and

southern Idaho. Beyond that area, populations are found that conform to the basic requirements of the species but differ in enough essential characteristics to cause them to be erected as geographic subspecies. There seem to be three such subspecific populations in addition to the basic species hereinafter referred to as *Thyanta pallido-virens pallido-virens* (Stål).

The most notable and least common of these distinctive populations is that group of individuals found in the more northeastern counties of California and the eastern portions of the states of Oregon and Washington, and in British Columbia. Here the individuals tend to develop long pilose hairs on the tibiae, rostrum, and antennae, yet maintain all other characteristics of the basic species. To this northwestern population has been given the name of *Thyanta pallido-virens setosa*.

The second population consists of those individuals from the southwestern United States and northern and southern Mexico, including the southern counties of California, the states of Arizona, New Mexico, and western Texas, and the states of Sonora and Chihuahua southward to Oaxaca in Mexico. Here the basic characteristics of *pallido-virens* hold but, added to these, are the presence of an orange rather than a yellow band on the abdominal margin and much produced, sharp, spinose, humeral angles. In view of the sharpness of the humeri, this subspecies is hereinafter referred to as *Thyanta pallido-virens spinosa*.

The third and last subdivision of the species includes all the populations of *pallido-virens* eastward to and including the piedmont regions of the eastern states, but not including the coastal plain except in certain sections of North Carolina, Virginia, and Maryland. These individuals do not possess the sharply produced humeri of the southwestern forms nor the excessive pilosity characteristic of the more northwestern subspecies but have added to the basic characteristics of *pallido-virens* a row of small black spots on the sides of the abdominal venter, one spot appearing behind the spiracle of each abdominal segment. Sometimes these spots are rather small and difficult to see, but for the most part they are recognizable though considerably smaller than the homologous structures in *Thyanta custator*. To this subspecific population there must, unfortunately, be assigned the name *Thyanta pallido-virens accerra* (McAtee).

The reason for this is that in 1919 McAtee described a form which he took to be a variety of *Thyanta custator* (Fabricius) and called it var. *accerra*. His type material represents individuals of the subspecies just defined. What McAtee described as a variety of a basic species is apparently only an overwintering generation of individuals not only of the

subspecies mentioned above, but also of the true species *custator* and *Thyanta calceata* (Say) as well. Sailer and I have found that the characteristics enumerated by McAtee (plus two other consistent ones that he missed) are found only in specimens of *Thyanta* that have been collected in the late autumn or very early spring, usually between the last week in September and the first week in April; most specimens, however, bear the collecting dates in October and March. The type series is dated October 15, 1916, October 21, and October 29. Neither Sailer nor I have found dates preceding or exceeding the above-mentioned range. This fact has led us to believe that those forms previously known as var. *accerra* are dimorphic forms that appear with the onset of cold weather and in preparation for hibernation. Below, in the present paper, I call this phase the autumnal-vernal (overwintering) brood.

In 1926, Blatchley elevated McAtee's var. *accerra* to full species rank, thus making it necessary at the present time to apply this name to the subspecies of *pallido-virens* in view of the fact that McAtee's type material is of this subspecies and not of the true *custator* as he inferred.

The very unfortunate part of this story is that the typical examples of the subspecies *pallido-virens accerra* do not at all match the description given by McAtee; only individuals of the overwintering or autumnal-vernal brood so conform.

#### OVERLAPPING OF SUBSPECIFIC POPULATIONS

Relatively little overlapping of the four subspecies is evident. A striking and clear-cut case is that of the populations of *pallido-virens accerra* and *pallido-virens spinosa*. *Thyanta pallido-virens accerra* is characterized by the presence of a single row of black spots on each side of the abdominal venter, but this subspecies does not have sharp spinose humeri. On the other hand, the typical subspecies *spinosa* lacks the abdominal maculations but is provided with sharp spinose shoulders. The range of *accerra* is from the eastern piedmont region westward through the Plains states and northward to North and South Dakota, Montana, and Wyoming, thence southward through the Rocky Mountains. On the other hand, the range of *spinosa* extends from Sonora and Chihuahua in Mexico northward to southern California and Arizona, Nevada, and Utah, and eastward to New Mexico and western Texas.

