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Title: THE LEAFHOPPER GENUS TIAJA OMAN (HOMOPTERA:

CICADELLIDAE), WITH A CONTRIBUTION TO THE

BIOSYSTEMATICS OF THE GROUP

Abstract approved: Redacted for privacy

Paul Oman

The genus Tiaja Oman consists of eight known species of flight-

less leafhoppers of the subfamily Megophthalminae found along the

western coast of North America between British Columbia and

northern Mexico. Species occurring from the San Francisco Bay

area northward are restricted to a narrow coastal zone within 1 km of

the ocean; some of those species that occur farther south may be

found inland as well as on the coast. Members of the genus occupy

an unusual habitat in that most individuals are found on the undersides

of their host plants or in the litter layer beneath them. Flightlessness

and the position the insects occupy on their host plants are seen as

adaptations to enhance survival in a windswept environment.

Life history studies of T. friscana (Ball) and T. arenaria Oman

show that nymphs normally pass through five nymphal instars

although some individuals may have four or six nymphal instars. The

final nymphal instar is of longer duration than any of the preceding

instars but the length of the developmental period appears to depend on temperature conditions in the rearing chamber. The northernmost species, <u>T. arenaria,</u> is univoltine with obligatory diapause while <u>T. friscana</u> and <u>T. montara</u> Oman, two species of the central California coast, are multivoltine with no diapause under favorable conditions. Other species are presumed to be multivoltine.

Host association studies show that members of the genus <u>Tiaja</u> are usually found associated with woody shrubs and that these shrubs may serve as feeding but not necessarily oviposition hosts. The oviposition host of <u>T. arenaria</u> is <u>Fragaria chiloensis</u> (L.) Duch.

Infraspecific variation in disjunct populations of <u>T. friscana</u> is examined. These populations lie 550 km apart and the range of another species, <u>T. montara,</u> intervenes. Crossbreeding experiments show that while there is some genetic differentiation as a result of isolation, the populations are similar enough and hybridize to a sufficient extent to be considered members of the same species.

Crossbreeding experiments between <u>T. friscana</u> and <u>T. montara</u> show that these allopatric species from the San Francisco Bay area hybridize to some extent when artificially placed together. However, fertility is considerably reduced compared to parental crosses and this is taken as evidence of the reliability of morphological features used for species differentiation in this genus. Factors influencing the success rates of these crosses are discussed.

The presence of members of the genus on islands and in populations isolated from the remainder of a species despite the limited mobility of the group is discussed. It is speculated that dispersal of T. arenaria to Vancouver Island subsequent to Pleistocene glaciation, dispersal of T. insula Sawbridge to Santa Barbara Island following its submersion in the late Pleistocene, and the colonization of San Simeon by T. friscana can be attributed to dispersal by drift of egg-containing host plant material aided by ocean currents and prevailing winds.

Taxonomic information includes a discussion of the place of the Megophthalminae within the Cicadellidae, recharacterization of the genus Tiaja, a revised key to the eight known species, and species recharacterizations including morphological data, distributions, seasonal occurrence, and host and habitat information. Criteria for differentiation of nymphal instars through setal patterns and wing pad development are discussed and illustrated.

It is concluded that further study of the habitats, life history, behavior, and cytogenetics of the Ulopinae and other members of the Megophthalminae will be necessary before current data on Tiaja can be used to help redefine relationships within and between these subfamilies.

The Leafhopper Genus <u>Tiaja</u> Oman (Homoptera:
Cicadellidae), with a Contribution to the
Biosystematics of the Group

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THE LEAFHOPPER GENUS TIAJA OMAN (HOMOPTERA: CICADELLIDAE), WITH A CONTRIBUTION TO THE BIOSYSTEMATICS OF THE GROUP

I. INTRODUCTION

Members of the leafhopper genus Tiaja Oman are small to medium-sized brown leafhoppers with rudimentary hindwings. They are restricted to the west coast of North America where each of the eight species has a limited distribution consisting of a series of isolated populations. The genus belongs to what is considered to be one of the more primitive subfamilies of leafhoppers, yet its members exhibit a number of unusual physical and behavioral attributes which presumably aid in their adaptation to an unusual habitat and coincidentally also render them a fascinating subject for biosystematic investigations.

Tiaja is one of the two North American genera of the tribe Megophthalmini. The taxonomic placement of the Megophthalmini is somewhat controversial. Evans (1947, 1966) recognizes a subfamily Ulopinae in which he places tribes Ulopini, Megophthalmini, and others. Oman (1949) recognizes subfamilies Ulopinae and Megophthalminae with included tribes Ulopini and Megophthalmini respectively. Morphological evidence has been the sole basis of past interpretation of these relationships. Ecological, distributional,

developmental, and behavioral information gained from a study of

the genus Tiaja should prove valuable for comparison with other

Megophthalmini, the Ulopini, and other Cicadellidae. Such informa-

tion could help clarify the relationship of these tribes to one another

and to the remainder of the Cicadellidae.

Inherent in any biosystematic inquiry are the questions "Why do

these organisms occur where they are and not in other areas where

apparently suitable conditions exist?", "What particular attributes do

they possess that enable them to survive in the environments they

occupy?", and "What factors of the geological past may account for

their present geographic distributions?" Leafhoppers are charac-

teristically vagile, with a capacity for dispersal by flight, yet

members of the genus Tiaja are flightless, slow-moving, and reluc-

tant to jump. Such specializations must play a significant role in

restricting the distributions of members of the genus and in keeping

members of each species isolated from one another. All members of

the genus occur within relatively circumscribed areas and would thus

seem to be appropriate subjects for studies that might contribute to a

better understanding of biogeography. But in seeking answers to bio-

geographic questions, it is essential that still other questions be

resolved, namely, "Are the isolated populations observed in fact

different kinds (species) or only structural variants of a widely

distributed species?" Hence, taxonomic analyses become prerequisites for biogeographic interpretations.

A recurring question in the systematics of nearly any group of arthropods, and certainly in the leafhopper family Cicadellidae, is the biological significance of morphological similarities and differences that are detected in various populations. Are these observed differences in structure reliable criteria for the definition of species? Species concepts in the Cicadellidae have traditionally been based almost entirely on morphological evidence and only within the last 50 years have the details of the internal structure of the male genitalia been included in this evidence.

Some recent studies of Cicadellidae, such as those of Le Quesne and Woodruff (1976), Vilbaste (1975), Sawbridge (1975b), Whitcomb (1972), and Muller (1957) have emphasized that some morphological dissimilarities may be a result of infraspecific variation and are not necessarily indicators of differentiation of species. Other studies such as those of Musgrave (1974), Nielson and Toles (1970), Severin and Klostermeyer (1950), and Severin (1940, 1945) have tended to confirm the taxonomic reliability of morphological criteria. Additional evidence from other taxa is obviously desirable in order to firmly establish the value of morphological criteria in species discrimination. In this study it seemed pertinent to examine whether

evidence from crossbreeding experiments would support or erode the current morphologically based species concept in _Tiaja_.

Although several species of _Tiaja_ have been known, largely as taxonomic curiosities, since 1902 when Ball described the first species that would later be placed in the genus _Tiaja_, until recently little was known about them other than the morphological features used in classification. Until _T. arenaria_ Oman was encountered and observed for a period of more than a year (Oman, 1972), all species were known only from limited samples and relatively few localities. Although _T. arenaria_ appears to occupy a discrete and well-isolated range, such is not the case with some other species that are morphologically rather similar to each other, particularly _T. friscana_ (Ball) and _T. montara_ Oman. Confusing occurrence records suggested that these groups might represent semispecies, subspecies, or a group of interbreeding morphs rather than distinct species. Thus a question implicit throughout the study was that of the biological discreteness of the populations known to exist along the coastline of western North America. Were the observed structural differences merely population differences or did they reflect isolating features sufficient to justify recognition as distinct species? This study endeavors to clarify the systematics of the genus _Tiaja_ through an analysis of structural, distributional, and biological evidence including experimental hybridization as a means of testing the specific discreteness of populations.

II. LITERATURE REVIEW

The major literature pertinent to a study of the genus _Tiaja_ falls into two categories: (1) that relating specifically to the genus and its member species, and (2) that dealing with the broader aspects of the position and relationships of the genus _Tiaja_ within the Tribe Megophthalmini and of the tribe within the Family Cicadellidae.

Members of the Megophthalminae are found in Europe, Africa, and the Americas; members of closely related subfamilies are found in Europe, Asia, Australia, Africa, and the islands of the South Pacific. Since all of these insects are considered primitive morphologically and have many unusual features, they have attracted the attention of many workers in all parts of the world. A summary of this literature up to 1956 is found in Metcalf's General Catalogue of the Homoptera (1962). Of primary interest to the current investigation are those papers which discuss the origin of the megophthalmines and their relationships to other leafhoppers. Only the most significant or controversial of these papers will be mentioned here.

Comparatively little has been published about the genus _Tiaja_ and its included species. The first of the species that would subsequently be placed in the genus _Tiaja_ were described by Ball in 1902. These were _T. interrupta_ (Ball) and _T. mexicana_ (Ball)l descriptions of _T. friscana_ (Ball) and _T. californica_ (Ball) followed in 1909. Ball

placed these four species in the Old World genus <u>Paropulopa</u> Fieber

along with a fifth North American megophthalmine leafhopper,

<u>Brenda</u> <u>arborea</u> (Ball) which has fully developed hindwings. In 1914

Van Duzee used the generic name <u>Koebelia</u> in a note on <u>interrupta</u> but

reverted to the generic name <u>Paropulopa</u> in his 1917 Catalogue. In

1941 the genus <u>Tiaja</u>, with <u>P. californica</u> as the type species, was

erected by Oman to contain the flightless members of the North

American Megophthalminae. He was of the opinion that the affinities

of this group of leafhoppers lay closer to the genus <u>Megophthalmus</u>

Curtis than to <u>Paropulopa</u> on the basis of the presence and placement

of the ocelli (Oman, 1941) but that there were sufficient differences

from the former to warrant creation of a new genus. At the same

time, Oman erected the monobasic genus <u>Brenda</u> to contain Ball's

<u>P. arborea</u>. Two new species described by Oman in his 1941 paper

were <u>T. montara</u> Oman and <u>T. ventura</u> Oman. A seventh species,

<u>T. arenaria</u> Oman, was discovered and described by Oman in 1972.

During the current investigation, an additional species, <u>T. insula</u>

Sawbridge, was discovered and described (Sawbridge, 1975a). With

the exceptions noted below, most other literature references to <u>Tiaja</u>

or its member species are merely cataloguings or parts of a species

list for a geographic area.

Published habitat and host plant information on members of the

genus <u>Tiaja</u> is sparse. The earliest such note is that of Van Duzee

(1914) for <u>T. interrupta</u>. Tilden (1951) makes brief mention of

<u>T. californica</u> in his study of the insect associates of <u>Baccharis</u>

<u>pilularis</u> DC. By far the most comprehensive treatment of the

habitat and host plants of a member of the genus <u>Tiaja</u> is that offered

by Oman (1972) in connection with description of <u>T. arenaria</u>. Mini-

mal host plant and habitat data are given for <u>T. insula</u> by Sawbridge

(1975a).

There has been considerable difference of opinion among

students of leafhopper classification centering on whether the

megophthalmine leafhoppers should be regarded as the Megophthal-

minae, a separate subfamily of the Cicadellidae, or as the Megoph-

thalmini, a tribe of Ulopinae. The main proponent of the latter

school of thought has been J. W. Evans who published "A Natural

Classification of Leafhoppers (Jassoidea:Homoptera)" in 1947 and

continued to espouse this viewpoint in 1966 and 1968 papers. Favoring

consideration of the megophthalmine leafhoppers as a distinct sub-

family of the Cicadellidae have been Oman (1949), Wagner (1951),

Linnavuori (1972), and Davis (1975). Halkka (1959) supports

Wagner's phylogenetic tree for the Cicadellidae on the basis of his

chromosome studies of 115 species of leafhoppers although his work

did not actually include data for the Megophthalmini. In this work, the

concurring opinions of the majority of recent workers is accepted and

the megophthalmine leafhoppers are treated as a distinct subfamily,

the Megophthalminae.

III. MATERIALS AND METHODS

Both living and preserved specimens were used during the course of this study. When the investigation was begun in 1972, the Oregon State University collection contained approximately 300 specimens of Tiaja, almost all representing the species T. arenaria. The majority of specimens examined in this study (several thousand in all) were collected specifically for this purpose during the study and were either maintained alive for observation and culture or preserved. Personal collecting was supplemented by several hundred preserved specimens, including types and representatives from many other localities, which were borrowed from the United States National Museum of Natural History (33 specimens), University of California at Riverside (3 specimens), California Academy of Sciences (225 specimens), California Department of Food and Agriculture (20 specimens), and University of Victoria (1 specimen). Additional information on the morphology, distribution, and seasonal occurrence of Tiaja species was gained from these specimens.

Population Sampling

Members of the genus Tiaja behave differently from most other leafhoppers and occupy unusual habitats; as a result, the customary collecting technique of sweeping vegetation is frequently not very

productive. Three methods were regularly used to obtain study samples of the different species. The first method was the "shovel" or "scoop" method for collecting specimens from upright, shrubby vegetation. This method involves placing the net under the shrub and agitating the plant so that the leafhoppers fall off into the net. _Tiaja_ tend to be slow to jump and fall into the net before jumping. To collect specimens living close to the ground under decumbent shrubby vegetation, or in clumps of grass or moss, a different technique is required. To sample such habitats, soil and litter samples, processed in a modified Tullgren funnel, were found to be most productive. Live specimens could be collected in a jar containing moist sand and a cutting of suitable plant material placed below the funnel; dead specimens could be collected by the traditional method of placing a jar of alcohol below the funnel.

First instar nymphs of _T. arenaria_ were also collected by a third method. Oviposition host plants were collected and placed on damp paper in refrigerator containers which were placed in a greenhouse room at $20^{\circ}C$ with a 16 hour photoperiod. As eclosion occurred, nymphs were transferred to laboratory host plants. This method was used to determine the oviposition site of _T. arenaria_. Samples of possible oviposition hosts were collected in the field and stored as described above. Plants were checked daily for eclosion of nymphs

and a tally was kept of the number of nymphs hatching from each test

species of plant.

Laboratory Culture Methods

Preliminary laboratory work was done with _T. arenaria_, the

species which Oman (1972) had successfully maintained in the labora-

tory for periods of up to 300 days. There were at that time no

established methods for rearing any species of _Tiaja_ through its

complete life cycle under laboratory conditions. Before a successful

culturing technique was established, a number of unsuccessful

attempts were made at rearing _Tiaja_ under artificial conditions.

Oman's (1972) maintenance technique of caging individuals on

sprigs of kinnikinnick (_Arctostaphylos uva-ursi_ (L.) Spreng.) in small

vials was the first used in the attempt to culture _Tiaja_ in the green-

house. A number of problems were encountered with this method

which, although useful for short term observation of individuals or

pairs, is not suitable for long term culture of large numbers of

insects. Water condensation on the tubes caused death by drowning,

particularly of young nymphs. Twigs became dry and brittle after

about a week, so were not suitable for oviposition or hatching experi-

ments. Only a few individuals could be placed in each tube.

Living kinnikinnick plants were next used in an effort to pro-

vide a long-lasting medium for producing large stock cultures. As

with the kinnikinnick cuttings, adults and nymphs were maintained (and nymphs matured) but no new nymphs hatched. Specimens had a tendency to become "lost" on the large plants and recovery of individuals was difficult. Additionally, large and costly cages had to be built to cover the kinnikinnick plants.

Attempts to use kinnikinnick as a laboratory culture plant were abandoned when it was discovered that the oviposition host of T. arenaria was beach strawberry, Fragaria chiloensis (L.) Duch. Cultivated strawberry plants and F. chiloensis transplanted from the field were then used to maintain stock cultures but again no evidence of oviposition was observed and no nymphs hatched. Strawberry plants have a disadvantage as a laboratory plant as they require nearly four months to grow from seed to the size required for culturing leaf-hoppers. Old plants need to be replaced before new ones are ready. Suitable facilities were not available for growing the thousands of strawberry plants that would have been needed for the various experiments in this study.

At about the time that strawberry plants were first used to maintain T. arenaria, a collection of T. friscana was brought in from the field and placed on a large Kenland red clover (Trifolium pratense L.) in the absence of the field host, Eriophyllum staechadi-folium Lag.var. artemisiaefolium (Less.) Macbr. Within three weeks, first instar T. friscana hatched from the plant. As a result of this

fortuitous discovery, Kenland red clover was used as the feeding and oviposition host in all subsequent laboratory work with Tiaja. Kenland red clover has an advantage over strawberry as a host plant in experimental work as it grows rapidly and plants are ready for use at the age of three to five weeks. Cultures of T. friscana and T. montara, a species later used in experimental work, were able to go through complete life cycles on the red clover. Stock cultures were maintained year round in greenhouse rooms with temperatures set at 20°C and with 16 hour daylight regimes. Since these greenhouse rooms are not controlled environment chambers and are affected by outdoor conditions, there was considerable fluctuation of temperatures in the rooms, especially during periods of extreme hot or cold outdoor temperatures. T. arenaria could be maintained on clover plants from hatching through to the adult stage but was never successfully cultured in the greenhouse.

Two types of cages were used for maintenance of cultures. Stock cultures were maintained within 22 cm x 23 cm x 44 cm tall rectangular wooden-framed cages with three net sides and one sliding glass side, set over 15 cm diameter clay pots containing red clover plants approximately 20-30 cm tall. Experimental work such as crossing and rearing of individuals or small groups of nymphs was done on red clover plants of a minimum age of three weeks (5 cm tall) growing in 10 cm diameter clay pots and caged by glass lamp globes

(Corning #2, volume 950 cc) with standard mesh cheesecloth covering the tops.

Oviposition Site Preference

To check oviposition site preference of T. friscana in the laboratory, a large red clover plant was exposed to gravid females for one week. After the females were removed, the plant was divided so that stems, leaves (including petioles), and flowers were placed in separate petri dishes. The number of nymphs hatching from each category of plant part was recorded.

Breeding Experiments

For the study of fecundity of T. friscana females, 40 virgin adult females were paired with males and each pair was caged on a Kenland red clover plant. For all crossbreeding trials and their controls, three adult virgin males and three virgin adult females were caged together on a red clover plant; ten replications were made of each cross. Adults were transferred to fresh plants every seven days. Each exposed plant was cut off at soil level and placed on filter paper in a glass petri dish marked with the type and number of the cross and the date adults were removed from the plant. Petri dishes were placed in plastic refrigerator containers with closely fitting lids and returned to the rearing room. The fecundity study was

continued for 24 weeks so that each female that remained alive for the entire period was exposed to 24 clover plants. The crossbreeding experiments were terminated after ten weeks (by which time numbers of parent individuals had declined markedly) so that each group of leafhoppers in this experiment was exposed to a total of ten clover plants.

Petri dishes were checked regularly for hatching nymphs. Nymphs were counted, then killed or placed on fresh clover plants for rearing. The measure of nymphs hatching per week per female was used rather than the measure of eggs laid per week per female because it was impossible to see the eggs in the host plant until immediately prior to hatching. This method has the disadvantages of producing a low estimate of the number of eggs actually produced and of not allowing a calculation of egg fertility to be made. An indication of the degree of inaccuracy involved in counting only nymphs hatched per female is given in Stoner and Gustin's (1967) study of Graminella nigrifrons (Forbes) where five females produced 80 eggs of which 70 were considered fertile, but of which only 49 hatched. In similar experimental work, Rabinovich (1972) found a statistically significant decrease in the percentage of hatching between eggs laid by females aged 4-28 weeks and females 49-87 weeks of age. The degree of inaccuracy could be expected to increase in interpopulation and interspecific crosses if hybrid

inviability were in effect. However, under the circumstances of the current investigation, the measure of nymphs hatching per week per female was considered the most accurate available.

Matings occurring in each cage were recorded as seen, although checks for mating were made only at irregular intervals as time permitted and as plant material was changed.

Each death was recorded as plants were changed. Death of a male, if it occurred more than a week after pairing, was not considered to be important. Deaths of females were, of course, of major importance, as they directly affected the nymphs per female per week ratio. The number of nymphs per female per week was calculated by dividing the number of nymphs hatching in a given week by the number of females present at the beginning of that week. It was arbitrarily decided that a female alive at the beginning of a week would be considered alive for the entire week. Results were graphed. Data were subjected to a t-test for the difference of two means.

Dissection Methods

Clearing and dissection of genitalia was necessary for detailed examination of male and female structures and usually for determination of species. Genitalia were prepared by the standard method of separating the abdomens from the insects with two microdissecting needles, then heating the abdomens in a 10% solution of NaOH for

approximately five minutes until the NaOH solution was just below

the boiling point and the non-sclerotized contents of the abdomen were

dissolved. After adequate maceration, the abdomens were then

rinsed twice with water before being transferred to glycerine for

observation, dissection, and storage. The styles, aedeagus, and

connective of males were removed from the genital capsule for close

examination by severing the dorsal attachment of the aedeagus to the

tenth segment and the ventral attachments of the styles to the plates.

The seventh sternum of the female was removed from the rest of the

abdomen for detailed examination. Cleared and dissected abdomens

were stored in glycerine in plastic microvials attached below the

insect on the pin.

Dissection of females for examination of ovarioles was done

according to the method for leafhoppers described by Kamm and

Ritcher (1972). The intersegmental membrane between segments 7

and 8 was severed by inserting a probe on each side of the seventh

sternum. The genital segments were then grasped with forceps and

pulled posteriorly to remove the ovaries from the abdominal cavity.

Nymphal Instar Determination

In order to determine the number of nymphal instars and the

duration of each instar, newly-hatched T. friscana and T. arenaria

nymphs were placed on individual red clover plants and caged in

cheesecloth-covered lamp globes. Each nymph was checked daily for moults. Nymphs were reared through to adulthood and a record of the number of moults and moulting dates was kept for each nymph.

It was also necessary to have nymphs of known instar in order to determine their diagnostic characteristics so that field-collected individuals could be identified. Individually-caged, newly-hatched T. friscana were checked daily for moults and at each instar an "early" and a "late" sample were taken. "Early" instar samples consisted of newly-hatched, first instar nymphs or newly-moulted nymphs in the other instars. "Late" instar samples consisted of nymphs that had last moulted 8-10 days before being killed, except for late fifth instar nymphs which had last moulted 12-15 days before being killed. Specimens were preserved in alcohol. The different stages were then studied and illustrated.

Measurements

Measurements of length were made with an American Optical Model 426 filar micrometer. Total body length was measured from the apex of the crown to the wing tips. Head length was measured as the median length of the crown; head width was measured as the width of the crown immediately anterior to the eyes. The ratio of head width to length (W/L) was calculated from these figures. Low W/L

values indicate an angular head while high W/L values indicate a

blunt head.

