CHROMOSOMAL SEQUENCES AND INTERISLAND COLONIZATIONS IN HAWAIIAN DROSOPHILA

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ABSTRACT

Of 103 picture-winged Drosophila species endemic to the high Hawaiian islands, all but three are endemic to single islands or island complexes. They are presumed to have evolved *in situ* on each island. The banding pattern sequences of the five major polytene chromosomes of these species have been mapped to a single set of Standard sequences. Sequential variation among these chromosomes is due to 213 paracentric inversions. An atlas of their break points is provided. Geographical, morphological and behavioral data may be used to supplement the cytological information in tracing ancestry. Starting at the newer end of the archipelago, the 26 species of the Island of Hawaii (less than 700,000 years old) are inferred to have been derived from 19 founders, 15 from the Maui complex, three from Oahu and one from Kauai. The existence of 40 Maui complex species is explicable as resulting from 12 founders, ten from Oahu and two from Kauai. The 29 Oahu species can be explained by 12 founder events, five from Kauai and seven from Maui complex (summary in Figure 5). Although the ancestry of two Kauai species can be traced to newer islands, the ten remaining ones on this island (age about 5.6 million years) are apparently ancient elements in the fauna, relating ultimately to Palearctic continental sources.

THE major high Hawaiian Islands, which are less than 6 million years old, harbor a group of approximately 110 species of large Drosophilas, loosely called the "picture wings." The banding patterns of all six polytene chromosomes of each of 103 of these species have been completely sequenced cytologically. Despite exciting new evidence for the mobility of DNA at the molecular level, the polytene chromosome orders, as manifested in these species, are highly stable. Each polytene band is qualitatively recognizable in even the most distant species; the gross order of each of the chromosomes ($2n = 12$ in all species) has been perturbed by 213 paracentric inversions, that is, an average of only about two per species.

In view of the sequential formation of the islands (those to the northwest are older, southeast newer), these genetic data are exceptionally useful in tracing the historical patterns of species formation. Whereas a chromosomal inversion "phylogeny" is intrinsically ambiguous as to rooting, the geological history of the islands provides the necessary outside information to give roots and direction to the relationships. These species display, furthermore, a very high degree of single-island endemism, greatly simplifying the reconstruction of ancient colonization patterns. Thus, of the 103 species, only three have been recorded

TABLE 1

Catalog of inversions found in chromosomes X and 4 of the picture-winged group of Hawaiian Drosophila

Chromosome		Species used for illustration	Subgroup	Break points published in:
X	4, 4a*	*grimshawi* (Standard)	I	C & S (1968a) shows Standard banding orders; C (1969)
	4b	*pilimana*	I	C & S (1968a); C (1969)
Xa, b*		*crucigera*	I	C (1966); C & S (1968a); C (1974)
Xc	4c*	*discreta*	I	C & S (1968a); C (1969); C (1974)
Xd, i, j, k, l	4h, i, j	*picticornis*	II	C & S (1968b)
Xe, f	4e, f, g	*punalua*	IV	C & S (1968c); C (1974)
	4k*, v*, g^{2*}, h^{2*}, i^{2*}	*disjuncta*	I	C & S (1968a); C (1969); C & Sato (1969): $4vg^2h^2i^2$ illustrated in BAIMAI (1975a)
Xg	4l	*engyochracea*	I	C & S (1968a)
Xh		*liophallus*	I	C & S (1968a); C (1974)
Xm, n	4m	*conspicua*	I	C & S (1968a); C (1974)
Xo p, q, r, s, t*		*planitibia*	II	C & S (1968b)
Xu, v, w, x, y	4o, p, q	*adiastola*	III	C & S (1968c); 4o break points corrected in C & J (1975); tip of X illustrated in RAIKOW (1973)
	4r	*spectabilis*	III	C & S (1968c); distal break corrected in C & J (1975)
Xz		*clavisetae*	III	C & S (1968c)
	4s (invalid)	*peniculipedis*	III	C & S (1968c); not an inversion, see C *et al.* (1970)
Xa^2	4u	*recticilia, heedi*	I	C & S (1968a); C (1974); tip of Xa^2 illustrated by RAIKOW (1973)
Xo^{3*}, t^{3*}, X_F*	4t*, k^{2*}, l^{2*}, m^{2*}, o^{3*}, p^{3*}	*silvestris*	II	C & S (1968c); 4 t, k^2, l^2, m^2 as *nigrifacies*; $4o^3$ not mapped but close to 4*t* (see caption, Table 2 Craddock & J 1979); $4p^3$, Xo^3, Xt^3 and X_F, Figure 2, this paper
Xb^2		*sproati*	I	C & S (1968a); C (1974)
Xc^2		*hemipeza*	II	C & S (1968b)
Xd^2, e^2, f^2, g^{2*}, h^2, i^2, j^2, k^2, l^{2*}	4w, x, y, z, a^{2*}	*primaeva*	V	C & S (1969)
Xm^2, n^2 o^{2*}, b^{3*}, n^{3*}, X_A*, X_B*, X_C*	$4b^2$, c^2, d^2, e^2, f^2, n^2, o^2, p^{2*}, q^{2*}, r^{2*}, s^{2*}, i^{3*}	*setosimentum*	III	C & S (1968c); see also C & J (1975) for corrected breaks for Xn^2, $4n^2$, $4q^2$, Xn^3 and constrictions X_A, X_B, X_C, this paper

