Biosystematics of the "*Leucopterus* Complex" of the genus *Blissus*

(Heteroptera: Lygaeidae)

David E. Leonard

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Biosystematics of the "*Leucopterus* Complex" of the genus *Blissus*

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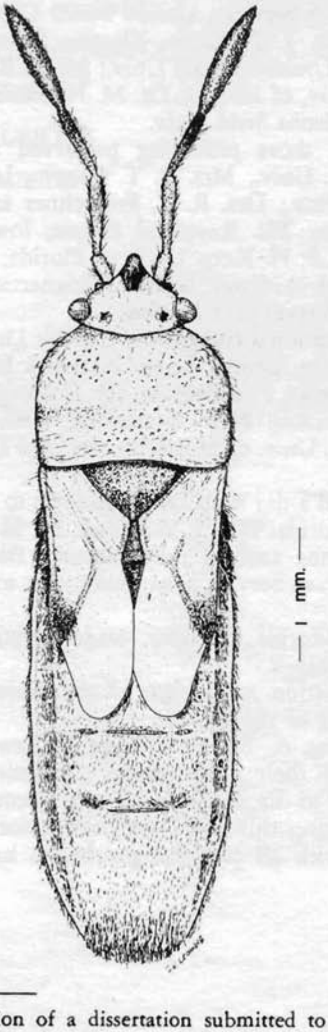

Holotype male of *Blissus arenarius maritimus* ssp. nov., dorsal view

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[1] A portion of a dissertation submitted to the Department of Zoology and Entomology, University of Connecticut, in partial fulfillment of requirements for the degree of Doctor of Philosophy.

HISTORICAL REVIEW

The first known North American species of *Blissus* was *Blissus leucopterus* described by Say in 1831 from a single specimen collected on the coast of Virginia. The first observation on this insect, however, antedated the formal description by nearly 50 years (Fitch 1856). This record was of damage to wheat in North Carolina in or about 1783. These insects spread through the Carolinas and Virginia for several years. In 1785 the grain fields of North Carolina were threatened with total destruction.

Thus early in North American history, *leucopterus,* commonly called the chinch bug, posed a potential (and in many years, an actual) threat to the economy of the agrarian society. Because of this threat probably more has been written about the chinch bug than any other North American insect; literature not restricted to scientific journals and books, but also daily and weekly newspapers.

After the initial report of damage in the 1780's chinch bug damage was not noted again until 1809 when, in some regions of North Carolina, wheat culture was abandoned for two years. In 1839 there was a bad infestation in the Carolinas and Virginia. In 1840 the infestation gave indications of being worse than in the preceding year. Albeit, Fitch (ibid.) records that the summer was wet instead of dry, and the insect was suppressed. This is the first reference to the effect of weather, which is of major importance in regulating the numbers of chinch bugs.

The discovery of *Blissus leucopterus* in the Midwest coincided with opening of western prairies for agricultural crops. In 1840 it was first noted in Illinois. Howard (1887) indicates that the first record for Missouri was 1839; Indiana, 1854; and Wisconsin, 1885. Forbes (1890) lists many early references in his extensive bibliography.

The first widespread damage in the Midwest did not occur until 1864, with losses in Illinois estimated at 73 million dollars. Since then, serious chinch bug outbreaks have occurred in many years. Heavy infestations are usually not continuous over wide regions, but are localized and dependent on temperature and rainfall. Effect of climate and weather on chinch bug numbers is reviewed by Shelford (1932).

According to Fitch (1856), chinch bugs had then been collected three times in New York State and once in Massachusetts, but no damage was reported. The first report of damage in the Northeast was in a timothy meadow at Hammond, New York (Lintner 1883). Van Duzee (1886) reported that *Blissus leucopterus* was very abundant in Buffalo, New York, for many years, and found it also in Lancaster, New York, and Ridgeway, Ontario. He noted these specimens as being uniformly larger, more robust, and with longer hairs on the pronotum than specimens collected from Kansas.

In 1893 Montandon described *Blissus hirtus* from a single specimen collected in Hazleton, Pennsylvania. This is certainly the form referred to earlier by Fitch, Lintner, and Van Duzee.

Blissus was unknown west of the Continental Divide until 1884 and 1885 when specimens were collected on three different occasions in California (Riley 1889). At least one of these latter records most likely refers to *Blissus mixtus* Barber (described in 1937).

Riley (1870) noted that chinch bugs occurred throughout the South, but there were no records of damage to grains south of the Carolinas.

Barber (1918) established three varieties of *Blissus leucopterus.* These were: (a) *Blissus leucopterus* var. *hirtus* Mont. about which he states (ibid.) "At most, this can only be considered a variety particularly common to the highlands of northeastern United States and Canada, where it is found in both macropterous and brachypterous condition." (b) *Blissus leucopterus* var. *arenarius* Barber, described from specimens collected in Sandy Hook, New Jersey, on a species of sand grass growing back of the sand dunes along the beach. According to Barber, this form differs from *leucopterus* in being longer and narrower, with additional differences in the antennal color patterns, villosity of the pronotum, hemelytra, and corium. Only macropterous forms were known to Barber. (c) *Blissus leucopterus* var. *insularis* Barber described from Punta Gorda, Florida, is characterized as being shorter and narrower than *leucopterus,* with a shorter terminal antennal segment, pronotal color and villosity differences, and color differences in the hemelytral veins and apical spot of the corium.

These taxa have subsequently been considered races, varieties, subspecies, species, and synonymies by various authors, including Barber himself. This confusion, coupled with differences in biology and the type of economic damage led to the initiation of the present study. In all ensuing discussion, *arenarius, leucopterus,* and *hirtus* will refer to the trinomial or subspecies.

MATERIALS AND METHODS

Rearing

In this study, two rearing methods were used. Petri dishes (9 cm or 5 cm) were used as cages, with fresh plant material (sudan grass stem plugs) introduced usually every other day. Ends of the stems were sealed in paraffin to prevent rapid desiccation. Four-dram lip vials were also used as rearing cages. A hole in the stopper plugged with cotton prevented condensation from forming on the vial sides.

The biggest difficulty was rearing early instar nymphs. Rearing on live plants was most efficient. Plants were grown in 3-inch clay pots and covered with round plastic cages 85 mm wide by 80 mm high (figure 1). Holes cut in the cages for ventilation were covered with Nitex nylon mesh screening (202 microns and 49 per cent open area). To prevent escape of bugs the cage was forced into the sand. Plants were watered through the base of the plastic pot.

Cultures were maintained either in a 29.5°C temperature cabinet, at room temperature which for the most part fluctuated between 23.4 and 24.5°C during the winter months, or in a greenhouse which had widely varying temperatures.

Crossing Experiments

Crossing experiments were set up either in Petri dishes or live plant cultures maintained in the greenhouse. Where overwintering adults were used, they were first kept in a temperature cabinet at 29.5°C for 10 to 14 days to break diapause. Most crosses were maintained in live plant cultures and frequently more than one pair of bugs was kept in the same culture.

Mortality in cultures was often high. Dead males were replaced whereas female mortality, if it occurred before egg laying, terminated the cross. If females were in contact with males for a month or more, results of the cross were recorded.

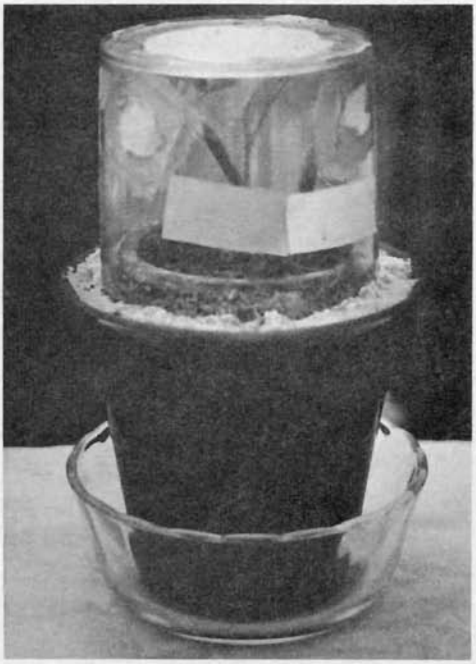


Figure 1. Cage used to rear specimens of *Blissus*. Bugs fed on plants grown in the inner clay pot.

Cytogenetics

The squash technique for the chromosome study followed is outlined by Ueshima (1963). Bugs were placed in modified isopropyl Carnoy's fixative (1 part glacial acetic acid, 3 parts absolute isopropyl alcohol) for 24 hours or more. The abdomens were removed and placed in acetocarmine stain for about 24 hours. Testes were more easily located after having been stained. Testes were dissected out and placed in a few drops of acetocarmine stain on a clean glass slide and covered with a coverslip which was tapped and pressed lightly. Excess stain was blotted up and edges of the coverslip sealed with a paraffin-balsam mixture.

Chromosomes were examined under a compound microscope using a magnification of 1350 times and Kohler illumination. Photomicrographs were made through the optics of the microscope on 35 mm Kodak Panatomic X film. A green filter was used to increase contrast.

BIOLOGY

Biological information obtained from these studies may apply to all species in the genus. This warrants including such information in a discussion of the biology of *Blissus*.

So far as is known, species of Blissinae feed on sap of Gramineae and thereby differ from most other Lygaeidae which are either seed feeders, predaceous, or both. The species of *Blissus* feed on a wide range of grasses, including grains. Some species feed on a number of different grasses, whereas others are host specific. Feeding by large numbers of bugs can kill plants.

The number of generations per year varies from one in species such as *iowensis* Andre (Decker and Andre 1938) and *breviusculus* Barber to continuous generations as noted in the southern limit of the range of *insularis*. Many species are bivoltine.

Diapause is important in the life cycle of some species. In *leucopterus, hirtus,* and *arenarius,* diapause was broken by 10 to 14 days continuous exposure to high temperatures (29.5°C) in the absence of light. The effect of light on diapause is poorly understood. *Leucopterus,* originally from Stillwater, Oklahoma, was maintained in a greenhouse culture in New Haven. The mean winter temperature in the greenhouse was 27°C but the fluctuation was considerable. During the week of December 22, 1963, daytime temperatures fluctuated mostly between 24.5 and 35°C, although a low of 14.5°C was recorded. Nighttime fluctuations were between 24 and 28.5°C. No eggs or nymphs were observed in the culture. Females kept at 29.5°C for 10 to 14 days laid only infertile eggs. Copulation and egg laying were not noted in the greenhouse until late in January. This coincided with lengthening of daylight hours and suggests that termination of reproductive diapause in *leucopterus* (and perhaps *hirtus* and *arenarius* as well) is influenced by daylength. However, this system can be overridden by continuous exposure to high temperatures in the absence of light in a temperature cabinet.

The species of *Blissus* have a definite courtship behavior in which antennae are involved. When males and females approach each other, the antennae usually establish the first contact. The female may show no additional interest and withdraw, but the male frequently pursues the female and mounts, with the antennae flailing the head and antennae of the female. At this point the effort may be terminated abruptly with the male rapidly dismounting and showing no further interest in the female. This is suggestive of the release of a chemical by the female, perhaps from the well-developed scent glands, although no odor is detected by smell.

With females, an increase in vibrations of the antennae, mostly in contact with the antennae and head of the male, appears to signify willingness to mate. The male mounts the female, both sexes maintain rapid vibrations of the antennae. The front legs of the male clasp the female about the pronotum and the hind legs stroke the venter of the abdomen of the female as the pairing is being effected. Once paired, the bugs characteristically face in opposite directions. During copulation the abdomens are ofttimes raised and vibrated for several seconds. Copulation has been noted for periods of up to 2 hours but undoubtedly can last for longer periods of time. During copulation bugs are often active with females the more active, walking about and sometimes feeding.

Copulation occurs in spring after initiation of activity by warm temperatures. In all species yet studied, females have a long oviposition period. Egg laying starts several days after adult females emerge. Females not mated will lay unfertilized eggs, but the preoviposition period is usually lengthened. Janes (1935) noted that females of *leucopterus* with few exceptions died shortly after the end of the oviposition period. This can also be recorded here for *hirtus, arenarius,* and *insularis*.

The accounts of number of eggs per female varies with each author. Janes (ibid.) found that egg laying in *leucopterus* was influenced by temperature. At 24.5°C the average number of eggs laid (12 females) was 532; at 29.5°C, 598 (11 females), and at 34.5°C 502 eggs (11 females). The highest number of eggs laid by one female was 1,091, an average of 15 per day laid at 24.5°C.

Because of the extended oviposition period of the females, all stages can be found in the field from July through fall in bivoltine forms. Some workers have taken appearance of eggs and early instar nymphs in fall to signify a partial third generation. Female *hirtus* and *arenarius* adults collected in late fall and early winter laid only infertile eggs and in males, no mature sperm was found. This signifies two rather than three generations per year.

The number of nymphal instars is five. In more temperate regions *Blissus* spp. overwinter as adults. Nymphs are known to seek winter quarters, but unless they transform to adults before cold weather they do not survive.

Species of *Blissus* can occur as either macropterous (long winged) or brachypterous (short winged). Some species are known only as brachypters, but this is most likely due to the small sample size from which these species are known. The following percentages of brachyptery are noted for the following taxa: *leucopterus* 0.1% (907 specimens); *hirtus* 63.7% (538 specimens); *insularis* 27.8% (389 specimens); *arenarius* 86.5% (1025 specimens); and *maritimus* ssp. nov. 92.5% (320 specimens).

Southwood (1960) noted there was an increase in flight activity in Heteroptera from temporary habitats. Later (1962 a, b) he showed that migration in the major taxa of terrestrial arthropods is positively correlated with impermanency of habitat. Sweet (1964) in his outstanding account of the biology and ecology of the Rhyparochrominae of New England (Lygaeidae) reviews much of the literature on habitat, dispersal, and brachyptery, and presents data which show a good correlation between the proportion of brachypters and permanency of habitat. The same type of correlation is evident in some species of *Blissus*. In collections of *leucopterus* from grains, few brachypters are found but in native bunch grasses the number of brachypters increases. A high percentage of brachypters is usually found in collections of *B. insularis* from St. Augustine grass lawns, but I found only macropters in isolated hammocks in the Florida Everglades. Where migration is a factor, there is apparently strong pressure against brachypters.