Illustrations

A micrometer disc ruled in 0.1 mm squares, placed in the

ocular of a stereoscopic microscope and drawing paper with a 5 mm

or a 1 cm square grid were used to prepare drawings of insect

structures. The following magnifications were used for these

drawings: male genitalia x90, female seventh sternum x90, heads

x90, first and fifth instar nymphs x45, developing wings from first

to fourth instar x90, and developing wings of fifth instar x45.

Genitalia drawn were preserved in glycerine, nymphs illustrated were

preserved in alcohol, and adults whose heads were illustrated were

preserved dry. Each page of illustrations includes a 1.0 mm or a

0.1 mm scale.

IV. DISTRIBUTION AND ECOLOGICAL ASSOCIATIONS

Members of the genus _Tiaja_ occur primarily along the west coast of North America where they show a distribution pattern consisting of isolated populations occurring in widely separated areas. _Tiaja_ have been found from southern British Columbia to northern Mexico (Figure 1). In the northern part of the genus' range, populations occur only in the narrow coastal strip west of the Coast Range which is known as the _Picea sitchensis_ zone (Franklin and Dyrness, 1973). This zone is considered to have the mildest climate in the northwest, with minimal extremes in moisture and temperature regimes (Franklin and Dyrness, 1973). The extremely mild climate is probably an important factor influencing _Tiaja_'s distribution along the northwest coast of the continent. Six species occur along the coast of central and southern California. Species in the more southerly part of the genus' range extend inland to the interior of California, Arizona, and Mexico's Sierra Madre Mountains. In the central part of _Tiaja_'s range, several species occur in very similar habitats.

T. arenaria, the species with the most northerly range, has been found in northern California, Oregon, Washington, and British Columbia. Negative collection records for _T. arenaria_ include sites from Gold Beach, Oregon south to Eureka, California and from

Figure 1. Distribution of members of the genus <u>Tiaja</u> in western
North America.

Vancouver Island

Tofino

Pachena

Victoria

Newport
Waldport

San
Francisco

San Simeon

San Diego

Key

T. arenaria ★

T. californica ✗

T. friscana ◉

T. insula ⊖

T. interrupta ◊

T. mexicana ●

T. montara ○

T. ventura ▫
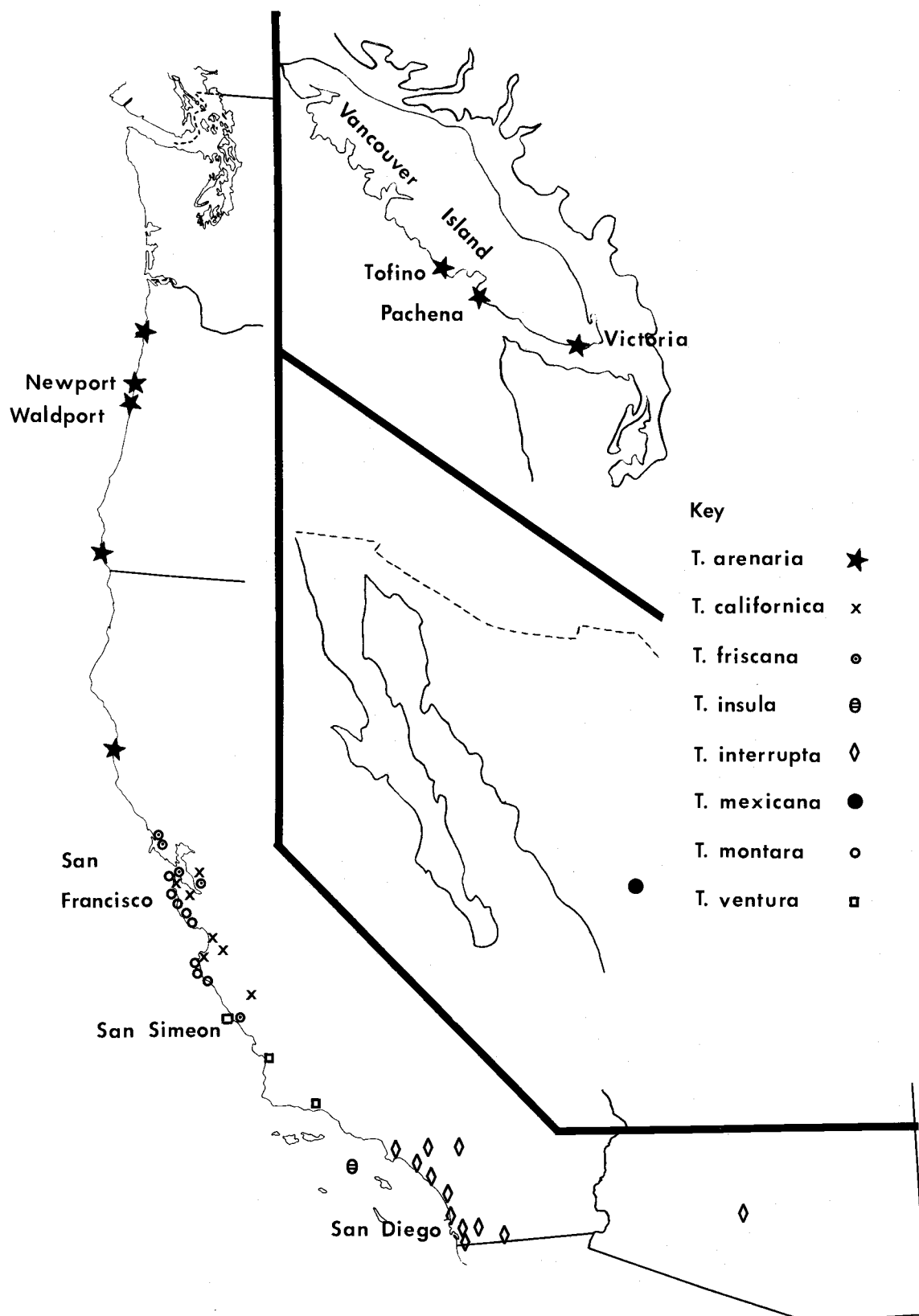
Astoria, Oregon north along the Long Beach Peninsula and Pacific

Beach areas in southern Washington. The habitats of T. arenaria

are discussed in detail as they have been studied most intensively

and can serve as a basis for comparison of the habitats of other

species of Tiaja.

In Oregon, Washington, and British Columbia, the habitats of

T. arenaria share a number of similarities, but at the same time

display several distinct differences. The indicator plants for this

leafhopper species are kinnikinnick (Arctostaphylos uva-ursi (L.)

Spreng. [Ericaceae]), and beach strawberry (Fragaria chiloensis (L.)

[Rosaceae]) in both regions. Populations of T. arenaria are usually

associated with sand dunes in Oregon. However, none of the British

Columbia sites studied so far has been located on a sand dune nor is

the single Washington site. Two of the sites in British Columbia,

Radar Hill and Point-No-Point, are characterized by thin mats of

kinnikinnick with a very thin layer of litter below, and are located on

large rocks immediately above the high tide mark on the west coast of

Vancouver Island. Beach strawberry is sparsely interspersed with

the kinnikinnick. Mosses are common at the Radar Hill site. Only

single specimens have been found at these sites. The third British

Columbia site, south of Wickininnish Beach, differs from the other

two in that no kinnikinnick is present. Beach strawberry is abundant

along with yarrow (Achillea millefolium L. [Compositae]) and a moss

Eurhynchium oreganum (Sull.) Jaeg. This site is on the sheltered side of a rocky seastack. An adult female and many early instar nymphs were collected from around the bases of the strawberry plants.

Unsuccessful attempts have been made to locate T. arenaria on the east coast of Vancouver Island and on the islands of the Gulf of Georgia. Although kinnikinnick is present, beach strawberry, a species that is restricted to the west coast of Vancouver Island, is absent. No strawberry of any kind was found associated with kinnikinnick on the east coast of Vancouver Island or the Gulf Islands.

The single Washington site at which T. arenaria was collected (16 km north of Queets) is characterized by the absence of kinnikinnick. The habitat consists of beach strawberry mixed with grass and is located at the top of a bluff approximately 35 m above beach level. There is evidence of recent disturbance of the area.

Sites in Oregon where T. arenaria occurs present a contrast to those in British Columbia and Washington/ The most thoroughly studied Oregon site, that near Waldport, is located on a stabilized dune. For sampling purposes, the site was considered as a series of sublocalities (Figure 2). The majority of work dealt with three main sublocalities:

(1) Sea side of first dune (Figure 2): This sublocality has a westerly exposure on the steeply-sloped ocean side of the dune closest to the sea. Kinnikinnick is the protective ground cover with

Figure 2.   Cross sectional diagram of the dune site 4 km north of Waldport, Oregon.

Beach

Sea side
of first
dune

Top of
first dune

Pinus
contorta
&
Picea
sitchensis

Lee side
of first
dune

Swale

Second
dune

Pinus
contorta
&
Picea
sitchensis
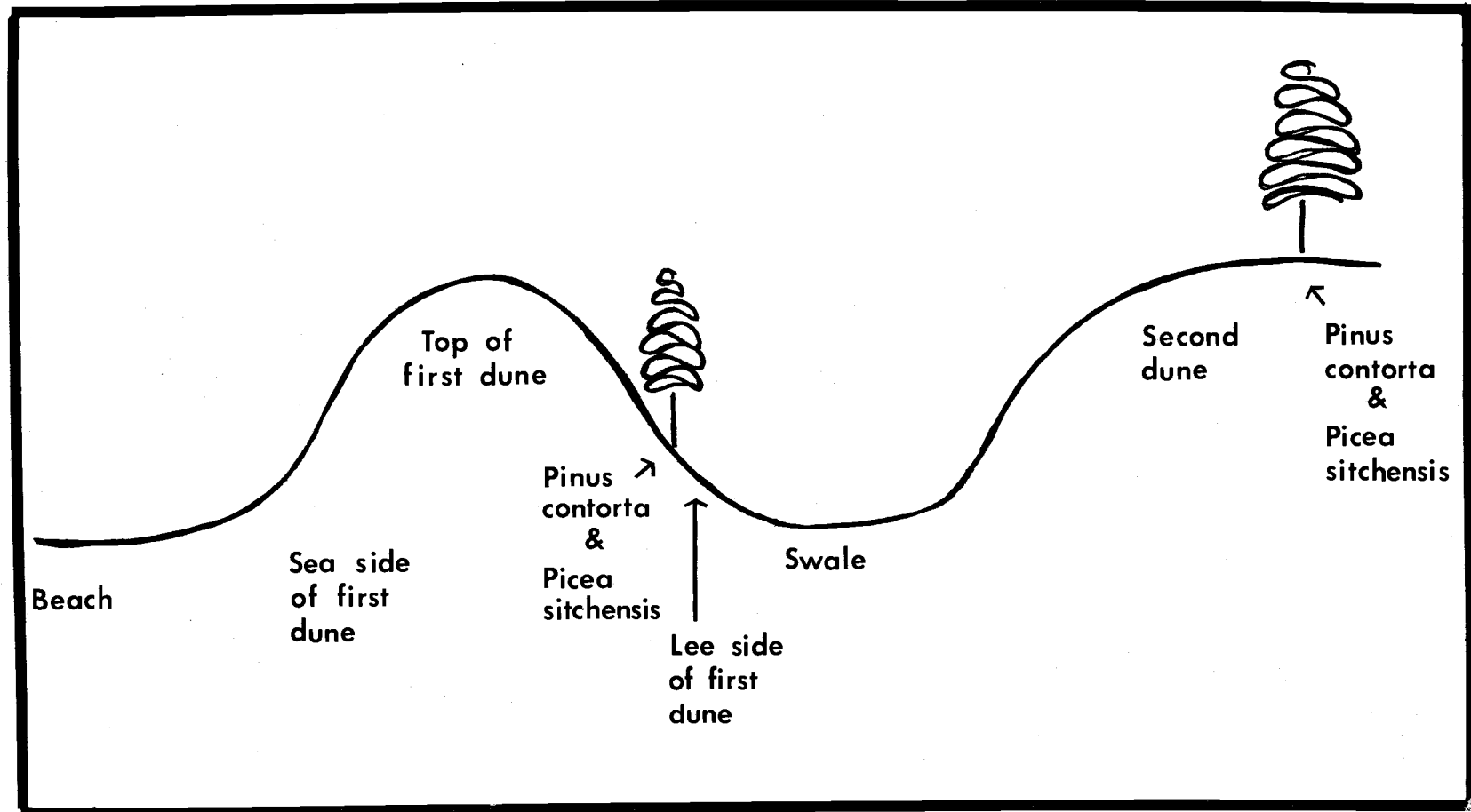
strawberry growing amongst it. The kinnikinnick mats are of

variable thickness but the litter and loose soil layer with spreading

kinnikinnick branches running through it is at least 8 cm deep in the

area sampled.

(2) Lee side of first dune (Figure 2): This sublocality lies at

the base of the first dune and is well protected by it from the wind. It

has an easterly exposure. Again, the main ground cover is kinnikin-

nick with interspersed beach strawberry and a loose soil-litter layer

at least 8 cm deep in the area sampled. A few Sitka spruce (Picea

sitchensis (Bong.) Carr [Pinaceae]) and lodgepole pine (Pinus

contorta Loud. [Pinaceae]) are scattered through this area.

(3) Second dune (Figure 2). This sublocality is on top of the

second ridge of the dune. Its western edge is fairly exposed to the

wind from the ocean although more sheltered than on the sea side of

the first dune ridge. A line of Sitka spruce and lodgepole pine

extends along the top of the ridge and shelters the area behind.

There is no kinnikinnick at this sublocality. Beach strawberry grows

amongst a protective cover of grass (Festuca rubra L.). Brackenfern

(Pteridium aquilinum (L.) Kuhn var. lanuginosum (Bong.) Fernald) is

a conspicuous feature of the vegetation in the summer months but

dies back at the onset of cold weather. In contrast to the sublocalities

where kinnikinnick is present, there is a minimum of litter and

surface cover consists primarily of the densely matted bases of the grass.

The T. arenaria sites in the Oregon sand dunes, surprisingly, give the impression of being considerably less xeric than those in British Columbia where kinnikinnick is present, despite the fact that average annual precipitation for Waldport, Oregon is 1682 mm compared to 3196 for Long Beach, B.C. (U.S. Weather Bureau, 1965 and Canada Department of Transport, Meteorological Branch, 1967). The kinnikinnick growth is much more dense and the litter layer may be as deep as 20 cm compared to a maximum depth of about 2 cm of litter at the British Columbia sites. There is a higher proportion of strawberry mixed in with the kinnikinnick at the Waldport site, and the plants appear much larger and more luxuriant. The British Columbia site where no kinnikinnick is present is most comparable to the second dune site at Waldport.

Most other Oregon sites are located at the edge of dune areas, for example, the sites at Newport and Moolach Beach north of Newport. The site 0.8 km north of Oceanside is on an old, well-stabilized dune. The only aberrant site is that at Ecola State Park where nymphs were found associated with sword fern, salal, deer-fern, alder, strawberry(?) and Douglas-fir. As yet little is known of a T. arenaria habitat at Pistol River, Oregon, although a specimen labeled from that locality has been examined.

The presence of T. arenaria south into California is indicated by the existence of a single male specimen from Fort Bragg. Fort Bragg was not visited during this study and nothing is known of the habitat from which that specimen was collected.

From Bodega Bay south along the coast of California and inland to some extent, there are records of numerous collections of several species of Tiaja, namely T. friscana, T. montara, T. californica, T. ventura, and T. interrupta.

At least three of these species occur in the San Francisco Bay area and on the coast of the San Francisco Peninsula, namely T. montara, T. friscana, and T. californica. They appear to occupy different habitats. All localities from which T. californica is recorded are inland, east or south of San Francisco Bay (Figure 3). This is in contrast to the coastal habitats in which T. montara and T. friscana have been found. T. montara has been collected only from localities exposed to the open ocean while T. friscana has been collected mainly in more sheltered areas (e.g. Marshall, Inverness, Lake Merced, and the north and east sides of the San Francisco Peninsula). However, T. friscana has been found also on the cliffs immediately above the ocean at San Simeon, San Luis Obispo County. This latter locality is approximately 400 km south of the Bay area and the presence of T. friscana this far south is extremely puzzling,

Figure 3. Distributions of <u>T. friscana</u>, <u>T. montara</u>, and <u>T. californica</u> on the central California coast.

San Francisco

Santa Cruz

Monterey

Pacific Ocean

Key

T. friscana   ⊚
T. montara   o
T. californica x
T. ventura   ●

San Simeon

San Luis Obispo
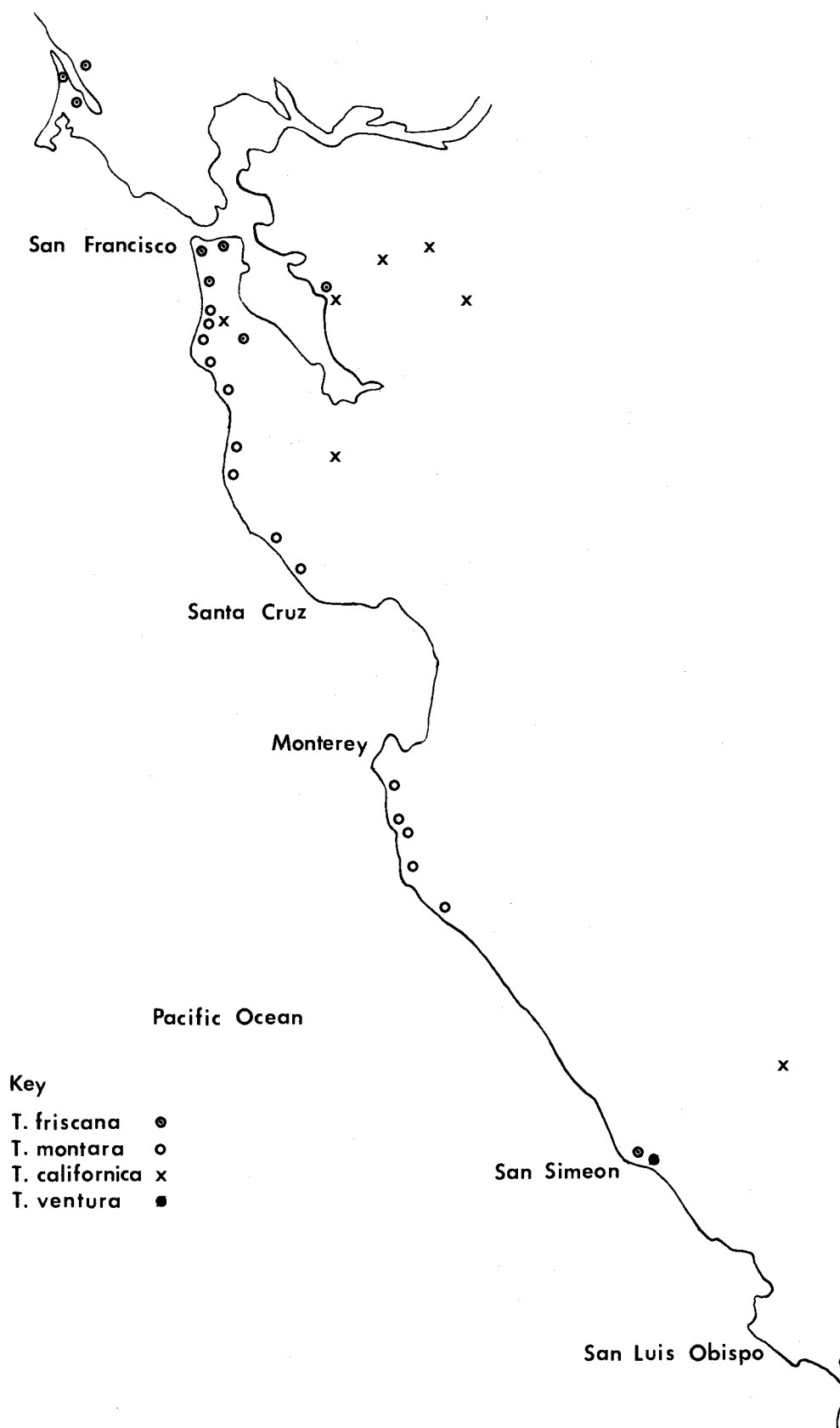
especially since the intervening coastline appears to be occupied

exclusively by T. montara.

T. ventura has been recorded only from coastal localities.

During this study it was collected on the bluffs at San Simeon along

with T. friscana. It is not certain that T. friscana and T. ventura

are actually sympatric at San Simeon; they could be occupying

adjacent microhabitats. Collecting at this site was not carried out in

a manner that could distinguish among specimens collected in

different sections of the site and the presence of the two species was

not detected until the specimens were later examined in the labora-

tory. Further investigation of the San Simeon site is necessary

before the sympatry or allopatry of these species can be determined.

Other localities from which T. ventura has previously been collected

are farther south toward Santa Barbara and Pismo Beach (Oman,

1941).

One plant serves as an excellent indicator for T. friscana and

T. montara (and possibly also T. ventura). That plant is the woolly

beach sunflower, Eriophyllum staechadifolium Lag. var. artemisiae-

folium (Less.) Macbr. (Compositae) and on the exposed hillsides of

San Francisco, San Mateo, Santa Cruz, Monterey, and San Luis

Obispo Counties it is perhaps the most conspicuous of the common

shrubs because of its bright yellow flowers. Woolly beach sunflower

grows along the Pacific Coast from Coos County, Oregon to Santa

Barbara County, California (Munz, 1964). Munz (1964) gives bloom time as being from April to September. A typical stem of woolly beach sunflower has narrow, green, pinnatifed leaves which are woolly-white on the underside on the upper part of the stem; the lower part of the stem has brown, dried-up, old leaves still attached.

There are usually no small plants growing beneath the woolly beach sunflower plant. A thin (1 cm) layer of litter formed from fallen dead leaves may build up under the shrub. Sometimes there is no litter layer at all as when the shrub is growing on a steep slope so that branches overhang a road cut.

Other shrubs frequently found along with woolly beach sunflower in the areas where these species of _Tiaja_ have been collected include _Baccharis_ _pilularis_ DC. (Compositae), _Artemisia_ _californica_ Less. (Compositae), _Rhus_ _diversiloba_ T. & G. (Anacardiaceae), and _Lupinus_ _arboreus_ Sims. (Leguminosae).

No new specimens of _T._ _californica_ were collected during the present study, consequently no direct information on its habitat was obtained. Tilden (1951) collected _T._ _californica_ from _Baccharis_ _pilularis_ but implies that its occurrence on _Baccharis_ was not sufficiently frequent to warrant inclusion of _T._ _californica_ as an "insect associate" of _B._ _pilularis_. Very likely, the occurrence of _T._ _californica_ on _Baccharis_ was accidental.

T. interrupta has been collected at numerous localities on the coast of southern California (Oman, 1941) and has also been found as far east as central Arizona. Its habitat preferences and ecological associations were not explored during the present study. However, Van Duzee (1914) notes that T. interrupta (he uses the name Koebelia interrupta) is "not uncommon on the chapparal from March to September" but unfortunately does not state with which plants of the chaparral association T. interrupta was associated.

