NUMBER 663 MARCH 9, 1972

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

EVOLUTION IN THE CANARY ISLANDS V. THE GENUS *CALLIPHONA* (ORTHOPTERA: TETTIGONIIDAE)

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INTRODUCTION

The tettigoniine genera *Calliphona* and *Psalmatophanes* are endemic to the Atlantic Islands. *Calliphona* is restricted to four of the seven Canary Islands, and *Psalmatophanes* is a monotypic genus represented only on the Madeira Island of the Madeira Archipelago (Fig. 1). Three species of *Calliphona* have been described: the short-winged *konigi* Krauss 1892 from Tenerife, the macropterous *alluaudi* I. Bolivar 1893 from Gran Canaria, and the medium-winged *palmensis* I. Bolivar 1940 from La Palma. Chopard (1938) erected the genus *Psalmatophanes* and described and assigned to it *barretoi,* a species with intermediate wing length from the Madeira Island.

At the time I. Bolivar (1940) described *palmensis,* he considered *palmensis* and *alluaudi* so dissimilar to *konigi* that he erected the subgenus *Calliphonides* to include them. Chopard (1938), in the description of his new taxon, indicated that he considered *barretoi* more closely related to *Tettigonia viridissima* than to any of the species of *Calliphona.* Thus the four proposed species clusters, *Tettigonia, Calliphona, Calliphonides* and *Psalmatophanes,* would seem to have varying degrees of relationship, one to the other.

In view of the close proximity of the Madeiran and Canarian Archipelagoes, the close affinities of the insular floras, and the morphological similarity between *Calliphona* and *Psalmatophanes,* a reevaluation of the implied polyphyletic origin of these groups from a *Tettigonia viridissima*-like ancestor (Chopard, 1938) was undertaken.

This study was supported by grants from the National Science Foundation, GB–6230 and GB–13104, to N. G. Hairston, The University of Michigan, for research in Systematic and Evolutionary Biology.

Field work in the Canary Islands was carried out in collaboration with the late Dr. Kornelius Lems, principal investigator under grant GB–3876 from the National Science Foundation, and with support from the John Simon Guggenheim Memorial Foundation.

MATERIALS

A male and a female of *Psalmatophanes barretoi* were made available to us by the authorities of the National Museum of Natural History, Paris. Dr. V. Llorente, Instituto Español de Entomología, Madrid, kindly placed at our disposal two pairs of *alluaudi* from Gomera, and one ♀ *palmensis* from La Palma. We are also indebted to Dr. David Ragge of the British Museum of Natural History who made available one pair of *alluaudi* from Gomera and one ♀ *palmensis* from La Palma. The remainder of the material of *Calliphona* was taken by

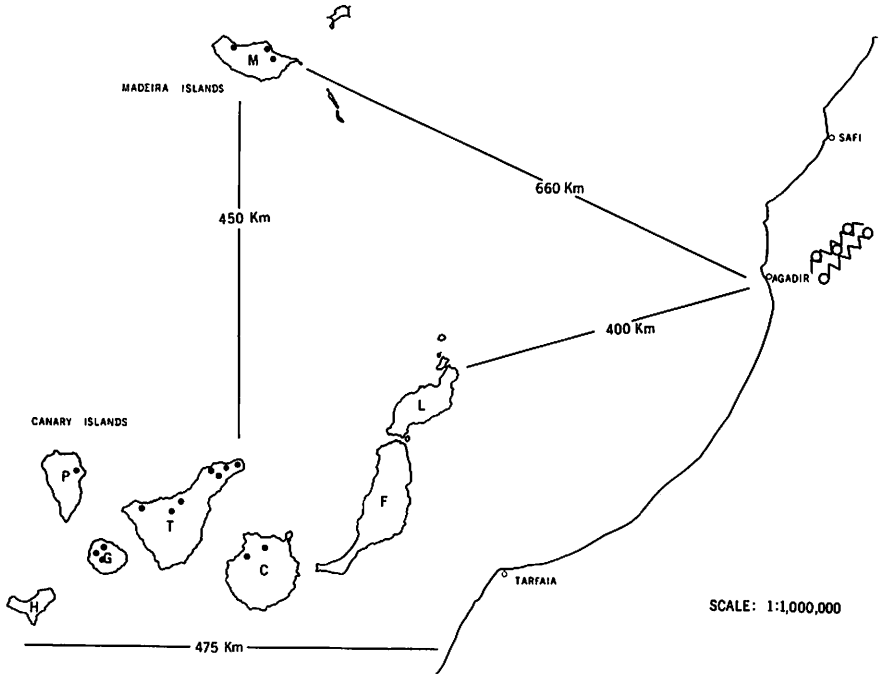

FIG. 1. Map of Madeira and the Canary Islands with specific collecting sites for *Calliphona*, and the distribution of the species. The Moroccan Coast and part of the Greater Atlas Mountains (jagged lines) from which *Tettigonia viridissima* is known are indicated. Relative position of land mass is maintained, although distance between islands is reduced.

Dr. Kornelius Lems and Christina Holzapfel in the Canary Islands during the year 1965–66. These latter specimens have been deposited in The University of Michigan Museum of Zoology and include 8 ♂ ♂ and 1 ♀ *konigi* from Tenerife, 6 ♂ ♂ *palmensis* from La Palma, 2 ♂ ♂ and 1 ♀ *alluaudi* from Gran Canaria and 1 ♂ *alluaudi* from Gomera. One pair of *Tettigonia viridissima* (UMMZ) from Skane, Sweden, was available for comparative study.

DOCUMENTATION OF ILLUSTRATED MATERIAL

Individuals used for text illustration are from the following localities:

Species	*Sex*	*Specific Locality*	*Date of collection*	*Museum*
C. palmensis		*La Palma*		
	♂	Puntallano	May 28, 1966	UMMZ
	♀	B^{co} San Bartolomé	May 17, 1934	Madrid
C. barretoi		*Madeira*		
	♂	Santana	August 9, 1936	Paris
	♀	Porto Moniz	August, 1953	Paris
C. alluaudi		*Gomera*		
	♂	Roque Valle Hermosa	March 22, 1966	UMMZ
		Gran Canaria		
	♂	Palmital-Moya	May 24, 1966	UMMZ
	♀	Tamadaba, 1000M	August 9, 1954	UMMZ
C. konigi		*Tenerife*		
	♂	Orotava, 600M	May 15, 1966	UMMZ
	♀	Orotava, 600M	May 19, 1966	UMMZ
T. viridissima		*Sweden*		
	♂	Skane	August 7, 1933	UMMZ
	♀	Skane	August, 1933	UMMZ