TABLE 1—Continued

Chromosome		Species used for illustration	Subgroup	Break points published in:
	$4j^{2*}$	*ciliaticrus*	I	C & S (1968a); C (1969)
Xp^2, q^2		*hirtipalpus*	I	C & S (1968a); C (1974)
	$4t^{2*}$	*hawaiiensis*	I	C & S (1968a); C (1969)
$Xr^2\ s^2, t^2$	$4v^2$	*ornata*	III	C & S (1968c) as n. sp. "A". $4v^2$ break points corrected in C & J (1975)
	$4u^2$	*basisetae*	IV	C & S (1968c)
Xu^{2*}		*obscuripes*	II	C & S (1968b)
Xv^{2*}, w^{2*}	$4a^{3*}, g^{3*}$	*neopicta*	II	C & S (1968b); C (1971b)
Xx^2	$4x^2, y^2, z^2, b^{3*}, c^{3*}$	*attigua*	V	C & S (1969)
	$4d^{3*}$	*ochrobasis*	III	C & J (1975)
Xy^2		*paenehamifera*	II	C & J (1975)
	$4e^{3*}$	*claytonae*	I	C (1971b)
Xz^2, a^3		*lineosetae*	I	C (1971b); C (1974)
	$4f^{3*}$	*neoperkinsi*	II	C (1971b)
	$4j^{3*}, k^{3*}$	*formella*	I	CLAYTON, CARSON and SATO (1972); $4j^3/k^3$ illustrated by BAIMAI (1975b)
Xc^3, d^3		*inedita*	I	C (1971b); C (1974)
	$4l^{3*}$	*flexipes*	I	CLAYTON, CARSON and SATO (1972)
Xe^{3*}		*oahuensis*	II	C (1971b)
	$4m^{3*}$	*aglaia*	I	CLAYTON, CARSON and SATO (1972)
Xf^3		*truncipenna*	II	C & J (1975)
Xg^3	$4d^*, n^*$	*fasciculisetae*	I	C & S (1968a); C (1969); C (1974)
Xh^3		*prostopalpis*	IV	C (1971b)
Xi^3	$4w^2$	*ingens*	II	C (1971b)
Xj^3	$4h^3$	*alsophila*	I	C (1971b); C (1974)
Xk^3, l^3	$4n^{3*}$	*assita*	I	C (1971b); C (1974)
Xm^3		*touchardiae*	III	C & J (1975)
Xp^3, q^3, r^3, s^3		*micromyia*	I	Figure 2, this paper
	$4_B, 4_C$	*affinidisjuncta*	I	Constrictions. Figure 3, this paper
X_D, X_E	4_A	*orthofascia*	I	Constrictions. Figures 2 and 3, this paper. X_D, 4_A, Maui complex; X_E, Hawaii

Lower case letters (alone and with superscripts) denote paracentric inversions. I–V refer to subgroups: I, *grimshawi*; II, *planitibia*; III, *adiastola*; IV, *punalua*; and V, *primaeva*. * = polymorphic within species: X_A, X_B, 4_A, etc. = constrictions: C = CARSON; S = STALKER; J = JOHNSON.

from more than one island in 20 years of intensive collecting. In discussions of single-island endemism, the closely-adjacent islands of Maui, Molokai and Lanai are considered as one island ("the Maui complex"), as all three were joined in the Pleistocene.

Beginning with CARSON, CLAYTON and STALKER (1967), a series of papers have

TABLE 2

Catalog of inversions found in chromosomes 2, 3 and 5 of the picture-winged group of Hawaiian Drosophila

Chromosome			Species used for illustration	Subgroup	Break points published in:
2	3	5	*grimshawi* (Standard)	I	C & S (1968a) shows Standard banding orders. STUART et al. (1981) shows base of Standard 3
	3a*		*crucigera*	I	C (1966); C & S (1968a); C (1974)
		5a	*ochracea*	I	C & S (1968a)
2a*	3b*		*fasciculisetae*	I	C & S (1968a); C (1974); C (1981b)
		5b, c*, m*	*prolaticilia*	IV	C & S (1968c)
	3c*, h*, p*		*discreta*	I	C & S (1968a); C (1974)
	3d, e	5e	*picticornis, planitibia*	II	C & S (1968b)
2c, d	3f	5f	*adiastola*	III	C & S (1968c)
2e			*clavisetae*	III	C & S (1968c)
2b	3g		*gradata*	I	C & S (1968a); C (1974)
		5k*	*silvarentis*	I	C & S (1968a); C (1981a) shows photograph of entire genome
	3i	5d	*liophallus*	I	C & S (1968a); C (1974)
2j			*hirtipalpus*	I	C & S (1968a)
	3j, k		*adiastola*	III	C & S (1968c)
2k, p*	3l, u*	5l*, p*, u*	*ochrobasis*	III	C & S (1968c); C & J (1975)
		5n*	*conspicua*	I	C & S (1968a)
2o*, t*	3r, m*		*silvestris*	II	C & S (1968b) as *nigrifacies*. 2t, this paper
2m*, n*			*neopicta*	II	C & S (1968b)
	3n*		*orthofascia*	I	C & S (1968a); C (1974)
2r			*inedita*	I	C *et al.* (1970)
	3o*		*orphnopeza*	I	C & S (1968a); C (1974)
2s*			*disjuncta*	I	This paper
	3p*		*discreta*	I	C & S (1968a); C (1974)
		5r	*claytonae*	I	C *et al.* (1970)
	3q		*hexachaetae*	I	C & S (1968a); C (1974)
		5s	*setosifrons*	II	C *et al.* (1970)
		5t*	*macrothrix*	I	C (1971b)
	3s*, v*	5g*	*recticilia*	I	C & S (1968a); C (1974); 3g/gsv illustrated in BAIMAI (1977)
	3t		*neogrimshawi*	III	C & S (1968c)
	3w		*ornata*	III	C & S (1968c) as n. sp. "A"
2i	3y	5o	*attigua*	V	C & S (1969) is incorrect. See Figure 3B and its caption, this paper