Blissus species have an X Y chromosome sex mechanism with males being the heterogametic sex. Segregation of sex chromosomes is unusual, for both the X and Y univalents undergo equational division at the first meiotic metaphase. At first division the chromatids of the Y chromosome separate precociously. Both sex chromosomes stain more lightly than autosomes. Species of *Blissus* also contains a chromosome called an *m* chromosome by Ueshima (via. Ashlock pers. comm. 1963). The *m* chromosome, like the sex chromosomes, stains lightly.

Of species of *Blissus* thus far surveyed, the most common diploid count in males is ten autosomes, an X, Y, and *m* chromosome. One pair of autosomes is distinctly larger.

SPECIES ACCOUNTS

Blissus leucopterus leucopterus (Say)

Life history

There are lengthy accounts of the life history of the chinch bug, including those of Walsh and Riley (1869), Forbes (1890), and Webster (1907). Unless cited, the following discussion of the life history is from these references.

Leucopterus overwinters as an adult; the preferred hibernating site is tufts of little blue stem grass, *Andropogon scoparius* Michx., but it is also commonly found in big blue stem, *Andropogon gerardi* Vitman, and in the southeastern part of its range, false redtop, *Triplasia purpurea* Walt. (Headlee and McColloch 1913). In regions that are intensively farmed, variations in hibernation can be noted, with adults hibernating in or under available plant refuse in fields or in plant material or debris bordering cultivated fields. Headlee and McColloch (1913) showed that winter mortality of chinch bugs is lower in clumps of *Andropogon* than in other hibernating sites. Decker and Andre (1937) found that winter mortality of *leucopterus* hibernating in blue stem and other bunch forming grasses was highest in sparse cover; also, the lack of snow cover increased mortality.

There are reports of flights to hibernating quarters in fall, and from hibernating quarters to crops in early spring.

Hosts Host plants of *leucopterus* are numerous but consist solely of species of Gramineae. Among grains, spring and winter wheat, sorghum, sudan grass, broom corn, Indian corn, field corn, millet, and rye are all fed upon. Oats appear to be less desirable than the above grains. Resistance of wheat varieties to *leucopterus* has been shown by Jones (1937) and resistance to corn varieties by Flint (1921), Holbert et al. (1937), Dahms and Fenton (1940), and Dahms and Sieglinger (1945).

Among cultivated and wild grasses, most notable hosts are Bermuda grass *Cynodon dactylon* (L.), foxtail grass, *Setaria lutescens* (Weigel), timothy, *Phleum pratense* L., blue grass, *Poa pratensis* L., crab grass, *Digitaria sanguinalis* (L.) and bottle grass, *Setaria viridis* (L.) Beauv.

The biology of *leucopterus* is influenced by susceptibility of the host, for with susceptible varieties Dahms et al. (1936) noted an increase in fecundity and an increase in size and speed of development of nymphs. Dahms and Fenton (1940) found that plants more susceptible to chinch bug attack are higher in nitrogen than more resistant varieties. In field and laboratory tests using soil treatments, resistance to chinch bug attack is consistently decreased by sodium nitrate, and in the majority of cases, increased by superphosphate.

Migrations of large numbers of chinch bugs from early crops of grains to later maturing grains are the most spectacular feature in the biology of *leucopterus*. Most of the literature deals with migrations and methods of curtailing them. For many years, construction and maintenance of barriers constituted the principal means of defense.

Predators and Parasites Among birds, only the Bobwhite devours the chinch bug in considerable numbers, according to Webster (1909). Webster also includes Prairie Chicken, Red-winged Black-bird, Catbird, Brown Thrush or Thrasher, Meadowlark, House Wren, Tree Swallow, Horned Lark, Western Kingbird, Trail's Flycatcher, Seaside Sparrow, Savannah Sparrow, Tree Sparrow, and Barn Swallow as predators.

Frogs will feed on chinch bugs. Small mammals may also be important predators, especially on overwintering bugs, but no records of small mammal predation can be recalled.

Among insect predators, species of coccinellids are often mentioned, but their effectiveness is questionable, as some observers note them feeding on aphids rather than on chinch bugs. Walsh (1861) notes *Hippodamia maculata* (Muls.) (= *Ceratomegilla fuscilabris*), *Coccinella munda* (Say) (= *Cycloneda munda*), *Cycloneda sanguinea* (L.), and two species of *Scymnus* as predators. *Pselliopus cinctus* (Fabr.) (Reduviidae) is noted as a predator by Howard (1887).

Ants are often mentioned as predators: *Lasius flavus nearcticus* Wheeler has been seen carrying off chinch bugs. *Lasius niger* (L.) and *Formica fusca* *subsericea* Say have been observed feeding on *leucopterus* (Forbes 1895 and 1916 respectively). In my greenhouse culture of *leucopterus, Leptothorax curvispinosus ambiguus* Emery was very active, and in its presence the culture declined. When the ants were eliminated the culture again increased in numbers.

A lacewing, *Chrysopa plorabunda* Fitch, has been noted in regions of high chinch bug numbers. Shimer (in Fitch 1856) describes their feeding on chinch bugs. *Orius insidiosus* (Say), an anthocorid, is often mentioned as a predator. Dahms and Kagan (1938) found *Collops quadrimaculatus* F. where chinch bugs were numerous. In their laboratory these beetles fed on *leucopterus* eggs but did not feed on nymphs or adults.

Only two insect parasites are known from *leucopterus:* a hymenopteran egg parasite, *Eumicrosoma benefica* Gahan (McColloch and Yuasa 1914, 1915) and a tachinid, *Phorantha occidentis* Walker, reared from specimens collected in South Carolina (Lugginbill 1922). Nematodes *(Mermis)* are also found in chinch bugs (Webster 1909).

Diseases Six species of fungi are reported as parasitic on *leucopterus,* but only two are of significance (Steinhaus 1949). These are the gray fungus, *Empusa aphidis* Hoff., and the more important, white muscardine fungus, *Beauveria bassiana* (Balsamo) Vuillemin, (= *Sporotrichum globuliferum,* = *Beauveria globulifera).* In 1954 MacLeod concluded that *Beauveria globulifera* (Spegazzini) Pickard, along with seven other species, were strains of *Beauveria bassiana.* A brief description of the characteristics of this disease organism is found in Steinhaus (1949).

The first report of fungi attacking chinch bugs is by Shimer (1865) but the importance of this was not generally recognized. In 1882, Forbes in Illinois and Popenoe in Kansas published accounts of disease. Soon after their rediscoveries, there was much interest in the possibility of artificial infection of white muscardine fungus to check chinch bug outbreaks. Many states adopted (and subsequently abandoned) programs to induce the disease artificially in the field. The most ambitious attempts were those of F. H. Snow in Kansas from 1886 to 1896. Early literature on chinch bug diseases is listed in a review by Forbes (1895).

The study of Billings and Glen (1911) showed that the white muscardine fungus is present naturally everywhere in fields throughout infested areas of Kansas. They concluded that artificial distributions would be too insignificant to be of practical use. Apparent absence of fungus among chinch bugs in fields is evidence of unfavorable climatic conditions rather than lack of spores.

Forbes (1882) found in the caecum of *leucopterus* a bacterium later named *Micrococcus insectorum* by Burrill (1883). Forbes considers this bacterium a normal constituent of the caecum and not a pathogen.

Distribution

Leucopterus extends from the east coast to the western plains. Specimens have been examined from as far north and east as Accomac, Virginia, and as far south as Escambia County, Alabama. Specimens of *leucopterus* have been examined also from North Carolina, South Carolina, Tennessee, Mississippi, Texas, Oklahoma, Kansas, Illinois, Iowa, Indiana, Ohio, Michigan, Wisconsin, Minnesota, and South Dakota. The northern limits of specimens examined are Hillsdale, Michigan; Okauchee, Wisconsin; Pine River, Minnesota; and Platte, South Dakota.

Figure 2 indicates the distribution of *leucopterus* as it is now known. A

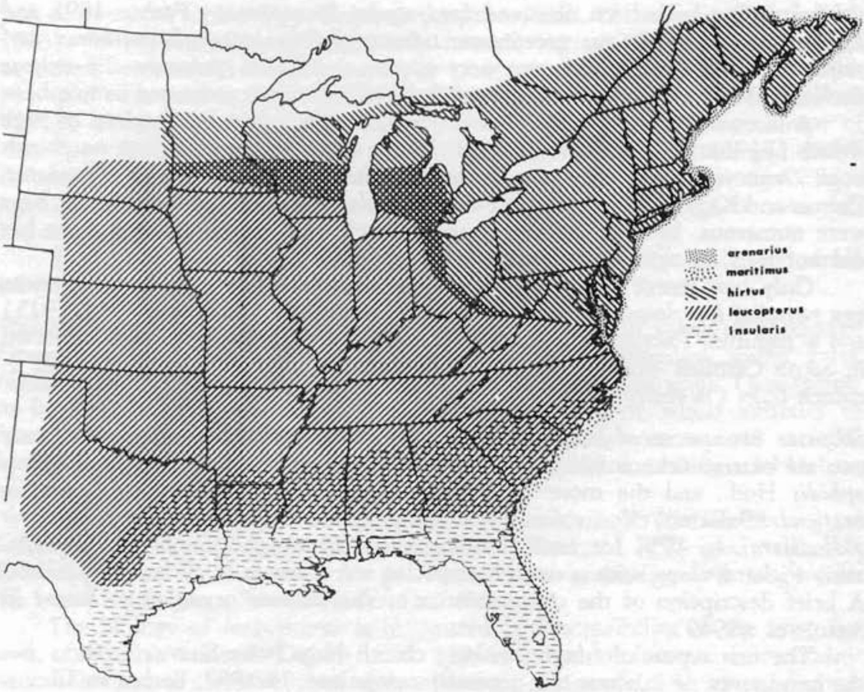


Figure 2. Distribution of the species and subspecies of the *leucopterus* complex. These forms occur in the areas designated only where suitable habitats prevail.

more precise knowledge of the limits of distribution will be possible only when extensive collecting is done in extremes of the range. Distribution maps can be misleading, for they infer continuous distribution rather than localized colonies, as pointed out by Mayr (1963).

Cytogenetics

The diploid chromosome complement of *leucopterus* males consists of ten autosomes, an X, Y, and *m* chromosome. Figure A of plate 1 shows first meiotic metaphase in *leucopterus* males. The length of the largest autosome at metaphase is 4.5 μ.

Blissus leucopterus hirtus Montandon

Life history

Hirtus overwinters as an adult, usually in tufts of meadow grasses or under plant debris in meadows or along borders of meadows. Where woods border fields inhabited by *hirtus,* adults may also be found under leaves along the border of woods. Bugs often hibernate in plant debris around the foundations of houses and under shingles or clapboards. Where numbers are high, they may also hibernate in houses.

Spring activity begins with periods of warm weather. Observations made at Storrs, Connecticut, in 1963 show that on April 25, *hirtus* was still hibernating but on May 9 most bugs had left hibernating quarters and some were copulating.

There seems to be no published accounts of flights of *hirtus* but in mid-

July, 1964, in Cheshire, Connecticut, specimens of *hirtus* were collected as they alighted on clothes hung outside to dry. Flight may be an important means of dispersal.

Winter mortality can be high and, as with *leucopterus,* mortality is most likely related to temperature and moisture in hibernating sites. In April 1963 mortality in a collection of 506 specimens from Mansfield, Connecticut, was 34.4 per cent.

Hosts In meadow habitats, timothy seems to be the preferred host plant. Most lawn grasses are also fed upon, with crab grass a notable exception (see figure 3). With lawn varieties, bent grasses are preferred. Where there are large numbers of *hirtus* and climatic conditions are favorable (hot and dry), lawns can be killed in less than one season. Most feeding takes place in sunny areas of lawns. High soil temperatures do not appear to be deleterious. In dry soil bugs are often found in soil cracks about the crown and roots of grass.

Parasites and Predators No parasites have been reared from *hirtus*. The predacious *Geocoris bullatus* (Say) and *G. uliginosus* (Say), are often found in the same habitat with *hirtus*. It is not known whether these species prey on *hirtus* or whether they simply share a habitat preference.

Disease A fungus, presumably white muscardine fungus, *Beauveria bassiana* (Balsamo) Vuillemin has been observed both in the field and in laboratory cultures. The effect of this fungus is evident, for *hirtus* is abundant only in prolonged periods of hot, dry weather unfavorable for sporulation of the fungus. During wet seasons, *hirtus* is not an economic problem.

Distribution

The range of *hirtus* extends both north and east of *leucopterus* (figure 2). Specimens were studied from Nova Scotia (locality unknown), Fredericton, New Brunswick; Montreal, Quebec; and Muskoka, Ontario, Canada.

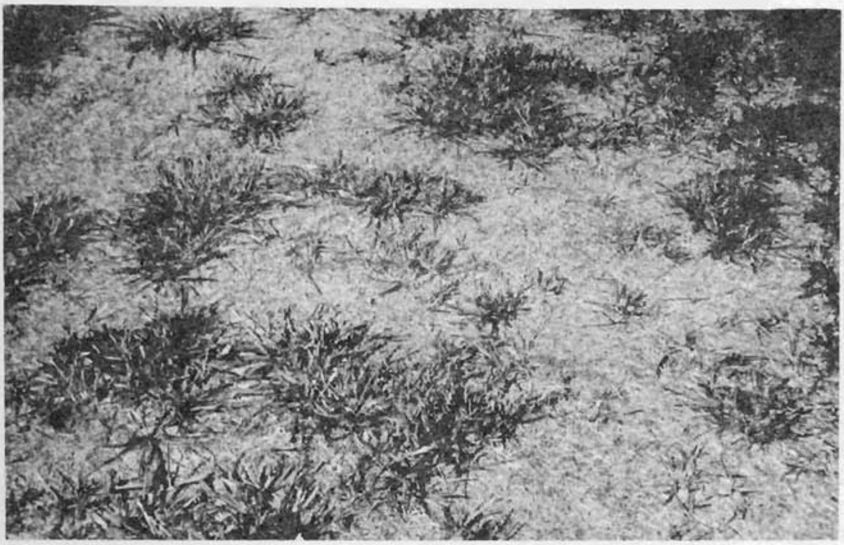


Figure 3. Feeding damage of *hirtus*. Feeding of large numbers of bugs killed all lawn grasses excepting crab grass, *Digitaria sanguinalis* (L).