T. insula, the Channel Island species known from Santa Barbara Island, has been collected from seablite, Suaeda californica Wats. (Chenopodaceae) (R. J. Gill, personal communication, 1975). A single female specimen from San Miguel Island appears to be T. insula also. It is likely that investigation of the other Channel Islands will uncover Tiaja on them too; whether or not they will prove to be T. insula remains to be seen.

T. mexicana is by far the least known member of the genus both structurally and ecologically. All that is known of the habitat of the two female specimens from which the species was described is that they were collected in the Sierra Madre Mountains, Chihuahua, Mexico at an altitude of approximately 2300 m on an unspecified date. There are no host or habitat data available. The record of T. mexicana in the relatively unstudied high elevation areas of northeastern

Mexico suggests that when this region is more closely explored,

other Tiaja species may be found.

It may be noted that all the Tiaja habitats studied or about which

any information is available have one major factor in common. At

least one species of shrubby plant or robust fern is present and in all

known cases, the shrubby species are the predominent ground cover.

Other herbaceous plants may or may not be growing among these

shrubby plants. All Tiaja species for which the habitat is known live

in areas that tend to be windy. The shrubby species may act as a

windbreak or else modify the environment by producing shade or

reducing moisture loss. This function is important regardless of

whether the shrubby plant is the actual feeding or oviposition host

of the Tiaja species in question.

The availability of a suitable habitat, including appropriate food

and oviposition host plants, may be related in part to whether the

suitable habitat is a successional stage or a climax community. As

an example, the Oregon dune habitat in which T. arenaria is found is

in a state of constant change. The successional stages present in the

dunes range from bare, unstabilized dune to the climax hemlock-

western red cedar forest (Wiedemann et al., 1969). The kinnikinnick-

beach strawberry association is but a transitory stage in plant

succession on the dune (Franklin and Dyrness, 1973). As sampling is

carried eastward into later successional stages such as the

Douglas-fir - salal community, the T. arenaria population disappears.
As the plants on a given section of the dune change over time, the
T. arenaria population presumably must shift in location with the host
plants. An eventual decrease in the area covered by kinnikinnick and
beach strawberry could result in a decrease in the T. arenaria popula-
tion. California species such as T. friscana and T. montara occupy
more stable habitats as their shrubby hosts are not successional stages
that will eventually give way to a climax community of trees.

The amount of disturbance of the habitat by man is also a factor
determining the availability of the habitat. Human population pres-
sure is severely affecting the amount of suitable habitat for T.
arenaria on the Oregon coast. Wiedemann et al. (1969) state, "The
present vegetation of the sand dunes . . . is a result of recurrent
sand movement, fires, and most importantly, the influence of man."
Increasing numbers of access roads are being built through the dunes
and with them more and more houses are being constructed. This
type of pressure is evident even at the Waldport site where T.
arenaria has been found most abundantly. A residential road provides
access to the Waldport site and along this road several small homes
have already been built. One can forsee the time when more roads
will be constructed to connect this area to the subdivision to the south
with more homes being built right on the T. arenaria site. Continued
development of the coastal strip in this manner could severely reduce

or destroy many of T. arenaria's natural habitats within the next few years.

A similar destruction of habitats for some California species of Tiaja has already taken place as a result of human population pressure over a number of years. Such localities as Alameda, Livermore, Newport Beach, Pasadena, San Diego, and Los Angeles which harbored populations of Tiaja in the early part of the century have been so changed by man that there is little hope of duplicating these occurrence records today. Where some individuals do still remain, as at Newport Beach, they may be existing in a habitat far different from that when original collections were made 70 or more years ago. Oman (field notes, 1971) notes that the one T. interrupta he collected at Newport Beach was on (unnamed) "vegetation at the edge of the tidal zone." He later stated (personal communication, 1973) that he did not believe this to be the normal host for T. interrupta. Destruction of the habitats of species with restricted distributions could eventually result in the extinction of these species unless they are able to adapt to the changed environment.

V. LIFE HISTORY STUDIES

Host Associations

The host plant of an insect can be defined as a plant which the insect utilizes directly for one or more life processes. In studying the biologies of leafhoppers, we are generally concerned with two types of hosts: feeding hosts or food plants, and reproductive hosts. Leafhoppers may be monophagous (restricted to one type of food plant) or polyphagous (having a wide range of food plants) or may be anywhere in between (DeLong, 1971). The feeding and reproductive hosts of a leafhopper may be the same or different plants. A reproductive host is a necessary part of a leafhopper's life cycle if eggs are deposited in it or if it is a vital food source which contains nutrients necessary to enable individuals to reach maturity and be fertile. The age and stage of the plant may influence its suitability as a leafhopper host (DeLong, 1971).

Host specificity has been investigated for several leafhopper species. A few leafhoppers, such as Baldulus tripsaci Kramer & Whitcomb, are restricted to a single plant species; B. tripsaci can survive only on Tripsacum dactyloides (Kramer and Whitcomb, 1968). Graminella villica (Crumb) is specific to Paspalum laeve while G. oquaka DeLong can survive only on two species of Panicum (Whitcomb, 1970). More frequently, leafhoppers are not restricted to one plant

species but are specific to a group of plants. Members of the genus

Giprus Oman are found on a variety of Gramineae (Sawbridge, 1975b).

Graminella nigrifrons (Forbes) is found on a wide range of grasses

while most species of Flexamia DeLong are found on Eragrostoid

grasses (Whitcomb et al., 1973). Friscanus friscanus (Ball) is

restricted to two species of Leguminosae (Lupinus arboreus and

Lathyrus littoralis (Nutt.) Endl.); Ankosus filamentus (Oman) has

been collected only from western hazel and alder, both members of

the Betulaceae (Oman and Musgrave, 1975). Oncopsis sp. are

specific to the Betulaceae (Claridge and Reynolds, 1972).

Whitcomb (1970) states that leafhoppers with a broad range of

host plants in the field tend to have an even broader range of hosts in

the laboratory while leafhopper species with a narrow range of hosts

in the field continue to show a narrow range of hosts in the laboratory

although usually these latter species are able to tolerate more than the

single host acceptable to them in the field. Such knowledge of the

host plant(s) of an insect is important in a biosystematic study

because upon this knowledge may rest the success or failure of work

with living animals. Successful laboratory culture and experimental

work depends on providing suitable plants for the insect's feeding

and reproduction. A plant suitable for maintaining adults may not be

suitable for completion of the life cycle. Field collection is expedited

if host or indicator plants are known; valuable clues to the insect's

range and distribution can be gained from the host plant's distribution

if an insect has specific feeding or reproductive hosts. Other factors

must be examined to explain the absence of the insect from some

parts of the host plant's range.

The species of Tiaja studied were not restricted to one food

plant. T. arenaria was maintained on kinnikinnick, beach strawberry,

cultivated strawberry, and red clover in the greenhouse. Feeding

preference tests, in which a choice of sprigs of kinnikinnick and straw-

berry was given to late instar nymphs and adults, showed no

preference of either plant species as a feeding host; when first instar

nymphs were similarly tested, they showed a preference for the

strawberry. T. friscana, T. montara, and T. ventura were also

maintained on red clover in the laboratory and were observed feeding

from woolly beach sunflower from which they were collected. T. mon-

tara and T. friscana have also been collected from Artemisia cali-

fornica and Lupinus arboreus which may serve as alternative feeding

hosts in the field.

Eggs of Tiaja are elongate-oval in shape and are laid singly

beneath the cuticle of the oviposition host, usually on the stem, but

occasionally on the leaf midrib, and rarely on the "fleshy" part of

the leaf or amongst the floral parts (Color Plate I). The oviposition

habits of T. friscana were studied briefly in the greenhouse. Of

1, 003 eggs hatching from red clover, 825 (82%) had been laid on the

Color Plate I. <u>T. friscana</u>, mature eggs in <u>Trifolium pratense</u> L.

stem of the plant; 177 (18%) had been laid on the leaves (almost always on the midribs), and one had been laid somewhere in the floral head. Although red clover is not the field host of T. friscana, these data confirm that eggs are deposited within the host plant and are not scattered on the soil at its base as was found for Aphrodes bicincta DeLong (Chiykowski, 1970). This information was utilized in the search for the natural oviposition host of T. arenaria.

The natural oviposition host of a leafhopper such as a species of Tiaja can be determined by separating samples of suspected host plant material in the laboratory and monitoring hatching from each plant species. The natural oviposition host of T. arenaria is Fragaria chiloensis, beach strawberry. All T. arenaria nymphs hatching from field collected plant material from the Waldport area hatched from beach strawberry. The oviposition host is not kinnikinnick as was suggested by Oman (1972). This explains why some T. arenaria have been found in areas where there is no kinnikinick present such as at the top of the second dune at Waldport and at Wickininnish Beach in British Columbia. The natural oviposition hosts of T. friscana and T. montara have not yet been determined by the method outlined above because of collecting difficulties due to distance of their habitats from Corvallis, Oregon. However, as nymphal specimens of T. friscana have been collected only from on and under woolly beach sunflower and not from surrounding plants, it

seems very likely that this plant is the reproductive host of T. fris-

cana. As T. montara nymphs have been found in association with both

woolly beach sunflower and Artemisia californica, the oviposition host

of this species requires further investigation. Both T. friscana and

T. montara will feed and reproduce on red clover in the laboratory,

indicating that they, like T. arenaria, are not specific to one host or

a taxonomically distinct group of hosts, at least when no choice is

available.

Immature Stages

Determination of the ages or instars of immature specimens

was particularly important in this study because the study was con-

cerned, in part, with sampling field populations and it was necessary

to be able to determine with some degree of accuracy what stages were

present in a given sample. This opened the door to a wealth of

information about the population such as data on egg hatching time,

number of generations per year under natural conditions, stage at

which parasitism becomes evident, stage at which death occurs as a

result of parasitism, and other factors relating to the study of living

insects. In a genus such as Tiaja, where little of a morphological

nature was known about the nymphs, there was even wider scope for

this study. Similarities and differences in the morphological features

of the different stages of each species needed to be studied.

There is an ongoing discussion amongst insect physiologists regarding the definition of an instar and the point at which each stage begins and ends. Traditionally an instar has been considered to last from one ecdysis (shedding of the old cuticle) to the next (Torre-Bueno, 1962). Hinton (1971, 1973, 1976) defines an instar as lasting from one apolysis (separation of the epidermis from the old cuticle) to the next apolysis. Wigglesworth (1973) argues in favor of continued use of ecdysis rather than apolysis to mark the end of one instar and the onset of the next on the bases that (1) the old integument remains functional until the moment of ecdysis, (2) apolysis is a gradual process, and (3) an instar, by definition, has a definite form, making it inappropriate to define an instar as beginning at apolysis. Whitten (1976), in support of Wigglesworth, points out again that apolysis does not take place simultaneously over the whole body but is a gradual process and is therefore less suitable than ecdysis for marking the beginning and end of each instar. Hinton (1976) stresses that growth is a continuous process and restates his contention that physiologically an instar begins at apolysis. In reply to Whitten (1976) he states that ecdysis, too, is not always synchronous over the whole body. He further states that, in his opinion, it is not necessary to abandon the traditional method of describing the stages of an insect by reference to ecdyses but that if one is doing so, one must use correct terminology to acknowledge this.

In this work, the terms "first instar," "second instar" and so on are used for simplicity. In Hinton's terms these would become "between hatch and first ecdysis," "between first and second ecdyses" and so on, acknowledging that physiologically the first instar ends with the apolysis before the first ecdysis, the second instar ends with the apolysis before the second ecdysis, and so on.

Separation of insects of differing instars has long been a problem although, in certain well studied groups, methods have been established for distinguishing among instars. Dyar's Law for lepidopterous larvae states that the increase in head width shows a regular geometrical progression in successive instars (Chapman, 1969). In the Cicadellidae, no such rules of thumb have been established. Gustin and Stoner (1968), while studying means to distinguish between the instars of the leafhopper Deltocephalus sonorus Ball, tried applying Dyar's Law but found that while averages for head capsule width increase in numerical value for each instar, individual measurements overlap to too great an extent to make such measurements a reliable means of instar discrimination. They also found that, except for the first instar, nymphs of that species could not be distinguished on the basis of color patterns or setal numbers or patterns.

There is, of course, a size differential between the instars but this too is extremely variable with overlaps in individual

measurements. Size is probably dependent on external (environmental) factors as well as internal (genetic) factors and is thus an unreliable means of distinguishing between instars.

Nymphs of the genus *Tiaja* are easily recognized. The body is robust and the head is particularly blunt so that it may almost appear squared in profile (Figures 4 and 5). The most striking attribute of a *Tiaja* nymph is that the entire head, face, and dorsal surface of the thorax and abdomen are setose. Nymphal instars may be distinguished from one another by the degree of development of the wing pads and to some extent by the number and position of the setae present on the wing pads. The smaller the nymph, the larger the setae appear in relation to the size of the nymph.

First instar nymphs of *T. friscana* show no development of the wing pads. There are eight prominent setae near the posterior edges of both the mesothoracic and metathoracic terga (Figures 5 and 6).

In second instar nymphs (Figure 7), the mesothoracic and metathoracic segments are essentially unchanged. The eight original setae on the posterior edge of each segment are present plus a few less prominent ones located anteriorly on each segment. A second instar nymph appears more robust than a first instar nymph.

Third instar nymphs show definite development of the mesothoracic wing pads which are elongated so that they cover
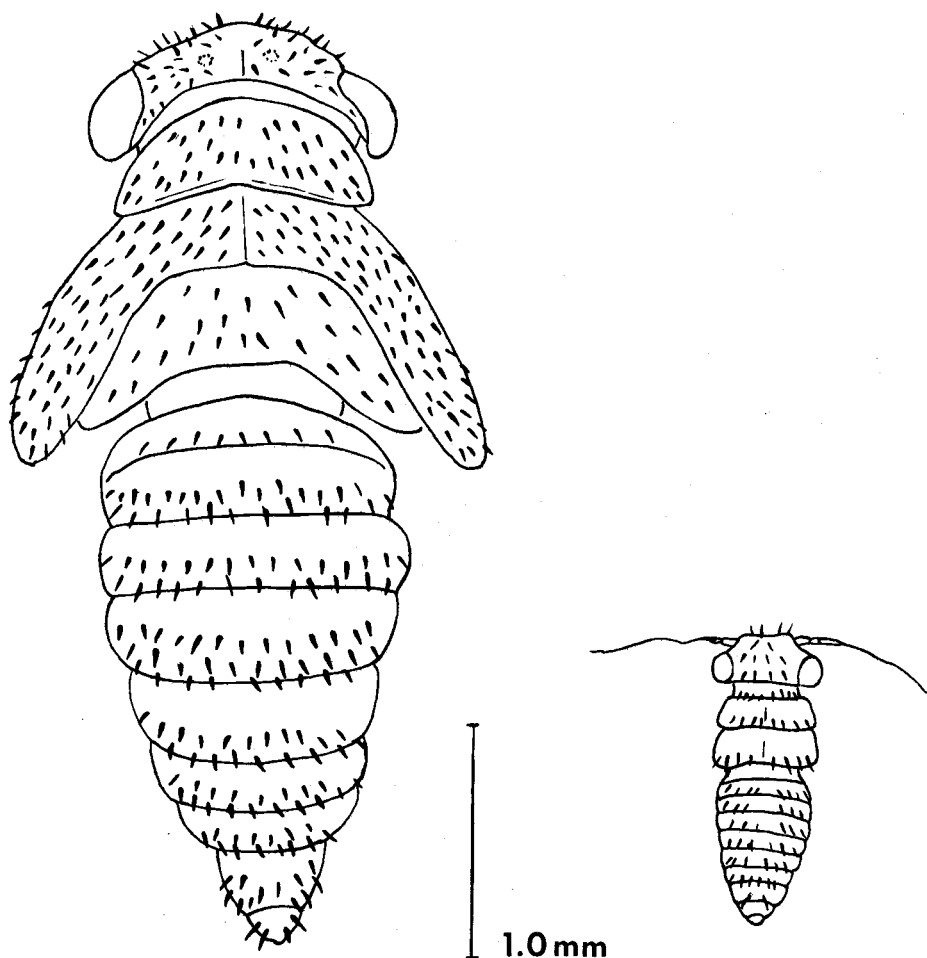
Figure 4. T. friscana: fifth instar nymph.

Figure 5. T. friscana: first instar nymph.

Figures 6-10. <u>T</u>. <u>friscana</u>: wing development.

    6.   First instar nymph
    7.   Second instar nymph
    8.   Third instar nymph
    9.   Fourth instar nymph
   10.   Fifth instar nymph

6

7

0.1 mm

8

10

9
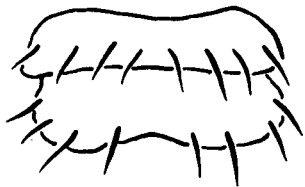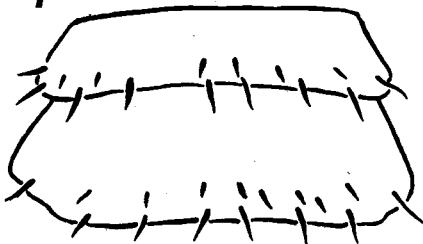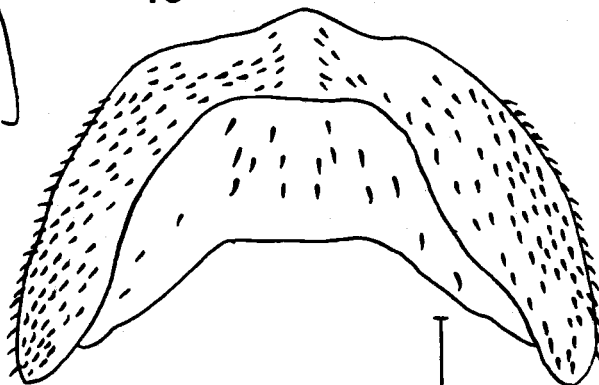
1.0 mm
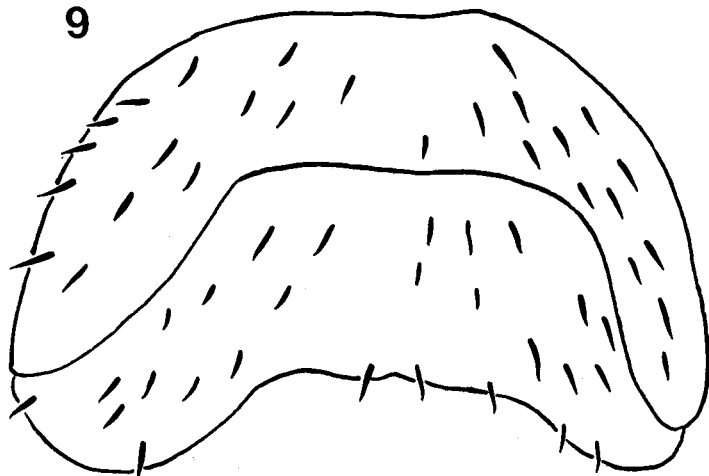
approximately half of the metathoracic wing pads at their outer edge
(Figure 8). The eight original setae on the posterior margins of the
wing pads are still present but are more difficult to distinguish from
about 16 other setae which are not present anteriorly on the wing
pads and do not seem to be arranged according to any particular
pattern.

Mesothoracic wing pads of fourth instar nymphs reach almost
to the posterior edge of the metathoracic wing pads (Figure 9). The
eight original setae on each wing pad appear no more prominent than
the other setae on each segment. Wing venation is not yet visible in
the fourth instar.

Mesothoracic wing pads of fifth instar nymphs are very distinct
and extend beyond the metathoracic wing pads (Figure 10). There is
some venation visible. The mesothoracic wing pads are covered with
fine setae; the visible part of the metathoracic wing pad is compara-
tively less setose.

T. arenaria and T. montara nymphs show a similar develop-
ment pattern of the wing pads to T. friscana. T. montara have setae
similar in length to those of T. friscana but the setae of T. arenaria
are much shorter and less prominent than those of T. friscana. This
setal length difference can be used to distinguish T. arenaria nymphs
from those of T. montara or T. friscana. A method for distinguishing

between T. montara and T. friscana nymphs has not yet been discovered.

Behavior

Information on the behavior of Tiaja was gathered from two sources: (1) field observation during collecting trips and (2) observation of caged individuals in the laboratory. These data can be combined to provide some insight into the habits of members of the genus Tiaja.

Tiaja appear to have a negative reaction to light. In their natural habitat, individuals apparently sit on the lower portions of the host plant and perhaps more frequently on the underside of leaves, as evidenced by the difficulty of collecting them by traditional sweeping methods and the much greater effectiveness of the "shovel" or "scoop" technique for T. friscana. T. arenaria are often found deep in the substrate litter layer, more so than would occur if they were simply knocked from the feeding host during collection. Young (first instar) T. arenaria located on beach strawberry plants in an area at which kinnikinnick was absent were observed to be clustered at the bases of the plants. Observations of all species maintained in the laboratory support evidence from the field. Tiaja are rarely seen on the tops of leaves or on the upper branches of the clover plants. More frequently they are found on the lower part of the main stem, on

the undersides of leaves, or on the undersides of lower branches.
They are also found in the crevices of the wooden culture cages,
amongst the lumps of soil and debris on the surface of the pots, and
buried amongst the cheesecloth which is used to seal the space between
the pot and the wooden cage.

The tendency toward sluggishness and reluctance to jump of
Tiaja individuals as noted by Oman (1972) was observed again with all
species studied live in this investigation. Nymphs placed on a
foreign surface such as a table top tend to walk around but rarely
jump. On occasion, when they do jump, young nymphs rarely go
farther than 15 cm and adults rarely jump more than 30 cm. It is
easy to knock both nymphs and adults from the host plant. When they
land on their backs they are unable to right themselves unless their
legs can grasp some object.

Mating behavior of T. arenaria was described in detail by
Oman (1972). No visible differences in courtship or mating ritual
were detected in numerous observations of T. friscana and T. mon-
tara. The male mounts the female from either side while facing in
the same direction (Color Plate II). He grasps her head and thorax
with his legs then uses the tarsi of his forelegs to tap or stroke her
in the head region. He then extends his abdomen downward so that the
apical dorsum of his genital capsule contacts the female near her
seventh sternum. The male styles are extruded along with the

Color Plate II. _T. friscana_ pre-mating or post-mating position,
male above female.

aedeagus and they probe the area at the base of the female pygofer.

If the female is receptive, copulation takes place shortly thereafter

(Color Plate III); if the female is unreceptive, she extends her genital

region downward at nearly a 90° angle to the rest of her abdomen so

as to prevent the male from attaching his styles. Unlike most leaf-

hoppers which initiate mating with the male above and facing in the

same direction as the female but which subsequently change to an end

to end position after copulation begins, _Tiaja_ maintain the position of

male above and oriented in the same direction as the female for the

duration of copulation. Successful copulation may last from several

minutes to several hours. The longest continuous copulation recorded

in this study lasted just over 11 hours. Multiple matings occur

frequently. One pair was observed mating on five separate occasions

but observations of two or three matings per pair were more

common.