TABLE 2—Continued

Chromosome			Species used for illustration	Subgroup	Break points published in.
	3z		*punalua*	IV	C & S (1968c): Figure 5 caption is wrong: upper figure is chromosome 3 lower is chromosome 5. Break points labeled "f" should be "z". See note, Table XI, C *et al.* (1970): C (1974)
	$3a^{2*}$	5q*	*lineosetae*	I	C (1971b): C (1974)
	$3b^{2*}$		*murphyi*	I	C (1971b): C (1974)
	$3c^{2}$		*ingens*	II	C (1971b)
2_A	$3d^{2*}$		*hawaiiensis*	I	C (1971b): C (1974): constriction 2_A illustrated in Figure 14.1. C (1981a) and Figure 3, this paper
2l*	$3e^{2*}$		*setosimentum*	III	C & J (1975)
2f, g, h, q*	3x*, f^{2*}	5h, i, j, v*	*primaeva*	V	C & S (1969): 3x, $3f^{2}$ and 5v, Figure 3, this paper

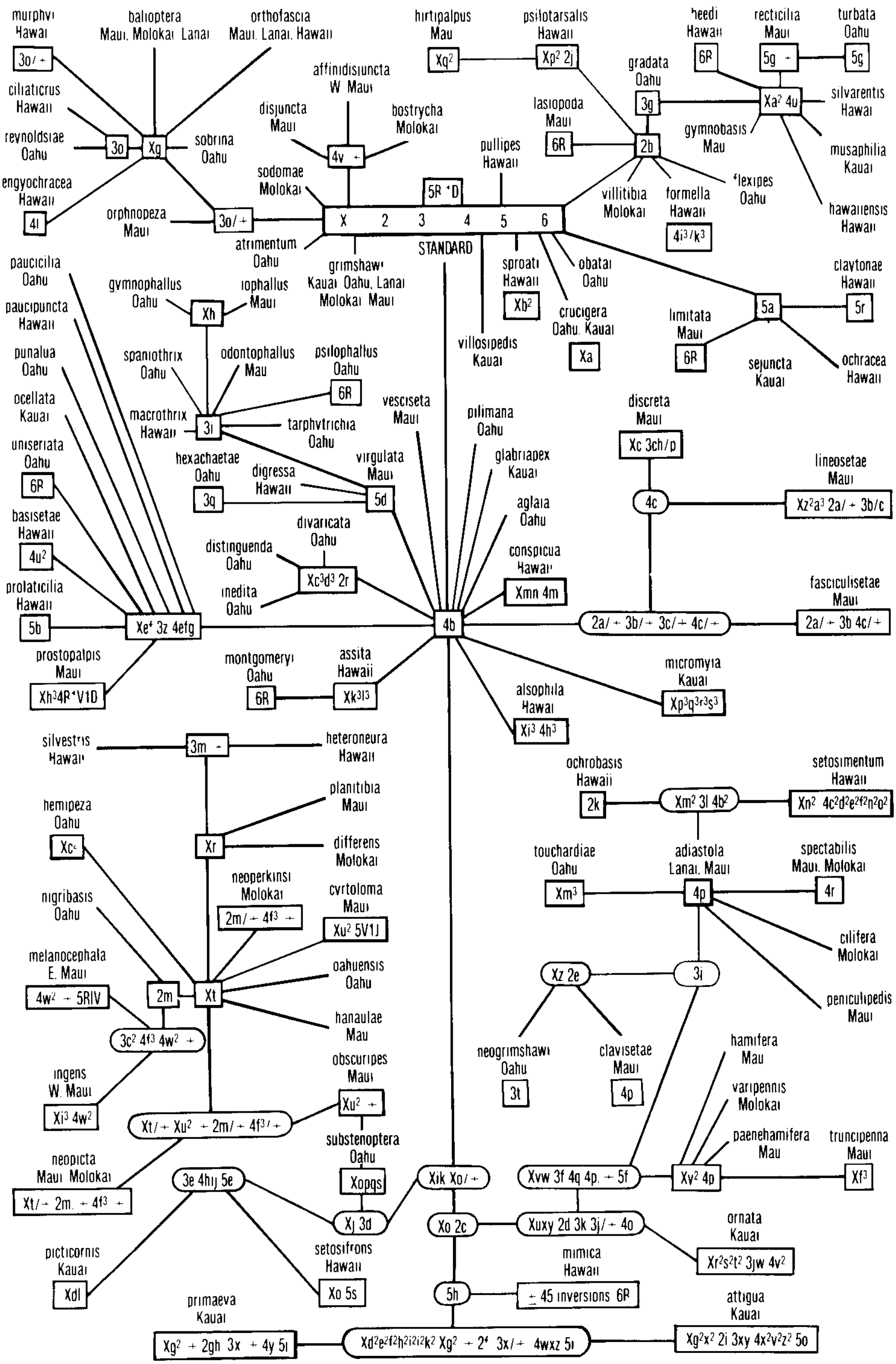
Abbreviations and symbols as in Table 1.

documented the accumulation of data over about 15 years on the polytene relationships of these species, culminating with a recent review (CARSON and YOON 1982). In this latter paper and several other recent ones (CARSON 1980, 1981a,b), the origin and geographical distribution of each species on the newer islands has been interpreted under the hypothesis that the islands were colonized by one or a few "founder" individuals. After each successful colonizing event (with the three exceptions mentioned before), one or more new morphologically and genetically distinct species have been formed.

The purpose of the present paper is twofold. First, an atlas of chromosomal data collected from diverse publications has been provided in summary form. Previously unpublished inversion breaks and other cytological features are presented in new chromosomal maps. Second, for each relevant species or related group of species on the newer islands, a hypothetical founder event is proposed. This includes an attempt to infer both the donor and recipient island and to specify the key chromosomal or other characters that may be used as tracers of ancestry. Each putative "founder" has been given a number and references to the prior literature provided.

