Separate Species or Polymorphism: A Recurring Problem in *Kapala* (Hymenoptera: Eucharitidae)

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Ann. Entomol. Soc. Am. 86(5): 517–531 (1993)

ABSTRACT Two species of *Kapala* known from northern South America and Central America are almost always collected in sympatry. A small percentage of the specimens are intermediate in some character states and thus cannot be assigned to one or the other species. To examine the hypothesis that samples represented a continuous array of morphotypes, the phenetic separation of the two species was analyzed using principal components analysis and canonical variates analysis. Clear separation of species and of geographical populations in Trinidad and Ecuador was found based on the first and second canonical variates, respectively. These discriminant functions were applied to a different set of individuals to determine if season or locality in a geographical area had consistent effects on morphology. Although morphometric analysis suggests a clear separation of the two species, a high coincidence of collections suggests a phenotypic polymorphism within one species. Descriptive notes are provided for *Kapala iridicolor* (Cameron), new combination, and *Kapala sulcifacies* (Cameron), new combination. *Lirata fulvicornis* Cameron and *Lirata nigriventris* Cameron are proposed as new synonymies under *Kapala sulcifacies*.

KEY WORDS *Kapala* spp., canonical variates, sympatry

WE ARE STRUCK by a puzzling pattern in Neotropical *Kapala*. Several closely related pairs of species are found virtually always in sympatry. Although the members of each pair appear quite distinct from each other, their geographical distribution suggests that they may represent phenotypic polymorphism within populations of single species. Here we begin study of this problem by investigating the nature of morphological differences between the members of one such pair, *Kapala iridicolor* (Cameron) and *Kapala sulcifacies* (Cameron). Both species are commonly collected in northern South America and Central America. They are distinct from other *Kapala* (see taxonomic notes in results section), and appear to belong at least to the same morphological group of species. Each species, as currently defined, is distinctive and can be separated from the other by the presence or absence of striae on the face, frons flat or swollen, and mesosoma with a high or low elevated profile (Fig. 1); the latter character states are attributed to *K. iridicolor*.

Other interesting features of these species causes us to question their status as separate species. Males of each species are collected in relatively high numbers wherever they co-occur, whereas females of *K. iridicolor* are rare. Different proportions of each species may be found in separate geographical areas, and similarities in morphology occur between the species at particular localities that are not found in the two species at other localities. Also, a few collections contain specimens with intermediate character states, in various combinations, that make it difficult to assign these individuals to a particular species.

Members of the genus *Kapala* Cameron are widespread throughout the Neotropical Region; a few species extend north into the southern United States and one disjunct species is found in central Africa (Heraty 1985) and Madagascar. Like other Eucharitidae, *Kapala* are specialized ant parasites (Clausen 1941, Heraty 1985). Accurate host associations were made for *Kapala* with *Pachycondyla* (Wheeler & Wheeler 1937) and *Odontomachus* (J.M.H., unpublished data) in South America (Formicidae: Ponerinae). *Kapala* belongs to a morphologically diverse group of Eucharitidae, many of which have undergone spectacular morphological modifications of the head and mesosoma. These morphological novelties do not appear to be the result of interactions with the host ants because adults spend only a brief time in the ant nest after emergence, and reports for other genera suggest that hosts are not antagonistic to the parasites (Wheeler 1907).