SYSTEMATICS

MORPHOLOGY.—In his generic description, Chopard (1938:227) indicated that, on the basis of the genitalia, narrowness of the frontal rostrum, and the hyaline caudal wings, *Psalmatophanes* was more closely related to *Tettigonia* than to *Calliphona*. He stated that his new genus differed from both *Calliphona* and *Tettigonia* in the elevation of the

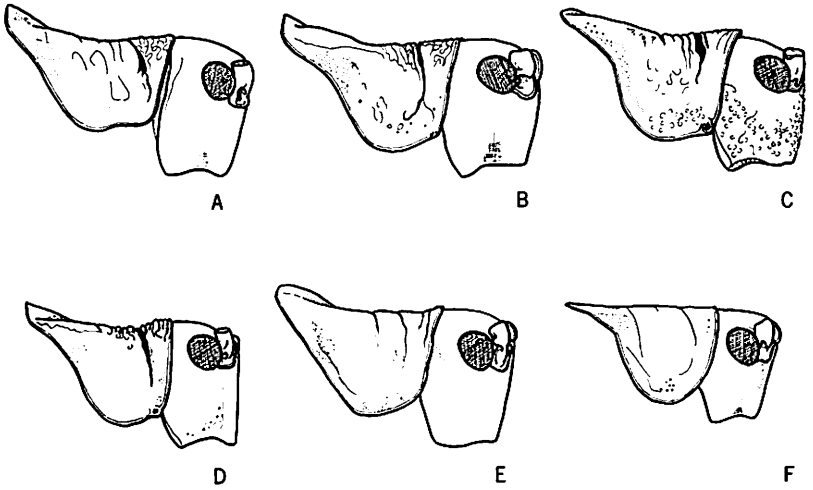

FIG. 2. Lateral view of the head and pronotum. A. *Calliphona konigi.* B. *Calliphona palmensis.* C. *Calliphona alluaudi* from Gran Canaria Island. D. *Calliphona alluaudi* from Gomera Island. E. *Calliphona barretoi.* F. *Tettigonia viridissima.*

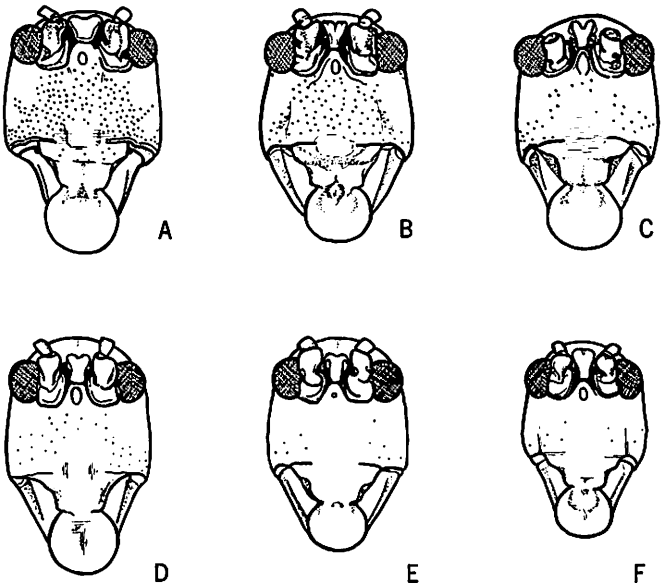

FIG. 3. Cephalic view of head. A. *Calliphona konigi.* B. *Calliphona palmensis.* C. *Calliphona alluaudi* from Gran Canaria Island. D. *Calliphona alluaudi* from Gomera Island. E. *Calliphona barretoi.* F. *Tettigonia viridissima.*

metazona, an observation which we question with regard to *Calliphona* (Fig. 2). I. Bolivar (1940) did not contribute to a clarification of the relationships of the three genera when he noted that "El nuevo género maderense se aproxima a *Tettigonia* quizá aun más que las *Calliphona* canarias, y no difiere al parecer de él sino por la apretada reticulación de los elitros y por presentar levantada la metazona pronotal."

In order to evaluate the morphological relationships between these groups, we have examined many characteristics, chiefly those of the head, pronotum, wings, and genitalia.

The head affords many conservative characters for species comparison. Laterally, it is broadly truncate in *Calliphona* and somewhat more narrow in *Tettigonia* (Fig. 2). Straightness of the frontal rostrum, a character used by Chopard to relate *barretoi* to *Tettigonia,* varies among species. *C. barretoi* more closely approaches *palmensis* in this feature than does *Tettigonia.* Except in *barretoi* and *T. viridissima* the faces of all species are punctate, *konigi* and *palmensis* most strikingly so (Fig. 3). Width of the fastigium of the vertex is relatively narrow except in *konigi,* which has a generally broad, square face. The frontal ocellus is conservative within species, and shows only one deviation. The Madeiran *barretoi* has a small, round ocellus, not a

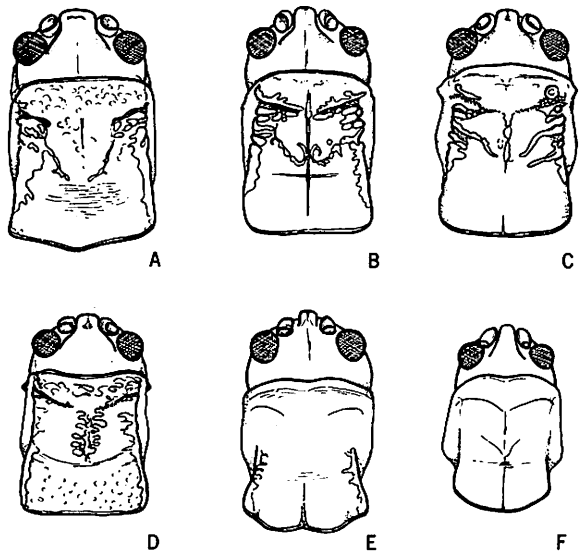

FIG. 4. Dorsal view of head and pronotum. A. *Calliphona konigi.* B. *Calliphona palmensis.* C. *Calliphona alluaudi* from Gran Canaria. D. *Calliphona alluaudi* from Gomera. E. *Calliphona barretoi.* F. *Tettigonia viridissima.*

large, oval structure as seen in the other taxa. The faces of all specimens studied are more or less hirsute.

The metazona of the pronotum is flat in *Tettigonia viridissima* but is raised dorsally in all other forms (Fig. 2). Sculpturing of the pronotum is a good species indicator; all species are strongly callous with the exception of *barretoi* and *Tettigonia viridissima* (Fig. 4). The lateral carina of the pronotum of *barretoi* is somewhat callous, while that of *T. viridissima* is smooth except for a few lateral punctations. A well-defined tooth located on the front ventral margin of the pronotum is present on all specimens of *alluaudi*. This structure is illustrated in both lateral and dorsal views (Fig. 2, 4), and is present in reduced form in *palmensis*.