MATERIALS AND METHODS

Wild-caught flies were brought to the laboratory, and isolated female specimens, previously mated in nature, were induced to oviposit. Aceto-orcein smears of polytene chromosomes of larval salivary glands were used exclusively. The basic polytene sequences of a species not previously studied were determined by comparing the sequences displayed by this species either with those of Standard for the entire group (*D. grimshawi*, subgroup I) or to the Standard arrangements for one of the other four subgroups (II, *planitibia*; III, *adiastola*; IV, *punalua*; V, *primaeva*). These compar-


murphyi Hawaii
3o/+
balioptera Maui, Molokai Lanai
orthofascia Maui, Lanai, Hawaii
ciliaticrus Hawaii
reynoldsiae Oahu
3o
Xg
sobrina Oahu
engyochracea Hawaii
4l
orphnopeza Maui
3o/+
affinidisjuncta W Maui
disjuncta Maui
4v +
bostrycha Molokai
sodomae Molokai
atrimentum Oahu
hirtipalpus Maui
Xq2
psilotarsalis Hawaii
Xp2 2j
lasiopoda Maui
6R
pullipes Hawaii
5R *D
X 2 3 4 5 6
STANDARD
grimshawi Kauai Oahu, Lanai Molokai Maui
sproati Hawaii
Xb2
obatai Oahu
crucigera Oahu, Kauai
Xa
villosipedis Kauai
heedi Hawaii
6R
recticilia Maui
5g +
turbata Oahu
5g
gradata Oahu
3g
Xa2 4u
silvarentis Hawaii
gymnobasis Maui
2b
musaphilia Kauai
flexipes Oahu
villitibia Molokai
formella Hawaii
4i3/k3
hawaiiensis Hawaii
claytonae Hawaii
5a
5r
limitata Maui
6R
sejuncta Kauai
ochracea Hawaii
paucicilia Oahu
paucipuncta Hawaii
punalua Oahu
ocellata Kauai
uniseriata Oahu
6R
basisetae Hawaii
4u2
prolaticilia Hawaii
5b
Xe4 3z 4efg
prostopalpis Maui
Xh34P*V1D
gymnophallus Oahu
Xh
iophallus Maui
spaniothrix Oahu
odontophallus Maui
psilophallus Oahu
6R
macrothrix Hawaii
3i
tarphytrichia Oahu
hexachaetae Oahu
3q
digressa Hawaii
virgulata Maui
5d
vesciseta Maui
divaricata Oahu
distinguenda Oahu
Xc3d3 2r
inedita Oahu
montgomeryi Oahu
6R
assita Hawaii
Xk313
pilimana Oahu
glabriapex Kauai
aglaia Oahu
conspicua Hawaii
Xmn 4m
4b
discreta Maui
Xc 3ch/p
4c
lineosetae Maui
Xz2a3 2a/+ 3b/c
2a/+ 3b/+ 3c/+ 4c/+
fasciculisetae Maui
2a/+ 3b 4c/+
micromyia Kauai
Xp3q3r3s3
alsophila Hawaii
Xi3 4h3
silvestris Hawaii
3m +
heteroneura Hawaii
planitibia Maui
Xr
differens Molokai
hemipeza Oahu
Xc6
neoperkinsi Molokai
2m/+ 4f3 +
cyrtoloma Maui
Xu2 5V1J
nigribasis Oahu
oahuensis Oahu
melanocephala E. Maui
4w2 + 5RIV
2m
Xt
hanaulae Maui
3c2 4f3 4w2 +
obscuripes Maui
Xu2 +
ingens W. Maui
Xi3 4w2
Xt/+ Xu2 + 2m/+ 4f3/+
substenoptera Oahu
Xopqs
neopicta Maui Molokai
Xt/+ 2m, + 4f3 +
3e 4hij 5e
Xj 3d
Xik Xo/+
picticornis Kauai
Xdl
setosifrons Hawaii
Xo 5s
Xo 2c
5h
primaeva Kauai
Xg2 + 2gh 3x + 4y 5i
Xd2e2f2h2i2i2k2 Xg2 + 24 3x/+ 4wxz 5i
ochrobasis Hawaii
2k
Xm2 3l 4b2
setosimentum Hawaii
Xn2 4c2d2e2f2n2o2
touchardiae Oahu
Xm3
adiastola Lanai, Maui
4p
spectabilis Maui, Molokai
4r
cilifera Molokai
Xz 2e
3i
peniculipedis Maui
neogrimshawi Oahu
3t
clavisetae Maui
4p
hamifera Maui
varipennis Molokai
paenehamifera Maui
truncipenna Maui
Xvw 3f 4q 4p, + 5f
Xy2 4p
Xf3
Xuxy 2d 3k 3j/+ 4o
ornata Kauai
Xr2s2t2 3jw 4v2
mimica Hawaii
± 45 inversions 6P
attigua Kauai
Xg2x2 2i 3xy 4x2v2z2 5o

isons are aided by the use of a drawing tube device fitting on a Wild M20 binocular compound microscope. This permits the image of the unknown sequence to be viewed at table level simultaneously with a cut-out photograph of the Standard sequence (see CARSON 1970).

