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# The Geographic Variation of Saperda Inornata Say (Coleoptera: Cerambycidae) in Eastern North America

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# THE GEOGRAPHIC VARIATION OF *SAPERDA INORNATA* SAY (COLEOPTERA: CERAMBYCIDAE) IN EASTERN NORTH AMERICA

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During the summers of 1962 and 1963 a study of the life history and behavior of what was thought to have been *Saperda moesta* LeConte in trembling aspen, *Populus tremuloides* Michaux, was completed in northern Michigan (Nord, 1968). After the field study, it became apparent that the original identification was doubtful. Furthermore, there was a possibility that two species were present in the study areas, thus the biological data collected may have represented not one but two species.

Two species of *Saperda* with similar habits had been reported to occur in *P. tremuloides: S. moesta,* a dark species, and *S. inornata,* a light species. The species under study was determined to be *moesta* mostly on the basis of what was considered to be a more reliable and consistent character than color, i.e. the shape of the egg-niche which the female gnaws in the host. The egg-niches of the study insect were U-shaped like those reported for *moesta,* not longitudinal slits as Hamilton (1888) reported for *S. concolor* (probably the eastern var. *unicolor = inornata*) in Pennsylvania. Although most of the few adults reared from *tremuloides* were light like *inornata,* there were darker specimens also. Therefore, the lighter individuals were considered to be only color variants of *moesta.*

After three summers, one, 1963, assisting Knight and two on this project, during which several thousand aspen suckers and twigs from larger trees were examined in several areas of Michigan and northern Wisconsin, it seemed odd that not a single *inornata (= concolor)* type egg-niche had been seen. After a second examination of the literature, it became apparent that the purported difference (Hamilton, 1888) between the egg-niches of *moesta* and eastern *concolor (= inornata)* was probably not reliable. Hamilton described the oviposition and egg-niche of *S. fayi* Bland in *Crataegus* spp., although he stated he did not see oviposition or eggs. Using almost the same words, he described these for *S. concolor* in *Salix longifolia,* "... the beetle makes a longitudinal incision through the bark with her jaws about three-fourths of an inch in length, and in each end deposits an egg." *S. fayi* does make longitudinal oviposition incisions and from his writing it is apparent that he assumed, erroneously, that the niches of *S. concolor* were like those of *S. fayi.* Felt and Joutel (1904), Peirson (1927), Harrison (1959), and Graham, *et al.* (1963) either quoted or paraphrased Hamilton's statement, thus perpetuating the error. Wong and McLeod (1965) were the first to note that both *moesta* and *concolor (= inornata)* made U-shaped egg-niches.

Now that the U-shaped egg-niche was determined not to be an exclusive character of *S. moesta* and because the beetles reared from *P. tremuloides* were more similar to *S. inornata,* the latter species name was considered to be most appropriate. This still did not rule out the possibility that two very similar species, separated only by slight morphological differences, might be present on *P. tremuloides* in the study areas. And because it was not yet possible to distinguish them by their egg-niches, galleries, or morphology, the biological data collected may represent not one but two species.

Considering the great similarity of the two morphs and the indication that there was considerable variation in the small sample of adults collected in this study, the following hypothesis was made: there is only one species of gall-making *Saperda* on species of *Populus* and *Salix* in eastern North America. The reported morphological variation in the literature, probably accounting for some of the nomenclatural confusion (Nord and Knight, 1972), and seen in our specimens might be attributable to geographic or local variation or to host plant interaction. It did not seem likely, even if two or more divergent populations had come about through geographic isolation, that two or more

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species were now living synchronously and sympatrically on the same host plants and exhibiting such similar activities without consistent morphological differences, even subtle ones. To shed some light on this hypothesis concerning the number of species present in the study areas, a study of the geographic variation of beetles collected during this study, supplemented by museum specimens from various parts of the range, was made.

## LITERATURE SURVEY

*SAPERDA INORNATA* SAY (= *CONCOLOR* LeCONTE).–The description and the nomenclatural status of *S. inornata* are given by Nord and Knight (1972).

*S. MOESTA* LeCONTE.–*S. moesta* was described in 1850 by LeConte (in Agassiz and Cabot. 1850). The original description follows:

> "*S. moesta.*–Nigra cinereo-pubescens, grosse confertim punctata, thorace latitudine vix breviore, basi leviter angustato, cinereo-bivittato, elytris apice rotundatis, antennis copore brevioribus annulatis, basi nigris. Long. .5. Pic."

He added, "The claws are entire, although at first view it would seem to be a *Phytoecia;* the head has a black, finely impressed frontal line. The eyes are almost divided." The type specimen is located in the Museum of Comparative Zoology, Harvard University. The type locality is the north side of Lake Superior (LeConte, 1852) and no host is given. It has since been reported living in several species of *Populus.*

Felt and Joutel (1904) considered *S. moesta* a variety of *S. populnea* Linne, a species found in Europe and in the Pacific Northwest. They described *S. populnea* as follows:

> "Black, shining, coarsely and deeply punctured, the punctures often contiguous and confluent on the eyltra; a few punctulations which are sometimes wanting occurring between the punctures; sparsely covered with a light gray or fulvous pubescence; thorax with a lateral band of dense fulvous or yellowish gray hairs; elytra with eight small spots of dense fulvous or yellowish hair, arranged in pairs, the first and third nearer the suture, the third pair being the largest; one or more pairs often obsolete, the third pair being the most permanent; antennae black, annulated with gray, first joint black."