Wing length is perhaps the most obvious character used to distinguish species in this complex. *C. alluaudi,* from both Gran Canaria and Gomera, and *Tettigonia viridissima* have long tegmina which well surpass the knee of the hind femur. *C. konigi* has short wings, less than the length of the abdomen. Wing length of *palmensis* and *barretoi* is intermediate between *alluaudi* and *konigi* (Fig. 5). Characters of the left tegmina, excluding the stridulatory file, are variable and difficult to analyse. However, the speculum region of the right tegmina shows interspecific variation in speculum shape, development of the speculum margin, and surrounding reticulation. The speculum of *barretoi* is

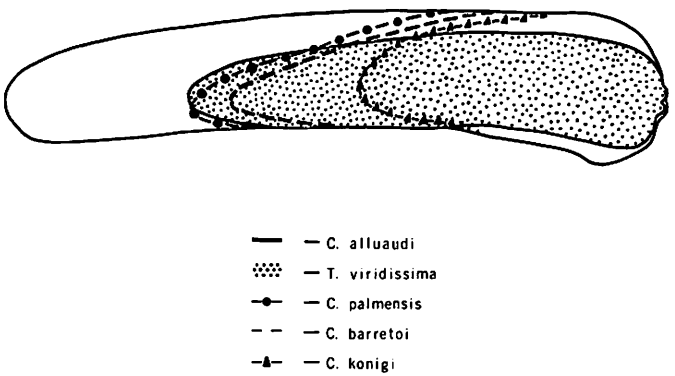

FIG. 5. Relative shape and dimensions of the elytra of *Calliphona* and *Tettigonia viridissima.*

round but predominantly ovate in all other species (Fig. 6). All species show abundant sensory hairs in the Cu_{1b} area, although subreticulation in this region varies from heavy in *barretoi* to weak in *T. viridissima.*

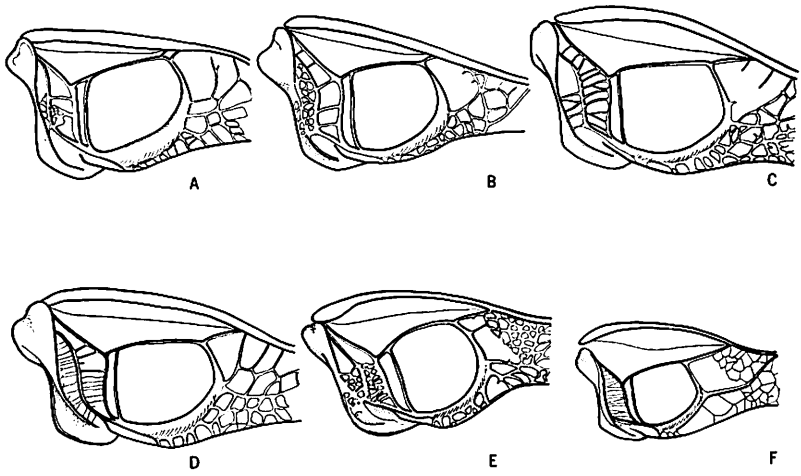

FIG. 6. Speculum and surrounding reticulation of the right tegmina of males. A. *Calliphona konigi.* B. *Calliphona palmensis.* C. *Calliphona alluaudi* from Gran Canaria. D. *Calliphona alluaudi* from Gomera. E. *Calliphona barretoi.* F. *Tettigonia viridissima.*

Characters of the male tenth abdominal tergite, cerci, and titillators are also useful in defining relationships. The most striking feature of any of the species is the enlarged, downcurved tenth tergite of *konigi* (Fig. 7, A; Fig. 8, A). Here the distal portion is produced into two large, strongly decurved, broadly obtuse lobes. All other species have relatively small tenth tergites, sculptured in a variety of ways depending on the species, and with terminally acute lobes. The median emargination of the plate is broad in *barretoi* and in *T. viridissima,* although in the former the lobes are straight, in the latter rather strongly outcurved (Fig. 8, E-F).

There is a consistent difference in the tenth abdominal tergite between males of *alluaudi* from Gomera and Gran Canaria. The caudal emargination is indistinguishable in the two populations. However, the median area of the lobes in Gran Canarian material is conspicuously folded, creating well-defined, rounded ridges which parallel the

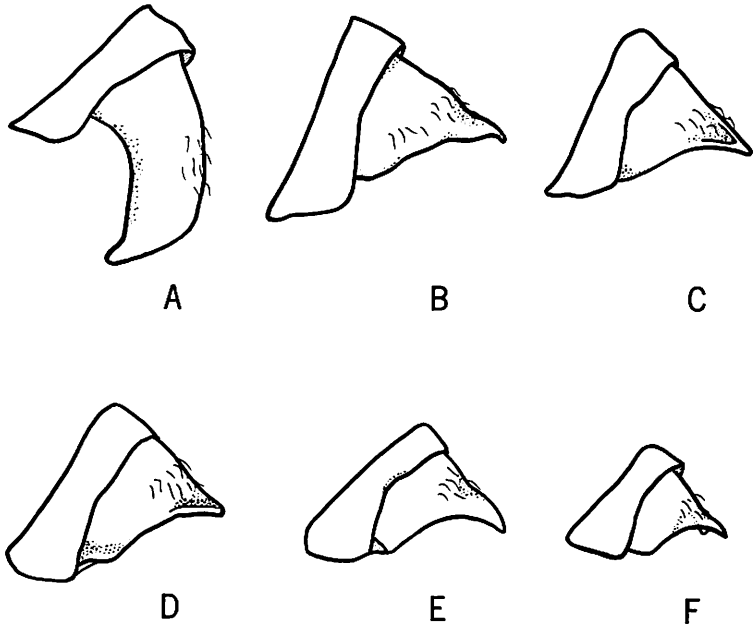

FIG. 7. Lateral view of the tenth abdominal tergite of males. A. *Calliphona konigi*. B. *Calliphona palmensis*. C. *Calliphona alluaudi* from Gran Canaria. D. *Calliphona alluaudi* from Gomera. E. *Calliphona barretoi*. F. *Tettigonia viridissima*.