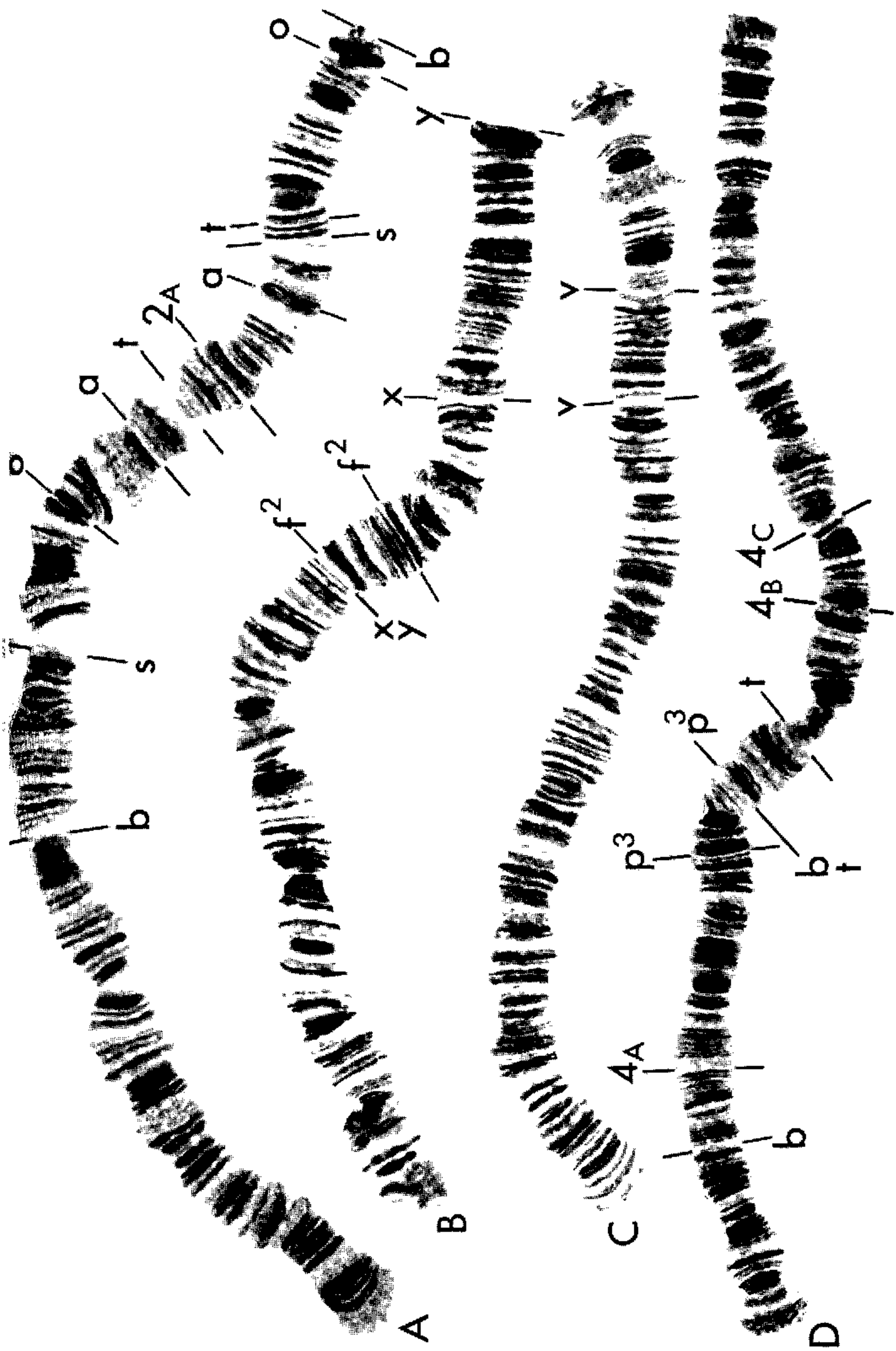
RESULTS

Tables 1 and 2 list by chromosome and identifying symbol the Standard sequences (*D. grimshawi*) and 213 inversions that have been recorded in the picture-winged group. References to published photographic illustration of the break points of these inversions, along with other notes, are provided. The microchromosome (no. 6) is invariant in these species; photographs appear in YOON and RICHARDSON (1978). Certain points in the polytene chromosomes are marked by precise and permanent constrictions (each is denoted by a subscript capital letter. e.g., X_A, X_B, 4_A, etc.). These markers are useful in tracing ancestry of species (for discussion, see CARSON and JOHNSON 1975; CARSON 1981b). These constrictions are also listed in Tables 1 and 2.

Table 3 gives a summary of these data. Other types of summaries appear in CARSON and YOON (1982). Figure 1 is reproduced from CARSON and YOON (1982). Although referred to by some as a "chromosomal phylogeny," it is best viewed as an informational display which enables the basic sequential formula of each

FIGURE 1.—Informational display of polytene chromosome sequence formulas and metaphase conditions in 103 species of picture-winged Drosophila of Hawaii. The sequences of *D. grimshawi* serve as an arbitrary General Standard for the group. Thus, X23456 is displayed in a box in upper center of the figure. Metaphase configuration of the Standard is five rods and one dot (5R1D). Boxes near the species names record any metaphase that differs from this, e.g.. 6R (six rods). The polytene element representing the microchromosome (6) is included. Each inversion is represented by a lower case letter (employed in the order of discovery) used as a suffix to the number of the chromosome. The large number of inversions have made it necessary to use the alphabet several times, i.e., the inversions of chromosome 4. discovered following 4z, are designated $4a^2$, $4b^2$, etc (These symbols are read "four-a-two, four-b-two".) When a symbol stands alone (e.g., 4b or 2b) this means that the sequence represented is present in the homozygous state. Some, but not all, known inversion polymorphisms are represented. Thus, "4v/+" (upper center) means that both the inverted sequence 4v and the relevant matching Standard section $4v^+$ (or simply, +) are segregating in the populations of the species. Most of the polymorphisms that are confined wholly to a single species are omitted from the diagram. Often, however, an inversion found polymorphic in one species will be found in another in either fixed or polymorphic state. A number of species may share the same fixed inversion but differ in other respects. For example, *orphnopeza* and *murphyi* (upper right) are polymorphic 3o/+, whereas several other species in the same phylad are fixed for either 3o or Standard, as the case may be. In some cases, repetition in the display of such facts has been avoided by adding to the diagram the inference that the species concerned arose from a common ancestral population having a certain inversion composition. The inversion formulas of these inferred ancestral populations are given within boxes with rounded ends. The conditions as directly observed within existing species have been placed within rectangular boxes. The Species Standard sequences for any species in the diagram can be determined by starting at the species name and reading the formulas of fixed inversions cumulatively by following the lines through all boxes back to the General Standard. Several examples may be used to illustrate this procedure. *D. liophallus* of Maui (upper left) has the formula Xh 3i 5d 4b 2, or, when arranged in order, Xh 2 3i 4b 5d. *D. lineosetae* of Maui (center right) may be read as Xz^2a^3 2 3h 4bc 5. *D. attigua* of Kauai (bottom of figure) differs from *grimshawi* Standard by 27 inversions: $Xikod^2e^2f^2g^2h^2i^2j^2k^2x^2$ 2cfi 3xy $4bwxzx^2y^2z^2$ 5hio. From CARSON and YOON 1982; reproduced by permission of Academic Press, Inc., London.