Hirtus extends to the south into northern Virginia and probably further south along the Appalachian Mountains. To the West, *hirtus* extends into Minnesota, with Page, Minnesota, the most western locality of specimens examined. Specimens were also examined from Maine, New Hampshire, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, Maryland, Delaware, Virginia and Ohio.

Cytogenetics

Hirtus males have a diploid chromosome complement of ten autosomes, X, Y, and *m* chromosome as shown in figure B of plate 1. In this figure, the large autosome has started to separate and the univalents are end to end, perhaps indicating the lack of a diffuse kinetochore in this genus. The length of the largest autosome at metaphase is 4.5 μ. The chromosomes of *hirtus, leucopterus,* and *insularis* appear to be identical in size.

Blissus arenarius arenarius Barber new comb.

Life history

This bug was described by Barber in 1918, and aside from the short note accompanying his description, there are no accounts of its biology. Barber noted that collections of this insect were made on grass growing in the back of a beach, and that only macropterous forms were known to him. In rather extensive collecting of this insect, from Cavendish, Prince Edward Island, Canada, to Chincoteague Island, Virginia, I have found *arenarius* only on coastal dunes in close association with American Beach grass, *Ammophila breviligulata* Fernald (figure 4). This is undoubtedly the plant mentioned by Barber. On examination of a thousand specimens, brachyptery as well as macroptery is found, and in fact, the majority (87.5%) are brachypterous.

Adults hibernate on or in close proximity to coastal dunes. A small percentage hibernate beneath dead sheaths of the host plants. Most hibernate in or under boards, stones and other debris such as beer cans, often found on coastal dunes. Usually these dunes are not much higher than the high water mark, and abnormally high tides in winter must account for some mortality. Many coastal sand dunes are bordered by marshy areas but these areas are not preferred as hibernating sites. Where woodlands border sand dunes, *arenarius* specimens have been collected under leaves in woods a few feet from the beach margin.

Winter mortality varies markedly. In February 1963, 78 per cent of males and 68 per cent of females were dead in a collection from West Haven, Connecticut. In January 1964, at the same locality, mortality was less than 5 per cent.

Copulation occurs early in spring. In 1962, in New Haven, Connecticut, pairing was noted on 29 March. In 1961, in East Lyme, Connecticut, pairing was observed on 6 April. Some bugs were still in winter quarters. Those bugs copulating were on the surface of the sand around the new shoots of the host plant.

Not all pairing takes place in warm weather. In West Haven, on May 10, 1963, copulation was observed on an overcast day. The air temperature was 15.2°C; the sand surface, 20.5°C; and under leaf sheaths where the bugs were, 16°C.

In spring, when the host plant shoots are new, *arenarius* can be seen on the grass blades. As the plants mature, *arenarius* is found between the dead sheaths, both above and below the surface of the sand. This undoubtedly helps insulate the bugs from high summer temperatures on the unshaded dunes.

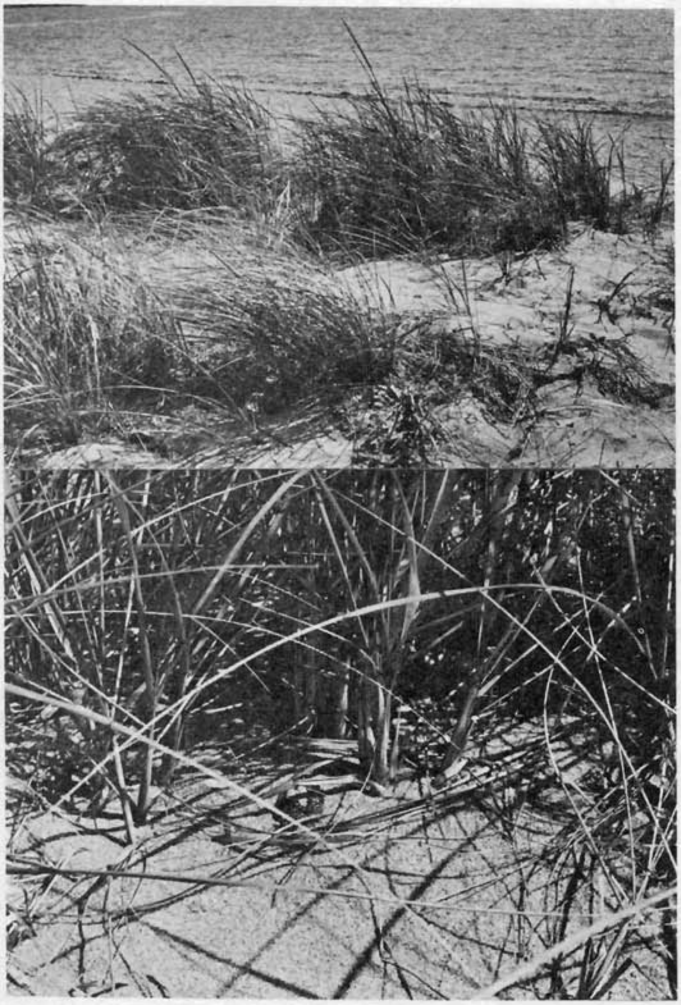


Figure 4. Habitat of *arenarius*. Bugs live and feed on *Ammophila breviligulata* Fernald which grows on coastal sand dunes.

Host The host of *arenarius* is *Ammophila breviligulata* Fernald, American beach grass, which grows along the coast on sand dunes above the high water mark. This plant is found from Newfoundland to North Carolina and on the shores of the Great Lakes from Lake Ontario to Lake Superior and Lake Michigan (Hitchcock 1950). (It would be of considerable interest to determine whether species of *Blissus* occur on American beach grass along the Great Lakes.) This plant is important in formation and maintenance of coastal sand dunes. *Uniola paniculata* L., found on coastal dunes south of Virginia, and *A. arenaria* L. on the West coast, play an analogous role.

Arenarius can be reared in the laboratory on a variety of grasses, including seaside creeping bent grass, oats, sudan grass, and corn seedlings. It does not adapt well to laboratory rearing, but whether this is due to poor diet is not known. No attempt was made to rear it on its own host in the laboratory due to the difficulty of culturing American beach grass.

Parasites and Predators No parasites are known for this insect. No predation was observed in the field. However, dune grass habitats abound with spiders, some of which may be preying on *arenarius*. In West Haven, Connecticut, two nabid nymphs, *Nabis subcoleopteurs* Kby. and *Pagasa fusca* Stein, were collected with *arenarius*. These predators fed on adult *arenarius, hirtus, leucopterus,* and *breviusculus* in the laboratory. The nabids insert their beak between leg segments of their prey, or between the head and prothorax. Apparently a toxin is involved for the prey is immobilized within a few seconds.

Disease Arenarius is susceptible to a fungus disease, most likely white muscardine fungus, *Beauveria bassiana* (Balsamo) Vuillemin.

Distribution

Arenarius extends from the Gulf of St. Lawrence southward along the eastern coast to southern Virginia. The northernmost locality of specimens examined was Cavendish, Prince Edward Island, and the southernmost, Chincoteague Island, Virginia. Specimens were examined from Prince Edward Island, Rhode Island, Connecticut, New York, New Jersey, Delaware, Maryland, and Virginia.

Cytogenetics

Males of *arenarius* have a diploid chromosome complement of ten autosomes, and an X, Y, and *m* chromosome. This is shown in figure D of plate 1. The Y chromosome has separated and the larger autosome has also started to separate. The lighter staining *m* chromosome is found in the upper right of the photograph. The large autosome is larger than any other species of *Blissus* examined thus far, and measures 6.5 μ at first meiotic metaphase.

Blissus arenarius maritimus ssp. nov.

General coloration of head and pronotum gray pruinose. Abdomen with silvery sheen from numerous short closely appressed silver setae. Hemelytra opaque white with veins very light at base becoming golden yellow at apices distal spot of corium brown, membrane opaque white. Legs golden yellow excepting last segment of tarsi and coxae castaneous.

Head lightly clothed with suberect light yellowish setae, length of head .43 mm, width of head .67 mm, interocular space .42 mm, pronotum clothed with yellowish-white suberect setae, length of pronotum .74 mm, width of anterior lobe .67 mm, width of posterior lobe 1.06 mm. Scutellum with slight median carina, anterior portion of scutellum depressed, scutellum width .54 mm, length .34 mm. Abdomen clothed with dense closely appressed silver setae with numerous suberect yellowish setae in the apical segment, length of abdomen and scutellum 2.69 mm, width of fifth abdominal tergite .86 mm. Length of antennal segments I:II:III:IV: .16 mm, .40 mm, .26 mm, .54 mm. Labium extending to basal half of metasternum, length of segments I:II:III:IV: .38 mm, .40 mm, .26 mm. Total length 3.78 mm.

Holotype: male. Fernandina Beach, Fla., Ft. Clinche Park, XI-21-1961, on *Uniola paniculata* L. (D. E. Leonard). In United States National Museum, USNM Type No. 67710.

Paratypes: 11 females, 15 males. Fernandina Beach, Fla., Ft. Clinche Park, XI-21-1961, on *Uniola paniculata* L. (D. E. Leonard): Jupiter, Fla., Palm Beach Co., May 19, 1948 (M. Cazier): Ft. George, Fla., July 29. 83, on Water Oats, collection T. Pergande. In United States National Museum, American Museum of Natural History, J. A. Slater collection, and author's collection.

For a general description of the genus *Blissus* (adults and nymphs) and *maritimus* nymphs, see Leonard (ms.). This subspecies is very similar to *arenarius* Barber, but *maritimus* is larger and differs in nymphal color patterns. Fourth instar nymphs of *maritimus* have a triangular yellowish area on the mesonotum.

Life history

Maritimus inhabits coastal dunes where it feeds on sea oats, *Uniola paniculata* L. References to this insect in the literature confuse this bug with other species of *Blissus*. This will be reviewed in a subsequent paper (Leonard ms.).

There are no accounts of the biology of *maritimus,* excepting Schwarz's (1888) notation that it occurs only on the upper regions of *U. paniculata.* This is curious, for *arenarius* is on the upper regions of its host only during warm days in early spring (see page ....). Schwarz (ibid.) thought these coastal forms were *leucopterus,* and a maritime origin for *leucopterus* was proposed and supported by some entomologists, particularly Webster.

Host The only known host is *Uniola paniculata* L. which, according to Hitchcock (1950), is found on coastal sand dunes from Northampton County, Virginia, to Florida, Texas, and eastern Mexico. It is also found in the northern West Indies. Wagner (1964) studied the ecology of *U. paniculata* and notes the occurrence of a lygaeid (presumably *maritimus*) as one of the 18 insect species in close association with this plant.

Parasites, predators, and diseases The parasites, predators, and diseases of this insect are unknown.

Distribution

Maritimus is found from northern North Carolina southward along the coast to the southern third of Florida (figure 2). No specimens have been found south of Jupiter, Florida. Specimens were examined from North Carolina, South Carolina, Georgia, and Florida. On a collecting trip in Florida in November and December 1961 I found no *maritimus* in the southern third of eastern Florida or on the Florida Keys. This corresponds to Schwarz's notation that *leucopterus (maritimus)* was absent from the Biscayne region of Florida and the Florida Keys. I could find no *maritimus* in several likely collecting sites on the Gulf Coast of southwestern Florida.

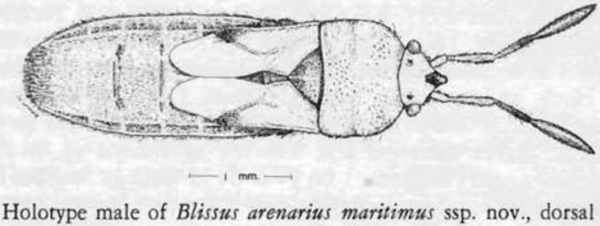


Figure 5. Holotype male of *Blissus arenarius maritimus* ssp. nov., dorsal view.
(See also page 6.)

Cytogenetics

The chromosome complement does not appear to differ from *B. a. arenarius,* with a diploid count of 10 autosomes, an X, Y, and *m* chromosome. Like *arenarius,* the largest autosome is larger than any other species of *Blissus* thus far studied, and measures 6.5 μ at first meiotic metaphase.

Blissus insularis Barber

Life history

This insect is a serious pest of St. Augustine grass lawns in southeastern and southcentral regions of the United States. Despite its economic importance, surprisingly little is known of the biology of this insect.

The taxonomic status of this insect has varied in a confusing fashion. This will be treated elsewhere (Leonard ms.) and will not be repeated here, excepting to note that most recent authors treat *insularis* as a distinct species. Kerr (1956) in a short discussion notes that *insularis* and *leucopterus* differ morphologically. He also states that *insularis* is not a pest of corn or other grains in Florida. Kerr also notes differences in susceptibility to DDT as well as differences in environmental conditions. I consider *insularis* to be a distinct species (see Leonard ms.).

The overwintering habits of *insularis* differ throughout its range. *B. insularis* is present in all stages in southern Florida during the winter. In northern Florida only adults are present, and these sometimes hibernate (Kelsheimer and Kerr 1957). In late November and early December of 1961 I collected adults and nymphs of *insularis* in the Miami area, Florida Keys, and the Everglades. In limited collecting in more northern areas of Florida I found only adults.

Eden and Self (1960) report that in the Mobile, Alabama, area, *insularis* overwinter as adults in debris and females mate after overwintering. They also found that females lay eggs 7 to 10 days after mating, and eggs hatch in 14 days. Kelsheimer and Kerr (1957) note that in summer in Florida eggs hatch in 7 to 10 days. In my laboratory cultures of *insularis,* females laid several eggs per day. Development from egg to adult varies with the locality; 49 to 56 days in Alabama (Eden and Self 1960); 35 days in Florida (Kelsheimer and Kerr 1957); 30 to 45 days in Mississippi (Burton and Hutchins 1958). Burton and Hutchins (1958) estimate females lay 100-300 eggs.