They described *moesta* as ". . . like *populnea;* but the vestiture is a uniform light gray without spots, and the lateral line on the thorax only faintly shown. The punctulations on the intervals between the punctures are more numerous than in *populnea.*" Breuning (1952) called *moesta* a subspecies of *populnea.*

## METHODS

Collections from major museums throughout the range of *P. tremuloides* and several bordering states were assembled. Specimens were compared and classified on the basis of external morphological characteristics. However, once the specimens were thus classified, the male and female genitalia and the mesonotal stridulatory file were compared between typical specimens in the two major morphological categories.

Museum specimens and some of those reared during the present study were sent to Dr. John F. Lawrence at Harvard University who compared them with LeConte's type-specimens of *S. concolor* (= var. *concolor* Felt and Joutel) and *S. moesta.* Some of the museum specimens were considered by him to be like the *concolor* type and others like the *moesta* type. Similar specimens were also sent to Dr. John A. Wilcox of the New York State Museum who compared them with Felt and Joutel's type-specimen of *S. concolor* var. *unicolor.* Nord made similar comparisons with the type of *unicolor.* Specimens reared in this study were also sent to Mr. Josef N. Knull of Ohio State University and Dr. John A. Chemsak of the University of California at Berkeley, both of whom identified them as var. *unicolor* (= *inornata* Say).

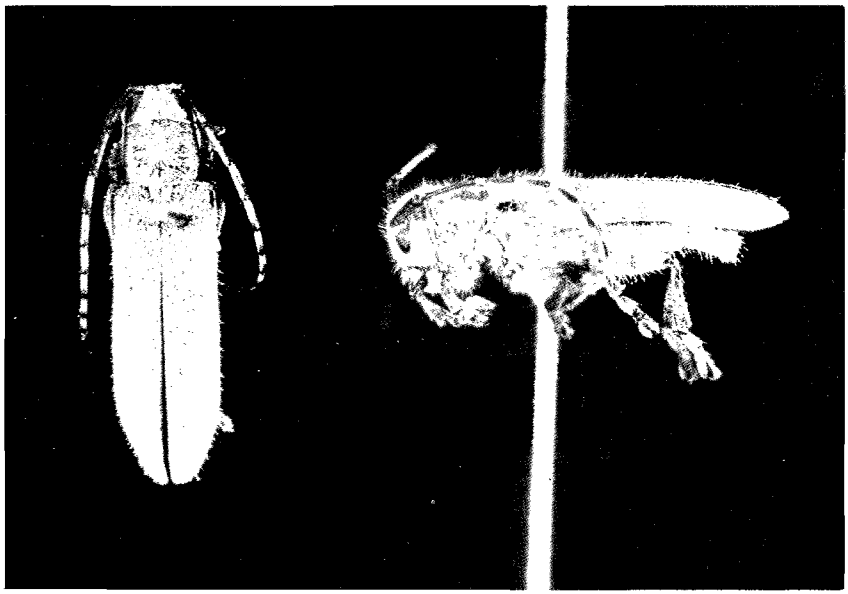

Fig. 1. Light *inornata* adults (= *S. inornata*).

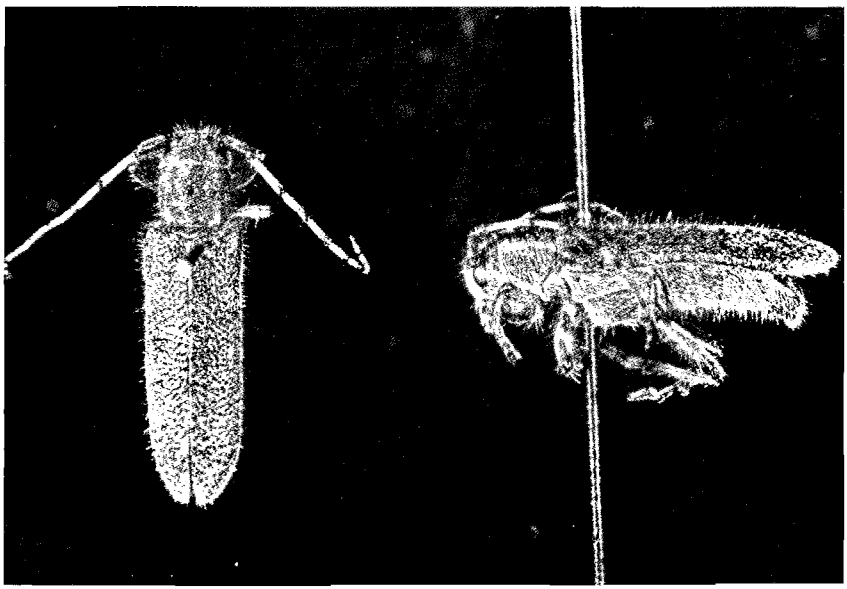

Fig. 2. Dark *inornata* adults (= *S. moesta ?*).