The process of oviposition was never observed in its entirety

during this study. On one occasion the final stages of withdrawal of

the ovipositor from the stem by a female was observed. Since

insects presumed to be ready to oviposit were observed from

6:00 a.m. to 11:00 p.m. without oviposition being fully observed, it

seems probable that oviposition usually takes place at night or in the

predawn or early dawn hours.
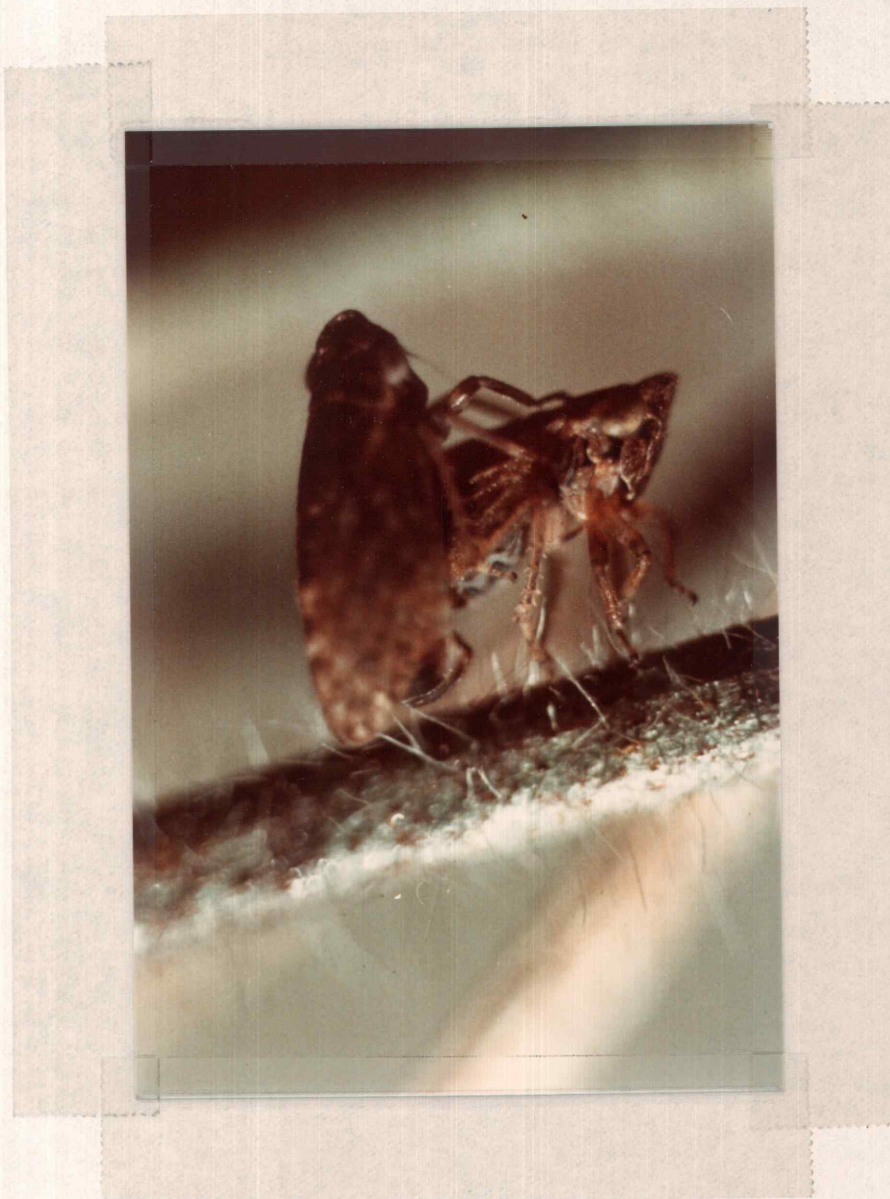
Color Plate III. <u>T</u>. <u>friscana</u>, copulating pair.

Hatching of eggs was observed at all times of the day but appeared to occur more frequently in the early morning. When petri dishes were checked for nymph hatching in the early morning, frequent observations of hatching or newly hatched nymphs were made. Few hatching or newly hatched nymphs were observed when petri dishes were checked for nymphs in the afternoon or evening.

Behavior of nymphs was observed. Like adults, nymphs seem to have a negative reaction to light. First instar nymphs have a tendency to congregate near the base of the host. First instar T. arenaria have been found in the field at the base of beach strawberry. In the laboratory, most first instar nymphs feed almost entirely from the midribs of the cotyledon when placed on a young (5 cm) clover plant and almost all of the early moults are in this position. A position on the underside of a leaflet or stem seems to be preferred on older plants. As nymphs develop, they move up the plant, and cast skins are more often attached to the stem or the underside of a leaflet. All cast skins observed have been in the head-up position.

Seasonal Occurrence

A field study of the seasonal occurrence of an insect is an integral part of a biosystematic study. At the simplest level, it is necessary to know when suitable developmental stages of the insect

are present in nature in order to collect immature and mature specimens for live observation, rearing, and study of preserved material. Field study on a long term basis can provide much information in such areas as the length of the life cycle, the number of generations per year, and the occurrence and duration of a diapause stage. Information about the preferred habitat and any seasonal habitat changes may also be gained from such a study.

T. arenaria received the most intensive field study since a large population at Waldport, Oregon was readily accessible at all times of the year. Except as indicated, the following discussion relates to observations made during the year 1973 at Waldport only. The population was sampled in three sublocalities which were located along a transect extending from the high tide mark to the Douglas-fir forest which lies beyond the pine-spruce line at the eastern edge of the dune area (Figure 2). The three sublocalities were: sea side of first dune, lee side of first dune, and second dune. Pooled sampling results for the site as a whole are considered first.

Information for 1973 and other seasons indicates that T. arenaria are present as adults all year at Waldport (Table 1). The presence of nymphs of increasingly advanced stages during late winter, spring, and summer and the lack of first and second instar nymphs after the end of May (Table 2) strongly suggests that there is only one generation per year.

Table 1. Record of _T. arenaria_ collected 4 km north of Waldport, 1973 by date, stage, and sex of adults.

Developmental stage	Feb 6	Mar 13	Apr 4	Apr 18	May 21	June 7	June 22	July 5	July 27	Aug 28	Oct 2
Adult	5 ♂	-	-	2 ♂	3 ♂	3 ♂	3 ♂	3 ♂	4 ♂	11 ♂ 8 ♀	4 ♂ 7 ♀
V	-	-	-	-	-	-	9	9	4	3	-
IV	-	-	-	-	1	11	11	5	3	-	-
III	-	-	-	3	10	5	2	-	-	-	-
II	-	-	2	15	1	-	-	-	-	-	-
I	10	27	5	3	1	-	-	-	-	-	-

Table 2.　Percent of <u>T. arenaria</u> nymphs at each instar, February to October, 1973.

Instar	Feb 6	Mar 13	Apr		May 21	June		July		Aug 28	Oct 2
			4	18		7	22	5	27		
V	-	-	-	-	-	-	40.9	64.3	57.1	100	-
IV	-	-	-	-	7.7	68.7	50.0	35.7	42.9	-	-
III	-	-	-	14.3	76.9	31.3	9.1	-	-	-	-
II	-	-	28.6	71.4	7.7	-	-	-	-	-	-
I	100	100	71.4	14.3	7.7	-	-	-	-	-	-

It is not known exactly when nymphs began hatching in the field in 1973. In view of data from later in the season, it is possible that although first instar nymphs are recorded as having been present in the February 6 sample, these nymphs may have hatched in response to the warmth and constant light in the Tullgren funnel. However, by April 4, some first instar nymphs had already hatched as both newly-hatched and older first instars and two second instar nymphs were retrieved from the litter samples and from plant material brought into the greenhouse for observation of hatching.

By mid-April, most of the nymphs collected were second instars; a few had reached the third instar (Table 2). By May 21, most of the nymphs in the sample were in the third instar. On June 7, the majority of nymphs collected were fourth instars and by June 21, almost all nymphs were fourth or fifth instars. All nymphs collected in July were either fourth or fifth instar. The only three nymphs found at the end of August were fifth instar. No collections were made between August 28 and October 2 on which date no nymphs were present. In 1970, at the same site, Oman recorded no male nymphs after August 17 and no female nymphs after September 15 (Oman, 1972).

Males mature first (Table 1) and newly-matured adult males were present in July. Females take longer to mature (see lab rearing data) and adult females were not found until August. Some adults

survive the winter and through the following spring as evidenced by collection of adults at all times of the year. It is notable that only adult males were taken in sampling during the winter and spring months of 1973 (Table 1). This may have been an accident in sampling due to small sample size. The only adult taken in British Columbia at Wickininnish Beach in May 1975 was a female.

It is impossible to say from field data whether or not any T. arenaria survive for more than one year. The longest recorded survival in captivity of an adult is over 300 days (Oman, 1972) which, when added to the time required to progress through the immature stages, would bring the total elapsed time from eclosion to death to at least a year.

Adults taken in samples up to and including June 7, 1973 were probably holdovers from the previous year as all nymphs present were either fourth instars or younger. The males collected on June 22, 1973 could have been either newly emerged or from the previous season, probably the latter as they did not have a teneral appearance. Adults collected from July onwards were probably mostly from the 1973 season.

The 1973 samples from the Waldport population were then considered by sublocality to determine if different segments of the population matured at different rates as a result of apparent

microclimatic differences due to such factors as exposure to wind or the type of plant providing ground cover.

Collection data by sublocality are summarized in Table 3. The small number of specimens involved in many of the samples and the fact that old and new season adults could not be distinguished made it impossible to subject these data to any meaningful statistical analysis. However, a few trends can be noted from the summarized data. Adult T. arenaria were present on the lee side of the first dune and on the second dune before any appeared on the sea side of the first dune. While the sublocality on the lee side of the first dune had third and fourth instar nymphs present at an earlier date, the sublocality on the second dune had a higher proportion of fifth instar nymphs present by late June and early July. By August 28, only the sublocality on the sea side of the first dune had any nymphs present.

A survey of daylight hour litter layer temperatures at the three sublocalities taken over a 24-hour period showed that for most of the day the site on the sea side of the first dune averages 2.5°C cooler than the site on the lee side of the first dune; only in the evening when the sun is low in the sky and the lee side of the first dune is in deep shade is the situation reversed. An ocean breeze cools the site exposed to the ocean and increases the temperature differential between the two sublocalities. During the same period the sublocality

Table 3. Record of *T. arenaria* collected 4 km north of Waldport, 1973 by sublocality, date, and developmental stage.

Developmental stage	Feb 6	Mar 13	Apr 4	Apr 18	May 21	June 7	June 22	July 5	July 27	Aug 28	Oct 2
Sea side of first dune											
Adult								3	2	9	2
V								2	1	3	
IV						2	2	1	2		
III					4	2	1				
II			1								
I			3								
Lee side of first dune											
Adult	2			1	3	2	2			6	4
V							1	2	1		
IV					1	4	3	2	1		
III				3	5	3	1				
II			1	10	1						
I	2	5	1	1	1						
Top of second dune											
Adult	3			1		1	1		1	4	5
V							8	5	2		
IV						6	6	2			
III						1					
II				5							
I	8	22	1	2							

at the top of the second dune had an average temperature of about
.2°C less than the lee side of the first dune.

These data suggest that maturation of T. arenaria is slightly
retarded by the greater exposure to the wind or the accompanying
cooler temperatures on the sea side of the first dune. Laboratory
rearing data have shown that increased temperatures lessen the
maturation time of Tiaja nymphs. From these samples, it does not
appear that the difference in dominant ground cover between the lee
side of the first dune and the second dune had any effect on the rate of
population maturation.

From collection data and the very limited success encountered
in propagating T. arenaria in the greenhouse, it seems probable that
T. arenaria undergo an egg diapause and that the period of low
temperature necessary to break diapause and allow development to
proceed (Danilevskii, 1965) had been completed when the first 1973
sample was taken on February 6.

The reason for the survival of adults over the winter is
uncertain. Field evidence suggests that eggs are probably laid in the
fall since females collected in the late summer and early fall and
dissected showed ovarioles with developing eggs. Additional evidence
is that egg-bearing plants can be found as early in the year as
February and that eggs are found in the stems of old strawberry plants
remaining from the previous summer but not in the stems of those

plants newly formed in the spring. Duration of fertility in female

T. arenaria was not determined because attempts to propagate

T. arenaria in the laboratory were unsuccessful. However, T.

friscana females reared under greenhouse conditions remained

fertile for approximately 14 weeks (see fecundity study) but very few

fertile eggs were laid after that time. This was despite the fact that

males were available so that reinsemination could take place at any

time. Unless female fertility in T. arenaria lasts for considerably

longer than in T. friscana, there is no satisfactory explanation of why

adults should survive through the winter since, if they are no longer

fertile, they cannot contribute to population survival. It was not

determined if overwintered males of T. arenaria were still fertile.

Regular sampling of populations of species other than T.

arenaria was prevented by distance of these populations from

Corvallis, Oregon. Data for T. friscana, while by no means com-

plete, suggest that this species has a bivoltine or multivoltine life

cycle since nymphs of all instars have been collected from July

through September. Adults and nymphs of all stages were collected

at Marshall, Marin County in July and September 1972 and at Fort

Point, San Francisco County in early July, 1974; adults and third

to fifth instar nymphs were collected at Fort Point in late November,

1973. It also appears that diapause, if any, in T. friscana is

facultative since it was possible to produce continuous generations in the laboratory (see laboratory studies of development from egg to adult).

There is no field information on seasonal occurrence or number of generations per year (except collection data) for other species of the genus _Tiaja_, as most collections by non-specialists have been of adults, usually only one or a few at a time at a given locality. However, T. _montara_ has a very similar life history to T. _friscana_ when reared under artificial conditions and it too may be bivoltine or multivoltine in nature. Some supporting field evidence for this hypothesis is that extensive collection of T. _montara_ in July 1974 yielded numerous adults and fifth instar nymphs as well as nymphs in the earlier stages of development. On the central California coast there would probably be ample time for another generation to be produced during the season.

Extreme weather conditions can influence the developmental stages present in a population on a given date. Laboratory rearing of T. _arenaria_ and comparison with field data has shown that temperature variation has a direct and obvious effect on the amount of time required for a nymph to progress from eclosion to adulthood. A very late spring and/or a very cool summer could theoretically slow down maturation to the extent that adults were not present until very late in the season. This followed by a sudden, early cold period

could kill off many adults before mating, egg development, and oviposition had taken place. The population the following year could thus be severely reduced. While this sequence of possibilities is unlikely to occur in such a climatically moderate area as the Oregon coast, it is still possible. Populations of species found in desert regions could be affected by extremely high temperatures or by drought.

Laboratory Study of Life History

Laboratory studies of an insect's life history can serve to supplement field studies to confirm or reject hypotheses about life histories formed from field observations of insect populations. Nuances of the life cycle that might go undetected from field studies alone may be seen more clearly in a laboratory study. Since conditions such as light, temperature, moisture, and food source can be controlled and manipulated in the laboratory, the effects of any or all of these variables on the life cycle may be assessed.

In the present study, it appeared from field collection data and preliminary culture attempts that at least two species (T. friscana and T. montara) had more than one generation per year and no obligatory diapause while another species (T. arenaria) had only one generation per year and apparent obligatory diapause. In addition, no information was available on the number of nymphal instars, the

relative time spent in the egg stage and in each nymphal instar, and the time required to complete the life cycle. This also seemed an appropriate time to investigate the late K. G. Swenson's speculation (personal communication, 1972) that the appearance of mature males in a leafhopper population before the appearance of mature females was the result of male eggs being laid first or hatching first. A carefully documented laboratory study was clearly necessary in order to gain information about these facets of _Tiaja_'s life history.

Development from Egg to Adult

T. friscana. Eggs used in this experiment were laid in the greenhouse and hatching occurred approximately 21 days after plants were exposed to gravid female _T. friscana_ when cultures were maintained at approximately 19°C. Of the 113 individuals which began the experiment, 71 became adults after five nymphal instars, 34 died or were lost during the experiment, 6 became adults after four nymphal instars, and 2 became adults after six nymphal instars. From this it is obvious that in _T. friscana_ five nymphal instars is the "normal" condition.

Table 4a summarizes the average time elapsed between hatch and emergence and the average time spent at each instar for individuals going through five nymphal instars. In all cases, the average length of an instar is less for males than for females. The duration of

Table 4. Number of nymphal instars and duration of nymphal period in T. friscana.

	I	II	III	IV	V	VI	H-A
(a) Average duration of each nymphal instar for individuals going through five nymphal instars.							
40 ♂	11.35 (10-15)	10.52 (9-15)	11.98 (10-15)	11.00 (9-16)	15.55 (11-20)		60.2
31 ♀	12.06 (9-15)	11.45 (10-15)	13.35 (10-22)	12.26 (7-22)	18.36 (9-24)		66.8
(b) Average duration of each nymphal instar for individuals going through four nymphal instars.							
3 ♂	10.33 (10-11)	11.33 (11-12)	14.33 (12-18)	21.33 (18-24)			57.33
3 ♀	11.67 (11-12)	11.67 (11-13)	21.67 (18-24)	19.33 (19-20)			64.33
(c) Average duration of each nymphal instar for individuals going through six nymphal instars.							
2 ♂	10	10	10.5 (10-11)	12	10.5 (10-11)	9	61.5

the first, second, third, or fourth instar is approximately 11 days

for males and approximately 12 days for females. For both males

and females, the duration of the fifth instar is considerably longer

than that of any of the previous four instars.

Only three male and three female T. friscana reached the adult

stage after only four nymphal instars (Table 4b). In all but one

instance females had a slower average rate of development than

males and the one instance may be a result of the very small sample

size. Overall time from hatch to adult was less for both males and

females compared to individuals going through five nymphal instars.

Females had both third and fourth instars prolonged while males

had only the fourth instar prolonged.

Both individuals going through six nymphal instars were males

(Table 4c). Although there was an extra nymphal instar, the total

time elapsed between hatch and adult emergence is only slightly

greater than the total time for males going through only five nymphal

instars. From the available data, it appears that instead of one

extra long fifth instar, these individuals had two instars of approxi-

mately the same length as each of the preceding four instars.

Newly-emerged adult females, when paired with males, were

able to mate and lay eggs beginning from one to two weeks after

pairing (see fecundity data). These eggs hatched approximately

21 days after they were laid, indicating strongly that there is no obligatory diapause in T. friscana.

T. arenaria. The eggs used for study of the duration of nymphal instars and the time elapsed from hatch to adult of T. arenaria were laid in F. chiloensis in the field and brought into the greenhouse where they hatched. It is not known how long before hatching oviposition occurred.

Of the 83 individuals originally present in this experiment, only 39 reached adulthood through five nymphal instars; 20 died or were missing during the experiment; 21 went through only four nymphal instars; and 3 went through six nymphal instars. In T. arenaria a full one-third of those reaching adulthood went through only four nymphal instars. In this instance "normal" would have to be considered to be either four or five nymphal instars.

Table 5a shows that T. arenaria males reared in the greenhouse and going through five nymphal instars took an average of 55.55 days from hatch to adult; T. arenaria females took an average of 57.87 days. As in T. friscana, the duration of the fifth instar is considerably greater than that of any preceding instar.

Table 5b gives the data for T. arenaria going through only four nymphal instars. Here also the final nymphal instar is of much longer duration than any of those preceding it. The total time

Table 5.   Number of nymphal instars and duration of nymphal period in _T. arenaria._

	I	II	III	IV	V	VI	H-A
(a) Average duration of each nymphal instar for individuals going through five nymphal instars.							
22 ♂	8.05	10.18	9.09	11.06	17.09		55.55
	(5-11)	(8-16)	(7-11)	(8-15)	(11-22)		(51-61)
15 ♀	9.13	9.27	9.87	11.93	17.47		57.87
	(5-11)	(4-17)	(6-12)	(8-16)	(11-20)		(53-63)
(b) Average duration of each nymphal instar for individuals going through four nymphal instars.							
11 ♂	7.73	10.82	11.18	20.18			49.91
	(5-12)	(6-20)	(8-13)	(17-28)			(46-63)
7 ♀	8.43	12.00	12.57	22.86			55.85
	(5-11)	(8-22)	(11-16)	(16-33)			(49-67)
(c) Average duration of each nymphal instar for individuals going through six nymphal instars.							
3 ♂	8.67	8.33	7.67	8.33	6.33	15.00	54.33
	(6-10)	(7-10)	(7-8)	(7-10)	(4-8)	(14-17)	(53-55)

elapsed between hatch and adult is in both instances less than that for individuals going through the full five instars.

The three individuals with six nymphal instars actually had a lower average time from hatch to adult than those with five nymphal instars (Table 5c). Unlike the sixth stage of T. friscana, the sixth stage of T. arenaria is considerably longer than any of the other five and the fifth appears to be slightly shorter.

Because of small sample size, data were not subjected to statistical analysis.

A striking illustration of the effect of environmental conditions on developmental time is that while nymphs used for the greenhouse study of T. arenaria hatched at the same time as those in the field, a comparison with Tables 1 and 2 shows that the first fifth instars collected in the field were not obtained until June 22, long after all the greenhouse reared individuals had become adults. The first adults in the field were collected in July (males) and August (females) (Table 1). The field population was not 100% adult until October 2, four months after all greenhouse reared individuals became adults. Average field temperatures in 1973 were: April, 9.5°C; May, 10.8°C; June, 12.9°C; and July, 13.7°C (U.S. National Weather Service, 1973) while laboratory temperatures averaged 21°C.

Discussion. The number of nymphal or larval instars varies among insect taxa. Primitive insects usually have a greater number

of immature instars than advanced groups (Chapman, 1969). For

example, in the Ephemeroptera there may be 30-45 nymphal instars

while in the Diptera (Nematocera) there may be as few as four larval

instars (Chapman, 1969). Within the Homoptera there is a variable

number of nymphal instars ranging from six in the Cicadidae to two or

three in the Coccidae; in the Cicadellidae there are usually five

nymphal instars (Imms, 1964).

It is interesting to speculate on the significance of the variation

in the number of istars required to reach adulthood. The high

incidence of T. arenaria individuals maturing after only four nymphal

instars suggests more than mere accident. One possible explanation

is that maturity in four instars is an adaptation by T. arenaria to life

in a cool climate. In a climate where, in an average year, maturation

of the population takes the whole summer, it would be an advantage,

in years when temperatures are abnormally cool, to have some

individuals that mature in a shorter time in order that they can mate

and lay eggs before the winter season begins. There could be a

physiological explanation for this phenomenon such as is found in

some Orthoptera species which have a variable number of nymphal

instars; in those species the females which are larger have an extra

instar and nymphs emerging from small eggs may have an additional

instar (Chapman, 1969). Variation in instar number occurs

occasionally in other species of leafhoppers. Chiykowski (1970)

reports two <u>Aphrodes</u> <u>bicinctus</u> (Schrank) that matured after only four nymphal instars. Stoner and Gustin (1967) recorded a <u>Graminella</u> <u>nigrifrons</u> (Forbes) that passed through six nymphal stages. Severin (1946, 1949) studied the life histories of <u>Hordnia</u> <u>circellata</u> (Baker), <u>Texananus</u> <u>lathropi</u> (Baker), and <u>T.</u> <u>spatulatus</u> (Van Duzee)and found several instances where individuals passed through four or six nymphal instars rather than the usual five. In these species, an extra instar occurred more commonly than a reduced number of instars.