No account of the number of generations per year was encountered. Continuous generations may occur in regions of southern Florida where nymphs are found in winter.

Hosts Reports of *insularis* damaging lawns in Florida date back to the turn of the 19th century according to Kerr (1956). Although heavily damaging to St. Augustine grass, *Stenotaphrum secundatum* (Walt.), this insect also feeds on other grasses, including torpedo grass, *Panicum repens* L., a pasture grass (Kelsheimer and Kerr 1957, Kerr and Kuitert 1955) and Pangola grass, *Digitaria decumbens* Stent. (Kerr and Kuitert 1955). According to Kelsheimer and Kerr, *insularis* is occasionally found on centipede grass, *Eremochola ophiuroides* (Munro) Hack, and rarely on Bermuda grass, *Cynodon dactylon* (L.) Pers. I have examined specimens of *insularis* collected on rice, *Oryze sativa* L.

Dr. H. R. Burke collected and sent me specimens of *insularis* which he collected on *Rubus sp.* (Rosaceae) on IV-9-64 in College Station, Brazos County, Texas. If these were feeding on *Rubus,* this is the first known record of Blissinae feeding on plants other than Gramineae.

In laboratory experiments, Kerr and Kuitert (1955) found that *insularis* could subsist in the laboratory for a time on several lawn grasses other than St. Augustine grass, but development was very slow. In my laboratory, *insularis* was reared primarily on sudan grass, field corn seedlings, and St. Augustine grass.

In some Florida Keys and the Everglades, *insularis* is found in native grasses. The abundance of this insect in hammocks in the Everglades is somewhat surprising. In one area (Snake Bight Trail), they were collected in a hammock well inside a swampy area. All *insularis* collected there were macropterous, which may signify some selective advantage for macropters in temporary habitats.

Parasites and Predators No records of parasites or predators are encountered.

Diseases No fungi are known to infect this insect. Kerr (1958) tried to control *insularis* in field tests with both *Beauveria globulifera* (Speg.) and *Metarrhizium anisphilae* (Metch.) Sorokin, but neither of the treatments resulted in reduction of numbers.

Distribution

Insularis extends from southern North Carolina southward to the Florida Keys (figure 2). Northernmost locality of specimens examined is Shallott Point in Brunswick County, North Carolina, and southernmost, Big Pine Key, Florida. Westward, *insularis* extends into Texas and most likely Mexico as well.

B. insularis extends throughout Florida but its distribution in Georgia, Alabama, Mississippi, and Louisiana is mostly in southern regions of these states. In Texas it is in the eastern and southeastern portion. Of specimens examined, northern limits in the Gulf Coast States and Georgia are Athens, Georgia; Okolona, Mississippi; Shreveport, Louisiana; and Tyler, Texas.

Barber (1918) lists paratypes of *insularis* from the West Indies. I have examined these specimens and they are not conspecific with paratypes of *insularis* from Florida.

Cytogenetics

The chromosome complement of *insularis* does not appear to differ from *leucopterus* or *hirtus*. The diploid number consists of ten autosomes, an X, Y, and *m* chromosome (figure C, plate 1). The size of the large autosome at first meiotic metaphase is 4.5 μ.

STATUS OF THE POPULATIONS OF THE Leucopterus COMPLEX

Comparative studies of morphology of adults of the *leucopterus* complex have shown that only subspecies of *arenarius* can be easily separated by this means. These differ from the others of the complex in general gray coloration, lighter colored distal spot of the corium, and in brachypters, a narrower and more sharply rounded membrane.

The habitat of *arenarius* and *maritimus* is an important consideration in separating these subspecies from other species in this complex. *Arenarius* and *maritimus* are known only from coastal dunes. *Leucopterus, hirtus,* and *insularis* have not been collected in this habitat.

In this study the length of the scutellum and abdomen is used rather than the total length for it is difficult to get specimens in the same plane for accurate measurements because of varying degrees of head declivity. The length of the abdomen and scutellum is easily measured and provides an adequate comparison of overall size differences.

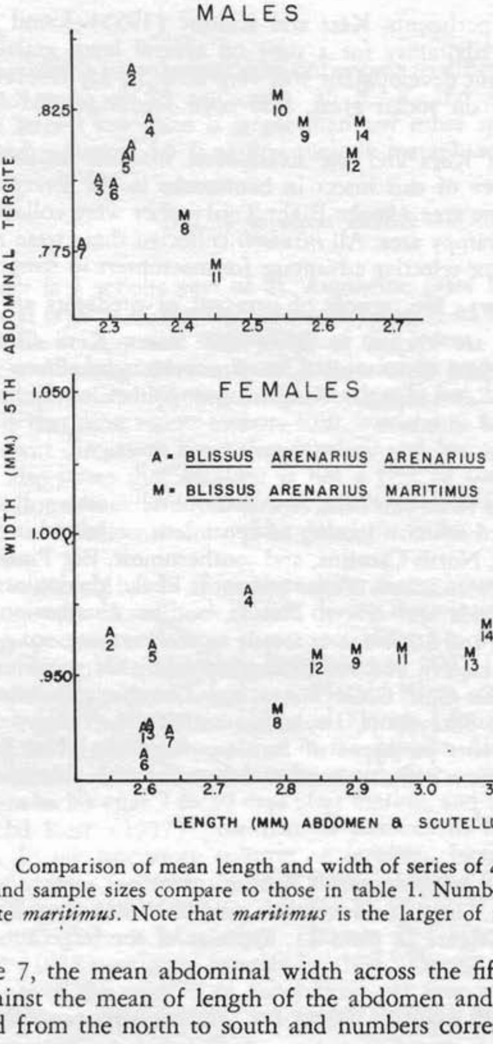


Figure 6. Comparison of mean length and width of series of *arenarius* and *maritimus*. The numbers and sample sizes compare to those in table 1. Numbers 1-7 denote *arenarius* and 8-14 denote *maritimus*. Note that *maritimus* is the larger of the two subspecies.

In figure 7, the mean abdominal width across the fifth abdominal tergite is plotted against the mean of length of the abdomen and scutellum. Localities are numbered from the north to south and numbers correspond to those listed in table 1.

Measurements of width of individuals of *arenarius* and *maritimus* show much variation but measurements of the length of abdomen and scutellum show a definite pattern. *Maritimus* is definitely the larger subspecies but there is some overlap as shown in figures 6 and 7. However, the means of the two forms differ significantly as seen in table 1, with *maritimus* the larger.

The difference in size of *arenarius* and *maritimus* more nearly approximates a cline than a sharp break. If strengthening of isolating mechanisms in the region of overlap increases character divergence between distinct but closley related species, then *arenarius* and *maritimus,* if distinct species, should show most divergence in the Virginia-North Carolina region. In *maritimus,* divergence in size shows up most strikingly in southern limits of its range. This suggests these two forms are interbreeding in the overlap zone and are not distinct species. Morphological and cytological similarity as well as differences in geographic

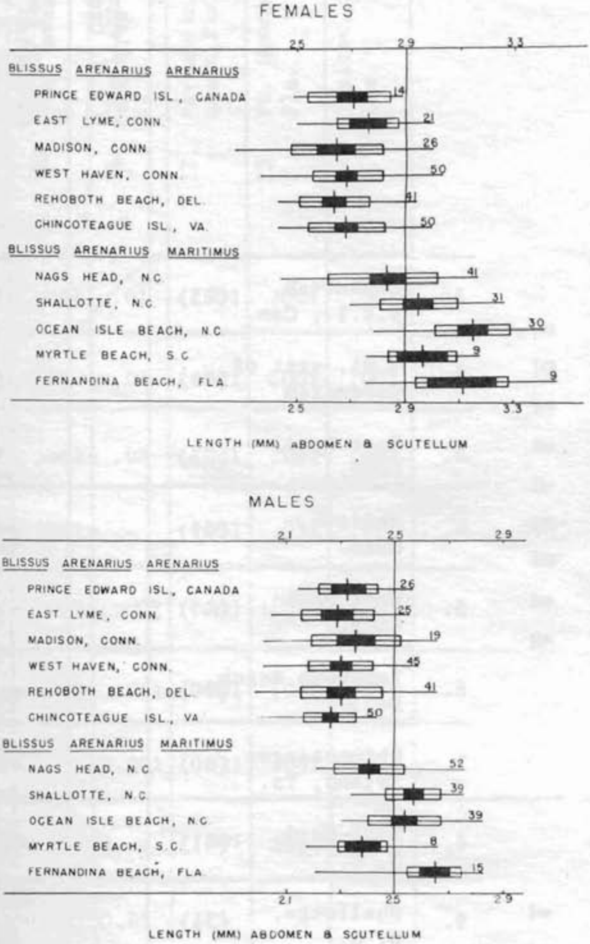


Figure 7. Statistical analysis of the length of abdomen and scutellum of *arenarius* and *maritimus*. The range is denoted by horizontal lines, the mean by vertical lines, the standard deviation by a rectangle, twice the standard error of the mean by solid black. Sample size is listed to the right above the range limits. Localities of both subspecies are listed from north (top) to south (bottom). Note that *maritimus* is the larger subspecies but size difference is less pronounced near the region of overlap. Difference of the specimens from Myrtle Beach, South Carolina, may be due to the small sample size.

distribution indicate that they are subspecies. The differences are hosts, size, and coloration of fourth instar nymphs.

Morphological differences found in *hirtus, leucopterus,* and *insularis* are more tenuous. As populations, these forms can be separated, but with single specimens or short series, identification is frequently very difficult. This is due to the large amount of variation in individuals, and morphological similarity.

In figures 8 and 9, only macropters are included. This is necessitated by morphological differences associated with brachyptery. Since *leucopterus* is found almost solely as macropters, only macropters are used. This reduces the

			ARENARIUS					
			1. Cavendish, P.E.I. Can. (14)	2. 7 mi. east Cavendish (10)	3. East Lyme Conn. (26)	4. Madison, Conn. (21)	5. West Haven, Conn. (50)	6. Rehoboth Beach, Del. (41)
ARENARIUS	1.	Cavendish, P.E.I., Can. (25)		-	-	-	-	-
	2.	7 mi. east of Cavendish (13)	-		-	-	-	-
	3.	East Lyme, Conn. (25)	-	-		-	-	-
	4.	Madison, Conn. (19)	-	-	-		-	-
	5.	West Haven, Conn. (45)	-	-	-	-		-
	6.	Rehoboth Beach Del. (40)	-	-	-	-	-	
	7.	Chincoteague Island, Va. (50)	.01	-	-	-	-	.02
MARITIMUS	8.	Nags Head, N. C. (41)	.02	.001	.001	.001	.001	.001
	9.	Shallotte, N. C. (31)	.001	.001	.001	.001	.001	.001
	10.	Myrtle Beach, S. C. (8)	.01	.001	.01	.001	.001	-
	11.	Charleston, S. C.	No males in collection.					
	12.	Fernandina Beach, Fla. (9)	.001	.001	.001	.001	.001	.001
	13.	Ft. George, Fla. (3)	.001	.001	.001	.001	.001	.001
	14.	Jupiter, Fla.		No males in collection.				

MALES

	MARITIMUS						
Isl.,Va. (30)	8. Nags Head, N. C. (41)	9. Shallotte, N. C. (31)	10. Myrtle Beach, S. C. (9)	11. Charleston, S. C. (5)	12. Fernandina Beach,Fla. (9)	13. Ft. George, Fla. (3)	14. Jupiter, Fla. (4)
	FEMALES						
-	.01	.001	.001	.01	.001	.001	.001
-	.01	.001	.01	.01	.001	.001	.001
-	.001	.001	.001	.02	.001	.001	.001
-	.001	.001	.001	-	.001	.001	.001
-	.001	.001	.001	.001	.001	.001	.001
-	.001	.001	.001	.001	.001	.001	.001
	.001	.001	-	.001	.001	.001	.001
.001		.001	.001	-	.001	.001	.001
.001	.001		.001	.01	-	-	-
.001	-	-		.02	.001	.001	.001
					-	.02	-
.001	.001	.02	.001	-		-	-
.001	.001	-	.01	-	-		-

Table 1. Levels of significance of differences in means of the length of abdomen and scutellum of specimens of *arenarius* (nos. 1-7) and *maritimus* (nos. 8-14). Sample sizes are in parentheses. *Maritimus* is the larger of the two forms, and the size of *maritimus*

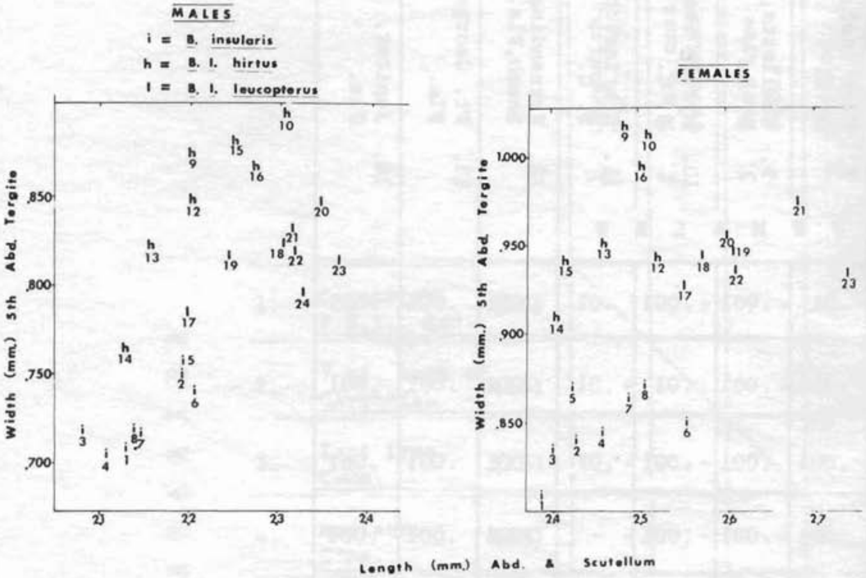


Figure 8. Means of the length and width of *leucopterus, hirtus,* and *insularis.* Note that *insularis* is less robust than *hirtus* but similar in length. *Hirtus* is generally more robust and somewhat shorter than *leucopterus*. Numbers refer to the following localities: 1. Key Largo, Fla.; 2. Orleans Parish, La.; 3. Baton Rouge, La.; 4. Lafayette, La.; 5. Bayville, La.; 6. Hathaway, La.; 7. Shreveport, La.; 8. College Station, Tex.; 9. Storrs, Conn.; 10. Milford, Conn.; 11. Mt. Washington, Md.; 12. Arlington Farm, Va.; 13. Arlington Farm, Va.; 14. Goodyear, Pa.; 15. Cleveland, Ohio; 16. Cleveland, Ohio; 17. Lafayette, Ind.; 18. Mahaska Co., Ia.; 19. New Sharon, Ia.; 20. Union Co., Ia.; 21. Webster Groves, Mo.; 22. Stillwater, Okla,; 23. Robstown, Tex.; 24. Lake Providence, La. Sample size is the same as shown in figure 9.

number of *hirtus* and *insularis* available for study, since both of these species are often found with a higher frequency of brachypters.