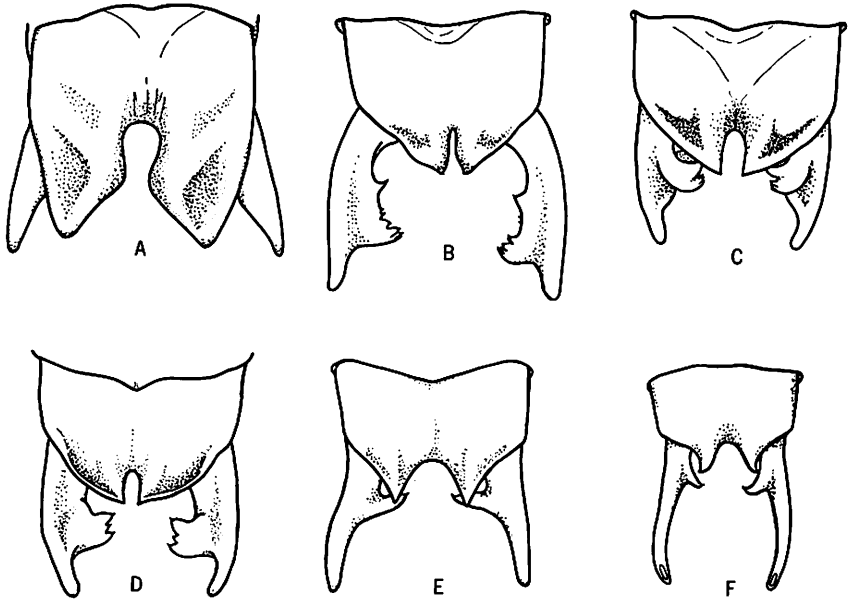

FIG. 8. Dorsal view of the tenth tergite and cerci of males. A. *Calliphona konigi*. B. *Calliphona palmensis*. C. *Calliphona alluaudi* from Gran Canaria. D. *Calliphona alluaudi* from Gomera. E. *Calliphona barretoi*. F. *Tettigonia viridissima*.

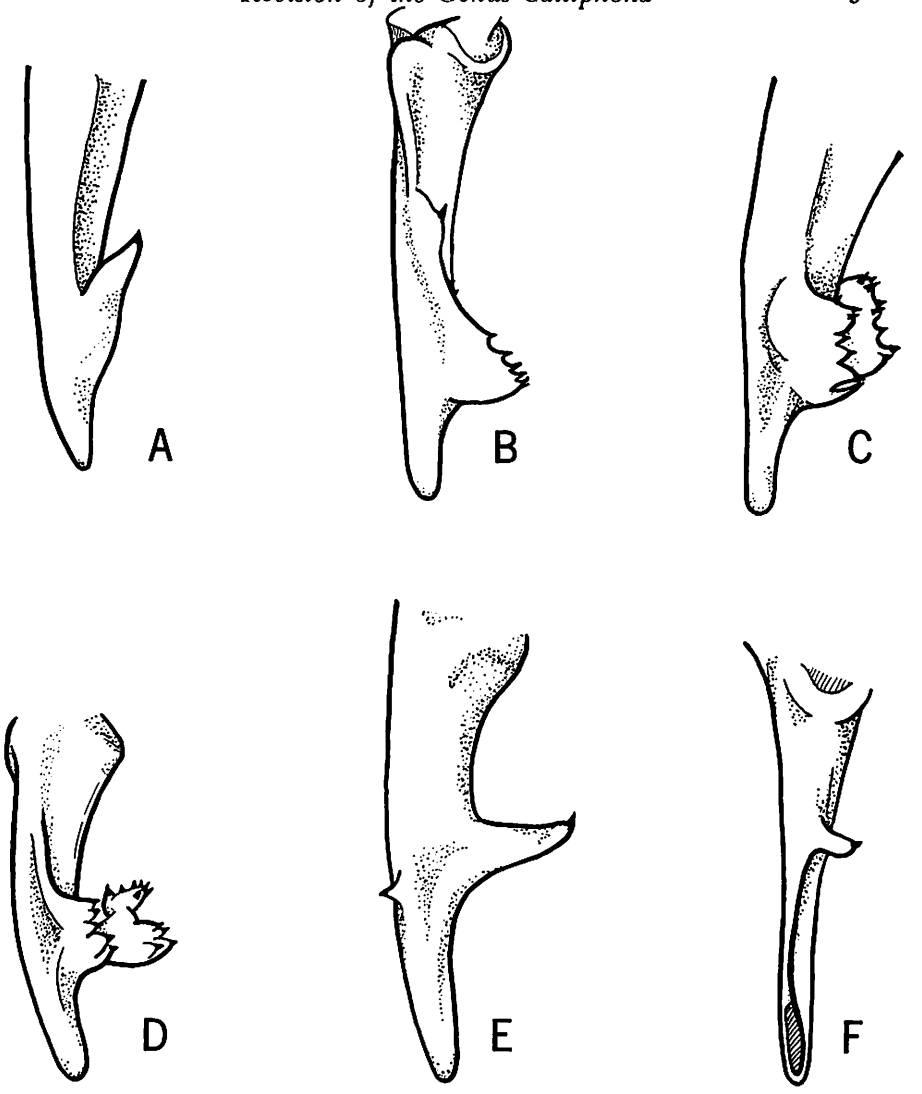

FIG. 9. Dorso-lateral view of the left cercus of males. A. *Calliphona konigi*. B. *Calliphona palmensis*. C. *Calliphona alluaudi* from Gran Canaria. D. *Calliphona alluaudi* from Gomera. E. *Calliphona barretoi*. F. *Tettigonia viridissima*.

emargination. The folding has also created a pronounced concavity lateral to each ridge (Fig. 8, C). These same ridges and concavities occur in Gomera males, but are much less well-developed (Fig. 8, D).

Two qualitatively different types of male cerci are evident in the

series of specimens before us, those with a simple internal tooth, and those bearing a complex multidentate internal appendage (Fig. 9). The former type characterizes *konigi, barretoi,* and *T. viridissima,* while *palmensis* and *alluaudi* are multidentate. The multidentate lobe varies from an oblique, flange-like process in *palmensis* (Fig. 9, B) to the variously shaped cup-like structure found in *alluaudi* (Fig. 9, C-D). The form of the cercal process of males of *alluaudi* from Gran Canaria is quite uniform, but there is considerable variation in the shape of this structure in the males of this species from Gomera. This is particularly evident in the degree of development of a finger-like ventral protrusion of the process. With the exceptions of shape and sculpturing of the tenth abdominal tergite and cerci, *alluaudi* males from Gran Canaria and Gomera overlap in morphological features (Figs. 2–4, C-D; 6-10, C-D). Although it seems clear that the populations of *alluaudi* on Gran Canaria and Gomera Islands have undergone some divergence, we feel that recognition of a distinct taxon on Gomera should await information on the comparative behavior of members of these populations as well as a more complete analysis of the range of morphological variation.