The relationship between the lengths of the instars and the differences in developmental times between the sexes is similar in both <u>T.</u> <u>friscana</u> and <u>T.</u> <u>arenaria</u>; however, a note of caution is warranted. Although the studies of the life histories of <u>T.</u> <u>friscana</u> and <u>T.</u> <u>arenaria</u> were carried out in the same greenhouse room, the study of <u>T.</u> <u>friscana</u> took place in the winter (November-January) and the study of <u>T.</u> <u>arenaria</u> took place in the spring (April-June). As temperatures and light quality in the greenhouse room are modified by outdoor conditions (growth chamber facilities were not available for use in this study), actual figures for time elapsed during development from hatch to adult (Tables 4 and 5) are not comparable since the experiments were not conducted simultaneously. Nor should the actual figures on the time elapsed from hatch to adult and for time spent within each instar be emphasized; such figures are too easily

modified by environmental conditions. The most important data to be gained from these studies are with regard to the number of instars, the relationship between the relative lengths of the instars, and the differences in developmental time between the sexes.

In all instances, the last nymphal instar is of longer duration than any of those preceding it. This is apparently a fairly common feature of the developmental pattern of many different leafhopper species. Examples of species in which this phenomenon has been recorded include Aphrodes bicinctus (Schrank) (Chiykowski, 1970), Deltocephalus sonorus Ball (Gustin and Stoner, 1968), Exitianus exitiosus (Uhler) Gustin and Stoner, 1973), Graminella nigrifrons (Forbes) (Stoner and Gustin, 1967), Colladonus geminatus (Van Duzee) (Nielson, 1968), Colladonus clitellarius (Say) (George and Davidson, 1959), Aceratagallia curvata Oman (Nielson and Toles, 1968), and Draeculacephala mollipes (Say) (Bridges and Pass, 1970). Table 6 expresses the duration of the fifth instar for each of these species as a percent of the period from hatch to adult. In all instances documented, the fifth instar occupies more than 20% of the total nymphal period and in some cases accounts for slightly over 30% of the nymphal period.

Both T. friscana and T. arenaria females take longer than males to reach maturity after hatching. Only a few of the afore-mentioned life history studies on other leafhopper species separated

Table 6. Duration of the fifth instar expressed as a percent of the total nymphal period for selected leafhopper species.

Species	Sex	% of Nymphal period spent in fifth instar
Tiaja arenaria	♂	30.8
Tiaja arenaria	♀	30.3
Tiaja friscana	♂	25.7
Tiaja friscana	♀	27.3
Aphrodes bicinctus	♂	26.7
Aphrodes bicinctus	♀	28.6
Deltocephalus sonorus	both	24.0
Exitianus exitiosus	♂	27.8
Exitianus exitiosus	♀	30.5
Graminella nigrifrons	both	21.7
Colladonus geminatus (California)	both	29.2
Colladonus geminatus (Oregon)	both	28.1
Colladonus clitellarius	both	22.7
Aceratagallia curvata	both	26.7
Draeculacephala mollipes	both	29.0

data by sex. Chiykowski (1970) noted that for A. bicinctus the mean

time per instar was slightly greater for females than for males in

all but the first instar. Overall time from hatch to adult was 2.8

days greater for females than for males. Gustin and Stoner (1973)

also compared the times required for the development of males and

females. Their data show that the time spent per instar for females

is the same or greater than that spent by males and that overall

development from hatch to adult requires an average of 6.5 days more

for females. Musgrave (1974) found that female Scaphytopius acutus

(Say) also take longer than males to develop. This information helps

to explain data from the field which consistently show that adult

females are not present until later than adult males.

Swenson speculated (personal communication, 1972) that the

presence of mature males in a population before mature females are

present might be due to male eggs being laid first. I have no

information as to whether male eggs are laid first or whether eggs of

both sexes are laid at the same time but the former possibility seems

unlikely. Both male and female leafhoppers are diploid and sex

determination in most species is by a single X chromosome although a

few species have both X and Y chromosomes (Halkka, 1959). Although

no chromosome studies of Tiaja have been made, the most closely

related species studied, Ulopa reticulata (L.), and leafhoppers of the

subfamily Agalliinae, had only an X chromosome. My data show that

eggs of both sexes hatch at the same time and that differences in developmental time during the nymphal stages lead to males maturing first. Under the slower development rates experienced in the field, it would be expected that the difference in the development rates between the sexes would be even more obvious.

Fecundity

Forty newly matured virgin female T. friscana were paired with males and exposed to a succession of red clover plants for one week intervals to determine the onset and duration of the egg laying period and average weekly nymph production. As explained previously, the measure of nymph production per week was used because eggs were impossible to see in the plant host until shortly before hatching occurred. Nymphs hatched approximately 21 days after adult females were removed from the plants.

During the first week after pairing, only two females laid eggs that produced nymphs (Figure 11); almost all females laid eggs the second week and the average number of nymphs produced per female increased to 3.59. The third week marked the onset of high nymph production which was maintained through the fourteenth week after pairing. Peak nymph production averaging slightly more than 16 nymphs per week per female occurred between the fourth and ninth weeks after pairing. Subsequent to the fourteenth week, average

Figure 11. Results of fecundity experiment for $\underline{T}$. $\underline{friscana}$ females.
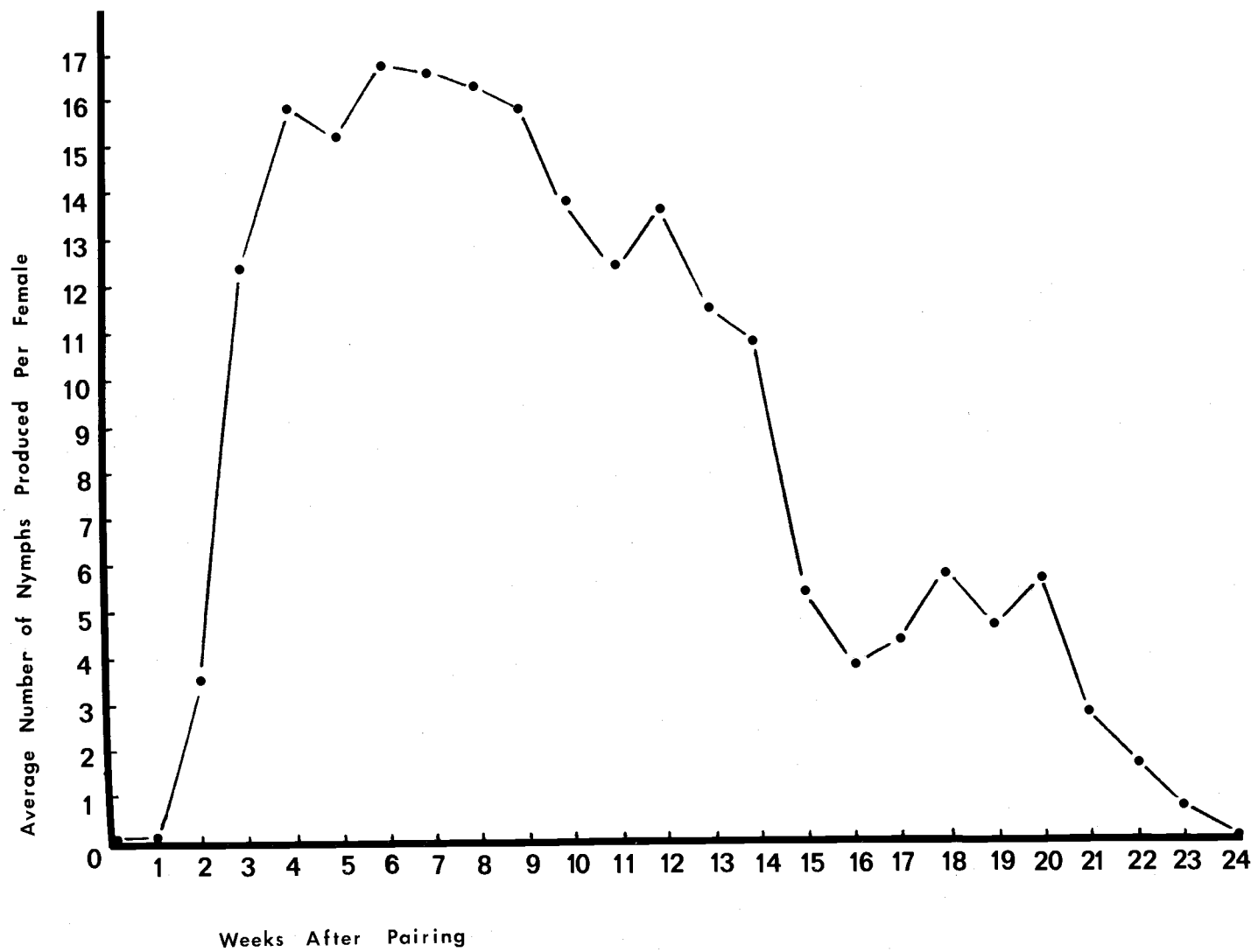
nymph production decreased markedly. By the twenty-fourth week after pairing, nymph production had ceased completely and only four females remained alive.

Parasites

Evidence of parasitism was noted during study of the genus Tiaja. Hymenopteran parasites of the Family Dryinidae were found affecting T. arenaria. Although attempts were made to rear the dryinid parasites to adulthood after they emerged from the dead host, these attempts were unsuccessful so identification of parasites was possible only to the family level.

Parasitized T. arenaria ranged in age from third instar to adult. Usually only one parasite per host was found, but one individual with two parasites was observed. Clausen (1940) states "a high percentage of parasitism of the host results in frequent duplicate oviposition, whereas the chance of this is slight in light infestation." This suggests that a low level of parasitism is in effect for T. arenaria. The egg of the parasite was apparently inserted into the leafhopper abdomen as larval sacs were observed protruding from the abdominal venter of affected individuals. The parasite emerges after the host's body contents have been consumed; pupation takes place outside the host.

It can be speculated that the occurrence of dryinid parasitism in T. arenaria may be related to the habitat occupied by this species. Despite collection of numerous specimens of T. montara and T. friscana in both immature and adult stages, no parasitized individuals of these species were observed. Nor have parasitized individuals been found in the other Tiaja species studied. T. arenaria is primarily found in the litter and soil layer below the host plant while other Tiaja species appear to live above ground on their host plant rather than in the thin layer of litter below it. This habitat difference may make T. arenaria a more accessible host. It is also possible that dryinids are not present in the habitats occupied by the other species of Tiaja, or if so, are not attracted to Tiaja.

The morphological effects of parasitism depend upon the stage at which the host was parasitized (Clausen, 1940). Parasitism of an early instar nymph usually results in the death of the host before it reaches maturity. Parasitism of a late instar nymph which matures before it dies may result in the reduction of the genitalia of both sexes so that the male assumes sexual characters of the female.

There are no concrete data on the effect of dryinid parasitism in population regulation of T. arenaria. What field data are available suggest the parasitism level in the population is about 8% (Oman, field notes, July 30, 1970). Clausen (1940) states that many dryinid species exert considerable population size control as not only are the

immature stages parasitic but the adults are predaceous so their effect may be felt at all stages of their development. In relation to this, it is interesting to note that Odum (1971) comments that parasitic insects are like predators in that they consume the entire host yet they tend to be host specific and have a high biotic potential like other parasites.

VI. CROSSBREEDING EXPERIMENTS

Introduction

Crossbreeding experiments were performed in this study as a means of testing the traditional species concept based on morphological similarities and differences among populations. Populations that are morphologically similar have traditionally been considered to be members of the same species while those that are dissimilar have traditionally been considered to belong to different species. The definition of species based on the biological species concept is that "species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1969). Early taxonomic work on leafhoppers was based almost entirely on structural characters and it is only in comparatively recent years that biological studies have been carried out to test the taxonomic reliability of these morphologically described species.

Some recent studies of leafhoppers have shown that certain morphological dissimilarities may be attributed to infraspecific variation and are not necessarily an indication of differentiation of species. Muller (1957) documents seasonal variation in the shape and length of aedeagal processes in _Euscelis plebjus_ (Fallen). Le Quesne and Woodruff (1976) found clinal geographic variation in the male genitalia of _Agallia laevis_ Ribaut, _Eupteryx stachydearum_

Hardy (=hortensis Curtis), and E. urticae (Fabricius). Whitcomb

et al. (1972) found that Stirellus bicolor (Van Duzee) and S. obtutus

(Van Duzee) are seasonal color variants of a single species and that

color form in this instance is controlled by photoperiod. Vilbaste

(1975) concluded that a number of southern Indian ulopine leafhoppers

described as distinct species are actually color variants of a single

species, Mesargus subopacus (Motschulsky). Sawbridge (1975b)

showed a wide range of infrapopulation variation in the aedeagal

processes of Giprus siskiyou (Oman) in series of specimens collected

at the same site on the same day.

Other biological studies have given support to taxonomic con-

clusions based on morphological criteria. Nielson and Toles (1970)

performed interspecific crosses between Carneocephala triguttata

Nottingham and C. nuda Nottingham, two morphologically very similar

but allopatric species of the southwest. Although the initial crosses

were fertile, partial or complete sterility was found when the F_1's

were crossed and in backcrosses to the parental types; when back-

crosses were crossed with each other, the majority were sterile.

From these experimental results, Nielson and Toles (1970) concluded

that C. triguttata and C. nuda should be retained as valid species

despite their morphological similarities and suggested that speciation

in these two groups has probably reached the semispecies level.

Severin (1945) attempted unsuccessfully to make reciprocal crosses

between Texananus lathropi (Baker) and T. latipex (DeLong). Copulation did not occur and although some females laid eggs, no nymphs hatched. These groups occur sympatrically and this biological evidence confirmed morphological indications that they are discrete species. Severin (1940) also attempted unsuccessfully to cross what appeared to be long-winged and short-winged forms of Macrosteles fascifrons (Stal) implying that they are distinct species despite the fact that they cannot be separated by morphological characters other than wing length. Purcell and Loher (1976) investigated the acoustical behavior of the two forms and made further attempts at hybridization. They report that the long-winged and short-winged forms have distinctly different songs and that one of the crosses was sterile (the few nymphs produced did not survive to maturity) while the reciprocal cross produced a very few fertile offspring. Despite this strong evidence of genetic and behavioral isolation of the long-winged and short-winged forms of M. fascifrons, Purcell and Loher have chosen not to separate them into two species because of the lack of morphological differentiation other than wing length, lack of evidence from other populations, and because they feel the taxonomic value of acoustical differences has not yet been shown conclusively. Severin and Klostermeyer (1950) reported unsuccessful attempts to cross Colladonus montanus montanus (Van Duzee) with C. geminatus (Van Duzee), and in doing so confirmed the taxonomic reliability of

these species. Musgrave (1974) investigated the Scaphytopius acutus complex; after crossbreeding experiments showed varying degrees of interpopulation fertility, three taxa previously described as species were reduced to subspecies of S. acutus.

During field work on Tiaja and the subsequent plotting of species distributions, two situations were presented which appeared ideal for tests of this kind, one involving two morphologically similar populations and the other involving morphologically dissimilar populations.

The first situation involved two populations of what appeared morphologically to be T. friscana. T. friscana ranges along the California coast from Tomales and Marshall in Marin County in the north to San Simeon, San Luis Obispo County in the south. Populations at these two extremes of the species' known range appear identical structurally although they live about 550 km apart and the distribution of the species is disjunct, with another species, T. montara, occupying the intervening coastal habitat. The present isolation of these populations is presumed to have been in effect for a very considerable period of time with gene flow severely restricted if not non-existent. Under these circumstances it seems possible that a reproductive barrier between the two populations might have arisen. Therefore, reciprocal crosses and the appropriate control crosses were conducted to test for this possibility.

The second situation involved T. friscana and T. montara, the latter species being that which separates the northern and southern populations of T. friscana. These species are based on morphological differences in their genitalia. T. friscana and T. montara appear to be essentially allopatric and are found in different localities on the San Francisco Peninsula. They appear to occupy different habitats with T. friscana found in sheltered areas away from exposure to the open ocean and T. montara found on bluffs and cliffs directly affected by ocean winds and salt spray. Despite habitat separation, it is quite conceivable that populations of T. friscana and T. montara (and possibly even T. californica) might, at times, occur close enough together that members of one species could occasionally contact members of the other species. A known example of such contact between species occurs at San Simeon where a few T. ventura were collected along with T. friscana although discrete microhabitats containing the two species might have been occupied but not detected during collecting. When two species have populations that are spatially close together, reproductive isolating barriers are often built up to prevent hybridization (Grant, 1963). Alternatively, the two populations could turn out to be interbreeding morphs of a single species, possibly with morphological features influenced by habitat. Reciprocal crosses were made between T. montara and T. friscana in an attempt to determine whether there are, in fact, sufficient

reproductive isolating mechanisms in effect between these two

morphologically and ecologically different groups to consider them

true species.

Interpopulation Crosses between Two
Populations of T. friscana

Results of interpopulation crosses and controls with Marshall

and San Simeon populations of T. friscana are given in Figure 12. The

data shown are in terms of nymphs produced from eggs laid each

week, even though actual hatching of nymphs occurred subsequent to

the weekly interval indicated. Very few nymphs were produced from

week 1, the week immediately following pairing. Nymphs were pro-

duced from all pairings in week 2, and peak production of progeny

occurred during the third to fifth weeks. Production declined in sub-

sequent weeks until the trials were terminated at the end of week 10.

Data for each replication are given in Appendix II, Crosses A, B,

D, and E.

The San Simeon male x Marshall female cross resulted in

nymph production very much like that of the two control crosses.

However, the nymph production of the cross of Marshall males x San

Simeon females was considerably lower than that of its reciprocal

and that of the controls between weeks 2 and 9. T-tests were

carried out to analyze the statistical significance of the difference in

Figure 12. Comparison of results of interpopulation crosses between
T. friscana from Marshall and San Simeon, California to
each other and to control crosses.
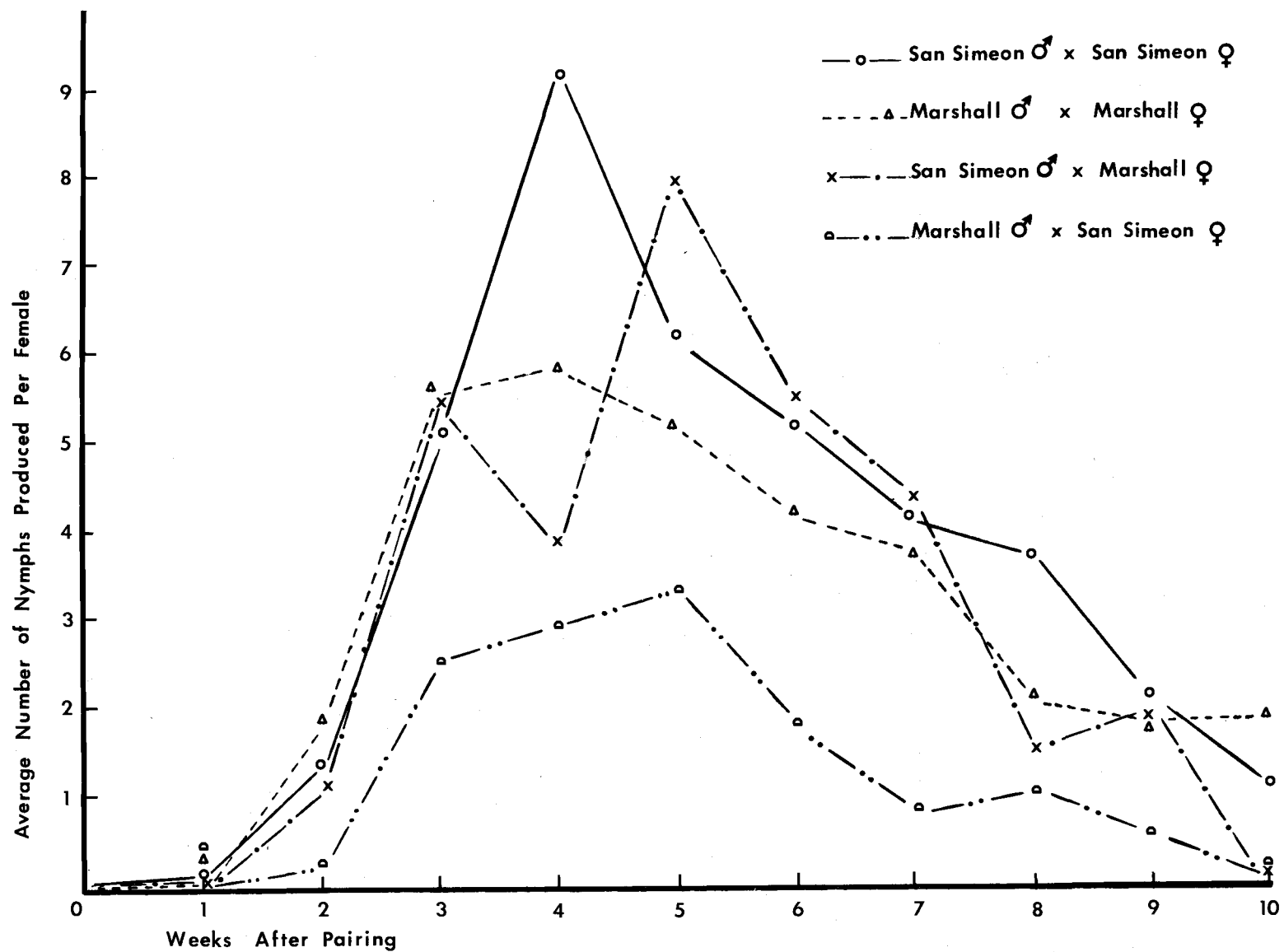
the mean number of nymphs produced per female for pairs of
samples as shown in Table 7. Calculations were made for each of
weeks 3 to 8. Controls (Marshall males x Marshall females and San
Simeon males x San Simeon females) had means that were not
significantly different from each other in five of the six weeks com-
pared. Week 4 showed significance only at the 5% level. Difference
in mean nymph production was highly significant (1% level) when the
Marshall males x San Simeon females cross was compared to the
controls in 50% of the comparisons, significant (5% level) in 25% of
the comparisons, and not significant in 25% of the comparisons.
When the reciprocal cross (San Simeon males x Marshall females)
was compared to the controls, the difference was highly significant
only 8.3% of the time, significant 16.7% of the time, and not signifi-
cant in 75% of the comparisons. When reciprocals were compared to
each other, the difference between them was highly significant (1%
level) in 66.7% of the comparisons and not significant in 33.3% of
the comparisons.

It appears that some factor is coming into play to reduce the
Marshall males x San Simeon females nymph production per female
below that for the reciprocal cross. One may speculate that this
could be a pre-mating isolating mechanism such as a courtship
behavior modification between the two populations that renders the
Marshall male less attractive to the San Simeon female than a

Table 7. Results of t-tests comparing reciprocal crosses with controls for interpopulation crosses between <u>T. friscana</u> at Marshall and San Simeon, California.