Figure 8 shows that *insularis* adults correspond in length to *hirtus*, but the mean width of *insularis* is smaller than *hirtus* or *leucopterus*. Means of width show no overlap but ranges of width show considerable overlap making identification by this character alone worthless.

Hirtus is generally more robust than *leucopterus* but there is considerable overlap in means of width of these two subspecies. There is also considerable overlap in length, especially in females.

Although figure 8 indicates three forms are involved, the difficulty of discrimination by size in short series can be seen in figure 9. *Hirtus* and *insularis* correspond roughly in length, whereas *leucopterus* is generally longer. However, the range, mean, standard deviation and standard error of the mean show much intraspecific and intrasubspecific variation. This variation is not restricted to length of abdomen and scutellum but is found also in head width, length of pronotum, width of anterior and posterior lobe of pronotum, and length and width of scutellum. There is some suggestion that *leucopterus* and *hirtus* are most divergent at the extremes of their range and more closely alike in regions of sympatry, supporting the consideration of these forms as subspecies rather than species.

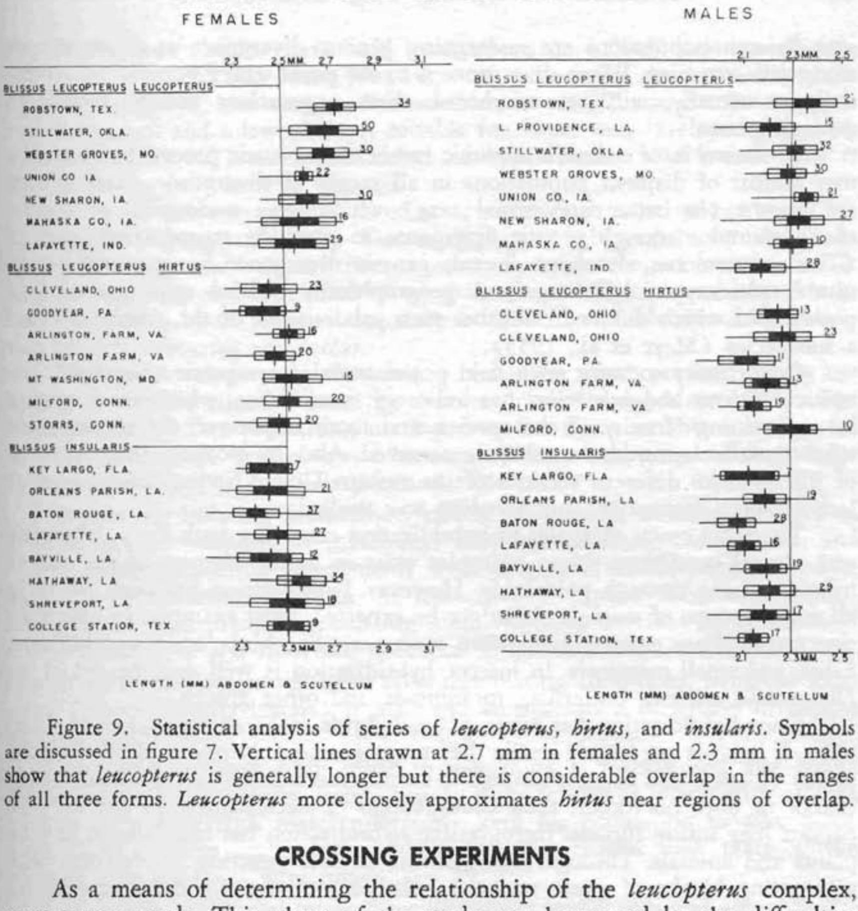


Figure 9. Statistical analysis of series of *leucopterus*, *hirtus*, and *insularis*. Symbols are discussed in figure 7. Vertical lines drawn at 2.7 mm in females and 2.3 mm in males show that *leucopterus* is generally longer but there is considerable overlap in the ranges of all three forms. *Leucopterus* more closely approximates *hirtus* near regions of overlap.

CROSSING EXPERIMENTS

As a means of determining the relationship of the *leucopterus* complex, crosses were made. This phase of the study was hampered by the difficulties in rearing specimens of *Blissus* in the laboratory. Rearing *hirtus*, *arenarius*, and *maritimus* was especially difficult, but since the former two were available locally, specimens were readily obtained for crossing. Several cultures of *maritimus* were acquired but efforts to maintain laboratory cultures failed.

The most widely held definition of a species is that it consists of groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups (Mayr et al. 1953). It is a recognizable fact that species as such do exist; how they have come about is more difficult to explain. Most theories accept spacial isolation as the starting point of speciation followed by genetic divergence and the establishment of isolating mechanisms. The most important factor is isolation; without isolation genetic divergence would not occur, for contiguous populations would share the same gene pool. Isolating mechanisms are genetically controlled and their establishment is dependent on genetic divergence. The one most important factor favoring spacial separation has been geographical isolation, where natural barriers prevent gene flow, and genetic divergence has taken place over a period of time. When, if ever, disjunct populations again become contiguous, isolating mechanisms (most often expressed or strengthened in the region of overlap) may prevent gene flow. It should be noted that biological systems are characterized by genetic plasticity and disjunct populations are undergoing genetic divergence at different rates along different lines. When divergence is to the point where populations, potentially or actually, will not interbreed, these populations can be considered distinct species.

Evolution is, of course, a dynamic rather than a static process and a species may consist of disjunct populations in all stages of divergence. Many groups are known (in better understood taxa) which have undergone phenotypic change without enough genetic divergence to preclude reproductive isolation. (The converse has also been shown; genetic divergence has preceded recognizable phenotypic differences.) A geographically defined aggregate of local populations which differs from other such subdivisions of the species is called a subspecies (Mayr et al., 1953).

Opportunity to work with field populations of sympatric species in Connecticut *(hirtus* and *arenarius)* has indicated some factors which are important in maintaining identity of the species, and more important, the consequences when these isolating mechanisms are removed. Also, by crossing different forms of *Blissus* from different sections of the eastern United States, the presence or lack of some "potential" interbreeding was studied.

There are many examples of hybridization occurring both under laboratory and natural conditions. More examples exist in plants because of the ease of hybrids arising through polyploidy. However, hybridization has been shown in all major groups of animals. As might be expected, most examples of hybridization are in those groups best known taxonomically: birds, anuran amphibians, fishes, and small mammals. In insects, hybridization is well documented in the *Drosophila,* crickets, butterflies, mosquitoes, and other groups.

Once hybridization has taken place, hybrids may radiate in several directions. If hybrids are largely sterile they may become stabilized through allopolyploidy (plants) and become adapted to an intermediate habitat. If allopolyploidy cannot or does not occur, then introgression or backcrossing to one or both parents may insure success. Introgressive hybridization has been shown in both plants and animals. Through introgression, natural selection is presented with segregating blocks of genic material belonging to entirely different adaptive systems (Anderson and Stebbins 1954).

Mecham (1961) in his discussion of isolating mechanisms in anuran amphibians grouped them into two categories, premating and postmating isolating mechanisms. Premating mechanisms are those which function prior to release of gametes and include sexual, habitat, temporal or seasonal, and mechanical isolation. Postmating mechanisms function after release of gametes and include gametic isolation, hybrid inviability, and hybrid sterility.

Sexual isolating mechanisms depend upon discrimination or specific response on the part of one sex in respect to the other sex. These isolating mechanisms include tactile, visual, and chemical discrimination, and behavioral isolation.

In observations of mating behavior of each form of this complex no gross differences were noted in intersubspecific, intraspecific, or interspecific crosses. This does not, however, preclude the existence of small differences. These behavioral patterns have not yet been studied in the field.

The importance of habitat isolation as a premating isolating mechanism has been shown in many animals. Most cases of hybridization have been correlated with the breakdown of habitat isolation. According to Sibley (1961) the most important barrier breaker now in existence is man, who by his modification of natural barriers is permitting hybridization in many parts of the world.

I have been able to make field observations on habitat isolation of only two forms, *arenarius* and *hirtus*. The niche of these forms differs in respect to habitat, host plants, and associated fauna. Yet, in a region where the environment was upset and a lawn habitat suitable for *hirtus* was developed adjoining a coastal habitat of *arenarius,* evidence of hybridization was found. This is discussed more fully later in the text.

Temporal isolation probably is of no importance in most species of *Blissus* because breeding seasons overlap. Due to egg laying habits of the female, adults of the first generation mature over a relatively wide range of time. Earlier springtime activity and copulation of overwintering adults observed in *arenarius* may conceivably be of some consequence in reducing the chance of hybridization between *arenarius* and *hirtus.*

Mechanical isolation or differences in terminalia which prevent mating has been shown to be effective in a few insects (reviewed by Mayr 1963). The "lock and key" effect preventing mating does not occur in this complex, for interspecific matings were observed between all forms. Also, no differences are found in the male phallus or clasper in this complex.

Postmating isolating mechanisms consist of gametic isolation (failure of fertilization), developmental inviability, adaptive inferiority of hybrids, and hybrid sterility. Crossing experiments were conducted to determine if these blocks to hybridization occur in the *leucopterus* complex. Laboratory experiments bypass such premating isolating mechanisms as isolation by habitat and temporal isolation, and may also influence sexual and behavioral mechanisms.

With *Blissus,* under the most favorable rearing conditions, nymphal mortality (especially early instars) is high and an evaluation of hybrid inviability was not attempted.

Intraspecific crosses were made to determine if mating and egg laying would occur under laboratory conditions. In these as well as interspecific crosses, females were kept with males sufficiently long for copulation to take place. Copulation in some intraspecific and interspecific crosses took place within minutes after the sexes were mixed.

In all intraspecific and intrasubspecific crosses fertile eggs and nymphs were obtained. This includes 14 pairings of *arenarius,* 18 pairings of *hirtus,* 12 pairings of *leucopterus,* and 15 pairings of *insularis.* In attempts to establish a culture of *maritimus* both fertile eggs and nymphs were obtained. Due to lack of specimens, no interspecific crosses were made with *maritimus.*

The localities from which the specimens were collected and used were as follows:

arenarius: Chincoteague Island, Virginia; Rehoboth Beach, Delaware (intraspecific crosses only); West Haven, Madison and East Lyme, Connecticut (intra- and intersubspecific and interspecific crosses).

maritimus: New Topsail Beach, Pender County, North Carolina (intersubspecific crosses).

leucopterus: Stillwater, Oklahoma (intra- and intersubspecific and interspecific crosses).

hirtus: Milford, Orange, and Storrs, Connecticut (intra- and intersubspecific and interspecific crosses).

insularis: Homestead, Flamingo Prairie, Everglades National Park, Miami, and Slater, Florida; Baton Rouge, Louisiana (intra- and interspecific crosses).

The results of the crosses are summarized in figure 10.

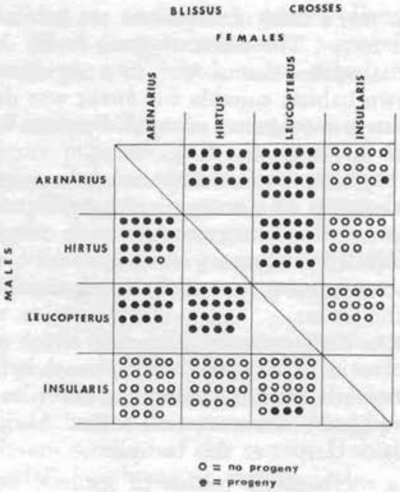


Figure 10. Summary of crosses of *Blissus*. *Arenarius* crossed with *leucopterus* and *hirtus* but cytogenetic abnormalities were found. In *insularis* crosses there was a high degree or total gametic isolation. *Leucopterus* and *hirtus* are inter-fertile.

arenarius × *maritimus*

These two subspecies were only paired three times. In these crosses, viable eggs were obtained.

Female *arenarius* and male *maritimus* were paired only once and fertile eggs and nymphs were obtained. The high nymphal mortality in intraspecific crosses of either of these two subspecies prevents any measure of hybrid inviability.

Female *maritimus* and male *arenarius* crossed in each of two pairings made, and as in the reciprocal, no complete gametic isolation is encountered. A male from one of these crosses was reared through to adulthood.

arenarius × *leucopterus*

In all cases in which these two species were crossed, fertile eggs and nymphs were obtained. Premating isolating mechanisms, if they occur, do not hinder mating in the laboratory. Actually, preliminary laboratory studies on mating choice experiments with these species indicate that there is no species discrimination.

In all 20 pairings of *leucopterus* females with *arenarius* males, hybrids were obtained. Not only are hybrids fertile, but one culture has been reared through five generations. This feat is not difficult with *leucopterus* but has been impossible to duplicate with *arenarius*. This strongly suggests that hybrids, which are intergrades, adapt better to laboratory conditions than *arenarius*.