Tettigonia viridissima has a membranous lacuna on the internal face of the tip of each cercus (Fig. 9, F). This is absent from all of the forms of *Calliphona.*

The titillators of all members of this complex of species differ from one another in length and in modifications of the basically biaciculate tip. Distally, all bear two well-defined aciculate processes (Fig. 10). However, supernumerary teeth are often seen in *palmensis* (Fig. 10, B) and in *alluaudi* (Fig. 10, C-D). The titillators of *Tettigonia viridissima* are much shorter than those found in the Calliphonas, measuring one-sixth rather than one-half the length of the cercus.

Distally, the female subgenital plate is either bilobate or trilobate (Fig. 11). The plates of *T. viridissima* and *C. barretoi* are more similar to each other than to those of other Calliphonas; in *viridissima* they are broadly rounded bilobate and broadly rounded emarginate; in *barretoi* they are more angulately rounded and acute-angled emarginate. The subgenital plates of *alluaudi* and *palmensis* are deeply and broadly rounded emarginate with cuspidate lobes. The same plate in *konigi* bears two long, aciculate lobes, separated by a small medial tooth lying at the base of the long, narrow emargination.

Systematic Analysis.—These various characters have been compiled and summarized in Table 1. All characters are given equal numerical value. The species have also been compared two at a time for all 20

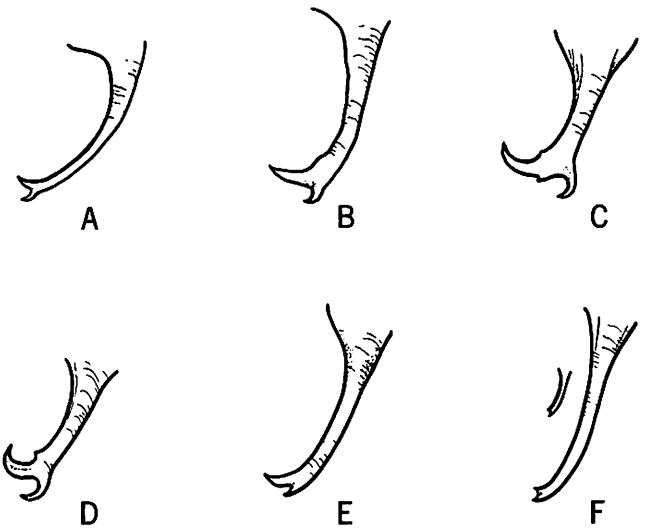

FIG. 10. Medio-dorsal view of the left titillator of males. A. *Calliphona konigi*. B. *Calliphona palmensis*. C. *Calliphona alluaudi* from Gran Canaria. D. *Calliphona alluaudi* from Gomera. E. *Calliphona barretoi*. F. *Tettigonia viridissima*.

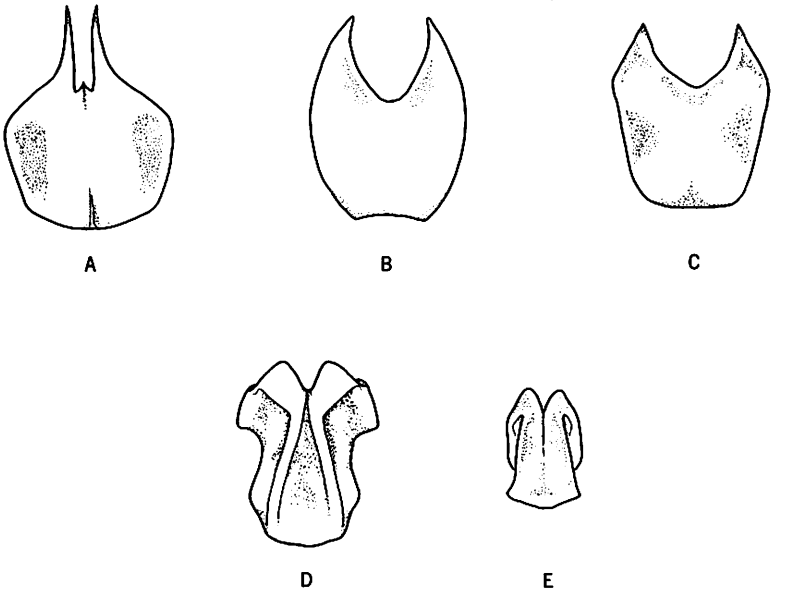

FIG. 11. Ventral view of the subgenital plate of females. A. *Calliphona konigi*. B. *Calliphona palmensis*. C. *Calliphona alluaudi*. D. *Calliphona barretoi*. E. *Tettigonia viridissima*.

TABLE 1
SUMMARY OF MORPHOLOGICAL CHARACTERS

Character	*T. viridissima*	*C. barretoi*	*C. konigi*	*C. palmensis*	*C. alluaudi*	*Fig. No.*
1) Width, fastigium of the vertex	<1.5 times first antennal segment	<1.5 times first antennal segment	>1.5 times first antennal segment	<1.5 times first antennal segment	<1.5 times first antennal segment	3
2) Frontal ocellus	oval, large	round, small	oval, large	oval, large	oval, large	3
3) Face	smooth	smooth	punctate	punctate	punctate	3
4) Pronotal shape	deplanate	elevated metazona	elevated metazona	elevated metazona	elevated metazona	2,4
5) Pronotal rugosity	absent	feeble	heavy	heavy	heavy	4
6) Callosity of the ventral cephalic angle of the lateral lobe of the pronotum	absent	absent	absent	present	present	2,4
7) Caudal margin pronotum	rounded	rounded; feebly emarginate	rounded; truncate	truncate	truncate	4
8) Subreticulation of Cu_{1b} area	feeble	heavy	medium	medium	medium	6
9) Development margin of the speculum	average	average	heavy	average	average	6

10) Shape of speculum	ovate	round	ovate	roundly ovate	ovate	6
11) Dimensions tenth tergite ♂	<¾ as long as wide	<¾ as long as wide	at least as long as wide	<¾ as long as wide	<¾ as long as wide	8
12) Shape tenth tergite ♂	terminally acute; laterally rounded	terminally acute; laterally rounded	terminally obtuse laterally flat	terminally acute laterally rounded; concave dorsally	terminally acute laterally rounded	7,8
13) Tenth tergite ♂ acute or obtuse; lateral margin-convex or concave	acute; concave	acute; concave	obtuse; convex	acute; subconvex	acute; convex	8
14) Shape subgenital plate ♀	bilobed	bilobed	tridentate	bicuspidate	bicuspidate	11
15) Titillator/cercus ratio	about 1.6	about 1:2	about 1:2	about 1:2	about 1:2	9,10
16) Distal end titillator	bidentate	bidentate	bidentate	tridentate	tridentate	10
17) Internal tooth cercus	unidentate	unidentate	unidentate	multidentate	multidentate	9
18) Terminal cercus lacunae	present	absent	absent	absent	absent	9
19) Ratio pronotum width/length	.71	.85	.83 ± .02	.80 ± .02	.83 ± .02	
20) Width of right tegmina ♂ at widest point	0.8	1.0	1.1 ± .1	1.1 ± .1	1.1 ± .1	

characters listed, and the percentages of similarity are given in Table 2. If the character compared was the same for the two species, 1 was scored; if partial overlap occurred, .5 was scored, and if the characters were totally different, 0 was rated. Percent of characters in common out of the total possible score of 20 was calculated for each pair of species. Redundant (mutually dependent) characters were discarded to avoid directional weighting of characters. For example, all Calliphonas from the Canary Islands and Madeira are heavy and robust as compared with *Tettigonia.* Hence only one character was used to indicate this feature (ratio of pronotum length/width), although many other size-dependent characters were apparent.