## RESULTS

MORPHOLOGY.–Because of the paucity and great variability of material available from western North America, little can be said about the situation there. However, there were enough specimens from eastern Canada and the northern U.S. east of the Mississippi River to establish a range of geographic variation. Although the general lack of host data, the small size of most collections, and the large gaps between the collection areas prevents one from arriving at positive suggestions, a description of the geographic variation in eastern North America and speculation on the number of species should be of interest to other workers.

The great majority of the eastern specimens fell into two rather distinct groups, which agreed closely with Felt and Joutel's (1904) descriptions of *S. concolor* var. *unicolor* (= light *inornata* Say of this study) (Nord and Knight, 1972) and *S. moesta* (= dark *inornata* Say of this study). The remainder were intermediate. Distinguishing characteristics of the two groups into which most specimens fell were:

1. Covered with dense, ash gray procumbent pubescence giving it an ash gray macro-color (Fig. 1). Elytra with short (0.08-0.56 mm; ave. 0.18 mm) white, suberect hairs (Fig. 1) and shallow punctures which are partly contiguous and partly confluent . . . . . light *inornata*.

1′. Procumbent pubescence sparse to very sparse and the brown to black ground color of the integument clearly visible giving it a very dark macro-color (Fig. 2). Elytra with longer (0.16-0.56 mm; ave. 0.36 mm), brownish to black suberect hairs (Fig. 2) and deep distinct punctures which are partly contiguous and partly confluent . . . . . dark *inornata*.

The light *inornata* specimens were a little larger than those of dark *inornata*. The females and males of light *inornata* averaged 9.9 mm and 8.5 mm in length, respectively, while those of dark *inornata* averaged 9.3 and 8.3 mm, respectively. Except for the suberect hairs, the characteristics in the above couplet were cited by Felt and Joutel (1904) as distinguishing *concolor* var. *unicolor* (= light *inornata*) from *moesta* (= dark *inornata*). All other characteristics mentioned by them or recorded in the present study were quite variable. The ground color varied from brown to black in both light *inornata* and dark *inornata*, but it was locally consistent. No differences in male or female genitalia were found between those assigned to light *inornata* or dark *inornata*.

The mesonotal stridulatory files of a small sample of males and females of dark and light *inornata* were compared. The size of the file varied with the size of the beetle, larger beetles having larger files. Larger beetles also had larger teeth or a smaller number per unit length. Comparing individuals of light *inornata* with those of dark *inornata* of the same sex and of similar size, there was very little difference in the number of teeth per unit length, and the files of one group were not consistently larger than those of the other. Measurements of a large number may show significant differences. Recordings and analyses of their sounds should be helpful.

Specimens intermediate in form, i.e. showing characteristics of both light and dark *inornata* in all combinations of the three main characters were also found, especially in Michigan and Canada. Their lengths averaged the same as light *inornata* for females (9.9 mm) but slightly larger than light *inornata* for males (8.7 mm). Because northern light *inornata* and some northern dark *inornata* were larger than southern individuals, and most of the intermediates were from Canada, this slightly larger size is not surprising.

According to Dr. Wilcox (*in litt.*) and by Nord's own comparison, Felt and Joutel's type of var. *unicolor* fits the description for light *inornata* in the couplet above. Seven specimens which were light *inornata*, using the above criteria, were compared with the type-specimen of *concolor* var. *unicolor* and all were conspecific with it, according to Dr. Wilcox. Five of these specimens were reared from hybrid aspens and trembling aspen in this study. Nord also found the *unicolor* type to be conspecific with light *inornata* of this study. The *unicolor* type was a female, ash gray in macro-color, 10.5 mm long and

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Table 1. Number of dark, light, and dark-light intermediate *inornata* reared from or associated* with each host species.