Examination of several thousand specimens of these two subspecies shows the following statistical data with regard to the occurrence of humeral spinescence and abdominal maculations in the respective populations:

TERRITORY	SUBSPECIES <i>accerra</i>	SUBSPECIES <i>spinosa</i>
Eastern states to Kansas, Nebraska, Oklahoma, and northern Texas	100% maculated 0% spinose	Does not occur
North and South Dakota, Montana, Wyoming, Colorado, and east- ern Utah	90% maculated 10% immaculate 0% spinose	Does not occur
Western Utah and southern and southwestern Nevada	50% maculated 50% immaculate 0% spinose	50% maculated 50% immaculate 100% spinose
Northern and central Arizona, New Mexico, and western Texas	Does not occur	36% maculated 64% immaculate 100% spinose
Southern California	Does not occur	23% maculated 77% immaculate 100% spinose
Southwestern Arizona	Does not occur	15% maculated 85% immaculate 100% spinose
Sonora and Chihuahua, Mexico	Does not occur	Fewer than 2% maculated; in most popula- tions 100% im- maculate and all spinose

The critical area of overlap between these two subspecies seems to be in the vicinity of western Utah and southern Nevada, where half of the population is spinose and the other half is not spinose, and where one-fourth is spinose and maculated, one-fourth spinose and immaculate, one fourth not spinose and maculated, and the remaining fourth not spinose and immaculate. Humeral spinescence does not occur in individuals from territory east and north of this region, but on the other hand maculation seems to carry well into the territory of the subspecies *spinosa*, gradually disappearing as the subspecies extends farther and farther southward and westward. Spinescence appears to be associated with the more arid southwestern desert areas, whereas maculation becomes a characteristic of the more northern and eastern regions.

*Thyanta pallido-virens pallido-virens* (Stål)

In a diagnosis of this basic species mere repetition of Stål's original description need be made. The body form is ovate, densely punctured with scattered small pale points on the elytra; the anterolateral margins of the pronotum are pale, usually the apex of the scutellum is bright red, and the elytral membranes are subvitreous without striking brown or tan



dashes along the veins; the humeri are not excessively produced and tend to be roundly rectangular; the edge of the abdominal venter is narrowly yellow or yellow-orange; the tibiae show some longer, seta-like hairs interspersed with the shorter pile; the abdominal venter is totally immaculate, no post-spiracular black points being present; the ventral abdominal punctures are more numerous and a little coarser laterally than they are on the middle of the disc. The over-all fine rugose texture of the pronotum and scutellum is much like that found in *Thyanta custator*.

As the name coined by Stål implies, the general color of this species is on the paler green side; many specimens have a tendency to become yellowish green. In range the basic species appears to be rather limited to central California, southwestern Idaho, Nevada, and parts of Utah (where it overlaps slightly with the subspecies *accerra*).

HOLOTYPE: Male 9 mm. long, 5.75 mm. wide across humeri; San Francisco.

ALLOTYPE: Female 10 mm. long, 6 mm. wide across humeri; San Francisco.

PARATYPES: None.

The types are deposited in the Riksmuseum, Stockholm, Sweden.

#### ***Thyanta pallido-virens setosa*, new subspecies**

The typical characteristics of *pallido-virens* are present but the antennae, rostrum, femora, and tibiae all become pilose by means of numerous seta-like hairs interspersed with shorter hairs, each of the longer hairs being longer than the lateral diameter of the respective structures to which they are attached. The pile is stiff but fine, easily recognized, and produces a definite hairy effect on the appendicular structures. The margin of the abdomen has a tendency to show considerable orange-yellow color, and the reddish banding on the pronotum frequently becomes intensified. The humeri remain angularly rounded to rectilinear, and the entire body color is pale green. The abdominal venter is devoid of black points; the puncturation is normal.

The distribution of the subspecies is confined to the northwestern portion of the United States and to British Columbia.

HOLOTYPE: Male 9.20 mm. long, 5.5 mm. across humeri; Pullman, Whitman County, Washington; July 21, 1928; deposited in the American Museum of Natural History.