A
B
C
p3
s3
q3
r3
X_E
X_D
t3
o3
X_F
n3
o2
X_C
X_B
X_A


A
B
C
D

of the 103 species to be read off the diagram (see caption of figure). Figures 2 and 3 present map positions for various inversions and constrictions. some for the first time.

DISCUSSION

As has been argued previously (CARSON *et al.* 1970; CARSON 1971a, 1982a,b; CARSON and YOON 1982), the geological and plate tectonic history of the major islands gives the outside information necessary for establishing the direction of evolution and phylogenetic relationships of these species. By and large, they appear to have evolved from the oldest (5.6 my) major high island (Kauai in the northwest) to the newest (<0.7 my) island (Hawaii, at the southeast end of the archipelago). Cytological conditions in *D. primaeva* of Kauai, furthermore, appear to provide a link between the Hawaiian picture-winged species and the *D. robusta* group of northern Japan and Korea (STALKER 1972). Colonization of the Hawaiian archipelago from Palearctic continental sources need not have been directly into the present island of Kauai but could have involved older islands, now severely eroded, further to the northwest.

The data presented here, however, pertain to evolution as it has occurred on the three newer islands or island groups (*i.e.*, Oahu, the Maui complex and Hawaii). The origin of most of the species that occur on the oldest high island (Kauai) cannot be traced by these data. Essentially, I deal here with the outcome

FIGURE 2.—Photographic maps showing break points of some X chromosome inversions and map points of constrictions. See Tables 1 and 2. Distal ends are to the left. A, Chromosome X of Standard *grimshawi*. $Xp^3q^3r^3s^3$ of *micromyia* is obtained as follows. Make tandem inversions p^3 and q^3; the proximal r^3 and s^3 break points should not be moved in this process. Then make r^3, followed by s^3. X_D and X_E are constrictions found in *orthofascia* from Maui and Lanai (see Table 1). B, Chromosome X of *planitibia*, differing from Standard *grimshawi* by nine inversions (Xijkopqrst, see CARSON and STALKER 1968a). Inversions o^3 and t^3 and constriction X_F are polymorphic within *silvestris* of Hawaii. C, Chromosome X of *D. setosimentum*. Relative to *adiastola* substandard, the arrangement shown is Xm^2n^2. A new polymorphic inversion of *setosimentum* (Xn^3) is shown, along with three constrictions characterizing the polymorphic complex chromosome of that species (for details see CARSON and JOHNSON 1975). The similar previously described polymorphic inversion Xo^2 is also shown.

FIGURE 3.—Photographic maps showing break points of some autosomal inversions and map points of constrictions. See Tables 1 and 2. Distal ends are to the left. A, Chromosome 2 of *crucigera* showing Standard banding order. Inversion 2s of *disjuncta* and 2t of *silvestris* are the only previously unpublished inversions shown. 2A denotes constriction A of chromosome 2. B, Chromosome 3 of *primaeva* showing Standard banding order. The break points of x and y are corrected from CARSON and STALKER (1969), Figure 2. If inversion x is made, followed by y, the fixed condition 3xy found in *attigua* will result. *primaeva* is polymorphic for both 3x and a new inversion, $3f^2$, from Mt. Kahili, Kauai. C, Chromosome 5 of *primaeva*, differing from Standard by 5hij (see CARSON and STALKER 1969). A new inversion in *primaeva* from Mt. Kahili, Kauai, 5v, is shown. D, Chromosome 4 of *obscuripes*, showing the 4b banding order found widely in the *planitibia* group. To convert to the banding order of Standard 4, inversion 4b must be made. Inversions b and t are shown since both of these inversions share a break point with a newly discovered *silvestris* inversion (p^3) from Maulua, Hawaii. 4_A–4_E represent constrictions, all of which occur in a Standard banding order (see Table 1).

TABLE 3

Number of fixed and polymorphic inversions among 103 Hawaiian species of Drosophila

	Subgroup no.												
	I. *grimshawi* (62)		II. *planitibia* (17)		III *adiastola* (14)		IV. *punalua* (8)		V *primaeva* (2)		I V (103)		
Chromosome	Fixed	Polymor phic	Fixed	Polymor-phic	Fixed	Polymor-phic	Fixed	Polymor-phic	Fixed	Polymor-phic	Fixed	Polymor-phic	I–V to-tal
X	22	1	12	7	14	3	3	0	8	2	59	13	72
2	3	2	0	4	4	2	0	0	4	1	11	9	20
3	3	12	3	2	6	2	1	0	1	2	14	18	32
4	5	17	3	9	13	6	4	0	7	3	32	35	67
5	3	5	2	0	1	3	1	2	4	1	11	11	22
Total	36	37	20	22	38	16	9	2	24	9	127	86	213

Inversions common to more than one subgroup have been entered only once. The base arrangements are standard *D. grimshawi*. Numbers in parentheses are numbers of species.

TABLE 4

Hypothetical founder events for the picture-winged Drosophila species of the Hawaiian archipelago