| State or Province | Dark *inornata* — Host Species | | | | Light *inornata* — Host Species | | | | | | Dark-light *inornata* intermediates — Host Species | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *P. tremuloides* | *P. blasamifera* | *Populus* sp. | *Salix* spp. | *P. tremuloides* | *P. balsamifera* | *P. grandidentata* | *Populus* sp. | *P.* hybrids | *Salix* spp. | *P. tremuloides* | *P. balsamifera* | *Populus* sp. | *P.* hybrids | *Salix* spp. |
| Alaska | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | . . | (1) |
| Connecticut | . . | . . | . . | . . | 5 | . . | (1) | (2) | . . | 3(2) | . . | . . | . . | . . | (1) |
| Illinois | . . | . . | . . | . . | . . | . . | . . | . . | . . | 21(5) | . . | . . | . . | . . | (1) |
| Massachusetts | . . | . . | . . | . . | (1) | . . | . . | 1(2) | . . | . . | . . | . . | . . | . . | . . |
| Michigan | . . | 21 | . . | . . | 43 | . . | . . | . . | . . | 4(1) | 46 | 5 | . . | . . | . . |
| Pennsylvania | . . | . . | . . | . . | . . | . . | . . | . . | . . | (2) | . . | . . | . . | . . | (1) |
| Wisconsin | . . | . . | . . | . . | . . | . . | . . | . . | 8 | . . | . . | . . | . . | 1 | . . |
| Manitoba | . . | 1 | . . | (1) | . . | . . | . . | . . | . . | 1(1) | . . | 3 | . . | . . | 3(2) |
| Ontario | 2 | (11) | . . | . . | 5 | . . | . . | . . | . . | . . | 14(3) | . . | . . | . . | (1) |
| Quebec | . . | (8) | . . | (1) | 1 | . . | . . | . . | . . | . . | 2(5) | (2) | . . | . . | . . |
| Saskatchewan | . . | 3 | . . | . . | . . | . . | . . | . . | . . | . . | (1) | 1 | . . | . . | . . |
| Yukon Territory | . . | . . | (16) | . . | . . | . . | . . | . . | . . | . . | . . | . . | (4) | . . | . . |
| N. W. Territory | . . | . . | . . | . . | . . | . . | . . | . . | . . | (1) | . . | . . | . . | . . | . . |
| Totals | 2(0) | 25(19) | 0(16) | 0(2) | 54(1) | 0(0) | 0(1) | 1(4) | 8(0) | 29(12) | 62(9) | 9(2) | 0(4) | 1(0) | 3(7) |

*Taken on or reared(?) from—number in parenthesis; the other number is the number of reared specimens.

3.0 mm wide, with shallow partly contiguous and partly confluent elytral punctures and medium length (0.30 mm) white, suberect hairs on the elytra.

According to Dr. Lawrence, LeConte's type of *moesta* fits the above description for dark *inornata*. The ground color was brown. The elytral punctures were contiguous as in a Goderich, Ontario, specimen and as deep as those on a Buffalo, New York, specimen, which were deep and distinct. The suberect hairs on the elytra of the type were longer and darker than those of light *inornata*. We have not seen this type.

## HOST AND LOCATION

HOST.–Not many of the dark *inornata* museum specimens had host records. Of those that did, all but 20 were taken on or reared from balsam poplar, *P. balsamifera* L. (Table 1). Sixteen of these were taken on *Populus* sp. which could have been *P. balsamifera*. Two specimens were marked "reared from *P. tremuloides*," one had a "*Salix discolor*" Muhl. (pussy willow) label, and one had a "*Salix* sp." label. Twenty-five specimens were labelled "reared from *P. balsamifera*," and 19 others were either taken from the foliage or reared from *P. balsamifera*.

There were more host records for light *inornata* specimens (Table 1). These were from *P. tremuloides, P. grandidentata* Michaux (bigtooth aspen), *Populus* sp., *Populus* hybrids, *Salix longifolia* (= *S. interior* Rowlee, sandbar willow), and *Salix* sp. Table 1 also shows the host records for the intermediates.

Felt and Joutel (1904) stated that, as far as known, *moesta* (= dark *inornata?*) had been reared only from *P. balsamifera*. With the exception of one collection from *P. tremuloides*, Wong and McLeod (1965) found *moesta* (= dark *inornata?*) only in *balsamifera* and never in willows, and they found *concolor* (= light *inornata*) mainly in willow and rarely in *tremuloides*. Both morphs occurred in their respective hosts growing in the same area (Wong, *in litt.*). It should be noted, however, that 10 of the 17 specimens with host records of Wong from Manitoba and Saskatchewan which were examined in this study were intermediate between light and dark *inornata* according to the above criteria. Although those reared from *P. balsamifera* as a rule were darker in macro-color than those reared from willow, they had much more procumbent pubescence than dark *inornata* from eastern Ontario, western New York, and Michigan.

The published host records which list *moesta* (= dark *inornata?*) from hosts other than *P. balsamifera* (Beutenmuller, 1896; Peirson, 1927; and Harrison, 1959) and one which lists *concolor* (= light *inornata*) from *balsamifera* (Cosens, 1914) are considered doubtful because no mention was made of reared specimens; and their criterion of distinguishing the morphs on the basis of egg-niche characteristics was found to be invalid in the present study. In other words, the "*moesta*" records could have been either dark or light *inornata*. Therefore, the evidence indicates that the dark *inornata* form is likely specific to *P. balsamifera*, and the light *inornata* form is likely specific to certain species of willow and to trembling aspen, *P. tremuloides*.

LOCATION.–Most of the dark *inornata* forms from the collections were found within the known range of *P. balsamifera* and *P. tremuloides* (Fig. 3). The continuous range of *P. balsamifera* occurs over much of Canada and, in the United States, across northern Minnesota and Wisconsin, most of Michigan, the Buffalo area and the Adirondacks in New York State, and across most of Vermont, northern New Hampshire, and most of Maine (Fowells, 1965). It also occurs in several small disjunct areas to the south. All but 11 specimens of the typical dark *inornata* form came from locations north of the southern boundary of the continuous range of *balsamifera*. Two of the 11 were from Erie County, Pennsylvania, and one was from Rensselaer County, New York, both of which fall within disjunct areas of the range. One each from St. Lawrence and Albany Counties, New York, and two from Olmstead County, Minnesota, were close to the southern extension of *balsamifera*. The other four, two from Galesburg, Illinois, and two from Atlantic City, New Jersey, were found well below the known range of *balsamifera*. None of these 11 had host records, and it is possible that they too were collected from *P. balsamifera*.