ALLOTYPE: Female 10.0 mm. long, 6.00 mm. wide across humeri; Dayton County, Idaho, July 4, 1937; deposited in the American Museum of Natural History.

PARATYPE MALES (17): *Idaho*: Lenore, May 19, 1937, one. *Nevada*:

Reno, August, 1940, one; Ormsby County, July, 1907, one. *California*: Sierra County, Downieville, July 8, 1952, collector Cazier, 10. *Oregon*: Hood River, July 28, 1921, one. All the above are deposited in the American Museum of Natural History. *British Columbia*: Saanich, May 5, 1918, one; September 9, 1918, one; Goldstream, May 11, 1925, one; Victoria, June 24, 1922, one. All the British Columbia specimens are in the collection of W. Downes.

PARATYPE FEMALES (9): *Idaho*: Emmett, July 29, 1940, one; Kendrick, August 13, 1938, one; Riggins, August 10, 1938, one; St. Maries, August 8, 1940, one. *Nevada*: Ormsby County, July 6, 1907, four; Reno, August, 1940, one. All are deposited in the American Museum of Natural History.

***Thyanta pallido-virens spinosa*, new subspecies**

In this subspecies the humeri become increasingly acute and in many instances, especially in the deeper southwestern and southern portions of its range, appear actually in the form of short spines. The pale edges of the pronotum and the orange-yellow margins of the abdomen become intensified, the orange markings being sometimes very conspicuous. The pile on the tibiae has fewer long, seta-like hairs in its composition than does that of the basic species, and there is little pilosity on the other parts of the legs, rostrum, and antennae. Like *pallido-virens*, this subspecies tends to be pale green to bright green. Reddish markings on the pronotum are usually lacking, fewer than 2 per cent of the population showing any trace of reddish tints.

It is pointed out above that some overlap occurs between this subspecies and the following (*accerra*), as evidenced by the presence of some fuscous or piceous maculations on the abdominal venter. In most cases the post-spiracular points common to *accerra* are rather weak and many times are difficult to discern; sometimes only the anterior two or three abdominal segments bear maculations, and these invariably are of a pale fuscous color; the posterior segments are totally immaculate.

In the many hundred specimens of this subspecies examined I have never found one in which excessive pilosity, such as is exhibited in the autumnal-vernal (overwintering) broods of *T. custator*, *T. calceata*, and *T. pallido-virens* subspecies *accerra*, occurs.

The distribution of this subspecies covers western and southwestern Texas, New Mexico, the southwestern part of Colorado, a good part of Utah and Nevada, all of Arizona and southern California, and at least Sonora and Chihuahua in Mexico.

HOLOTYPE: Male 9.25 mm. long, 5.8 mm. wide across humeri; Patagonia, Santa Cruz County, Arizona, July 23, 1937; collection of H. Ruckes; deposited in the American Museum of Natural History.

ALLOTYPE: Female 10.0 mm. long, 6.20 mm. across humeri; Las Cruces, Dona Ana County, New Mexico, August 28, 1937; collection of H. Ruckes; deposited in the American Museum of Natural History.

PARATYPE MALES (74): *Arizona*: Jacobs Lake, July 24, 1952, 36; Gray Mountain, July 25, 1952, five. *New Mexico*: Red Rock, July 15, 1937, 16; Las Cruces, August 27, 1937, seven. *Sonora*: Minas Nuevas, August 7, 1952, seven; Kino Bay, August 14, 1952, three. All are deposited in the American Museum of Natural History.

PARATYPE FEMALES (50): *Arizona*: Organ Pipe National Monument, June 10, 1952, 11; Ramsey Canyon, Huachuacha Mountains, July 15, 1941, nine. *New Mexico*: Red Rock, July 15, 1937, 10; Las Cruces, August 28, 1937, 10. *Sonora*: Minas Nuevas, August 7, 1952, 10. All are deposited in the American Museum of Natural History.