	Donor island	Chromosomal configuration of founder	Founder no.	References and remarks
A. Island of Hawaii (26 species)				
setosifrons	Kauai	3e 4hij 5c	3	CARSON and YOON (1982). Figure 12
assita	Oahu	Xk^3l^3	27	CARSON and YOON (1982), Figure 13
formella	Oahu	2b 2_{AA}	35	CARSON (1981b). Figure 14.2 This number supercedes no. 24 [see CARSON (1971a). Table 1 where *formella* was referred to as "n.sp. no. 2"]. No. 24 has been reassigned to *prostopalpis* of Maui (see CARSON and YOON 1982. Figure 10).
basisetae *paucipuncta* *prolaticilia*	Oahu	Xef 3z 4efg	10	CARSON and YOON (1982). Figure 10
ciliaticrus	Maui	Xg 3o	38[a]	CARSON (1980), Figure 12.2
digressa	Maui	5d	30	CARSON and YOON (1982), Figure 13
engyochracea	Maui	Xg 3	36[a]	CARSON (1980), Figure 12.2
hawaiiensis	Maui	Xa^2 4u 2_{AA}	32	CARSON (1981b). Figure 14.2
macrothrix	Maui	3i 5d	31	CARSON and YOON (1982). Figure 13. This number supercedes no. 23 used by CARSON (1971a). Table 1. No. 23 has been reassigned to *touchardiae* of Oahu (CARSON and YOON 1982. Figure 11).
murphyi	Maui	Xg 3/3o	20	CARSON (1980), Figure 12.2
orthofascia	Maui	X_E	37[a]	CARSON (1980), Figure 12.2
psilotarsalis	Maui	Xp^2 2j	33	CARSON (1981b), Figure 14.2
sproati	Maui	X 2 3 4 5[b]	39[a]	No longer considered to be from the same founder as *D. pullipes* (see CARSON 1971a, Table 1)
alsophila *conspicua*	Maui	4b	18	CARSON and YOON (1982), Figure 13
heedi *silvarentis*	Maui	2_{A+A+}	19	CARSON (1981b). Figure 14.2
ochrobasis *setosimentum*	Maui	Xm^2 3l $4b^2$	15	CARSON and YOON (1982), Figure 11
claytonae *ochracea*	Molokai	5a	22	CARSON (1980), Figure 12.1
heteroneura *silvestris*	Molokai	Xr	17	CARSON and YOON (1982), Figure 12
pullipes	Lanai	X 2 3 4 5[b]	21	CARSON (1981a), Figure 3. Referred to as "n. sp. no. 1" in CARSON (1971a)

TABLE 4—Continued

	Donor island	Chromosomal configuration of founder	Founder no	References and remarks
B. Maui complex (Maui-Molokai-Lanai) (40 species)				
limitata	Kauai	5a	13	CARSON (1980). Figure 12.1
adiastola *cilifera* *clavisetae* *hamifera* *paenehamifera* *peniculipedis* *spectabilis* *truncipenna* *varipennis*	Kauai	Xikouxy 2cd 3k 3j/+ 4bo	1	CARSON and YOON (1982). Figure 11
grimshawi	Oahu	[c]	41[a]	CARSON (1981a). Figure 3
virgulata	Oahu	5d	9	CARSON and YOON (1982). Figure 13
liophallus	Oahu	Xh	29	CARSON and YOON (1982). Figure 13
odontophallus	Oahu	3i	28	CARSON and YOON (1982). Figure 13
prostopalpis	Oahu	Xcf 3z 4efg	24	CARSON and YOON (1982). Figure 10
gymnobasis *recticilia*	Oahu	2b 3g	11	CARSON (1981b), Figure 14.2. Supercedes no. 11 as described in CARSON *et al.* (1970)
hirtipalpus *lasiopoda* *villitibia*	Oahu	2b 2_{A+A+}	34	CARSON (1981b). Figure 14.2
discreta fasciculisetae lineosetae vesciseta	Oahu	4b	8	CARSON and YOON (1982). Figure 13
affinidisjuncta *balioptera* *bostrycha* *disjuncta* *orphnopeza* *orthofascia* *sodomae*	Oahu	X 2 3 4 5[b]	6	CARSON *et al.* (1970). Figure 16 and CARSON (1981a). Figure 3
cyrtoloma differens hanaulae ingens melanocephala neoperkinsi neopicta obscuripes planitibia	Oahu	Xpqs 3d 4b	25	CARSON and YOON (1982). Figure 12

TABLE 4—Continued

	Donor island	Chromosomal configuration of founder	Founder no	References and remarks
C. Oahu (29 species)				
grimshawi	Kauai	X 2 3 4 5[c]	40[a]	CARSON (1981a), Figure 3
substenoptera	Kauai	Xpqs	2	CARSON and YOON (1982), Figure 12
atrimentum *crucigera* *gradata* *flexipes* *obatai*	Kauai	X 2 3 4 5[c]	5	CARSON (1981b), Figure 14.2. This founder is now assumed to be separate from that from *D. grimshawi*. The latter has been assigned no. 40. See also CARSON (1980), Figure 3
paucicilia *punalua* *uniseriata*	Kauai	Xef 3z 4efg	7	CARSON and YOON (1982), Figure 10
aglaia *distinguenda* *divaricata* *gymnophallus* *hexachaetae* *inedita* *montgomeryi* *pilimana* *psilophallus* *spaniothrix* *tarphytrichia*	Kauai	4b	4	CARSON and YOON (1982), Figure 13
turbata	Maui	5g 2_{A+A+}	42[a]	CARSON (1981b), Figure 14.2
neogrimshawi	Maui	Xz 2e	14	CARSON and YOON (1982), Figure 11
touchardiae	Maui	Xvw 3fj 4q 5f	23	CARSON and YOON (1982), Figure 11
nigribasis	Maui	2m	26	CARSON and YOON (1982), Figure 12
reynoldsiae	Maui	Xg 3o	43[a]	CARSON (1980), Figure 12.2
sobrina	Maui	Xg 3	44[a]	CARSON (1980), Figure 12.2
hemipeza *oahuensis*	Maui	Xt	16	CARSON and YOON (1982), Figure 12
D. Kauai (2 species)				
crucigera	Oahu	[c]	45[a]	CARSON (1980), Figure 12.1. Now considered to have colonized Kauai from Oahu (GIDDINGS and CARSON 1982)
musaphilia	Maui	Xa^2 4u 2_{A+A+}	12	CARSON (1981b), Figure 14.2

For each species, the probable island of origin is listed. This is followed by the inferred chromosomal configuration of the founder individual(s). Each of the 45 inferred founder events is given a number (3rd column in body of table).

[a] New number assigned in this paper.

[b] Although both *pullipes* and *sproati* have standard X 2 3 4 5 tracer sequences, the former species is very close to *grimshawi* morphologically and behaviorally, so that separate founders are assumed for *pullipes* and *sproati* (see also OHTA 1978).