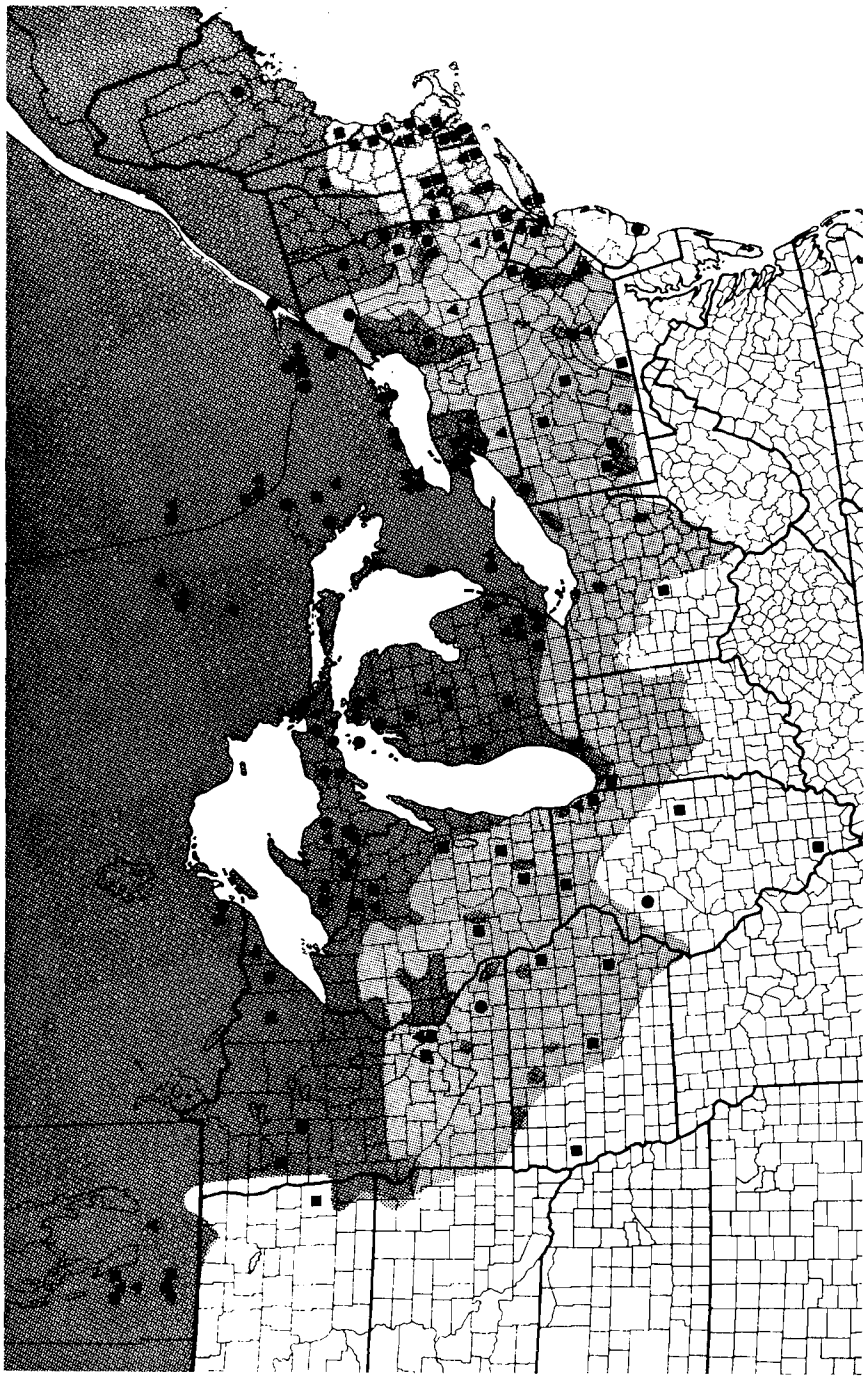

Fig. 3. Distribution of *S. inornata* in relation to the distribution of *P. tremuloides* (entire shaded area of map) and *P. balsamifera* (darkly shaded areas only) in southeastern Canada and northeastern United States. Squares, light form of *S. inornata;* circles, dark form; triangles, intermediate forms. Tree distributions from Fowells, 1965.