Comparison	Week					
	3	4	5	6	7	8
Marshall ♂ x Marshall ♀ & Marshall ♂ x San Simeon ♀	**	**	-	**	**	-
San Simeon ♂ x San Simeon ♀ & Marshall ♂ x San Simeon ♀	*	**	*	*	**	-
Marshall ♂ x Marshall ♀ & San Simeon ♂ x Marshall ♀	-	*	*	-	-	-
San Simeon ♂ x San Simeon ♀ & San Simeon ♂ x Marshall ♀	-	**	-	-	-	-
Marshall ♂ x Marshall ♀ & San Simeon ♂ x San Simeon ♀	-	*	-	-	-	-
San Simeon ♂ x Marshall ♀ & Marshall ♂ x San Simeon ♀	**	-	**	**	**	-

- not significant
* significant (α = .025)
** highly significant (α = .005)

San Simeon male would be, resulting in a lower proportion of the San Simeon females being fertilized by the Marshall males than is true for the reciprocal so that fewer nymphs per original female are produced. Individual trial totals (Appendix II, Cross D) suggest that this might be so as two trials have high total nymph production (67 and 58) while the insects in the other trials produced 30 or fewer nymphs per trial. Other possibilities are that there is greater incompatibility of the San Simeon egg and the Marshall sperm than in the reciprocal, or greater hybrid inviability once the egg is fertilized.

It appears that interpopulation differences, as indicated by lowered fertility in at least one direction of the reciprocal cross, are present in the two populations from the extreme ends of the range of T. friscana. However, genetic isolation of the two populations is far from complete and the nymphs per female per week production of the interpopulation crosses does not appear sufficiently different from that of the controls to warrant any interpretation other than that they are populations of a single species.

Interspecific Crosses between T. friscana and T. montara

Figure 13 shows results for the reciprocal crosses between T. montara and T. friscana. Peak nymph production for the controls,

Figure 13. Comparison of results of reciprocal interspecific crosses between T. friscana from Marshall, California and T. montara from Pillar Point, California to each other and to control crosses.
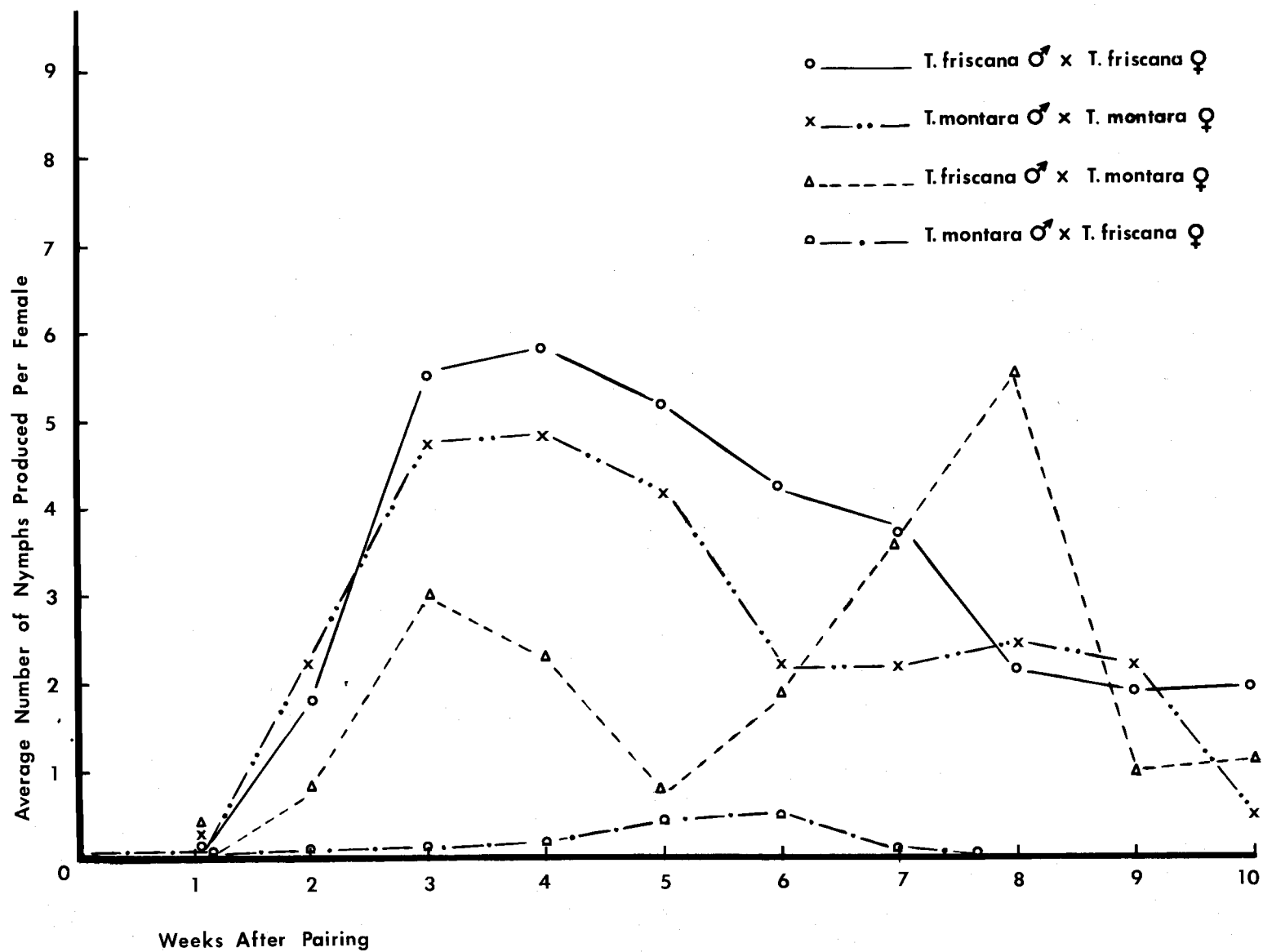
an average of four to six nymphs per female per week, occurs between the third and fifth week after pairing. The experimental cross involving T. montara males and T. friscana females resulted in extremely low nymph production per female per week. A slight increase in nymphs produced per female per week is seen in the fifth and sixth weeks. Of the nine cages involved in the T. montara male x T. friscana female cross (Appendix II, Cross G), five failed to produce any offspring. Twenty-five of the total of 31 nymphs produced in this cross came from one set of three females and could have been the result of only one female being successfully inseminated. A second set of females produced four nymphs and two other groups produced only one nymph each.

The experimental cross between T. friscana males and T. montara females shows an unusual bimodal pattern of nymph production. Peak nymph production occurs during the third, fourth, seventh, and eighth weeks after pairing. Production falls off sharply between peaks and after the eighth week. A closer look at nymph production within each cage (Appendix II, Cross F) reveals that in the T. friscana male x T. montara female cross, the leafhoppers in two of the eight cages failed to produce any offspring, two cages had very low nymph production, two cages had fairly low nymph production, and two cages had very high nymph production. In this cross, the second peak in the nymphs per female per week ratio (week 8) is largely a

result of production of 51 nymphs by three females in that week.
It is likely that if the sample size had been sufficiently large, the
bimodal pattern of nymph production in this cross would not have
appeared.

T-tests were used to compare the difference in the mean nymph
production of the reciprocal crosses and the controls for weeks 3 to 8
(Table 8). Controls (T. friscana males x T. friscana females and
T. montara males x T. montara females) were not significantly differ-
erent from one another in 83.3% of the comparisons. In week 6 the
mean nymph production per female of the control crosses was
significantly different at the 5% level. The T. montara male x T.
friscana female cross was found to be highly significantly different
from both controls in all weeks (1% level). The difference of the
T. friscana male x T. montara female cross from control crosses
was highly significant (1% level) in 33.3% of the comparisons,
significant (5% level) in 16.7% of the comparisons, and not significant
in 50% of the comparisons. When the reciprocals were compared
to each other, differences were highly significant (1% level) in
66.7% of the comparisons, significant (5% level) in 16.7% of the
comparisons, and not significant in 16.7% of the comparisons.

The greatly lowered nymph production of the reciprocal crosses
between T. friscana and T. montara, particularly when T. montara
males were crossed with T. friscana females, and the erratic

Table 8. Results of t-tests comparing reciprocal crosses with controls for interspecies crosses between T. friscana and T. montara.

Comparison	Week					
	3	4	5	6	7	8
T. friscana ♂ x T. friscana ♀ & T. montara ♂ x T. friscana ♀	**	**	**	**	**	**
T. montara ♂ x T. montara ♀ & T. montara ♂ x T. friscana ♀	**	**	**	**	**	**
T. friscana ♂ x T. friscana ♀ & T. friscana ♂ x T. montara ♀	**	**	**	*	-	-
T. montara ♂ x T. montara ♀ & T. friscana ♂ x T. montara ♀	-	*	**	-	-	-
T. friscana ♂ x T. friscana ♀ & T. montara ♂ x T. montara ♀	-	-	-	*	-	-
T. friscana x T. montara & T. montara x T. friscana	**	**	-	*	**	**

- not significant
 * significant (α = .025)
** highly significant (α = .005)

pattern of nymph production in the reciprocal cross, support the conclusion based on morphological evidence that two distinct species are involved and suggest that a number of isolating mechanisms are operational to maintain the integrity of each species in localities where their ranges are adjacent or overlapping. A similar conclusion was reached by Nielson and Toles (1970) who had limited success in interbreeding two morphologically based species of Carneocephala, C. triguttata Nottingham and C. nuda Nottingham.

These data provide a foundation for speculation on interspecific isolating mechanisms present in Tiaja. It must be kept in mind that the artificial conditions of the experiments (placing individuals of different species at close quarters with no choice of mating with members of their own species) eliminated geographical and ecological isolation, either of which could be important prereproductive isolating barriers in nature. Both geographic and ecological isolation of these species do appear to exist in nature. T. friscana and T. montara, as far as is known, are allopatric; they have never been collected at the same site. As mentioned previously, the habitats of the two species differ in that T. montara is always found in areas directly exposed to the ocean while T. friscana is almost always found in sheltered areas. If spatial and ecological barriers effectively prevent crossing in nature, it is possible that reproductive isolating mechanisms would be lacking and that when members of the

two populations came together, there would be relatively free hybridization between the two groups. However, since fertility in the test crosses is drastically reduced, such is obviously not the case, suggesting that physiological and behavioral reproductive barriers exist, at least under the stated laboratory conditions.

This reproductive isolation may take any of several forms. Firstly, mating may not be taking place as frequently as in con- specific crosses because of ethological factors such as differing courtship stimuli (possibly auditory ones as found by Claridge and Reynolds (1973) for the Oncopsis flavicollis group) that could have reduced mating frequency although no visible differences in courtship between the two species were observed. Secondly, there could be a mechanical and/or ethological isolating factor operating due to the disparity in size between the two species. The T. montara males used were considerably smaller than T. friscana males and the T. friscana females with which they were paired. The smaller males may not have been able to copulate with the larger females because of this size difference. The genital hooks on the T. montara males could be too short to effectively grasp the seventh sternum of the T. friscana female.

The once popular "lock and key" theory of Dufour (1844 in Mayr, 1963) provides another possible but less likely mechanical isolating factor. If the male genital structures of one species do not

fit the female of the other species, insemination cannot take place. It appears that insemination is not always taking place in these interspecies crosses since over half the T. montara male x T. friscana female crosses failed to produce any offspring. While courtship and apparently successful copulation were observed, it is impossible to say whether insemination was accomplished in these cases (i. e. that the sperm of the male reached the spermatheca of the female) since obtaining such evidence would have required killing and dissecting the test animals.

Once insemination occurs, other isolating factors may come into play (Grant, 1963). Cytoplasmic incompatibility could result in reduced fertilization. As some fertilization obviously did take place, partial hybrid inviability may have been a factor so that only a very few of the fertilized eggs survived to hatch as nymphs.

VII. TAXONOMY

Position of the Genus *Tiaja* within the Cicadellidae

Tiaja is a member of the leafhopper tribe Megophthalmini. The relationship of the Megophthalmini to the other tribes of the Cicadellidae, particularly the Ulopini, has long been a subject for discussion amongst those concerned with leafhopper taxonomy and phylogeny. Evans (1947, 1966) considers the Megophthalmini, Ulopini, Myerslopiini, Monteithini, and Cephalelini to be tribes of the subfamily Ulopinae. Oman (1949) treated the Megophthalmini as a tribe of a separate subfamily, the Megophthalminae. Wagner (1951), in considering relationships among the leafhoppers, constructed a phylogenetic tree for the Cicadellidae which shows the Ulopini as a branch near the base of the Cicadellid line and the Megophthalmini as a branch near the base of the Iassid line. Halkka (1959) compared the results of his chromosome studies of 115 species of leafhoppers to Wagner's phylogenetic tree and found that cytogenetic evidence gives strong support to many points in Wagner's scheme. Unfortunately, although a chromosome study was made of the ulopine species *Ulopa reticulata* L., there are no data for any megophthalmine leafhoppers so no new genetic information regarding the degree of relationship of the Ulopini and the Megophthalmini was obtained.

Linnavuori (1972) has provided a recent interpretation of the relationship of the megophthalmines to the ulopines. He argues that the megophthalmines are so greatly differentiated from the ulopines that they rate subfamily rank. He bases his argument for subfamily status on differences in the facial sclerites, ocellar position, tibial shape, tibial spine pattern, and male genital structures that are evident in the two groups. Linnavuori also groups three of Evans' subfamilies, the Ulopinae, Cephalelinae, and Monteithinae, into a single subfamily, the Ulopinae, and states that they are the most primitive group in the Cicadellidae. He suggests that the Megophthalminae and a third subfamily, the Myerslopiinae, may have derived from ulopine stock in the Mesozoic era. Both Oman and Linnavuori see strong similarities between the Megophthalminae and the Agalliinae. Linnavuori states that the Agalliinae were probably derived from ancestral megophthalmines in the Tertiary period.

Davis (1975) studied the female genitalia and the metathoracic legs of leafhoppers and came to the conclusions that the Megophthalminae should be a separate subfamily from the Ulopinae, the Cephalelini should be a tribe of the Ulopinae, and that the Megophthalminae and the Agalliinae are closely related. The latter conclusion was reached after a detailed study showed a number of similarities in the valvulae and the arrangement of setae on the metathoracic leg of the two groups. It is noteworthy that Davis reached the same

conclusions as Linnavuori and Oman although his study was based on different anatomical features. In this work, the opinions of the majority of recent workers are accepted, and the megophthalmine leafhoppers are treated as the subfamily Megophthalminae.

There are no known members of the Megophthalminae in South America, Asia, Australia, or on the islands of the western Pacific Ocean. In these regions and in southern Africa are found leaf-hoppers of the Tribes Ulopini (Europe, India, and Madagascar), Cephalelini (South America, Australia, and New Zealand), Monteithini (New Guinea), and Myerslopiini (New Zealand, Chile, and Madagascar).

The Subfamily Megophthalminae with its one included tribe, the Megophthalmini, is represented in Europe, Africa, and North America. The group takes its name from <u>Megophthalmus</u> Curtis (=<u>Paropia</u> Germar) which has three included Palearctic species: <u>M. decimquartatus</u> (von Schrank), <u>M. scabripennis</u> Edwards, and <u>M. scanicus</u> (Fallen). The latter species has the widest distribution and occurs throughout Europe from Sweden and Great Britain to the islands of the Mediterranean, Algeria, and Turkey. This also appears to be the widest distribution by far of any species of Tribe Metophthalmini.

The genus _Paropulopa_ Feiber has only one species, _P. lineata_ Fieber which is found in France and Spain.

In Africa, the tribe Megophthalmini is represented by two genera, _Odomas_ Jacobi, which includes nine species (Linnavuori, 1973) and _Dananea_ Linnavuori with one species, _D. inflaticeps_ Linnavuori. _Dananea_ has fully developed hindwings while the hindwings of _Odomas_ are not developed.

In North America, there are two genera of megophthalmine leafhoppers. _Tiaja_ Oman is differentiated from _Brenda_ Oman on the basis that _Tiaja_ has rudimentary hindwings and is flightless while _Brenda_ has fully developed hindwings and is capable of flight; additionally, _Tiaja_'s criwn is longer medially than next to the eye while _Brenda_'s crown is the same length medially as next to the eye. Both genera are restricted to western North America.

Characterization of the Genus

Members of the genus _Tiaja_ range from 2.5 to 5.0 mm in length with females of each species tending to be slightly larger than the males. The head is wider than the pronotum and flattened apically. The median length of the crown is greater than the length of the crown next to the eye, giving the head a somewhat angular appearance which

varies with the individual species. Angularity of the head, as meas-
ured by the ratio of the width of the crown at the anterior margin of
the eyes to the median length of the crown (W/L) tends to be constant
within species and varies among species. W/L ratios for _Tiaja_ range
from 2.20 to 3.68; low W/L values indicate a relatively angular head
(Figure 14) while high W/L values indicate a relatively blunt head
(Figure 15). Newly moulted individuals are white (Color Plate IV) but
begin to darken immediately and within hours have become shades of
brown ranging from rust to chocolate to fuscous. The head, pronotum,
and forewings have a pitted texture. Forewings are fully developed
and leathery; venation is somewhat obscured by the pitted texture of
the wings. There is no membranous appendix. The posterior mar-
gins of the forewings are contiguous along the commissural line for
their entire length. The forewings probably serve mainly to protect
the body. Hindwings show only rudimentary development, rendering
the insects flightless. Observation of live specimens showed that they
are unable even to flex their forewings. The male valve is very
small while the partially fused genital plates are very large. The
tenth abdominal segment is equipped with genital hooks used to clasp
the female during copulation. While the size and general shape of the
genital hooks serves as a good generic characteristic, the shape,
number, and position of the processes on the hooks are distinct in
each species as are the shapes of the styles and the aedeagus. The
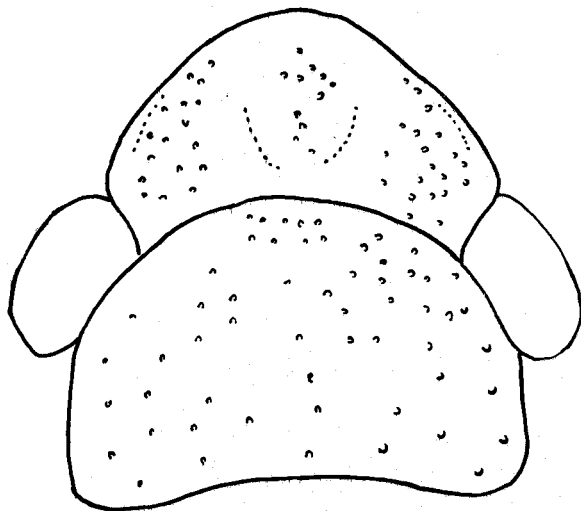
14

Figure 14. _T. insula_: head and pronotum.
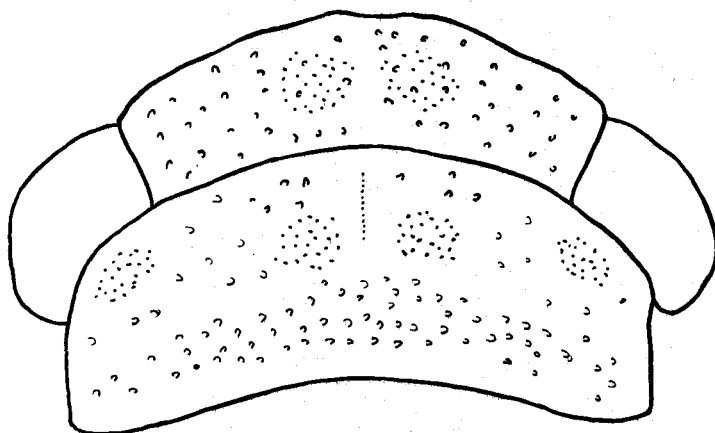
1.0 mm

15

Figure 15. _T. arenaria_: head and pronotum.

Color Plate IV. <u>T</u>. <u>friscana</u>, newly-emerged adult and cast skin.

female seventh sternum is relatively short laterally throughout the genus but otherwise varies considerably among the species, being bandlike in some and extremely emarginate or with projections in others. The type species for the genus Tiaja is Paropulopa californica Ball, type by original designation.

Tiaja nymphs are easily distinguished from those of other genera. Their most prominent features are the strongly flattened head seen most clearly in first instar nymphs (Figure 5) and the numerous fine setae covering the face, head, pronotum, developing wings, and the abdominal dorsum. Colors are of a similar range to those of adults. Characters of each instar were discussed previously.

Species Groups

The eight species in the genus Tiaja can be arranged in two groups on the basis of morphological characteristics and to some extent distribution. Group I includes the three more northern species of the genus, T. arenaria, T. friscana, and T. montara. The species in Group II which include T. californica, T. insula, T. ventura, T. interrupta, and T. mexicana, inhabit the southern portion of the genus' range.

Members of Group I are the larger-sized species in the genus with body length ranging from 4.0 mm to 5.0 mm. They are

characterized by blunt heads resulting in W/L ratios greater than
3.00. In Group I the styles and genital hooks extend beyond the
genital plates and are clearly visible in undissected specimens.
There appears to be a wide range of color variation among non-
teneral individuals in each species in Group I. Individuals may range
from light reddish-brown to almost black in color.

Species included in Group II tend to show the reverse
morphological characteristics to those listed for Group I. Body
length of species in Group II is less than 4.0 mm. Head shape is
more angular, with W/L values ranging from 2.20 to 2.85. The
genital hooks and styles are not visible unless specimens are dis-
sected. Color appears less variable in Group II species; most
individuals are light brown in color and extreme color variants have
not been found.