*Thyanta pallido-virens accerra* (McAtee)

By far the largest population of any subspecies of *pallido-virens* is that to which McAtee's varietal name of *accerra* must be given. The prime characteristic by which it is distinguishable from the basic species is the presence of a single row of post-spiracular black points on each side of the abdominal venter. The spots are invariably larger than those found in some of the population of the subspecies *spinosa* but always smaller than those found in the species *custator*. In this vast population there is some tendency for seta-like hairs to occur on the tibiae but usually less abundantly so than in the typical species, and the pile is much less conspicuous than that found in *pallido-virens setosa* but much more striking than that found in *custator*. Otherwise the basic characteristics, such as the pale lateral margin of the pronotum, the orange-yellow maculation of the abdominal margin, the scattered pale points on the elytra (sometimes obsolescent), the scutellar proportions, and pronotal dimensions, are present.

The distribution of this species covers the major portion of the United States and southern central Canada. In general the range extends from the piedmont area of the central Atlantic states westward to eastern Colorado, Wyoming, Montana, and North and South Dakota, and south-westward through northern Alabama, Mississippi, Louisiana, and most of Texas.

HOLOTYPE: Female; Barachias, Alabama; October 15, 1916; E. G. Holt, collector; deposited in the United States National Museum.

PARATYPES: *Alabama*: Barachias, October 21, 1916 (2). *Texas*: San Antonio, October 29, 1916 (1).

#### KEY TO BROODS

Forms for the most part green or yellow-green, without a pale longitudinal raised linea on the scutellum; lateral margins of head, pronotum, and abdomen devoid of seta-like pubescence; humeri rectilinear, angulated or spinose but not bluntly rounded. Collecting dates range from April to October. . . . .

. . . . . summer broods  
Forms for the most part tan, brownish, or olivaceous, with a pale longitudinal raised linea on the scutellum; lateral margins of head, pronotum, and abdomen provided with a delicate halo of wide-spaced, seta-like hairs; humeri bluntly rounded; pronotum, scutellum, and elytra provided with a scattering of well-defined pale points; abdominal incisures bordered with a narrow, dark brown band of color; tibia strongly setose. Collecting dates range from October to April. . . . . autumnal-vernal broods

#### KEY TO SUMMER BROODS

1. Anterolateral margin of the pronotum, apical angles of the abdominal segments, a row of prominent post-spiracular points on each side of the abdominal venter, and a point in the inner angle of each pronotal cicatrice piceous; humeral angles rectilinear to acute spinose; elytra usually without scattered pale points; appendicular pile inconspicuous, consisting of short stiff hairs, in length less than the diameter of the tibiae. . . . . 2  
Anterolateral margins of the pronotum and apical angles of the abdominal segments pale or concolorous; with or without a row of post-spiracular black points on each side of the abdominal venter; no black points in the inner angles of the pronotal cicatrices; elytra usually provided with scattered pale points; appendicular pile varied, frequently provided with interspersed longer, seta-like hairs; humeri roundly rectilinear to acutely spinose . . . . . 4
2. Anterolateral margins of pronotum distinctly concave; humeral angles strongly produced outward and forward and terminating in strong spines; length, 10 mm. to 14 mm. Florida, Mexico, West Indies, Central and South America. . . . . *perditor* (Fabricius), 1794  
Anterolateral margins of pronotum straight or nearly so; humeral angles not much produced, rectilinear to acute; length, 7 mm. to 10 mm. . . . . 3
3. Form somewhat elongate oval; tip of scutellum surpassing the inner angles of the coria; tongue of the scutellum one-third of the length of the scutellum; apical margin of the male genital segment provided with a minute median notch in its transverse border and subtended by a clearly defined rectangular impression on the cup. Coastal area of the Gulf states and the Atlantic seaboard to New York. . . . . *custator* (Fabricius), 1803