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Table 2. Number of light, dark, and intermediate* *inornata* collected south of the continuous range of *Populus balsamifera*.

| State | Light *inornata* | Intermediates more . . . | | | | | | Sum | Dark *inornata* | Grand Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | | . . . like light *inornata* | | | . . . like dark *inornata* | | | | | |
| | 2-2-1 | 2-1-1 | 3-2-1 | 2-2-2 | 3-1-1 | 2-1-2 | 3-2-2 | | 3-1-2 | |
| N. Dakota | 4 | . . | . . | . . | . . | . . | . . | 0 | 0 | 4 |
| Minnesota | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 7 |
| Wisconsin | 10 | . . | . . | . . | . . | . . | . . | 0 | 0 | 10 |
| Iowa | 5 | . . | . . | . . | . . | . . | . . | 0 | 0 | 5 |
| Illinois | 154 | 5 | 0 | 0 | 2 | 0 | 0 | 7 | 2 | 163 |
| Indiana | 2 | . . | . . | . . | . . | . . | . . | 0 | 0 | 2 |
| Michigan | 0 | . . | . . | . . | . . | . . | . . | 0 | 0 | 0 |
| Ohio | 1 | . . | . . | . . | . . | . . | . . | 0 | 0 | 1 |
| Pennsylvania | 95 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 100 |
| New Jersey | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 5 |
| New York | 56 | 5 | 5 | 0 | 0 | 1 | 0 | 11 | 3 | 70 |
| Connecticut | 33 | 2 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 36 |
| Rhode Island | 5 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 6 |
| Massachusetts | 52 | 2 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 55 |
| New Hampshire | 3 | . . | . . | . . | . . | . . | . . | 0 | 0 | 3 |
| Maine | 1 | . . | . . | . . | . . | . . | . . | 0 | 0 | 1 |
| Total | 427 | 18 | 7 | 0 | 3 | 1 | 1 | 30 | 11 | 468 |
| Percent | 91.2 | . . | . . | . . | . . | . . | . . | 6.4 | 2.4 | 100.0 |

*Intermediates indicated by code number of the 6 possible combinations of the three principle distinguishing characters: Macro-color–2, ash gray; 3, brown to black. Elytral punctures–1, deep; 2, shallow. Suberect Elytral Hair–1, white (usually short); 2, dark (usually long).

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Table 3. Number of light, dark, and intermediate* *inornata* collected north of the southern boundary of the continuous range of *Populus balsamifera.*

| State or Province | Light *inornata* | Intermediates more . . . | | | | | | Sum | Dark *inornata* | Grand Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | | . . . like light *inornata* | | | . . . like dark *inornata* | | | | | |
| | 2-2-1 | 2-1-1 | 3-2-1 | 2-2-2 | 3-1-1 | 2-1-2 | 3-2-2 | | 3-1-2 | |
| Minnesota | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 5 |
| Wisconsin | 9 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 10 |
| Michigan | 68 | 14 | 5 | 31 | 3 | 5 | 4 | 62 | 56 | 186 |
| New York | 3 | 0 | 1 | 1 | 0 | 0 | 6 | 8 | 44 | 55 |
| New Hampshire | 1 | . . | . . | . . | . . | . . | . .. | 0 | 0 | 1 |
| Maine | 0 | . . | . . | . . | . . | . . | . . | 0 | 7 | 7 |
| Labrador | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 |
| New Brunswick | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 7 | 9 |
| Quebec | 1 | 0 | 0 | 7 | 0 | 0 | 3 | 10 | 33 | 44 |
| Ontario | 15 | 1 | 4 | 34 | 3 | 15 | 12 | 69 | 64 | 148 |
| Manitoba | 4 | 0 | 0 | 9 | 0 | 1 | 4 | 14 | 4 | 22 |
| Saskatchewan | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 3 | 5 |
| N. W. Territory | 1 | . . | . . | . . | . . | . . | . . | 0 | 3 | 4 |
| Yukon Territory | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 | 17 | 21 |
| Alaska | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 |
| Total | 105 | 15 | 11 | 86 | 6 | 23 | 35 | 176 | 240 | 521 |
| Percent | 20.1 | . . | . . | . . | . . | . . | . . | 33.8 | 46.1 | 100.0 |

*See footnote, Table 2.

South of the southern boundary of the continuous range of *balsamifera,* most of the specimens (91.2%) were of the light *inornata* form (Fig. 3). In fact, these specimens, including large series from Illinois, Pennsylvania, the New York City area, Connecticut, and Massachusetts, are remarkably similar morphologically. Only a small percentage (6.4%) of the specimens from this region were intermediate and most of them were more like light *inornata* than dark *inornata.* Table 2 shows the number of specimens collected south of the continuous range of *balsamifera* by each of eight categories of possible combinations of the three principle distinguishing characters. Of the 30 intermediate specimens, 25 were more similar to light *inornata* than to dark *inornata.*

North of the continuous southern extension of *balsamifera,* there was much more variation. Most of the intermediates were found there (Fig. 3). Of all the specimens found in this region, 33.8 percent were intermediates (Table 3), 20.1 percent were of the light *inornata* form and 46.1 percent were of the dark *inornata* form. The proportion of light *inornata*-like intermediates to dark *inornata*-like intermediates was about two to one as compared to five to one to the south. In only a few locations both light and dark *inornata* forms were represented, and then, except for Iron County, Michigan, only one or two of the "odd" form occurred. More detailed observations need to be made in these specific areas.