Key to the Species of Tiaja

1. a. Female 2
    b. Male 3
2. a. Total length about 3.6 mm.
        Female 7th sternum large in relation to total body
        size with a deep V-shaped median emargination and
        two elongate, divergent, triangular-shaped pro-
        jections, one on each side of the median
        emargination (Figure 20) . . . . T. mexicana

b. Female 7th sternum truncate, shallowly emarginate, or with projections not triangular-shaped 3

3. a. Styles and genital hooks of males extending beyond plates and clearly visible without dissection. Mean W/L 3.00 or greater. Total length greater than 4.0 mm 4

b. Styles and genital hooks not normally visible without dissection. Mean W/L less than 3.00. Total length less than 4.0 mm 6

4. a. Female with 7th sternum small in relation to 6th sternum, sometimes only visible laterally and with basal margin of pygofer exposed and strongly deflexed. Male plates rounded apically with a flared, V-shaped median incision (Figure 27). Styles tapered apically (Figure 24). Genital hooks with one sharp spine and one blunt projection (Figure 39) . . . . T. friscana

b. Female with 7th sternum large in relation to 6th sternum and with basal margin of pygofer not deflexed. Male with styles enlarged apically or with plates with a very narrow median incision 5

5. a. Female 7th sternum with broad, shallow, U-shaped median emargination (Figure 16). Male plates rounded apically with a flared, V-shaped median incision (Figure 27). Styles enlarged and footlike apically (Figure 23). Genital hooks with two sharp spines (Figure 42) . . . . T. montara

    b.   Female 7th sternum with a shallow, more V-
shaped median emargination (Figure 18). Male
plates sharply angled subapically with a narrow
median incision (Figure 28). Styles very broad
distad of attachment to connective (Figure 22).
Genital hooks with 3 spines, one very large and
dorsal and 2 small and ventral (Figure 37). . T. arenaria

6.   a.   Female 7th sternum with a pointed or rounded
projection each side of a deep, narrow, U-shaped
medium emargination (Figure 21). Male plates
longer than wide, almost parallel-sided, and
rounded apically (Figure 25). Median incision
narrow and one-half the length of the plates.
Genital hooks with 4 spines (Figure 38). . . T. californica

    b.   Female 7th sternum truncate or with broad,
shallow emargination. Male plates truncate,
angled subapically, or as in T. californica but
with genital hooks with only 3 spines   7

7.   a.   Female 7th sternum with a broad, shallow,
U-shaped emargination with a well-defined,
rounded projection on each side (Figure 19).
Male plates angled subapically (Figure 29).
Genital hooks with 2 small spines (Figure 40). . T. insula

    b.   Female 7th sternum truncate or with no definite
projections (Figure 17). Genital hooks with
3 or more spines 8

8.   a.   Length 3.2 mm or less for females; 3.0 mm
or less for males. Female 7th sternum truncate
or shallowly emarginate, may appear to be under
the 6th sternum and visible only laterally. Male

Figure 16.   <u>T</u>. <u>montara</u>: seventh sternum

Figure 17.   <u>T</u>. <u>ventura</u>: seventh sternum

Figure 18.   <u>T</u>. <u>arenaria</u>: seventh sternum

Figure 19.   <u>T</u>. <u>insula</u>: seventh sternum

Figure 20.   <u>T</u>. <u>mexicana</u>: seventh sternum

Figure 21.   <u>T</u>. <u>californica</u>: seventh sternum
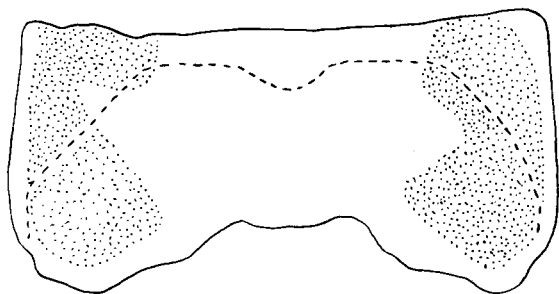
16
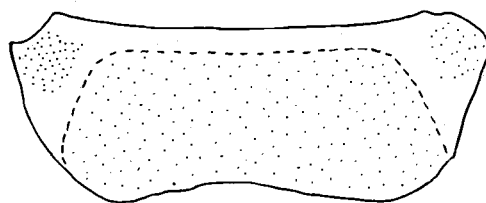
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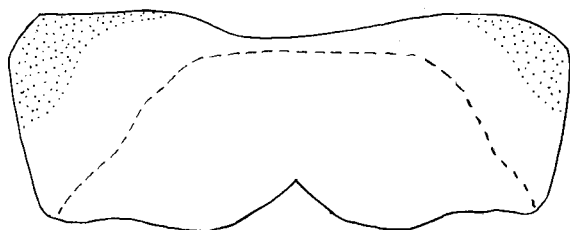
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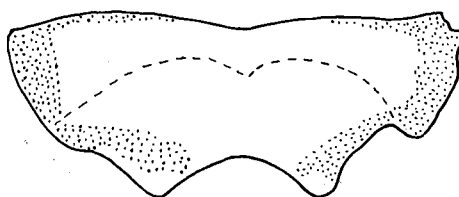
19
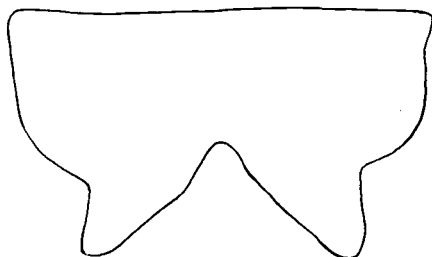
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0.1mm
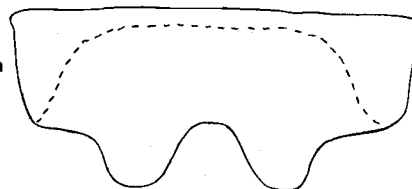
21

Figure 22. T. arenaria: right style

Figure 23. T. montara: right style

Figure 24. T. friscana: right style

Figure 25. T. californica: genital plates

Figure 26. T. interrupta: genital plates

Figure 27. T. friscana: genital plates

Figure 28. T. arenaria: genital plates

Figure 29. T. insula: genital plates
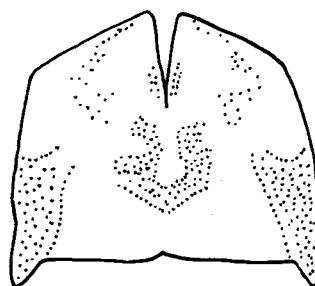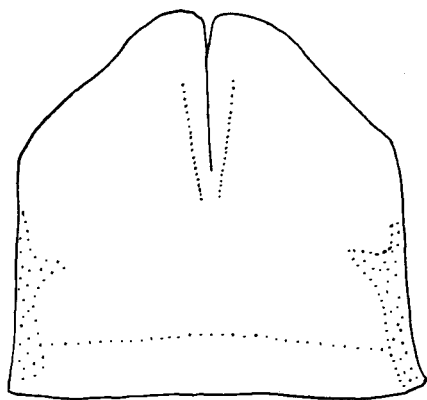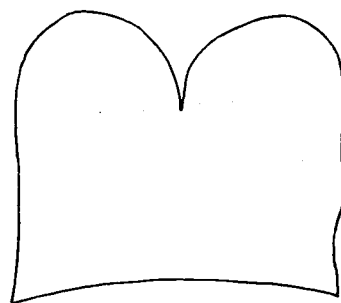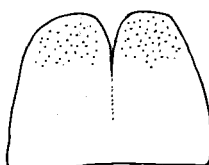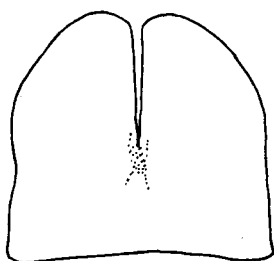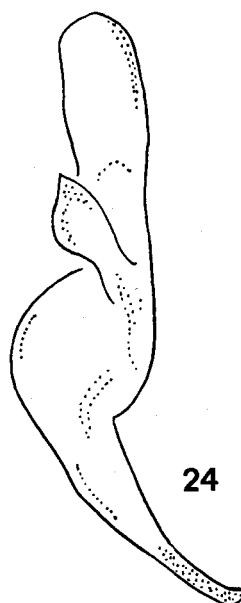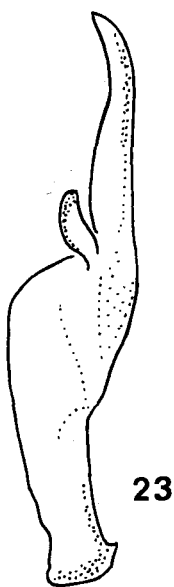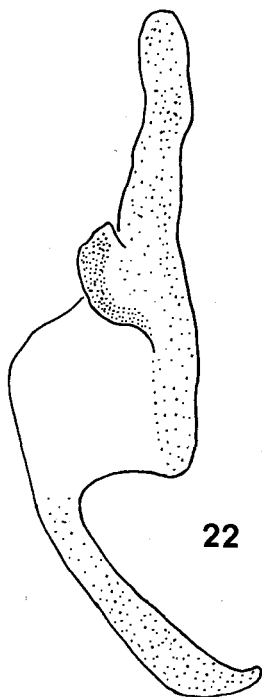
0.1 mm

Figures 30-36. Aedeagus

           30. *T. arenaria*
           31. *T. californica*
           32. *T. insula*
           33. *T. interrupta*
           34. *T. friscana*
           35. *T. montara*
           36. *T. ventura*

Figures 37-43. Left genital hook

           37. *T. arenaria*
           38. *T. californica*
           39. *T. friscana*
           40. *T. insula*
           41. *T. interrupta*
           42. *T. montara*
           43. *T. ventura*
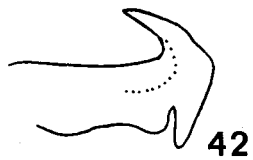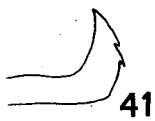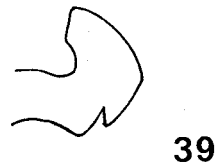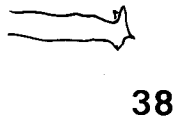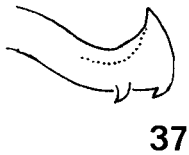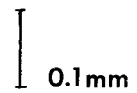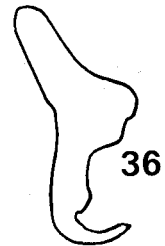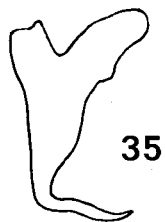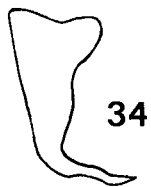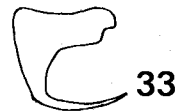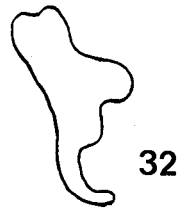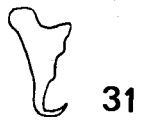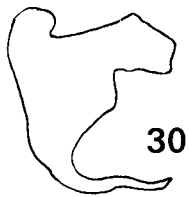
plates very small and truncate apically (Figure 26).
Genital hooks with one long, tapering spine and
3 short spines (Figure 41). Aedeagus with
elongate distal portion (Figure 33) . . . . . T. interrupta

b.　Total length 3.5 mm or greater. Female 7th
sternum truncate or very shallowly emarginate
Male plates rounded apically with narrow median
incision. Genital hooks with one dorsal and
2 ventral spines (Figure 43). Distal portion of
aedeagus relatively short (Figure 36) . . . . T. ventura

Species Descriptions

T. arenaria Oman

(Figures 15, 18, 22, 28, 30, 37)

Tiaja arenaria Oman 1972, p. 70

Mean W/L: 3.68, very blunt head

Total Body Length: Male: 4.4-4.5 mm. Female: 4.2-4.8 mm

Color: Variable, ranges from light reddish-brown to almost black
in non-teneral specimens.

Female Genitalia: Seventh sternum large with shallow, almost
V-shaped median emargination.

Male Genitalia: Styles and genital hooks extending beyond plates and
clearly visible in undissected specimens. Plates large and
sharply angled subapically; median incision minute. Genital

hooks with 3 spines: 1 large and dorsal; 2 small and ventral.
Styles broad distad of attachment to connective and relatively
broad subapically.

Holotype: ♂, "Oregon, Lincoln County, 2.5 mi N Waldport,
17-VIII, 1970, P. Oman" (USNM)

Material Examined: (1000+ specimens) OREGON: Tillamook County:
Cannon Beach, Ecola State Park, 1 mi N. Oceanside, 1.2 mi S
Oceanside. Lincoln County: Newport, 2.5 mi N Waldport.
Curry County: Pistol River, Nesika Beach. BRITISH
COLUMBIA: Pachena, Point-No-Point, Radar Hill Beach,
Wickininnish Beach. CALIFORNIA: Mendocino County: Fort
Bragg. Marin County: Muir Woods? WASHINGTON: 10 mi N
Queets.

Published Records Not Verified: None

Seasonal Occurrence: All year; nymphs present April to August

Host: Fragaria chiloensis

Habitat: Within 100 m of the ocean on stabilized sand dunes or rocky
foreshore; may be in a kinnikinnick/strawberry association or
a grass/strawberry association.

T. friscana (Ball)

(Figures 24, 27, 34, 29)

Paropulopa friscana Ball 1909, p. 183

Tiaja friscana, Oman, 1941, p. 209

Mean W/L: 3.14, head relatively blunt

Total Body Length: Male: 4.4-4.7 mm. Female: 4.7-4.9 mm

Color: Variable; most specimens are a mottled, grey-brown;

   extremes may be pale reddish-brown to almost black.

Female Genitalia: Seventh sternum small and may only be visible

   laterally. Basal margin of pygofer strongly deflexed.

Male Genitalia: Styles and genital hooks extending beyond plates and

   clearly visible in undissected specimens. Plates rounded, with

   flared, V-shaped median incision. Genital hooks with a blunt

   projection and one sharp spine. Styles tapered apically.

Lectotype: ♀, "S. Francisco, Cal., 27 Ap. 08, E.D. Ball,

   Collector" (USNM)

Material Examined: (1000+ specimens) CALIFORNIA: Marin County:

   Tomales Bay, Millbrae, 3.3 mi N Marshall, Inverness. San

   Francisco County: San Francisco, Lake Merced, Fort Point.

   Alameda County: Alameda. Sonoma County: Bodega Bay?.

   San Luis Obispo County: San Simeon.

Published Records Not Verified: None

Seasonal Occurrence: Adults probably all year; collection data con-

   firm presence May through December

Host: Eriophyllum staechadifolium var. artemisiaefolium

Habitat: Usually within 100 m of the ocean in sheltered habitats in

   association with E. staechadifolium var. artemisiaefolium,

<u>Lupinus</u> <u>arboreus</u>, and <u>Artemisia</u> <u>californica</u>. Rarely (at San Simeon) on an exposed bluff.

<u>T.</u> <u>montara</u> Oman

(Figures 16, 23, 35, 42)

<u>Tiaja</u> <u>montara</u> Oman 1941, p. 210

Mean W/L: 3.02, head quite blunt

Total Body Length: Male: 4.2-4.4 mm. Female: 4.4-4.7 mm

Color: Variable; most specimens are a mottled grey-brown; extremes may range from pale reddish-brown to almost black.

Female Genitalia: Seventh sternum large with a broad, shallow, U-shaped median emargination.

Male Genitalia: Styles and genital hooks extending beyond plates and easily visible in undissected specimens. Plates rounded, with a flared, V-shaped median incision. Genital hooks with 2 well-developed spines. Styles footlike, broad apically.

Holotype: ♂, "Montara, Calif., June 13, 1935, P.W. Oman" (USNM)

Material Examined: (1000+ specimens) CALIFORNIA: San Mateo County: Halfmoon Bay, Pillar Point, Moss Beach, 1 mi N Montara, San Gregorio State Beach, Pebble Beach State Park. Santa Cruz County: 17 mi NW Santa Cruz, 6.4 mi N Jct. Hwy. 1 & Hwy. 84, 6.5 mi N Davenport. Monterey County: Carmel,

Big Sur, 2.8 mi S. Pt. Lobos, 8.2 mi S. Pt. Lobos, 13.3 mi S

Pt. Lobos.

Published Records Not Verified: None

Seasonal Occurrence: Adults probably present all year; collection

data confirm presence of adults March through November.

Host: Eriophyllum staechadifolium var. artemisiaefolium

Habitat: Exposed coastline of central California in association with

E. staechadifolium var. artemisiaefolium, Lupinus arboreus,

and Artemisia californica.

T. californica (Ball)

(Figures 21, 25, 31, 38)

Paropulopa californica Ball 1909, p. 184

Tiaja californica, Oman, 1941, p. 208

Mean W/L: 2.53, head relatively pointed

Total Body Length: Male: 3.0-3.2 mm. Female 3.3-3.5 mm

Color: Variable; ranges from pale beige to almost black; most

specimens intermediate in color

Female Genitalia: Seventh sternum with a deep, U-shaped median

emargination and a well-defined pointed or blunt projection on

each side of the emargination.

Male Genitalia: Styles and genital hooks not usually visible in

undissected specimens. Plates almost parallel-sided but

rounded apically; plates appear longer than wide; median

incision is 1/3 the length of the plates but very narrow. Genital

hooks with 4 spines. Connective broad and aedeagus small.

Lectotype: ♀, "Salinas, Cal., 20 Je'08, E.D. Ball, Collector"

(USNM)

Material Examined: (51 specimens) CALIFORNIA: Alameda County:

Alameda, Livermore, Niles. Santa Clara County: Los Altos,

Sargent. Monterey County: Bradley, Bryson. Contra Costa

County: Moraga Valley, Mt. Diablo. San Mateo County:

Spring Valley Lake Road, Montara. Madera County: Bass Lake.

Published Records Not Verified: Napa County: Oakville. Santa

Clara County: Watsonville. San Mateo County: Burlingame.

Monterey County: Monterey. San Mateo County(?): Honda

(sic), (?) County: Leona Heights

Seasonal Occurrence: Adults probably present all year; collection

data confirm presence of adults from April through November

Host: Unknown

Habitat: Not found on the ocean shore; plant associations unknown

T. insula Sawbridge

(Figures 14, 19, 29, 32, 40)

Tiaja insula Sawbridge 1975a, p. 268

Mean W/L: 2.20, head very pointed

Total Body Length: Male: 3.0-3.5 mm. Female: 3.5-3.75 mm.

Color: Pale sandy brown

Female Genitalia: Seventh sternum with broad, shallow, U-shaped

emargination with a rounded projection on each side.

Male Genitalia: Genital hooks not visible in undissected specimens.

Plates angled subapically with median incision extending 1/3

the length of the plates. Genital hooks each with 2 small spines.

Styles tapered. Aedeagus stocky.

Holotype: ♂, "California: Los Angeles County, Santa Barbara

Island, VI-6-74, E. L. Paddock & R. F. Hobza" (California

Academy of Science)

Material Examined: (7 specimens) CALIFORNIA: Los Angeles

County: Santa Barbara Islands. Santa Barbara County: San

Miguel Island(?)

Published Records Not Verified: None

Seasonal Occurrence: Adults present in May and June; no data for

the remainder of the year

Host: Suaeda californica

Habitat: Near the shore on California coastal islands

<u>T. interrupta</u> (Ball)

(Figures 26, 33, 41)

<u>Paropulopa interrupta</u> Ball 1902, p. 21

<u>Tiaja interrupta</u>, Oman 1941, p. 208

Mean W/L: 2.65, head relatively pointed

Total Body Length: Male: 2.7-2.8 mm. Female: 2.9-3.25 mm

Color: Variable, usually light greyish-brown

Female Genitalia: Seventh sternum truncate or very shallowly

emarginate and may appear to lie partly under the sixth

sternum.

Male Genitalia: Styles and genital hooks not normally visible in

undissected specimens. Plates very small, narrowed and

truncate apically. Genital hooks with one long tapering spine

and 3 short, hooklike spines.

Lectotype: ♀, "Los Angeles Co., Cal., Collection Coquillet"

(USNM)

Material Examined: (44 specimens) ARIZONA: Pinal County:

Maricopa. CALIFORNIA: Los Angeles County: Pasadena,

Los Angeles. San Diego County: Alpine, Del Mar, E of

Jacumba. Orange County: Newport Beach, San Clemente.

Riverside County: ANZA. (?) County: Newton.

Published Records Not Verified: Riverside County: Beaumont,

Cabazon, San Jacinto Mts. San Diego County: Carlsbad,

Miramar, Tiajuana. San Bernardino County: Ontario.

(?) County: Cuyamaca Lake, Hurkey Creek, La Mesa.

Seasonal Occurrence: Probably present all year; collection data

confirm presence March through November.

Host: Unknown, found on chaparral plants

Habitat: Both near to shore and well inland, presumably on plants of

the southern California chaparral association.

<u>T. mexicana</u> (Ball)

(Figure 20)

<u>Paropulopa mexicana</u> Ball 1902, p. 207

<u>Tiaja mexicana</u>, Oman 1941, p. 21

Mean W/L: 2.50, head quite pointed

Total Body Length: Female: 3.6 mm

Color: Light brown

Female Genitalia: Seventh sternum distinctive; relatively large

with a deep, flared, V-shaped emargination and two long,

triangular-shaped projections, one each side of the median

emargination.

Male Genitalia: Unknown

Lectotype: ♀, "Sr. Madre Mts. Mex. 7500'," C.H.T. Townsend,

Collector

Material Examined: Material from the type locality only

Published Records Not Verified: None

Host: Unknown

Habitat: Unknown

T. ventura Oman

(Figures 17, 36, 43)

Tiaja ventura Oman 1941, p. 209

Mean W/L: 2.85, head not particularly pointed or blunt

Total Body Length: Male 3.7-3.8 mm. Female: 3.8-3.9 mm.

Color: Mottled, sandy brown

Female Genitalia: Seventh sternum truncate or very shallowly

emarginate.

Male Genitalia: Styles and genital hooks not usually visible in

undissected specimens. Plates longer than wide and rounded

apically with a minute median incision. Genital hooks with 3

spines, 1 dorsal and 2 ventral. Aedeagus with distal portion

relatively short. Styles tapered apically.

Holotype: ♂, "Pismo Beach, Calif., July 19, 1933, R.H. Beamer"

(USNM)

Material Examined: (18 specimens) CALIFORNIA: San Luis Obispo

County: San Simeon, Pismo Beach. Santa Barbara County:

Montecito

Published Records Not Verified: Santa Barbara County: Santa

Barbara, Gaviota. Ventura County: Oxnard.

Seasonal Occurrence: Adults present in June and July; no data for the

remainder of the year

Host: Unknown, possibly *Eriophyllum staechadifolium* var. *arte-*

misiaefolium

Habitat: Coastal, plant associates unknown except for San Simeon

where associated with *E. staechadifolium* var. *artemisiaefolium*

VIII. SUMMARY AND CONCLUSIONS

This investigation of the genus Tiaja proved to be extremely

rewarding in that during its course both predictable and unexpected

discoveries were made. Many of the initial aims of the study,

especially those regarding life histories, habitat and host associa-

tions, and distributions of the species of Tiaja were realized. A pre-

diction written into an early draft of this thesis was that Tiaja would

be located on the California Channel Islands; only a few months

later, specimens of the species later described as T. insula were

received for identification. Other facets of this study such as the

interpopulation and interspecies crosses were made possible and

deemed necessary because of new information gained as the study

evolved. A notable failure of the experimental work was the lack of

success in culturing T. arenaria in the laboratory although the effort

provided information about the species. At this point a recapitulation

of the knowledge gained from this study and an attempt to relate it to

the broad field of cicadellid biosystematics are in order.

Fossil evidence of the past history of the Homoptera is scarce,

probably due to the insects' relatively soft bodies. Evans (1947)

has suggested that the Ulopinae (including the Megophthalmini)

probably originated in the early Jurassic. Linnavuori (1972) has

suggested that the Ulopini and the Megophthalmini probably became

differentiated in the late Jurassic. Evans (1965) goes on to suggest

that the Ulopini and the Megophthalmini originated in the southern

hemisphere and that the few representatives of these groups now

present in the northern hemisphere are probably a result of post-

Eocene dispersal factors. However, he does not give any indication

of what these dispersal factors might be. It is likely that the early

Megophthalminae were all winged and capable of flight. If so, when,

where, and why did some genera and species lose their capacity for

flight?