An inspection of Table 2 reveals that *barretoi* has about the same number of characters in common with the Canary Island Calliphonas as with *Tettigonia viridissima,* that *konigi, palmensis,* and *alluaudi* have essentially the same number of characters in common with *T. viridissima,* that *konigi, palmensis,* and *alluaudi* have approximately the same number of characters in common with *barretoi,* and that *palmensis* and *alluaudi* are strikingly similar in the characters analyzed.

TABLE 2

PERCENTAGE OF SIMILARITY AMONG FIVE TETTIGONIINE SPECIES, CALCULATED FROM 20 CHARACTERISTICS

	Tettigonia viridissima	*Calliphona barretoi*	*Calliphona konigi*	*Calliphona alluaudi*
C. barretoi	50			
C. konigi	30	48		
C. alluaudi	32	53	53	
C. palmensis	30	53	53	90

The distinctions between *barretoi* and *konigi,* and between *konigi* and *palmensis* and *alluaudi* are not sharp. These taxa have numerous characters in common and probably represent the evolutionary products of a monophyletic group. We believe that this relationship is obscured by the recognition of the genus *Psalmatophanes* and of the subgenus *Calliphonides,* and that, in the interests of a better understanding of phylogenetic relationships, these names should be suppressed. Hence, we consider *Psalmatophanes* Chopard 1938 and *Calliphonides* I. Bolivar 1940 as synonyms of *Calliphona* Krauss 1892.

VOCALIZATION.—Sound recordings of *alluaudi* (from Gran Canaria), *konigi,* and *palmensis* were made at 72°F in a laboratory in the Canary Islands. Sonagrams were produced on a Kay Electric Vibralizer at the University of Michigan Museum of Zoology. In preparation of the sonagrams, pattern setting was normal, bandwidth wide, vibralizer drum speed HL.

The distribution of wing strokes and frequency is similar for *palmensis* and *alluaudi* (Fig. 12, B-C), but number of strokes per second varies in both species. The call usually begins with short intervals of vibrations (c), and then develops into a long series of repetitive sounds (b).

Although *konigi* sounds much like these two species and has been heard calling in syncopation with *palmensis* in the laboratory, each wing stroke of *konigi* appears to be double (Fig. 12, A).

The double stroke of *konigi* is correlated with approximately twice the number of file teeth found in other members of this genus (Fig. 13). However, the file teeth are regularly spaced and not paired as are the apparent strokes illustrated in Fig. 12, A. It is possible that the double stroke results from the files making contact on both forward and backward action of the wings. *C. konigi* was found to have an average of 240 ± 5 teeth per file (file length 4.3 ± .3mm), *alluaudi* from both Gomera and Gran Canaria have approximately 115 teeth (file length 3.7 ± .2mm), and *palmensis* from La Palma has 120 ± 3 teeth (file length 3.4 ± .1 mm). Although *barretoi* has somewhat fewer file teeth (105), it also has a shorter file than the other Calliphonas (=2.8mm). The file of *T. viridissima* from Skane, Sweden, is 2.1mm. long and has approximately 95 file teeth.

Thus an analysis of vocalization patterns also indicates a close relationship between *palmensis* and *alluaudi. C. konigi* is unique in song and stridulatory morphology.