In addition to F_1 hybrid crosses, a hybrid male was backcrossed to a *leucopterus* female with fertile eggs and nymphs obtained.

In the reciprocal crosses the same general situation occurred with all 14 *arenarius* females crossing with *leucopterus* males. This number does not include an experiment where 14 virgin *arenarius* females were placed with *leucopterus* males. This culture was neglected by mistake and all females died before they could be segregated to determine if they were laying fertilized eggs. Some, if not all females were fertilized, for dead nymphs and viable eggs were found.

From the cross of *arenarius* females with *leucopterus* males the F_1 and F_2 adults obtained were fertile but no hybrids could be reared beyond F_2. This contrasts with the relative ease of maintaining progeny from the cross of *leucopterus* females with *arenarius* males, and suggests the effects of postmating mechanisms.

It has been suggested by Dr. Peter D. Ashlock that Dr. Norihiro Ueshima, Department of Entomology and Parasitology, University of California, Berkeley, would be willing in the course of his survey of Lygaeidae chromosomes to examine *Blissus* chromosomes for me. In his examination of an F_1 hybrid from a *leucopterus*×*arenarius* cross, Ueshima found interesting cytogenetic differences. The haploid number of both species is alike, but in *arenarius* the large autosome is larger than the large autosome of *leucopterus* (figures E, F, G, plate 2). All autosomes including the heteromorphic ones paired during meiosis (figure G, plate 2), but bridging was found during first anaphase (figure H, plate 2). Ueshima's preparation contained no second division figures. My preparations show anaphase bridging in second meiotic division of crosses involving *leucopterus* or *hirtus* crossed with *arenarius* (figure J, plate 3).

An F_1 *arenarius-leucopterus* hybrid female was backcrossed to a *leucopterus* male and progeny were obtained. The cytogenetic examination of adult male progeny from this backcross shows anaphase bridging. Heteromorphic autosomes are shown in figures M and N of plate 4, and figure O of the same plate shows some chromosome configurations during late diplonema or early diakinesis.

Anaphase bridging in first meiotic division is not an uncommon phenomenon and where studied has been shown to be caused by crossing over within confines of an inverted segment in inversion heterozygotes. Frequency of crossing over within an inversion in most cases is dependent on the length of the inversion. Little if any inviability accompanies anaphase bridging. Sturtevant and Beadle (1936), from their studies of bridging in the X chromosomes of *Drosophila melanogaster,* hypothesized that since the axes of the second division spindles lie in a straight line it is assumed that non-crossover chromatids disjoin from the centromeres of the dicentric and move into terminal nuclei, one of which is the ootid nucleus. In this manner chromatids which formed the bridge would be lost in polar bodies and no loss in viability of females would result. The study of Carson (1946) on *Sciara impatiens* Johan. eggs verified this theory. Using a stock with long inversions, Carson found genetic and cytological evidence for the selective elimination of bridging chromatids.

If in *Blissus* hybrids bridging chromatids are likewise eliminated in oogenesis in females, there would be no loss in fecundity. However, in males the condition is different than that discussed in *Drosophila melanogaster* and *Sciara impatiens,* for in *Blissus,* autosomal bridging occurs rather than bridging in sex chromosomes. One could expect that bridging chromatids would not produce functional sperm. Fifty per cent of the sperm would be inviable if bridging occurred in every first meiotic anaphase. However, bridging does not occur in all first divisions.

The loss of some sperm due to anaphase bridging should be of selective disadvantage to hybrids. The amount of selective disadvantage would be dependent on inversion length since the chance of crossing over (and subsequent bridging) is directly proportional to the length of inversion.

The occurrence of bridging during second meiotic division is more difficult to explain. McClintock (1938) shows that in maize anaphase bridging could occur with crossing over in inversion heterozygotes. If this inversion is sufficiently long, a four strand double crossover within the inversion can occur. When a four strand double crossover and subsequent anaphase bridging occur at first division, bridging also occurs at second division. This second meiotic anaphase bridging is caused by fusion of the two longitudinal halves of the chromatid at the position of breakage. Perhaps bridging in second anaphase of *Blissus* hybrids is analagous to this condition.

The effects of anaphase bridging at second division should have more drastic results on viability than bridging at first division. Anaphase bridging at second division will cause sperm or ootids to have in their complement a large or small portion of the heteromorphic autosome, depending on where the breakage occurs. If bridging occurs in all second divisions, theoretically all of the gametes could be inviable. However, the frequency of secondary bridging is not high, but any reduction in viability should place *Blissus* hybrids at a selective disadvantage if hybridization were to occur in the field.

It should be noted that in heteropteran chromosomes Schrader (1932) has found what he termed an interzonal fibre which he considers basically a hollow tube composed of the viscous elastic covering which envelops a chromosome at metaphase. There seems to be little doubt that anaphase bridging is occurring in *Blissus* hybrids. Figure H, plate 1, shows a definite lagging of the joined autosomes.

Although *arenarius* and *leucopterus* interbreed and produce viable offspring in the laboratory, I still consider them to be distinct species based on morphological and cytological differences including meiotic abnormalities, as well as their very different habitat requirements.

arenarius × *hirtus*

In all pairings but one of *arenarius* with *hirtus*, viable eggs and nymphs were produced. *Hirtus* has a chromosome complement which morphologically appears to be identical to *leucopterus*. The same meiotic aberrations as discussed in *arenarius* × *leucopterus* crosses are found in *arenarius* × *hirtus* crosses.

Arenarius females and *hirtus* males produced offspring in 18 of 19 pairings. Complete blocks to adult development do not exist, for hybrid adults are obtained. Viable eggs were obtained from F_1 hybrid crosses. Anaphase bridging in F_1 hybrid males is shown in figures I and J of plate 3.

Hirtus females crossed with *arenarius* males a total of 15 times and all 15 females laid viable eggs. The few adults reared were preserved for cytological examination. High nymphal mortality may have been due to developmental inferiority of hybrids, but *hirtus* was reared through a generation with about equal difficulty.

Although interbreeding and viable offspring are obtained in the laboratory in crosses of *arenarius* and *hirtus*, I consider these to be distinct species on the basis of the larger autosome in *arenarius* and the anaphase bridging (as well as differences in morphology and habitat preferences).

arenarius × *insularis*

A high degree of genetic inviability exists between these two species. *Arenarius* females were crossed with *insularis* males in 24 pairings. None of the eggs produced were viable. The absence of viable eggs was not due to premating isolating mechanisms for copulation was frequently noted. The number of unsuccessful pairings suggests complete gametic isolation.

In the reciprocal crosses of *insularis* females crossed with *arenarius* males, one female of the 20 crossed laid viable eggs and one adult was reared through. Mating occurs frequently but gametic isolation is nearly complete.

The high gametic inviability between *arenarius* and *insularis* indicates that they are distinct species.

leucopterus × *hirtus*

Leucopterus females successfully crossed with *hirtus* males in all 20 pairings. Some nymphs have been reared through to adults and F_1 hybrid adults are fertile.

An F_1 hybrid male was examined cytologically by Ueshima who found the number and morphology of the chromosomes is identical and pairings at meiosis normal (Ashlock 1963 pers. comm.).

Hirtus females crossed with *leucopterus* males in all 19 pairings. Nymph mortality is high as with intrasubspecific crosses of *hirtus*. F_1 hybrids were fertile.

The complete interfertility between *leucopterus* and *hirtus* and lack of cytogenetic differences, combined with morphological similarity, and different geographic distributions support the consideration of *leucopterus* and *hirtus* as subspecies rather than distinct species.

leucopterus × *insularis*

A large degree of genetic incompatability exists between these two taxa. Only three *leucopterus* females crossed with *insularis* males and produced viable eggs, whereas 21 females laid non-viable eggs. Copulation occurred; partial genetic incompatability exists between these species.

From the three successful crosses a total of one adult male and two females were reared through, but F_1 crosses were not possible since the production of the male and females was not coincident. The male crossed with two *leucopterus* females. These females laid fertilized eggs but no nymphs were obtained.

In reciprocal crosses of *insularis* females with *leucopterus* males all 14 females laid non-viable eggs, suggesting total gametic inviability. Copulation was observed in some crosses and presumably took place in others.

Morphological differences in *leucopterus* and *insularis* indicate that genetic divergence has taken place between these species. The high degree of gametic inviability supports the view that these are distinct species. Because of greatly reduced gametic viability, isolating mechanisms should develop rapidly in regions of sympatry.

hirtus × *insularis*

A high degree of gametic isolation exists between these two forms but it is not complete.

Hirtus females were paired with *insularis* males in a total of 19 pairings but produced non-viable eggs. In a test where 10 female *hirtus* were paired with *insularis* males the females were all dead before they could be segregated to determine if they were laying viable eggs (after 30 days). In this culture a few nymphs were recovered from which three adults were reared.

Although copulation between these two species occurs, gametic isolation is nearly complete.

Insularis females paired with *hirtus* males in 13 pairings produced only non-viable eggs, although copulation was noted in some pairings and presumably occurred in all. Gametic isolation appears to be complete, and *hirtus* and *insularis* are considered distinct species.

NATURAL HYBRIDIZATION

The ease in which *arenarius* and *hirtus* interbreed in the laboratory raised the question of whether these two forms cross in nature. Since the area of sympatry would be near the coastal dune habitat of *arenarius*, coastal regions in Connecticut were sought where the habitat of *arenarius* and the turf or meadow habitat of *hirtus* were contiguous, or nearly so. These habitats normally do not overlap, for coastal dunes are unsuitable for the variety of grasses on which *hirtus* subsists. On Lighthouse Point, at the mouth of New Haven Harbor, is an area in which the habitats of *hirtus* and *arenarius* are nearly contiguous (figure 11). A lighthouse constructed near the water's edge has a lawn around its base. Lawns are also found throughout the adjoining park. The area between the lighthouse and the water is rocky but adjacent to the lighthouse is a narrow region of sandy beach on which *Ammophila breviligulata* grows.

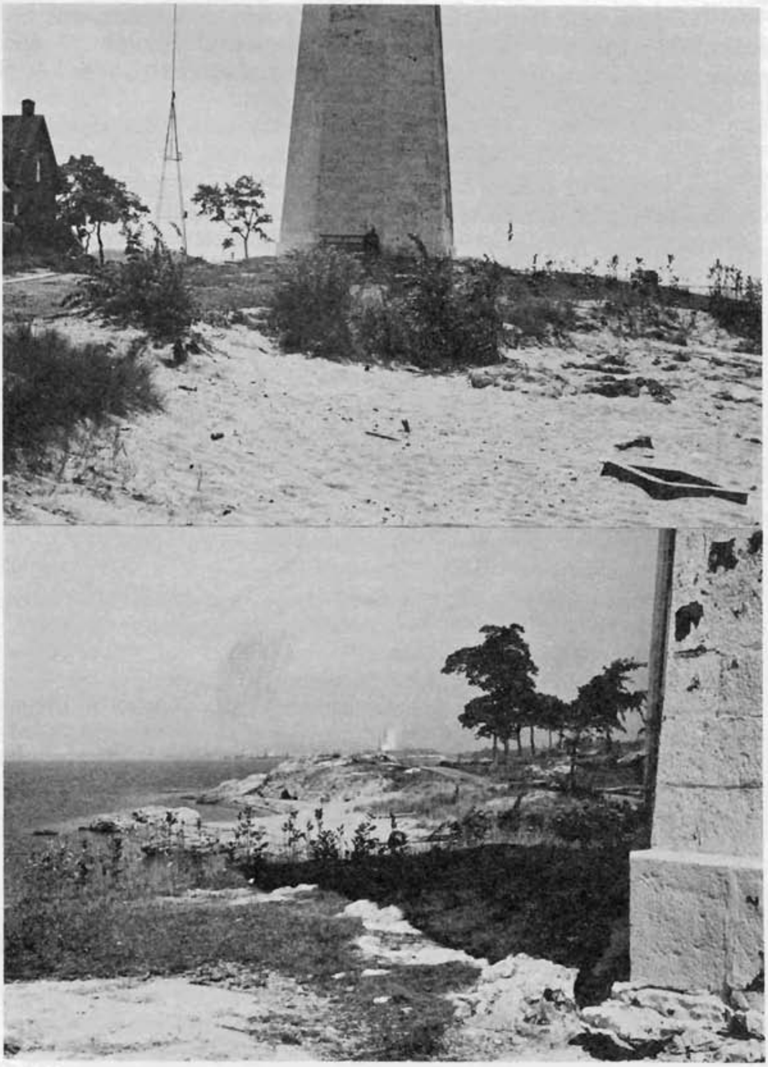


Figure 11. Area in which *arenarius—hirtus* introgressants are found. The top photograph is taken from the coastal sand dunes with beach grass shown in the left foreground. The bottom photograph is taken from the lawn with the beach grass in the background. Evidence of introgression was found in specimens collected in both habitats.