In the present study, which was concerned with one host species, *P. tremuloides*, only light *inornata* and intermediate forms were found. This was also true of a larger series of specimens reared from *tremuloides* in Iron County, Michigan, by Grimble. Of a total of 89 specimens reared in this study and by Grimble from *tremuloides,* 44 were typical of light *inornata* and 45 were intermediates, 37 of the latter were closer to light *inornata* than to dark *inornata* (Table 4). All intermediate combinations of the three main characters occurred but not one typical dark *inornata* was found in *tremuloides.*

In 1967, Grimble reared 26 specimens from *balsamifera* in Iron County, Michigan. Twenty-one were like dark *inornata* and five were intermediate, three of which were closer to light *inornata* than to dark *inornata* (table 4). No typical light *inornata* specimens were found in *balsamifera.*

In summary the following was found in this study of preserved specimens:

1. Most of the specimens could be assigned to one or two distinct groups or morphs, the dark form to dark *inornata* (fitting the description of *moesta*), and the ash gray form to light *inornata* (fitting the description of *concolor* var. *unicolor*). The remainder were intermediates, which in total, showed all combinations of the three main distinguishing characteristics.

2. Three main host species were evident: *P. balsamifera, P. tremuloides,* and *Salix* spp. Host records were very few. Of those available, most of the dark *inornata* individuals were reared from or associated with *P. balsamifera,* while most of the light *inornata* individuals were reared from or associated with *P. tremuloides* or *Salix* spp.

Table 4. *Saperda* specimens reared from *P. tremuloides* and *P. balsamifera** in Upper Michigan.

| County | Light *inornata* | Intermediates† more . . . | | | | | | Total | Dark *inornata* | Grand Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | | . . . like light *inornata* | | | . . . like dark *inornata* | | | | | |
| | 2-2-1 | 2-1-1 | 3-2-1 | 2-2-2 | 3-1-1 | 2-1-2 | 3-2-2 | | 3-1-2 | |
| Iron | 38 | 6(3) | 2 | 24 | 1(2) | 5 | 1 | 39(5) | (21) | 77(26) |
| Dickinson | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 4 |
| Ontonogan | 4 | 0 | 1 | 2 | 0 | 0 | 1 | 4 | 0 | 8 |
| Total | 44(0) | 6(3) | 4(0) | 27(0) | 1(2) | 5(0) | 2(0) | 45(5) | 0(21) | 89(26) |

*Specimens reared from *P. balsamifera* in parentheses; others reared from *P. tremuloides.*
†See footnote for Table 2.

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3. All dark *inornata* specimens except 11 were from north of the southern edge of the continuous range of *balsamifera*. South of this line almost all specimens were light *inornata* and a few were intermediates, most of which were more like light *inornata* than dark *inornata*. North of the line, both dark and light *inornata* occurred along with most of the intermediates.

4. All of the 89 specimens reared from *tremuloides* in this study and Grimble's (1966) were like light *inornata* or intermediates. Most of the intermediates were more like light *inornata* than dark *inornata*. The typical dark *inornata* form was not found in *P. tremuloides* in either study.

5. Of 26 specimens reared from *P. balsamifera* by Grimble, 21 were typical dark *inornata*, 5 were intermediates. Three of the intermediates were closer to light *inornata* than to dark *inornata*, but no typical light *inornata* forms were found in *balsamifera*.

## DISCUSSION

There are two possible explanations for this pattern of geographic variation. (1) There are two species present—a more northern species, represented by the dark *inornata* morph (perhaps *moesta*), which is more or less host specific to *balsamifera*; and a more southern species, represented by the light *inornata* morph, which is more or less host specific to *tremuloides* and *Salix* spp. In the northern areas where both forms have been found and where all three host species occur, often in the same stand, intermediates commonly occur. This could be due to hybridization or intraspecific variation, but one would expect two closely related species to become more distinct in such areas. (2) There is just one eastern species of gall-forming *Saperda, S. inornata,* which lives on *balsamifera, tremuloides,* and *Salix* spp. and which varies in color and possibly size according to which host and in what part of the country it matured. In the northern areas where all three hosts occur, there is much morphological variation, from the dark-colored *inornata* form, living in *balsamifera*, and intergrading to the light *inornata* form, living in *tremuloides* or *Salix* spp. In the southern part of the range where only *P. tremuloides* or only *Salix* occurs, there is less morphological variation among the adults which are almost always light *inornata*.

The pattern of geographic variation does not clearly suggest how many species are present, although all data taken together suggest one species as the most parsimonious present choice. Mayr (1963) states that the variability within infra-species populations is greater near the center of the species range and decreases toward the periphery. In the case of *Saperda inornata* (assuming one species to be present) variability is greatest in Michigan and Ontario where dark and light *inornata* occur along with intermediate forms. In the southern part of the range, the variability is much less; almost all specimens are light *inornata*. It is possible that this decreased variability is a response to the simplification of the environment to the south, namely, a) the absence of one of the host species, *balsamifera,* in most of the United States portion of the range, and b) the absence of *tremuloides* also in the southern-most portion of the range.