[c] On morphological and/or behavioral traits, judged to be a separate founder from other species with similar sequences.

of evolutionary events stemming ultimately from colonists arising in Kauai and becoming established on the newer islands.

Table 4 presents a series of hypotheses evoking the "founder effect" to explain the origin of many of the species on the newer islands. Older hypotheses have been revised in view of newer data. Colonization of an island is proposed to have been accomplished, for most lineages, by the arrival there of a single gravid female (the founder) usually stemming from an older (donor) island. Each founder has a putative chromosomal configuration and is assigned a number. After arrival there may or may not be a proliferation of species on the recipient island. In any event, the invocation of separate interisland founders is done in a parsimonious manner, that is, only if morphological, behavioral or geographical data suggest such a conclusion. Basically, however, the establishment of putative founders rests largely on the use of the cytological markers, an especially precise way to infer ancestry (see CARSON 1971a).

Table 4 lists a total of 45 inferred founders, each having an individual chromosomal configuration. These pertain to 97 species currently existing on the islands of Kauai, Oahu, Maui complex and Hawaii. The remaining ten

DONOR ISLAND \ RECIPIENT ISLAND	Kauai	Oahu	Maui Complex	Hawaii	Total founder donations
Kauai	[12]	5	2	1	8
Oahu	1	[29]	10	3	14
Maui Complex	1	7	[40]	15	23
Hawaii	0	0	0	[26]	0
Total founder receipts	2	12	12	19	45

FIGURE 4.—Numbers of picture-winged Drosophila species on four Hawaiian islands or island groups (boxes on diagonal) and the numbers of hypothetical founders donated (rows) or received (columns) by each island.

species, or populations of species, endemic to Kauai, are considered to be ancient; their origin cannot be inferred from these data. Subgroup I (see Table 3) members in this category are: *villosipedis*, *sejuncta*, *glabriapex* and *micromyia*. The Kauai population of *grimshawi* is also considered ancestral to other populations of this species on the newer islands (see OHTA 1978). The other ancient Kauai species include, except for subgroup V, only a single member from each subgroup, *i.e.*, *picticornis* (subgroup II), *ornata* (III), *ocellata* (IV) and *primaeva* and *attigua* (V).

Figures 4 and 5 present general summaries of the conclusions from the data reviewed in this paper. The arrows in Figure 5 indicate the direction of colonization; their width is proportional to the number of founders. Note that in the case of two colonizations of Kauai and seven of Oahu, the founders are inferred to have arisen on a younger island and colonized an older one. The number of species on each island is given in parentheses. For further discussion of the number of founders as related to the age and area of the islands, see CARSON (1982b).

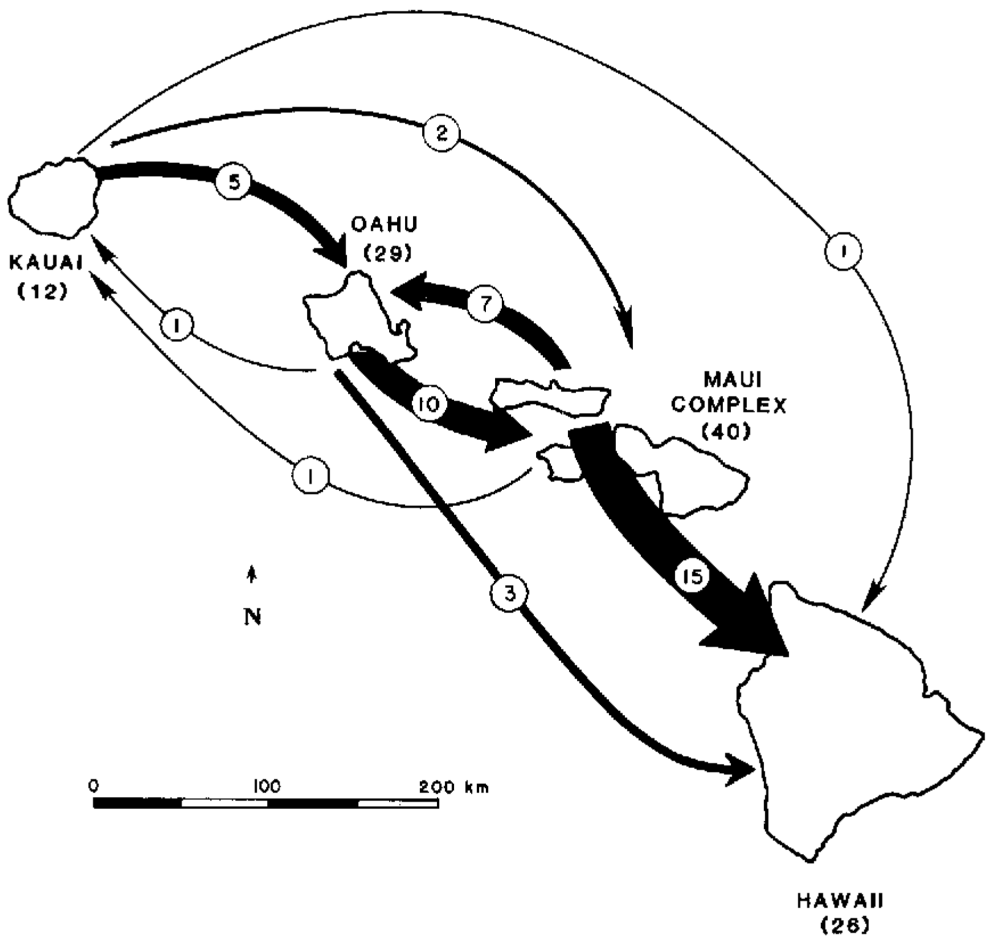


FIGURE 5.—Geographical summary of the proposed founder events invoked to explain the origin of the fauna of each island. The width of the arrows is proportional to the number of proposed founders. The number of species found on each island is given in parentheses.

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