- Form more broadly ovate; tip of scutellum just about reaching the inner angles of the coria; tongue of scutellum one-fourth of the length of the scutellum; apical margin of male genital segment provided with a minute, median, erect tubercle on its transverse border and subtended by a vague semicircular impression on the cup. Virginia, North and South Carolina, Georgia, Florida, Alabama, eastern Texas, Arkansas to Illinois. . . . . *calceata* (Say), 1831
4. Abdominal venter immaculate, i.e., no row of post-spiracular black points on each side . . . . . 5
- Abdominal venter provided with a row of post-spiracular small black points on each side . . . . . 7
5. Humeral angles conspicuously produced into acute to spinose tips; appendicular pile with only a few, if any, long, seta-like hairs interspersed with the shorter hairs, each long hair, when present, longer than the diameter of the tibia. Western Texas, New Mexico, Arizona, southern California, Chihuahua, Sonora, and southward to Oaxaca. . . . . *pallido-virens spinosa*, new subspecies
- Humeral angles not produced into acute or spinose tips, usually slightly rounded or rectangular; appendicular pile with a few or many long, seta-like hairs interspersed with the shorter hairs, each longer than the lateral diameter of the tibia . . . . . 6
6. With only a few interspersed, long, seta-like hairs on the tibia, none on the rostrum, antennae, or femora. Central and western California, western Nevada, and southwestern Idaho. . . . . *pallido-virens pallido-virens* (Stål), 1859
- With numerous interspersed, long, seta-like hairs on the tibia as well as on the femora, rostrum, and antennae. Northeastern counties of California, Oregon, Washington, and British Columbia (western Great Basin). . . . . *pallido-virens setosa*, new subspecies
7. Humeral angles weakly rounded to rectangular, not much produced. Central, northern, and southern areas of the United States and southern Canada not inhabited by other subspecies; eastward to the Appalachian piedmont behind the coastal plains . . . . . *pallido-virens accerra* (McAtee), 1919
- Humeral angles conspicuously produced into acute to spinose tips. Western Utah, southern and southwestern Texas, western Texas, northern and central Arizona, and New Mexico . . . . . *pallido-virens spinosa*, new subspecies

KEYS TO AUTUMNAL-VERNAL BROODS

1. Anterolateral margin of pronotum, apical angles of the abdominal segments, a row of prominent post-spiracular points on each side of the abdominal venter, and a point in the inner angle of each pronotal cicatrice piceous . . 2
- Anterolateral margin of pronotum pale or concolorous; no black points in the pronotal cicatrices; post-spiracular black points small and inconspicuous. (Previously known as *T. custator* var. *accerra* McAtee.) Distribution same as the summer broods. . . . . *pallido-virens accerra* (McAtee), 1919

2. Form elongate oval; tip of scutellum surpassing the inner angles of the coria; tongue of the scutellum one-third of the length of the scutellum; apical margin of the male genital cup provided with a median minute notch and subtended by a clearly defined rectilinear impression on the surface of the cup. Distribution same as that of the summer broods. . . . . *custator* (Fabricius), 1803
- Form more broadly ovate; tip of scutellum just about reaching the inner angles of the coria; tongue of the scutellum one-fourth of the length of the scutellum; apical margin of the male genital cup provided with a minute erect tubercle and subtended by a vague semicircular impressed area on the face of the cup. Distribution same as that of the summer broods. . . . . *calceata* (Say), 1831

### SUMMARY

1. About 8000 specimens of both *Thyanta custator* (Fabricius) and *Thyanta pallido-virens* (Stål) were studied.

2. *Thyanta custator* and *Thyanta pallido-virens* are not subspecific but two distinct species difficult to differentiate from each other.

3. *Thyanta custator* is restricted in its distribution to a territory extending roughly along the maritime portions of the Gulf states and the Atlantic seaboard northward to at least Long Island, New York, and in itself is not very variable.

4. *Thyanta pallido-virens* is a very plastic species and has, in addition to the basic species *T. pallido-virens pallido-virens* (Stål), at least three subspecific (geographical) populations: *T. pallido-virens setosa*, new subspecies; *T. pallido-virens spinosa*, new subspecies; and *T. pallido-virens accerra* (McAtee).

5. The phase previously described by McAtee as *Thyanta custator* var. *accerra* is apparently an autumnal-vernal (overwintering) dimorphic seasonal generation occurring in the species *pallido-virens*, *custator*, and *calceata*.

6. If the contents set forth in the foregoing article are accepted, a great part of the literature and bibliography dealing with these species must be revised.

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