The presence of all distinguishing dark *inornata (= moesta ?)* characteristics, dark macro-color, deep, distinct punctures, and longer, darker suberect elytral hairs in the specimens reared from *P. tremuloides* in this study and in Grimble (1966) strongly supports the hypothesis of one species. In other words, it seems likely that offspring from light *inornata* developing in *balsamifera* may look like dark *inornata (= moesta)* as adults, through some unknown process. Also, the one-species hypothesis is supported by the fact that several specimens of unknown parentage reared from *balsamifera* in Manitoba and Saskatchewan were intermediate, showing some characters of light *inornata,* especially denser procumbent pubescence and shallow elytral punctures. Therefore, offspring of typical dark *inornata (moesta?)* growing up in *tremuloides* or willow might, for similarly unexplained reasons, look like light *inornata* as adults.

There is a reported behavioral difference between individuals from *balsamifera* and those from willow and *tremuloides*. Wong and McLeod (1965), and both Carlson and Grimble (*in litt.*), reported that *moesta* (= dark *inornata ?*) galleries in *balsamifera* are

found on smaller diameter twigs and that usually only one U-shaped egg-niche is gnawed instead of one to several egg-niches as made by light *inornata* which occur on willow and *tremuloides*. The number of egg-niches might be governed by diameter of the twig in dark *inornata* as it is with light *inornata* (Grimble *et al.*, 1969), but disposition toward oviposition on small twigs may be the real difference. Saunders (1874) reported that ovipositions of "*moesta*" on *balsamifera* were localized at the base of buds and Grimble (*in litt.*) stated that most egg-niches of dark *inornata* are located just above the base of a leaf petiole. In the present study, light *inornata* oviposited on twigs from 5 to 15 mm in diameter, and their ovipositions were not associated with buds or petioles.

Strong speculation that there is only one species is as far as one can go with the present evidence from a study of preserved specimens and the few rearings from known hosts. A field study similar to that made by W. J. Brown (1956, 1959) to distinguish sympatric sibling species of *Chrysomela* living on species of *Salix*, *Populus*, and *Alnus* will probably be necessary before conclusive evidence can be assembled. Brown was able to distinguish several host-specific cryptic species by making special collections of all stages of the insects and studying aspects of the biology, particularly host preferences and mating behavior. Utilizing some of his methods and others, the following studies could be made to determine how many species of *Saperda* exist on poplar and willow in the northeastern area of North America:

1. In areas where all hosts occur together, collect a series of specimens from each host species to determine the range of variation and the frequencies of the variants on each host. Compare the ranges and frequencies between hosts. If these ranges and frequencies are the same, it would support the one-species hypothesis. If they are different, it would indicate that there may be more than one species, but it could also mean that the differences are due to differences in the host.
2. Confine females from one host on the other hosts to see whether or not they will oviposit. Record survival of the larvae on "non-hosts" and compare percent survival on the host to that on the "non-host" if eggs are laid. If oviposition does not take place on the "non-host," particularly when the female is given no choice, it would support the hypothesis of more than one species present. If oviposition occurs on the "non-host" but the larvae die, the conclusion would be the same. However, if oviposition occurs on the "non-host" when the female is given no choice, and at least sometimes when given a choice, and the percent survival is comparable to that on the host, it would support the one-species hypothesis.
3. If females oviposit on "non-hosts," determine whether or not they behave the same or differently with regard to oviposition site selected and the number of egg-niches gnawed at one site.
4. Determine whether or not the seasonal histories are the same on each host, specifically whether the adults are in flight at the same time.
5. See whether reciprocal matings take place between individuals reared from different hosts. If they do, are the offspring viable and fertile in both hosts of the parents, or one, or neither?
6. If reciprocal matings take place, determine whether an individual from one host will copulate with one reared from a "non-host" on the "non-host" species (usually takes place on the host). If the adults from one host are not attracted to the "non-host," even when occupied by receptive individuals reared from that "non-host" species, this would constitute an isolating mechanism which prevents interbreeding. This would support the existence of two species.
7. Record sounds made during courtship, copulation, or disturbance and analyze them to see if there are consistent differences among recognizable kinds.
8. Rear the young of mated females of the typical kinds in typical and reciprocal hosts and then compare adult appearances.

After assembling this information, which would be no small task, there should be strong evidence as to whether there is only one, two, or more species of *Saperda* commonly found on poplar and willow in northeastern North America. Furthermore, as

Brown (1959) says, "... after he [the taxonomist] has segregated sibling species by ecological or ethnological characters, he can often find [formerly] obscure morphological characters to [readily] separate them." If one knew how many species were involved, it would be much easier to find morphological characteristics separating the kinds.

Even if there should turn out to be two species, one specific to *tremuloides* and *Salix* spp. and the other specific to *balsamifera*, the field data of this study pertained to one species, the light gray one inhabiting *tremuloides, Saperda inornata* Say. If there is only one species of gall-making *Saperda* present, which varies at least morphologically according to the host species in which it grew up, the data are still valid for individuals in *tremuloides*. However, the life history and behavior of the insect on *balsamifera* should be explored to determine whether or not there are differences which could affect the population dynamics as well as our understanding of the identity of the insect on trembling aspen. Among the many questions which need to be answered are: (1) Does *balsamifera*, or willow, absorb much of the population produced in *tremuloides*, and vice versa? (2) Are there differences in mortality factors and rates on the sub-population living in *balsamifera* and willow, and how does this affect the dynamics of the total population?

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