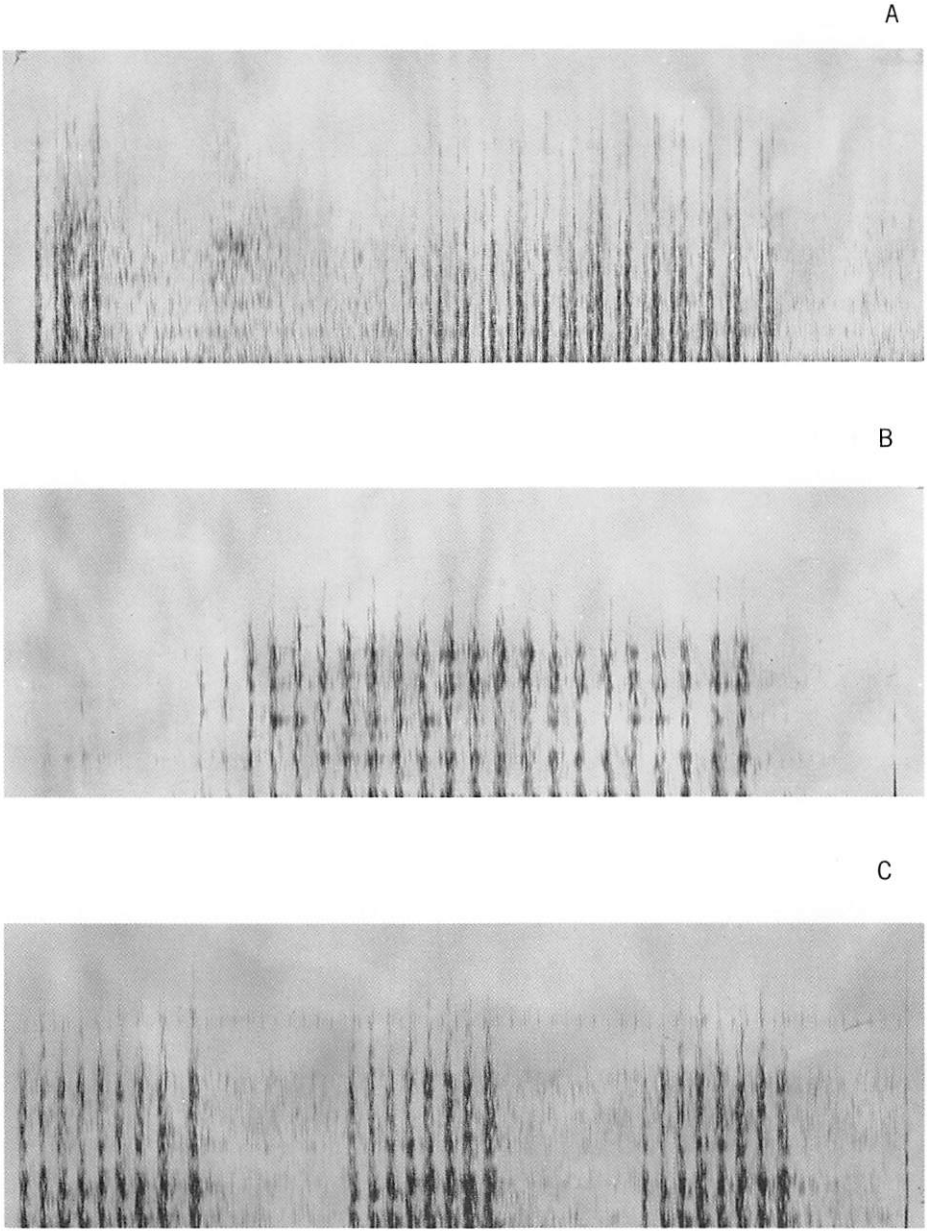

FIG. 12. Sonagrams of vocalizations of male *Calliphona konigi* (A), *C. palmensis* (B), and *C. alluaudi* from Gomera (C). Laboratory temperature: 72° F, time interval illustrated: 2.23 seconds, frequency: 44–4400 kilocycles per second.

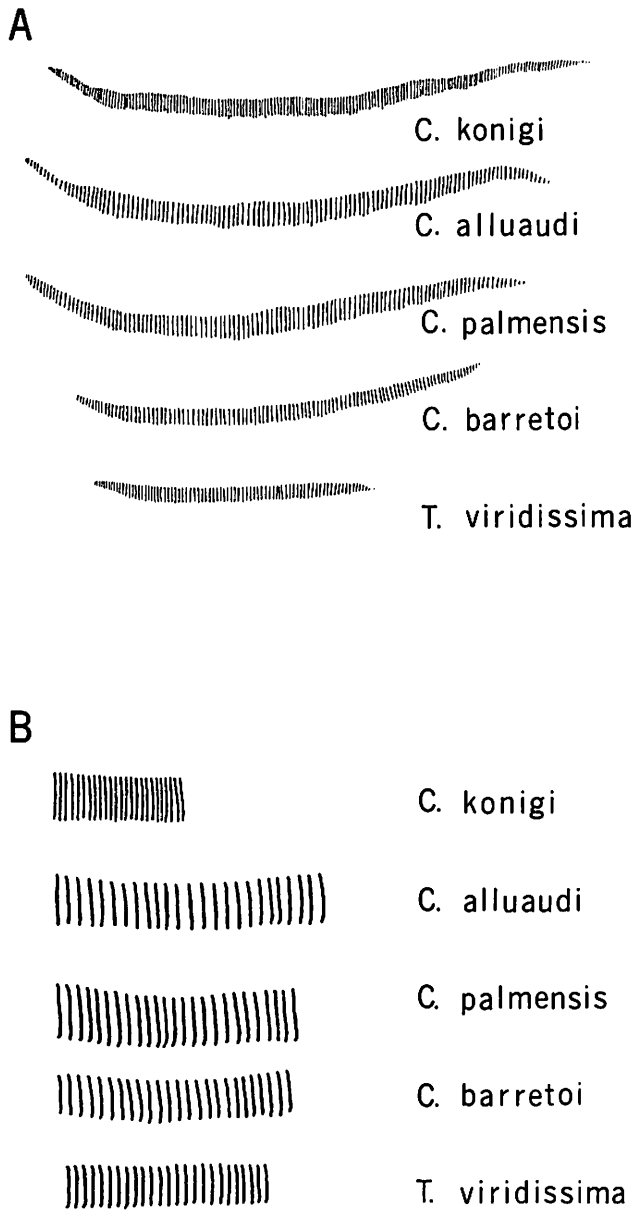

FIG. 13. A. Stridulatory files showing rib shape and arrangement of teeth.
B. Detail of 25 central teeth showing size and relative distribution.

KEY TO THE SPECIES OF *CALLIPHONA*

1. Pronotum smooth or weakly calloused, deplanate or the metazona elevated caudally, the caudal margin distinctly rounded or broadly emarginate and broadly bilobate (Fig. 2, E–F; 4, E–F); tenth abdominal tergite of male broadly U-shaped emarginate, the emargination wider than deep (Fig. 8, E–F); male cercus with internal tooth directed medially, unicuspidate (Fig. 8, E–F; Fig. 9, E–F); female subgenital plate ventrally bearing two anterior-posteriorly directed ridges, distally bilobate, the lobes broadly rounded (Fig. 11, D–E); macropterous 2

1′. Pronotum strongly calloused, the caudal margin truncate or feebly rounded truncate, metazona strongly elevated caudally (Fig. 2, A–D; Fig. 4, A–D); tenth abdominal tergite of male deeply emarginate, the notch deeper than wide (Fig. 8, A–D); male cercus with internal tooth unicuspidate and directed anteriorly (Fig. 8, A) or with internal tooth an arcuate, multicuspidate flange-like process (Fig. 9, B–D); female subgenital plate ventrally smooth, without ridges, distally bi- or trilobate; the lobes sharply pointed (Fig. 11, A–C); brachypterous or macropterous 3

2. Pronotum smooth, deplanate, metazona not elevated, caudally broadly and distinctly rounded (Fig. 4, F) tegmina normal; titillators (Fig. 10, F) about 1/6 the length of the male cercus; male cercus (Fig. 9, F) with a terminal internal, membranous lacuna (Europe, North Africa, Temperate Asia) ..... *Tettigonia viridissima* Linnaeus

2′. Pronotum feebly calloused, metazona elevated caudally, broadly bilobate (Fig. 4, E); tegmina reticulate, veinlets raised; titillators (Fig. 10, E) at least 1/2 as long as the male cercus; apical portions of male cercus (Fig. 9, E) lacking a terminal, internal, membranous lacuna (Madeira Island) ..... *Calliphona barretoi* (Chopard)

3. Fastigium of the vertex more than 1.5 times as broad as the first antennal segment (Fig. 3, A); ventro-cephalic angle of of lateral lobes of pronotum without a distinct callosity (Fig. 2, A; Fig. 4, A); tegmina shorter than the abdomen, the posterior margin of the speculum of the male right tegmen strongly enlarged (Fig. 6, A); hind wings infuscated with veins and crossveins, hyaline margined; tenth abdomi-

nal tergite of the male strongly down-curved, obscuring the cerci (Fig. 7, A; Fig. 8, A); female subgenital plate distally tricuspidate (Fig. 11, A) (Tenerife Island) ..... *Calliphona konigi* Krauss