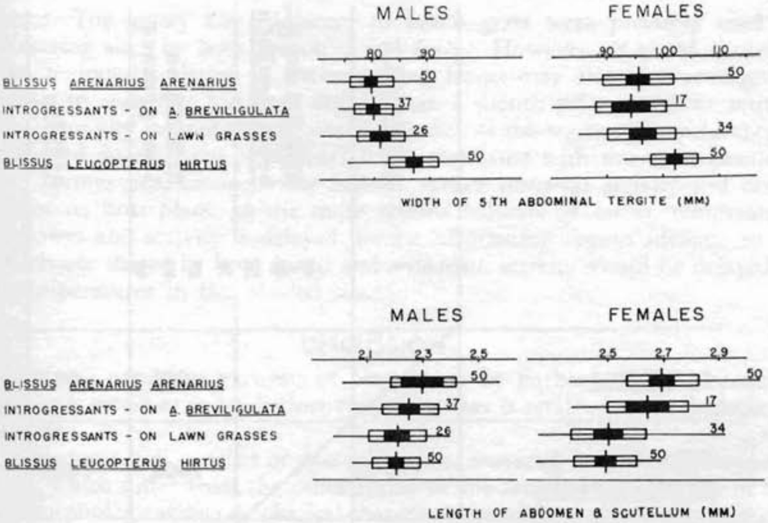


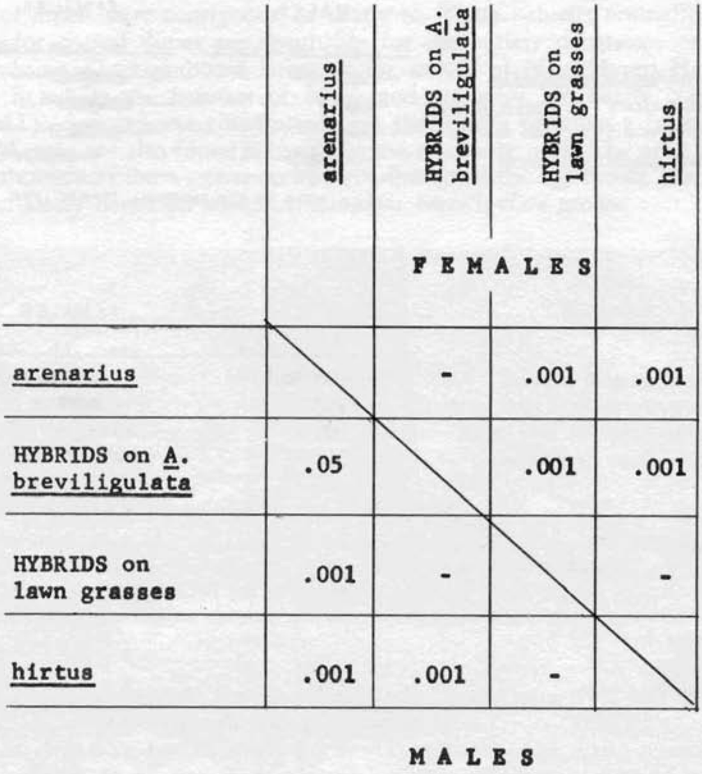
Figure 12. Statistical analysis of samples of *arenarius* and *hirtus* and samples of introgressants collected on the hosts of *arenarius (A. breviligulata)* and *hirtus* (lawn grasses). The symbols used are explained in figure 7. Note that the hybrid specimens on *A. breviligulata* more closely approximate *arenarius,* and the hybrids on lawn grasses most closely approximate *hirtus.*

Both the lawn area around the lighthouse and the beach grass contained specimens of *Blissus.* Specimens in both habitats showed evidence of introgression between *hirtus* and *arenarius.* These are characterized in length and width (figure 12) and in such less easily definable characters as pronotal coloration and color of the distal spot of the corium. The significance of difference in means of length is shown in table 2. Brachypterous forms of *hirtus* and *arenarius* differ in mean length of wing membrane with membranes of *arenarius* usually longer. These measurements show the same pattern found in abdominal length and width.

Specimens from *A. breviligulata* were at first thought to represent typical *arenarius* forms, but closer examination shows some evidence of introgression. There is apparently strong selection against introgressant forms in the dune habitat. This population does not differ significantly from a population of *arenarius* collected across the harbor on a sand bar jutting into the harbor and isolated from *hirtus* habitats by a tidal marsh.

Specimens collected from the lawn habitat immediately suggest hybridization has taken place. This habitat, consisting of a poor stand of a variety of grasses, is apparently more favorable to introgressants and these (at least presently) do not appear to be subjected to as strong selective pressures as those on beach grass. Bugs from both habitats are inter-fertile and specimens collected on the lawn have been maintained for three generations in the greenhouse.

The same cytological abnormalities found in preparations from laboratory crosses are found in the introgressants collected in the field (figures K and L, plate 3). A heteromorphic autosome (figure K, plate 3) and anaphase bridging (figures 1, plate 3) are found. How long this population can continue with a pair of heteromorphic autosomes and anaphase bridging is not known.



MALES \ FEMALES	arenarius	HYBRIDS on A. breviligulata	HYBRIDS on lawn grasses	hirtus
arenarius		-	.001	.001
HYBRIDS on A. breviligulata	.05		.001	.001
HYBRIDS on lawn grasses	.001	-		-
hirtus	.001	.001	-	

Table 2. Significance of difference in means of the length of abdomen and scutellum of specimens of *arenarius* from West Haven, Conn., *hirtus* from Storrs, Conn., and introgressant specimens collected in New Haven, Conn., on American beach grass, *A. breviligulata,* the host of *arenarius,* and lawn grasses, the hosts of *hirtus*. These data correspond to figure 12 and indicate that individuals on *A. breviligulata* more closely approximate *hirtus*. This may be the result of strong selective pressure against the *arenarius* genetic complement in the *hirtus* habitat, and an even more pronounced selective pressure against the *hirtus* genetic complement in the *arenarius* habitat. Evidence of introgression expressed phenotypically is most readily found in the specimens on lawn grasses.

It is of interest to show that introgression can and does occur in species *Blissus,* but it is important to attempt to determine the conditions under which the initial hybridization took place. For hybridization to occur, premating isolating mechanisms, if such existed, must have broken down. It seems obvious that the most important of these is habitat isolation. Sexual isolation in the form of behavioral patterns during courtship might be of importance but not under laboratory conditions where mating occurred and no obvious differences in mating behavior were noted. The most striking difference between *hirtus* and *arenarius* is their different habitat requirements. In this case, as with most other known cases of introgression in animals, habitat change by man seems to be the major factor in eliminating or reducing the effect of this isolation.

The initial contact between species may have occurred with overwintering forms. The overwintering site of *arenarius* is usually on coastal dunes, but in another locality hibernating adults have been found in woods and trash behind the dunes. The grassy areas adjacent to beach grass were probably used for overwintering sites by both *arenarius* and *hirtus*. However, as noted earlier in the text, temporal isolation of overwintering forms may exist, for activity and copulation in *arenarius* has been noted about a month prior to *hirtus* activity. This early activity in *arenarius* is most likely due to the warmer temperatures on the unshaded dunes. Activity appears to be correlated with warm temperatures and the warmer sand environment induces earlier *arenarius* activity and earlier growth of its host plant. In the more shaded habitats of *hirtus,* temperatures remain lower and activity is delayed. In the hibernating region adjacent to the dune probably shared by both *hirtus* and *arenarius*, activity would be delayed by cooler temperatures in this shaded site.

DISCUSSION

Although named as varieties of *leucopterus* by Barber (1918), I consider *insularis* and *arenarius* to be distinct species. *Hirtus* is retained as a subspecies of *leucopterus.*

Blissus arenarius consists of two subspecies, *arenarius* Barber and *maritimus* ssp. nov., which differ from the other forms of the *leucopterus* complex in biological, morphological, and cytological characteristics which indicate that *arenarius* is a distinct species. Both subspecies of *arenarius* differ from the other forms of the *leucopterus* complex in general coloration. As with many animals inhabiting dunes, *arenarius* is lighter in color. This coloration may be a useful adaptation for heat reflection in a habitat characterized by heavy solar radiation and lack of shade. That lighter coloration is not being maintained solely as a phenotypic response to environmental factors but rather is a genetic trait is shown by the fact that *arenarius* reared through two generations in laboratory cultures did not differ in color from field collected specimens. However, other species of *Blissus* living on coastal dune grasses do not have this gray coloration.

In size, *arenarius* closely approximates *leucopterus,* and is slightly larger than *insularis* or *hirtus*. *Maritimus* is larger than the other forms of this complex. (See figures 6-9)

The percentage of brachyptery in populations of *arenarius* is normally higher than the percentage of macroptery, which contrasts with the condition found in *leucopterus*. The total lengths of the hemelytra/membrane differ in brachypters of *arenarius* and *hirtus*. In *hirtus,* the membrane is less than three-fourths the length of the hemelytra (mean of .63 mm) whereas in *arenarius* the membrane is more than three-fourths the length of the hemlytra (mean of .83 mm).

Both subspecies inhabit coastal dunes; both live on ecologically similar plants. In this respect *arenarius* and *maritimus* are not unique in this genus. *B. mixtus* Barber inhabits *Ammophila arenaria* L. in California (Prendergast 1943), and *minutus* (Blatch.) lives on U. *paniculata* L. on the Florida Keys and presumably on the west coast of Florida.

The subspecies of *arenarius* differ cytologically from the rest of the complex in the size of the largest autosome in the diploid complement of ten autosomes shared by each species of this complex. The larger autosome in *arenarius* is larger than the analogous autosomes in *insularis* and both subspecies of *leucopterus*. In crossing experiments of *arenarius* with *leucopterus, hirtus,* and *insularis,* complete gametic isolation was found only in *arenarius* female × *insularis* male crosses. In crosses of *arenarius* with *leucopterus* and *hirtus* the picture is quite different, for in hybrids anaphase bridging between the heteromorphic autosome is found in both meiotic divisions. In male cells, bridging at first division would result in half of the sperm being non-viable, but in females it is likely that no inviability would be evident. In *Drosophila* (Sturtevant and Beadle 1936) and in *Sciara* (Carson 1946) it is shown that only non-crossover chromatids form the ootid. Bridging in second division may be due to crossing over within a four strand double crossover. In cells where second meiotic bridging occurs, all cells would contain varying amounts of the bridging chromosome depending on where the break occurs. Theoretically all of these cells would be non-viable. The amount of anaphase bridging is dependent on the number and length of inversions. Selective pressure against hybrids with these genetic abnormalities could be high. An indication of whether successful hybridization and subsequent introgression could occur in nature is shown in the introgressant population found in New Haven, Connecticut. Specimens are fertile but the degree of fertility has not been studied. Introgression is most evident on the poor turf habitat, which may represent a habitat in which the introgressants may successfully compete with *hirtus*. Evidence of introgression on the dune grass habitat of *arenarius* is much less, indicating stronger selective pressure against these forms in this unique habitat.

The major isolating mechanism which maintains *arenarius* as a closed genetic system is habitat isolation. Where this isolation is removed, hybridization can occur, for behavioral isolating mechanisms, if present, do not prevent hybridization. Complete gametic isolation does not exist, but this genetic system which contains a heteromorphic autosome and anaphase bridging might be at a selective disadvantage.

Blissus arenarius is here considered a distinct species. Although interbreeding may occur between *arenarius* and *leucopterus* or *hirtus,* and although introgression has been described in a natural population, it is not inconsistent with the biological species concept to consider these distinct species. In regions where man has altered the habitat there are many recorded cases of "good" species hybridizing and producing viable offspring, especially among amphibians and birds (Sibley 1961).

Arenarius has been separated from the other forms long enough for divergence (both genotypic and phenotypic) to occur. Reproductive isolation is sufficiently well developed to prevent, under normal conditions, introgression with other forms. Where hybridization takes place, isolating mechanisms should be strengthened, for those bugs with genetic complements with more poorly developed isolating mechanisms that "allowed" hybridization to occur should be removed from the population. Those genomes containing no introgressant genes, although subject to the same selective pressures, might benefit (in per cent survival) from reduced competition of introgressants. Perhaps one characteristic on which selective pressure is most harsh is the aberrant chromosome complement of the introgressants.

There may be some question whether *arenarius* and *leucopterus* are conspecific. A valid argument for such a consideration is the production of viable F_1 hybrids in the laboratory and the discovery of an introgressant population in nature. Under most circumstances this evidence in itself would indicate conspecificity. However, high, if not complete fertility, is known for many species crosses throughout the animal kingdom. Mayr (1963) lists some fully cross-fertile species and notes that cross-fertility does not prove conspecificity.

In its relationships to other members of this complex, the subspecies of *arenarius* appear more closely related to the subspecies of *leucopterus* than to *insularis*. This is best characterized by the degree of gametic isolation between *insularis* and *arenarius*. In general characteristics of size and shape, *arenarius* more closely approximates *leucopterus* than *hirtus*.

Blissus arenarius is broken into two subspecies on the basis of adult size. There are also differences in nymphs. Both subspecies share a similar habitat but differing hosts. The significance of the host difference is not known but host preference might be a strong factor isolating populations of these subspecies. Both subspecies are difficult to rear, hampering crossing experiments, but those crosses attempted indicate that complete gametic isolation between subspecies does not occur. If isolating mechanisms are in effect in regions of sympatry, then character divergence might be expected to be most pronounced in this region. Examination of specimens from Virginia and North Carolina indicates *maritimus* shows most divergence at the opposite (southern) limit of the range, suggesting that these two species are interbreeding in regions of sympatry. *Arenarius* and *maritimus* fit well into the subspecies concept. Although *insularis* is described as a subspecies of *leucopterus* by Barber, *insularis* is here considered a distinct species. *Arenarius* and *insularis* are readily separated, but separation of *insularis* from the subspecies of *leucopterus* is more tenuous. All taxa of this complex are highly variable with no one character holding up in long series. Often this makes positive identification of individual adults difficult. *Blissus insularis* is generally smaller than *leucopterus,* more closely approximating the length of *hirtus,* but is less robust than either *hirtus* or *leucopterus*. The labium of *insularis* extends further than in either other form, extending to the midpoint or beyond (often surpassing the caudal margin of) the metasternum. *Insularis* is frequently found in series consisting of a high percentage of brachypters (see page 11), but brachypterous *leucopterus* constitute a small percentage of a population. With *hirtus* brachypters are common, but since *hirtus* and *insularis* are allopatric, identification of species is usually not as much a problem as separation of sympatric series of *insularis* and *leucopterus*. The hemelytra and membrane of *insularis* is generally whiter than the other forms. The veins on the hemelytra are white basally but piceous or nearly so caudally as is the distal spot of the corium. There are subtle differences in the shape of this spot in *insularis* and *leucopterus*. The contrast in coloration of the anterior and posterior lobes of the pronotum is often more striking in *insularis*. Punctation on the scutellum is often more sparse and the punctures less wide; seldom does the scutellum appear rugose as in *leucopterus*.

Often all of these characteristics have to be used to separate *insularis* from *leucopterus,* but if a series of nymphs is available, the task is simplified. In fourth instar nymphs of *insularis* the head and pronotum is ochraceous, not castaneous or piceous as in *hirtus* and *leucopterus*.