The relatively great distances currently separating some

populations of certain species of Tiaja raises questions about how

dispersal took place, especially in some of the more widespread

species. Several physical and behavioral characteristics of Tiaja

work in opposition to dispersal in the adult stage. The absence of

hindwings is a specialization that makes active flight impossible.

The apparent inability of Tiaja to flex their forewings and the relatively

large overall size of the adults of some species makes use of air

currents for dispersal by gliding unlikely. The apparent negative

reaction of Tiaja to light as seen by insects of all stages keeping to

the lower parts of host plant stems and the undersides of leaves

further reduces the likelihood of the insects being carried away from

their habitat by wind. These characteristics of Tiaja would be

especially important in windy areas with sparse, widely separated

patches of suitable host vegetation in habitats such as sand dunes and seastacks on the coast and chaparral or desert inland. In such habitats population survival would depend on lack of dispersal.

There are a number of possibilities to explain the dispersal of Tiaja although each may be argued. Dispersal could have taken place very early on before the capacity for flight was lost and subsequent speciation could have been a result of isolation since that time. This possibility is not acceptable for all species as will be made apparent shortly. Tiaja could have dispersed simply by walking although large areas of unsuitable terrain (including saltwater) separating areas of suitable habitat make walking as the sole means of dispersal unlikely. Adults or nymphs could have been moved by wind currents although, as previously mentioned, behavioral studies suggest Tiaja avoid areas where they are subject to wind action. Dispersal could have taken place in the egg stage if the host plants which contained the eggs were moved, either as drifting plant material or by man's or another animal's actions.

The presence of T. arenaria and T. insula on islands requires special consideration of these species and the means by which they came to be on these islands. Vancouver Island, where T. arenaria has been found in four separate localities, was the subject of Pleistocene glaciation. At maximum glaciation, some 20,000 years ago, ice extended a considerable distance beyond the present shoreline

of the island (Howden, 1969). As little as 6,000 years ago, ice was present in the area where T. arenaria is now found. This means that the presence of T. arenaria on Vancouver Island today cannot be explained by dispersal prior to the loss of flight and certainly cannot be explained by early Cenozoic land links. A means of colonization within recent time must be found. Since dispersal of the adult and nymphal stages appears unlikely because of structural and behavioral characteristics that work against dispersal, it is suggested that colonization of Vancouver Island after the glaciers receded was carried out not by adults or nymphs but by translocation of the egg stage. Observation of the relative positions of the Oregon and Washington coasts and the west coast of Vancouver Island, coupled with the fact that the California Current flows northward along the coast suggests that T. arenaria could have been introduced to Vancouver Island through drifting debris which included T. arenaria eggs embedded in beach strawberry.

The presence of T. insula on the California Channel Islands could be related in part to the many changes which the California coastline has undergone during the Mesozoic and the Cenozoic. Reed (1933) details these changes as follows: during the Cretaceous all eight islands were joined in a single land mass, Catalinia; during the Eocene the northern four islands were submerged while Santa Barbara, San Clemente, and Santa Catalina Islands were probably

above sea level; in the Oligocene all the islands were submerged;

during the Lower Miocene all eight islands were connected to the

mainland and formed the "San Pedro Peninsula"; in the Upper

Miocene all islands except San Nicolas were submerged; during the

Pliocene all islands were joined to each other but not to the main-

land; in the Pleistocene the islands were separate from each other.

Some islands may have had mainland links in the early Pleistocene

as evidenced by mammalian fossils, but due to fluctuating ocean

levels in the late Pleistocene, some of the islands, including Santa

Barbara and San Nicolas, were submerged (Raven, 1967). It is

possible that T. insula or a species ancestral to it could have dis-

persed to the islands overland during the Lower Miocene. In the

Upper Miocene, San Nicolas Island, the only one to remain above sea

level, could have served as a refuge, with reintroduction to the other

islands following during the Pliocene. Reintroduction of T. insula to

Santa Barbara Island would have to have taken place across water,

probably from one of the other islands, in recent times. It might

be questioned why the simpler route of colonization of Santa Barbara

and other Channel Islands directly from the mainland in recent times

is not proposed. The explanation for this is that T. insula, unlike

T. arenaria has not been found on the mainland, suggesting relatively

early isolation from other species.

The adventitious means of colonization by water routes suggested above for T. arenaria and T. insula need not be restricted to the colonization of islands. The isolated population of T. friscana at San Simeon, some 450 km south of San Francisco and separated from it by territory occupied by T. montara, suggests that the introduction of T. friscana at San Simeon may have been accidental. The fact that this is the only T. friscana population known from a site exposed to the open ocean further suggests that the introduction of this species may have come via the ocean. A problem encountered by these ideas is that the California Current moves northward while dispersal almost certainly was southward. There are two possible ways around this dilemma: (1) egg-containing drift may have moved west in the ocean far enough to be caught by the southward moving North Pacific Current before being regained by the California Current and moved northward onto the shore at San Simeon, or (2) colonization of San Simeon by T. friscana could have been a result of freak conditions encountered during a major storm or subsequent to earthquake action. There is, of course, no concrete evidence to support this speculation and it is extremely unlikely that the actual means of T. friscana's colonization of San Simeon will ever be known.

Collection of new specimens and collation of data from previously collected specimens provided a useful picture of the range and distribution of the species of Tiaja. Each of the three northerly

species in the genus was found to have a much greater range than was previously known. Within its range, each species was found to be more common than previous collection data had suggested. For example, T. montara, previously thought to be restricted to a small area around Montara, San Mateo County, is the dominant species of the central California coast with an apparently continuous distribution from Montara to Big Sur (and possibly farther south). T. arenaria is not restricted to the central Oregon coast but has populations extending as far north as Tofino, British Columbia and as far south as Fort Bragg, California. T. friscana has a population as distant from the San Francisco Bay area as San Simeon in San Luis Obispo County, California. Although the southern members of the genus received less attention than those of the north, collation of previous collection records shows T. interrupta extending as far inland as central Arizona. The discovery of T. insula on the Channel Islands and of a specimen from San Martin Island that fits no known species suggests that the offshore islands of southern California and Mexico may harbor additional as yet undiscovered species of Tiaja. The fact that T. mexicana occurs in the mountains of northwest Mexico suggests that other species of Tiaja may be found at similar altitudes farther south.

The question arises as to how gene flow is maintained in species which for the most part consist of isolated populations. For

species that have almost continuous distributions such as <u>T</u>. <u>montara</u>, it is conceivable that a fair amount of gene exchange could take place relatively easily. However, other species with distinctly discontinuous distributions such as <u>T</u>. <u>friscana</u> and <u>T</u>. <u>arenaria</u> must have very restricted gene flow between populations. Intraspecific (interpopulation) crossing experiments show that some reproductive isolating barriers have been built up between populations at the extremes of <u>T</u>. <u>friscana</u>'s range. Since no other <u>T</u>. <u>friscana</u> populations have been found south of San Francisco County, it may be that the lowered fertility of the interpopulation crosses indicates long term isolation from other populations and that the San Simeon population is on its way to becoming even more greatly genetically differentiated from the species' northern populations and may eventually reach the point where even the degree of hybridization found possible in these experiments is decreased. This population, if isolation from others remains in effect, could eventually become sufficiently altered to become a different species.

The three species found in the San Francisco Bay area appear to be ecologically separated by adaptation to different habitats, <u>T</u>. <u>montara</u> being found in exposed coastal areas, <u>T</u>. <u>friscana</u> being found in sheltered coastal areas, and <u>T</u>. <u>californica</u> being found inland away from the coast. Reciprocal crosses between <u>T</u>. <u>friscana</u> and <u>T</u>. <u>montara</u> demonstrated that a certain amount of interspecific hybridization

was possible if populations of the two species were to occur side by side although the artificial conditions of the laboratory did not take into account possible preference for conspecific mates. Fertility was greatly reduced in the cross between male T. montara and female T. friscana while nymph production was erratic in the cross between male T. friscana and female T. montara. This evidence supports the taxonomic conclusion based on morphological evidence that T. montara and T. friscana are indeed discrete species. Although other species in the genus Tiaja were not subjected to reciprocal crosses, results for T. montara and T. friscana suggest that in this genus a high degree of confidence may be placed on morphological characteristics as evidence of the biological discreteness of species.

Further work on the isolating mechanisms operating in Tiaja is desirable. Investigation into the importance of habitat separation in maintaining discrete species would be useful as would an investigation of some of the other plausible reproductive isolating factors. For instance, it is feasible that the species of Tiaja have different courtship songs. Such species-specific songs have been found in other cicadellid genera in recent years, e.g. Oncopsis (Claridge and Reynolds, 1973), Circulifer (Smith and Georghiou, 1972), and Empoasca (Vargo, 1973). Although no Tiaja have been tested for sound-producing capabilities, Ossiannilsson's (1949) study of sound production in Swedish Auchenorrhynchous Homoptera in which the

related species, _Megophthalmus scanicus_ (Fallen), was found to produce a song, suggests that _Tiaja_ likely have this capability also. If a method could be found to locate newly laid eggs in the host plant, this would facilitate determination of fertility and related data in interspecific and interpopulation crosses.

In the laboratory studies of life history, differences in diapause requirements were found between _T. arenaria_ and the two more southerly species, _T. friscana_ and _T. montara_. _T. arenaria_ is apparently adapted to its northern range by having obligatory diapause; even under long days (16 hours light and 8 hours dark) and warm temperatures (21°C), _T. arenaria_ did not reproduce in the laboratory. _T. montara_ and _T. friscana_ have no diapause under the continuously favorable conditions in the laboratory. In nature they may experience facultative diapause as collection records show a lack of first and second instar nymphs in November. The diapause requirements of the southern five species have not been studied and although collection records suggest that adults are present all year, no nymphs of these species are known to have been collected so there is no indication of the duration of the reproductive period. One might speculate that, since their environment has warmer winters than in the north, there is no need for diapause to guard against exposure to cold winters in the southern species. Reproduction may be continuous throughout the year.

Studies of development from hatch to adult showed that T. fris-cana usually go through the five nymphal instars normally associated with the Cicadellidae. However, a high proportion of T. arenaria passed through only four nymphal instars. Other species whose life histories have been documented rarely pass through only four nymphal instars and it is speculated that this could possibly be an adaptation of this univoltine species to its environment. A few individuals that passed through six nymphal instars were found in both Tiaja species reared but this is consistent with the situation found in other leafhoppers whose life histories have been studied.

This study represents a step towards a biological comparison of Tiaja with the other genera in the Megophthalminae and of the Megophthalminae with other closely related subfamilies such as the Ulopinae and the Myerslopiinae. Comparisons as to habitats and microhabitats occupied, feeding and oviposition host plants, oviposition habits, nymphal development, diapause requirements, and behavior including sound production should yield information that could be used to substantiate or reject taxonomic conclusions based on structural attributes. A continuation of the cytogenetic studies begun by Halkka (1959) would be illuminating. An expanded electro-phoretic protein analysis as described by Norment et al. (1972) for a few members of the Cicadellidae and the Membracidae could also help to resolve problems in the higher classification of the Cicadellidae

including the relationships of the genera, tribes, and subfamilies. This, of course, would require a tremendous amount of detailed study of the other genera and species in the Megophthalminae and Ulopinae.

Surprisingly little work of a biological nature has been done so far on leafhoppers closely related to _Tiaja_. No biological data are available for _Brenda_, the winged megophthalmine genus in North America. A comparative study of _Brenda_ and _Tiaja_ and their respective specializations to their habitats should be made. There are likewise no comprehensive studies of the biologies of any of the Ulopini, Cephalelini, Myerslopiini, Monteithini, or Megophthalmini other than _Tiaja_. Biological notes in papers of taxonomic significance (e.g. Evans, 1966, 1968) suggest that members of these tribes have somewhat similar habits and habitats to _Tiaja_ but the extent of these similarities remains undocumented. Only when comparable studies are made of the other megophthalmine, ulopine, and myerslopiine genera can the data available for _Tiaja_ be used to begin to unlock the puzzle of the relationships of the oldest sub-families of the Cicadellidae.

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APPENDICES

APPENDIX I

Numerical values for the average number of nymphs produced

per female per week for all interpopulation and interspecific

crosses and their controls.

Cross	Week									
	1	2	3	4	5	6	7	8	9	10
T. friscana ♂ (Marshall) x T. friscana ♀ (Marshall)	0	1.79	5.62	5.88	5.15	4.21	3.50	2.09	1.90	2.00
T. friscana ♂ (San Simeon) x T. friscana ♀ (San Simeon)	0.11	1.36	5.09	9.25	6.20	5.27	4.15	3.80	2.14	1.17
T. montara ♂ x T. montara ♀	0	2.24	4.75	4.82	4.26	2.19	2.18	2.38	2.17	0.50
T. friscana ♂ (Marshall) x T. friscana ♀ (San Simeon)	0	0.24	2.58	2.95	3.35	1.75	0.86	1.09	0.60	0.14
T. friscana ♂ (San Simeon) x T. friscana ♀ (Marshall)	0	1.11	5.44	3.81	8.00	5.45	4.38	1.63	2.00	0
T. friscana ♂ (Marshall) x T. montara ♀	0	0.76	3.00	2.30	0.74	1.75	3.54	5.46	1.00	1.13
T. montara ♂ x T. friscana ♀ (Marshall)	0.04	0.04	0.12	0.20	0.38	0.45	0.10	0	0	0

APPENDIX II

Nymphs produced per week by culture pot showing deaths

of females for all interpopulation and interspecific crosses

and their controls.

A. T. friscana (Marshall) ♂ x T. friscana (Marshall) ♀.

Pot no.	Week										Total
	1	2	3	4	5	6	7	8	9	10	
7	0x	1	10	19	21	10x	2	0x	–	–	63
27	0	23	21	14xx	0	0x	–	–	–	–	58
28	0	13	22	33	16	21	6xx	3	1x	–	115
29	0	1	2	13xx	4	14x	–	–	–	–	34
30	0	1	10x	10	10	6	11x	6	4	0	58
38	0	0	17	12	11	13	7	0	1x	0x	61
39	0	0	26	6	8	3xx	0	0	1	3	47
40	0	2x	14	0	2x	0	2	5	3	4	32
54	0	10	16	34	31	13	21	9	9	9	152
60	0x	1x	8x	–	–	–	–	–	–	–	9
Total nymphs	0	52	146	141	103	80	49	23	19	16	629
Total females	30	29	26	24	20	19	13	11	10	8	–

x = death of a female

B. <u>T. friscana</u> (San Simeon) ♂ x <u>T. friscana</u> (San Simeon) ♀.

Pot no.	Week										Total
	1	2	3	4	5	6	7	8	9	10	
2	0	0	14	46	28x	11	0	2	14	6	121
11	0	7	28	42	22	0	18	4xx	1x	-	122
16	0	0	13	35	28	33	12x	5x	0	1	127
23	0x	2x	11	9	10	1	11x	-	-	-	44
24	0x	1	34	34	25	29	13	27	0	0	163
35	0	14	14x	6	10	4xx	-	-	-	-	48
46	2	4x	3	6	0xx	-	-	-	-	-	15
47	0	0	0x	5	1	1	0x	0x	-	-	7
57	1	6	0x	2	0xx	-	-	-	-	-	9
Total nymphs	3	34	117	185	124	79	54	38	15	7	656
Total females	27	25	23	20	20	15	13	10	7	6	-

x = death of a female

C. <u>T. montara</u> ♂ x <u>T. montara</u> ♀.

Pot no.	Week										Total
	1	2	3	4	5	6	7	8	9	10	
9	0	2	16	14	12	9	9	15x	10	0x	87
14	0	0	19xx	11	5	0	0	0	0	0	35
15	0x	5	6x	11	8	4	2	2	3	3x	44
17	0	18	16	25	5	7	13x	2x	0	0	86
19	0	7	14	0	12	6x	0x	0	0	0	39
31	0	0x	5xx	-	-	-	-	-	-	-	5
32	0	4	1	31	34x	2xx	-	-	-	-	72
44	0	17	37	3x	5x	4x	-	-	-	-	66
45	0	12	19	11x	0x	3x	-	-	-	-	45
52	0	0	0x	0x	0	0	0x	-	-	-	0
Total nymphs	0	65	133	106	81	35	24	19	13	3	479
Total females	30	29	28	22	19	16	11	8	6	6	-

x = death of a female

D. T. friscana (Marshall) ♂ x T. friscana (San Simeon) ♀.

Pot no.	Week										Total
	1	2	3	4	5	6	7	8	9	10	
20	0	2	20	8	23	8	4xx	2	0	0	67
25	0	1	0	7	12	5	1x	2	0x	0	28
33	0	0	1	0	0	0	0	4x	1x	0	6
34	0	0	6	5	5	10	0	1	3x	1	30
36	0	2	10	20	11x	3x	7	3	1	0x	58
48	0	0	2	11xx	0	2	0	0	1	0	16
59	0	0xx	10	5	6	0x	-	-	-	-	21
Total nymphs	0	5	49	56	57	28	12	12	6	1	226
Total females	21	21	19	19	17	16	14	11	10	7	

x = death of a female

E. <u>T. friscana</u> (San Simeon) ♂ x <u>T. friscana</u> (Marshall) ♀.

Pot	Week										Total
no.	1	2	3	4	5	6	7	8	9	10	
4	0	0x	15	22	29	16	2	2x	1	0	87
10	0x	0	0	7	22	16	10	1	0x	0	56
26	0	8	11x	9	6	12	13	5	2x	0	66
21	0	5	31x	6	2x	8	8	4	9	0	73
37	0	7	23	0	26	0xxx	-	-	-	-	56
41	0x	0	0	11	18x	8	2	1x	-	-	40
49	0	1	18	6xx	9x	-	-	-	-	-	34
Total nymphs	0	21	98	61	112	60	35	13	12	0	412
Total females	21	19	18	16	14	11	8	8	6	4	

x = death of a female

F. <u>T. friscana</u> ♂ x <u>T. montara</u> ♀.

Pot no.	Week										Total
	1	2	3	4	5	6	7	8	9	10	
1	0	4	29	23	0	15	4	20x	0xx	–	95
5	0	0	0	0	0	0xx	0	0	3	0	3
8	0	0	3	16	10	13	30	51	7	9	139
18	0	0	16	3	4x	0x	0	0	0	0	23
22	0x	0x	0	0	0x	–	–	–	–	–	0
51	0x	6	7	4	0	0	12	0	0	0	29
53	0x	0	0	0	0x	0	0	0	0	0	0
55	0	6	5	0x	0	0	0	0xx	–	–	11
Total nymphs	0	16	60	46	14	28	46	71	10	9	300
Total females	24	21	20	20	19	16	13	13	10	8	

x = death of a female

G. T. montara ♂ x T. friscana ♀.

Pot no.	Week										Total
	1	2	3	4	5	6	7	8	9	10	
3	0	0	1	5	9	10	0x	0	0xx	-	25
6	0	1	0	0	0	0	0x	0x	0	0	1
12	1	0	1	0	0	0x	2	0	0	0	4
13	0	0	0	0	0x	0	0	0	0x	0	0
42	0	0	1	0x	0x	0	0	0	0x	-	1
43	0	0	0	0	0	0	0x	0	0x	0	0
50	0	0	0	0	0	0	0	0x	0	0xx	0
56	0	0x	0	0	0	0	0	0	0	0x	0
61	0	0x	0	0	0	0	0	0	0	0	0
Total nymphs	1	1	3	5	9	10	2	0	0	0	31
Total females	27	27	25	25	24	22	21	18	16	11	

x = death of a female

APPENDIX III

Computed "t" values for comparison of results of interpopu-

lation and interspecific crosses and their controls.

A. T. friscana interpopulation crosses and their controls.

Comparison	Week					
	3	4	5	6	7	8
Marshall ♂ x Marshall ♀ &	3.97**	2.97**	1.73	2.83**	3.60**	1.42
Marshall ♂ x San Simeon ♀	(43)	(41)	(35)	(33)	(25)	(20)
San Simeon ♂ x San Simeon ♀ &	1.99*	4.28**	2.27*	2.45*	3.64**	1.71
Marshall ♂ x San Simeon ♀	(40)	(37)	(35)	(29)	(25)	(19)
Marshall ♂ x Marshall ♀ &	0.19	1.78*	2.12*	0.98	-0.53	0.67
San Simeon ♂ x Marshall ♀	(42)	(38)	(32)	(28)	(19)	(17)
San Simeon ♂ x San Simeon ♀ &	0.26	3.58**	1.17	-0.09	-0.18	1.16
San Simeon ♂ x Marshall ♀	(39)	(34)	(32)	(24)	(19)	(16)
Marshall ♂ x Marshall ♀ &	0.48	-2.25*	-0.82	-0.69	-0.39	-0.99
San Simeon ♂ x San Simeon ♀	(47)	(42)	(38)	(32)	(24)	(19)
Marshall ♂ x San Simeon ♀ &	2.74**	-0.88	3.60**	3.84**	3.61**	1.17
San Simeon ♂ x Marshall ♀	(35)	(33)	(29)	(25)	(20)	(17)

* significant (α = 0.025)

** highly significant (α = 0.005)

B. Interspecies crosses between <u>T. friscana</u> and <u>T. montara</u> and their controls.

Comparison	Week					
	3	4	5	6	7	8
<u>T. friscana</u> ♂ x <u>T. friscana</u> ♀ &	11.18**	7.27**	6.81**	5.14**	7.18**	4.10**
<u>T. montara</u> ♂ x <u>T. friscana</u> ♀	(49)	(47)	(42)	(39)	(32)	(27)
<u>T. montara</u> ♂ x <u>T. montara</u> ♀ &	6.42**	5.50**	4.91**	4.43**	5.05**	4.58**
<u>T. montara</u> ♂ x <u>T. friscana</u> ♀	(51)	(45)	(41)	(36)	(30)	(24)
<u>T. friscana</u> ♂ x <u>T. friscana</u> ♀ &	3.00**	3.43**	5.26**	2.51*	0.17	1.51
<u>T. friscana</u> ♂ x <u>T. montara</u> ♀	(44)	(42)	(37)	(33)	(24)	(22)
<u>T. montara</u> ♂ x <u>T. montara</u> ♀ &	1.70	2.23*	4.01**	0.68	-0.98	1.18
<u>T. friscana</u> ♂ x <u>T. montara</u> ♀	(46)	(40)	(36)	(30)	(22)	(19)
<u>T. montara</u> ♂ x <u>T. montara</u> ♀ &	1.10	0.91	0.78	2.35*	1.83	0.27
<u>T. friscana</u> ♂ x <u>T. friscana</u> ♀	(52)	(44)	(37)	(33)	(22)	(17)
<u>T. friscana</u> ♂ x <u>T. montara</u> ♀ &	-3.99**	-3.50**	1.00	-2.22*	-3.77**	3.30**
<u>T. montara</u> ♂ x <u>T. friscana</u> ♀	(43)	(43)	(41)	(36)	(32)	(29)

*significant (α = 0.025)

**highly significant (α = 0.005)