3'. Fastigium of the vertex less than 1.5 times as broad as the first antennal segment (Fig. 3, B–D); ventro-cephalic angle of lateral lobe of pronotum bearing a distinct callosity (Fig. 2, B–D; Fig. 4, B–D); tegmina at least as long as the abdomen, the posterior margin of the speculum of the male right tegmen much less strongly developed (Fig. 6, B–D); hind wings hyaline, not pigmented; tenth abdominal tergite of male not strongly downcurved, the internal process of cercus visible from above (Fig. 7, B-D; Fig. 8, B-D); female subgenital plate bicuspidate (Fig. 11, B-D) 4

4. Tegmina about three times as long as wide (Fig. 5); medial projection of male cercus an arcuate flange (Fig. 9, B); emargination of female subgenital plate as deep, or deeper than wide (Fig. 11, B) (La Palma Island) ..... *Calliphona palmensis* I. Bolivar

4'. Tegmina more than four times as long as wide (Fig. 5); medial projection of male cercus an arcuate multidentate flange bearing a secondary ventrally projecting multidentate lobe (Fig. 9, C–D); emargination of female subgenital plate wider than deep (Fig. 11, C) (Gran Canaria and Gomera Islands) ..... *Calliphona alluaudi* I. Bolivar

FAUNISTIC AND FLORISTIC AFFINITIES OF THE CANARY ISLANDS AND MADEIRA

Both the Canary Islands and Madeira are of volcanic origin and lie west of the Moroccan coast in the Atlantic Ocean (Fig. 1). At least the Canarian Archipelago is probably of Tertiary origin (Ceballos and Ortuño, 1951), and is thought to have been formed in connection with the Atlas orogeny in Morocco.

The Orthopteran fauna of Madeira is generally impoverished, with approximately 26 known Orthopteran species compared to over 90 in the Canaries (Chopard, 1938, Johnston, 1956). No endemic genus of Acridoidea occurs both in Madeira and the Canaries, and most species of Orthoptera which are present in both have wide distributions in Europe, Africa and often Asia (for example, *Oecanthus pellucens* Scopoli, *Phaneroptera nana sparsa* Stål, *Aiolopus thalassinus*

Fabricius, and *Aiolopus strepens* Latreille). On the other hand, *Acheta meridionalis* Uvarov is endemic to both the Canaries and Madeira, as is the genus *Calliphona.*

The vegetation of Madeira and the Canary Islands is strikingly similar, both in zonation and in floristics (Lems, 1958). A typical relevee from either island group taken in the heath zone, the characteristic habitat of all Atlantic Island Tettigoniinae, is defined by species of the genera *Erica, Echium, Leucophae, Phyllus, Bystropogon, Lytanthus, Ilex, Laurus* and sometimes *Pinus.* In this regard, it is particularly interesting to note that in the Canaries and Madeira, *Calliphona* is present only on those islands with well developed heath and pine. Heath and pine are absent on Lanzarote and Fuerteventura; heath is impoverished and subclimax on Hierro. The pine forest on Hierro has been nearly eradicated by fire and only recently has undergone artificial reforestation. *Calliphona* is absent from all of these three islands. Furthermore, *Calliphona* is found only in heath and adjoining cultivated and pine areas on the islands on which it is found. On Madeira, for example, the most commercial of the Atlantic Islands, *barretoi* is found only in and around the forests of the northern and north-central area (Fig. 1).

The species with which *Calliphona* was first compared historically is *Tettigonia viridissima* L. (I. Bolivar, 1893). This species has a wide distribution in Europe, North Africa and temperate Asia (Ragge, 1965) and in Morocco it is known from both the Great Atlas and Middle Atlas chains (Chopard, 1943). Unlike the Atlantic Island forms, it occupies quite a wide range of habitats. In the British Isles, for example, where it occurs mainly along the south coast, it is found in nettles, bracken fern and often among garden plants (Ragge, 1965).

THE PATTERN OF EVOLUTION IN *CALLIPHONA*

Although it is not possible to determine the course of evolution in *Calliphona* on the Atlantic Islands on the basis of our data, several relationships seem likely.

The large number of characters in common between *barretoi* of Madeira and *Tettigonia viridissima* on the mainland suggests that the stock ancestral to *Calliphona* first reached Madeira. These *Tettigonia viridissima*-like ancestors adapted to life in the heath forest of Madeira and gradually became more robust and *Calliphona*-like. Subsequently members of this stock, approaching *barretoi* in appearance, spread

southward to the Canary Archipelago. Here differentiation continued, giving rise to *konigi, palmensis* and *alluaudi.*

The timing of introduction and the subsequent evolution of *Calliphona* on the Canaries, are, in part, uncertain. Evidence from general body and stridulatory morphology, as well as sound production, point to a recent divergence of *palmensis* and *alluaudi.* In terms of distribution, it is most reasonable to assume that *alluaudi* developed from *palmensis* stock, first reaching Gomera and then spreading to Gran Canaria. *C. konigi,* evolved from migrants from Madeira Island, has, in many respects, diverged farther from the ancestral stock than the other Calliphonas, but shape and configuration of the male cerci and titillators are remarkably similar to those found in *barretoi* and *T. viridissima.* The long-winged *alluaudi* is not known from Tenerife, the island which is occupied by *konigi* and which lies between Gomera and Gran Canaria, both inhabited by *alluaudi.* We suspect this is owing to competition for a single niche in the heath zone, the unique habitat of *Calliphona.*

It is interesting to note that all of the Calliphonas, except *alluaudi,* exhibit some degree of wing reduction. This is most extreme in *konigi,* in which the wings cover about two-thirds of the abdomen. The wings of *barretoi* and *palmensis* are a little longer, reaching the knee of the caudal femur. It is possible that this reduction is a response to living in the permanent heath zone (Darlington, 1943).

SUMMARY

A comparison, using 20 morphological characters, was made between the four Tettigoniines occurring on Madeira and the Canary Islands and the species, *Tettigonia viridissima.*

As a result of this comparison we are placing *Psalmatophanes* Chopard 1938, and *Calliphonides* I. Bolivar 1940 into synonymy with *Calliphona* Krauss 1892.

We conclude that the four species of *Calliphona, konigi, barretoi, palmensis,* and *alluaudi,* are derivatives of a single invasion from the African mainland by a *Tettigonia viridissima*-like ancestor.

The several characters common to *barretoi* of Madeira and *Tettigonia viridissima* suggests that the original stock giving rise to *Calliphona* reached Madeira first, and later spread southward to the Canary Archipelago.

Although the direction in evolution of *Calliphona* is uncertain, it is likely that *alluaudi* and *palmensis* have been derived more recently

than *konigi,* since they are strikingly similar in most morphological characters studied, as well as produce similar patterns of vocalization.

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