There is some degree of gametic isolation between *insularis* and *leucopterus* and *hirtus*. At present, this isolation is of less importance in preventing gene exchange in *insularis* and *hirtus,* for these forms are allopatric. This might be of significance with *insularis* and *leucopterus* for these two species appear to be sympatric along the northern border of the range of *insularis*. In Texas there appears to be broad overlap of ranges. Laboratory crosses indicate that hybridization can occur only between *hirtus* or *leucopterus* females and *insularis* males. In most crosses, gametic isolation is complete but in a few crosses progeny are obtained. Other isolating mechanisms are unknown, and a study of populations of these two species in regions of sympatry should be enlightening. *Blissus insularis* in St. Augustine grass habitat might well be isolated from *leucopterus* which has not yet been found on this host. However, *insularis* is found in other grasses, and whether these hosts are shared by *leucopterus* is not known.

If interbreeding between these species occurs in the field, a rapid selection of isolating mechanisms might be predicted. Those bugs which interbreed would be the ones in which premating isolating mechanisms are weaker. These genetic complements would be either lost with complete gametic isolation or greatly reduced with a high degree of gametic incompatibility.

Hirtus was described as a species by Montandon and as a variety of *leucopterus* by Barber. Here, *hirtus* is retained as a subspecies. The number of morphological characters which distinguish *hirtus* from *leucopterus* are relatively few. Adult *hirtus* are somewhat more robust and shorter than *leucopterus,* but both forms are very variable. The setae of *hirtus* are golden yellow, especially in more eastern regions of its range, whereas the setae of *leucopterus* are silver or light straw yellow. The color of the abdomen of *hirtus* is darker. Perhaps the most characteristic difference is the higher percentage of brachypters in *hirtus.* Macroptery appears to be correlated with permanency of habitat. Selection against brachypters would be most strong in an agricultural ecosystem where migration is often a necessity. In the more stable turf and meadow habitats of *hirtus* migration is rarely necessary. Spring and fall flights to and from hibernating quarters are common in *leucopterus* but unknown in *hirtus.* Slight color differences are found in fourth instar nymphs, with the underside of the head, thorax, femora and tibiae of *hirtus* more rufescent.

The ease in which hybridization occurs in the laboratory and fertility of hybrids suggests that these two forms will interbreed. A study of populations in regions of sympatry should determine what (if any) isolating mechanisms are in effect. Isolation by habitat and host may be important. *Leucopterus* is found in native prairie grasses but adapts readily to cultivated grains. *Hirtus* is not known to feed on *A. scoparius,* a prairie grass found in the East, nor has it adapted to feed on small grains. Studies are necessary in regions of sympatry where hosts common to both forms (such as timothy) occur to determine possible isolating mechanisms.

The relative ease in rearing *leucopterus* in contrast to the difficulties encountered with *hirtus* indicates that genetic divergence has taken place. The relatively small morphological differences, interfertility and different geographic distributions supports the consideration of *leucopterus* and *hirtus* as subspecies rather than species.

CONCLUSIONS

On the basis of morphological, biological, and cytological evidence, *Blissus arenarius, insularis,* and *leucopterus* are considered distinct species. *Arenarius* consists of the subspecies *arenarius* Barber and *maritimus* ssp. nov. *Leucopterus* is comprised of the subspecies *leucopterus* (Say) and *hirtus* Montandon.

The subspecies of *arenarius* are characterized by general coloration, coastal dune habitat, and a larger autosome. *B. insularis* is characterized by subtle differences in adults and nymphs and a total or large degree of gametic isolation in interspecific crosses. *B. leucopterus* contains the subspecies *hirtus* and *leucopterus.* These subspecies are interfertile, have only slight morphological differences, and differ in geographic distribution, percentage of brachptery, host, and habitat preferences.

The chromosome complements of *arenarius, maritimus, insularis, leucopterus,* and *hirtus* are described. All have a diploid chromosome number of ten autosomes, an X, Y, and *m* chromosome. The only known exception to this number in species of *Blissus* is found in *breviusculus* Barber, which contains 14 autosomes, an X, Y, and *m* chromosome (Leonard ms.). All species surveyed have one large autosome. In *arenarius* and *maritimus* the large autosome is larger than any other species studied.

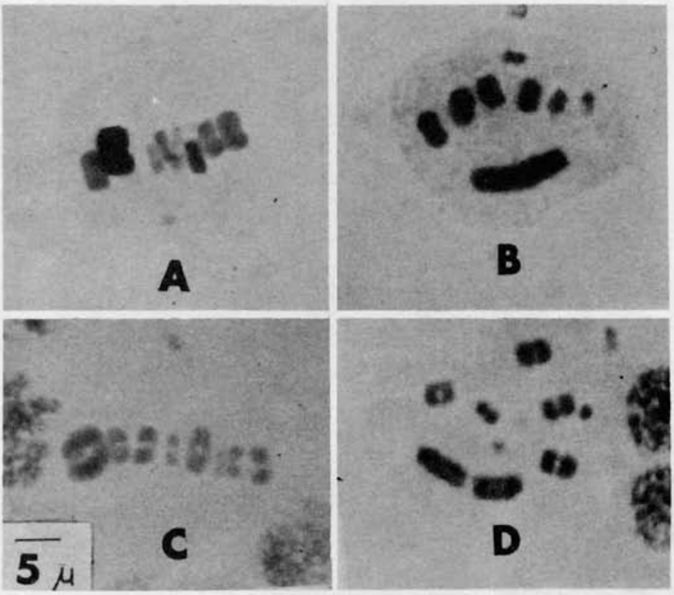


Plate 1. First meiotic anaphase of *Blissus* spp.

A. *Blissus leucopterus leucopterus* (Say) male with a diploid complement of ten autosomes, an X, Y, and *m* chromosome.

B. *Blissus leucopterus hirtus* Montd. male with a diploid complement of ten autosomes, an X, Y, and *m* chromosome. The largest autosome has started to separate and the chromatids are end to end. This may preclude a diffuse kinetochore in *Blissus*.

C. *Blissus insularis* Barber male with a diploid complement of ten autosomes, an X, Y, and *m* chromosome.

D. *Blissus arenarius arenarius* Barber male with a diploid complement of ten autosomes, an X, Y, and *m* chromosome. The larger autosome chromatids have separated as have the Y univalents. The lighter staining *m* chromosome is seen in the upper right.

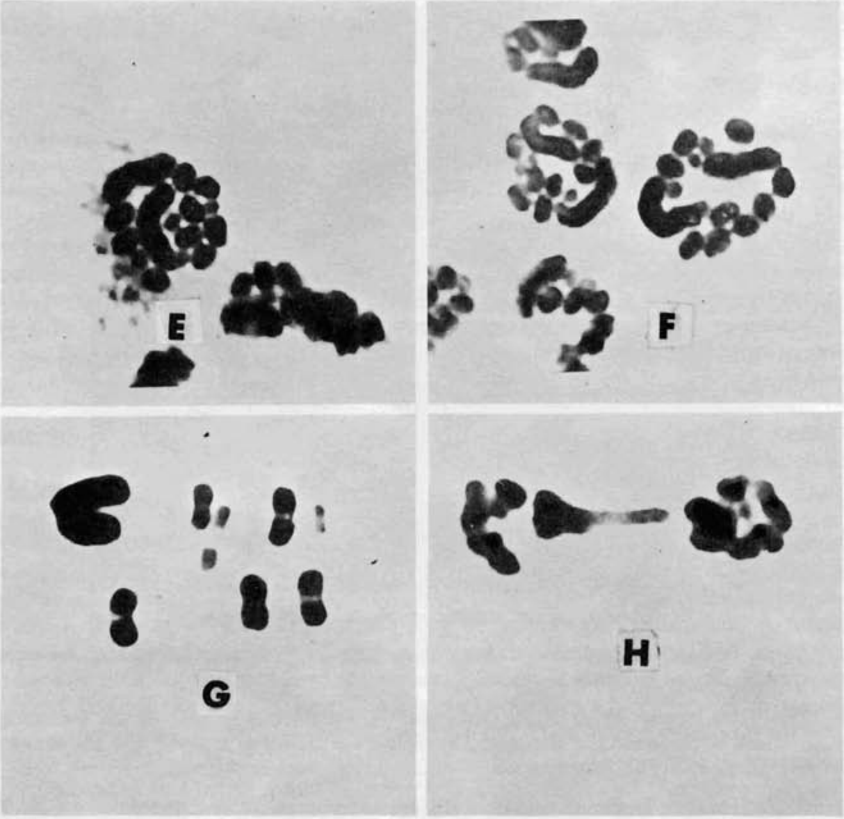


Plate 2. First meiotic anaphase of an F₁ *leucopterus-arenarius* hybrid. Preparations and photographs by N. Ueshima.

E. and F. Heteromorphic autosomes in an F₁ *leucopterus-arenarius* hybrid. The largest autosome is from the *arenarius* parent.

G. First metaphase showing pairing. Note the heteromorphic bivalent. The Y univalents have separated.

H. Anaphase bridging between heteromorphic autosomes of *leucopterous—arenarius* hybrid.

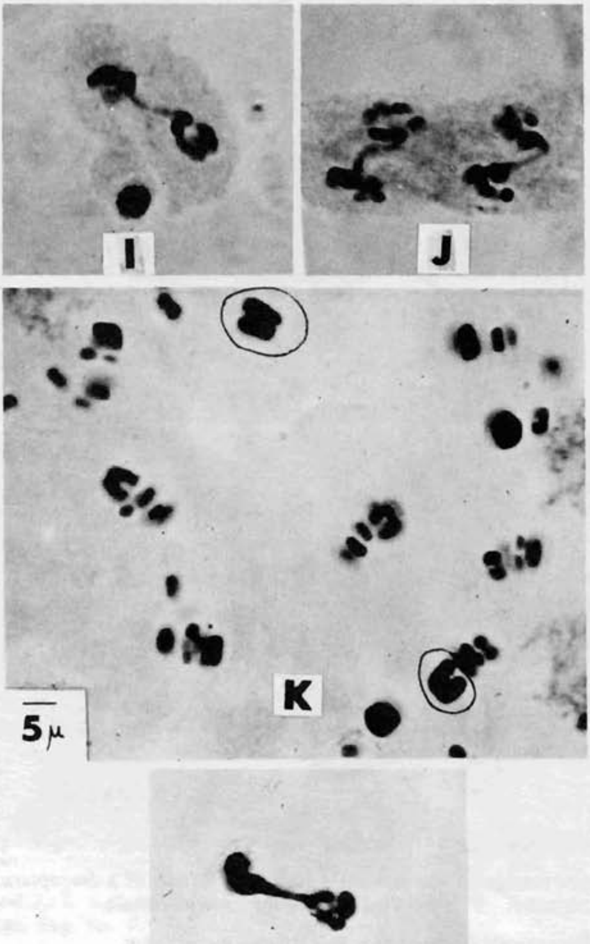


Plate 3. Anaphase bridging in a *Blissus* hybrid male (upper photographs) and meiotic abnormalities in a natural hybrid male (lower photographs).

I. and J. Anaphase bridging in an F_1 hybrid from an *arenarius* × *hirtus* cross.

K. Heteromorphic autosomes (circled) in male from natural population of *hirtus*—*arenarius* introgressants.

L. Anaphase bridging from the same preparation as K above.

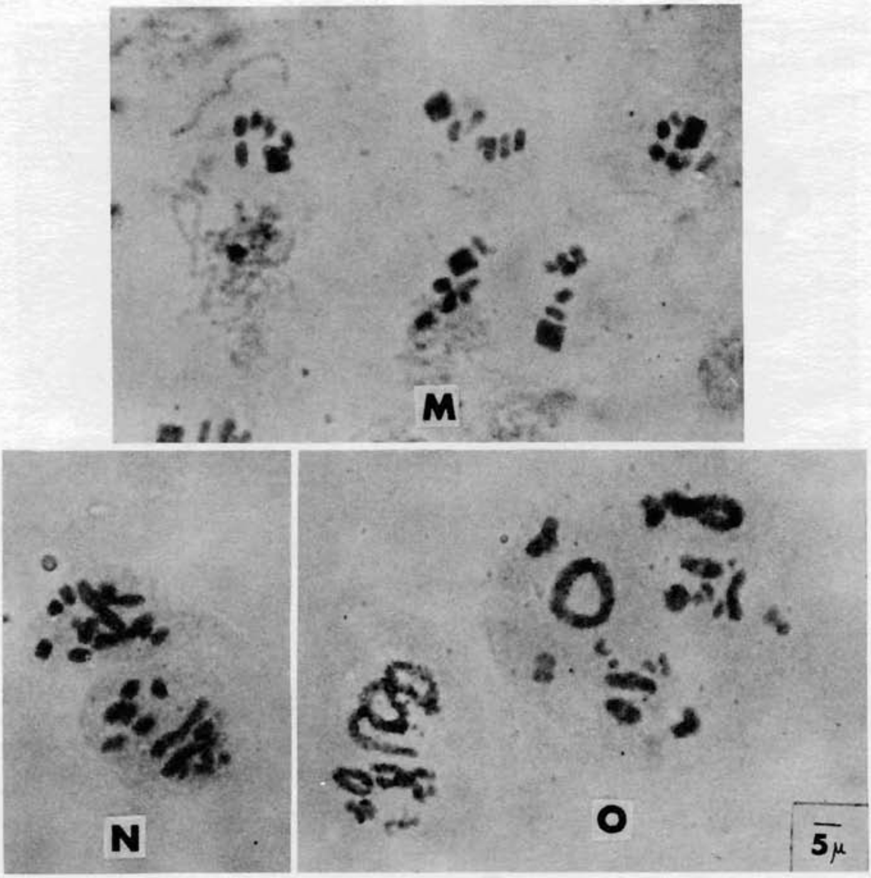


Plate 4. Meiotic configurations in a male from a backcross of a *leucopterus* male with an F_1 hybrid *arenarius—leucopterus* female.

M. and N. Heteromorphic autosomes in first meiotic division.

O. Late diplonema or early diakinesis configurations.

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