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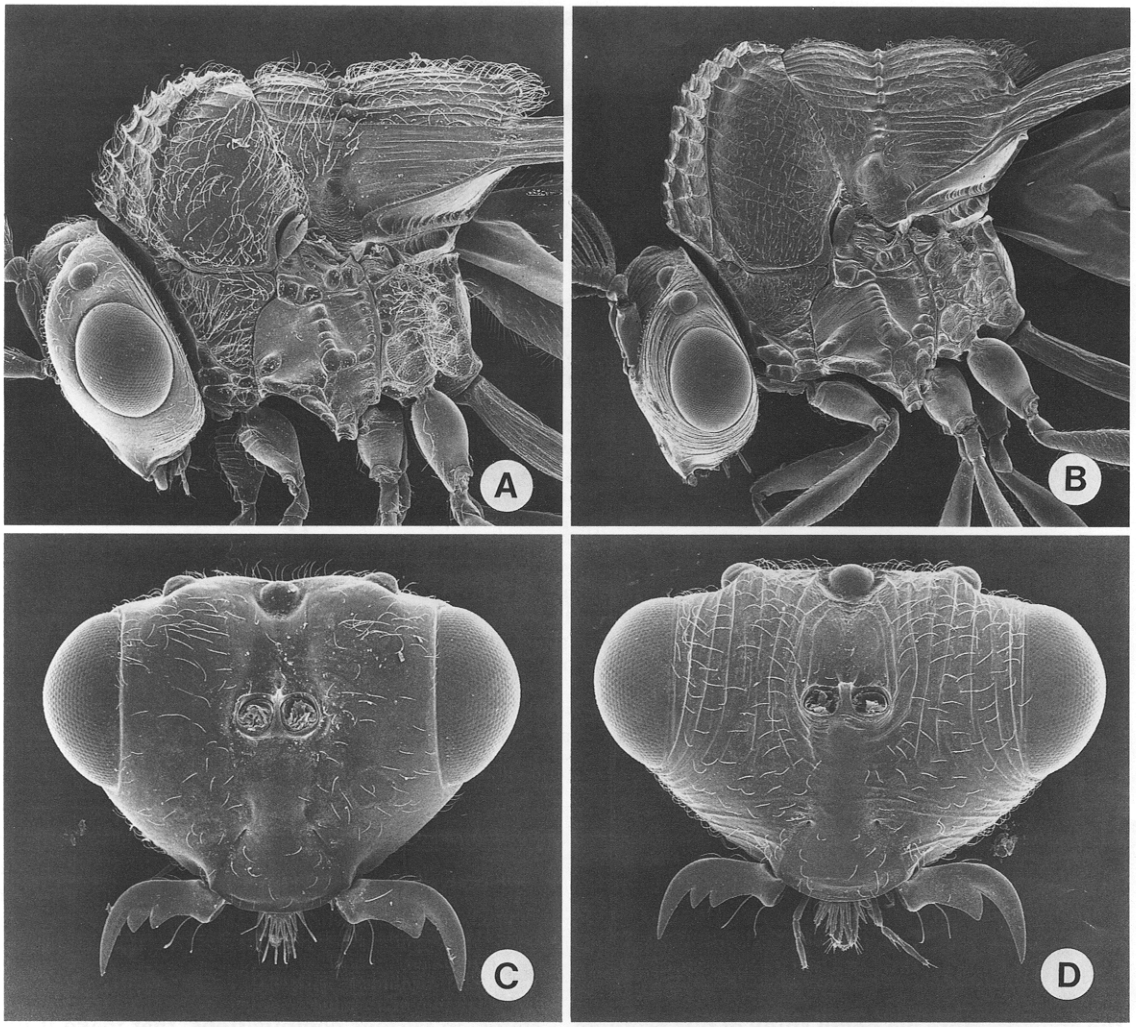


Fig. 1. A and C, *K. iridicolor:* (A) Lateral view of mesosoma. (C) Frontal view of head. B and D, *K. sulcifacies:* (B) Lateral view of mesosoma. (D) Frontal view of head.

Kapala is one of the most commonly collected genera of Eucharitidae in the Neotropical Region, yet only a few of the species can be accurately identified. In total, there are 18 described species; J.M.H. estimates that as many as 48 species will eventually be recognized. The current species descriptions are poor and a taxonomic revision is needed. A major obstacle to a proper characterization of species is the large degree of morphological variation within apparent species and a lack of reliable characters to separate species. There is little information available on behavior, oviposition habits, or mating preferences; therefore, species boundaries in *Kapala* are estimated by observing phenetic gaps between groups of individuals. Before defining the criteria for recognition of species within *Kapala,* it is necessary to analyze the morphological variation both within and among species to avoid gross errors.

Are the species mentioned above truly different species of *Kapala,* or are they two distinctive phenotypes belonging to the same species? If one assumes a single polymorphic species, one might expect a certain degree of overlap in morphology between the two forms, and that individuals classified as "questionable" would be intermediate in form. We have used morphometric methods to characterize size and shape differences between these forms at several localities. The results of this study will have substantial implications for our concepts of species in *Kapala* and therefore the number of species that will eventually be recognized.

Materials and Methods

Populations Sampled. For morphometric studies of *K. iridicolor* and *K. sulcifacies*, two separate data sets were analyzed. The first data set was used as a training data set for developing discriminant functions and studying morphological structure in the two species. The training data set was sampled from single collections from Trinidad and Ecuador that contained representatives of each species. Samples consisted of 150 male *Kapala* collected from 15 July to 15 August 1976 in Curepe, Trinidad (single collection from malaise trap, all from The Natural History Museum, London [BMNH]), and 80 male *Kapala* collected during February 1983 at Rio Palenque, Ecuador (all from the Canadian National Collection, Ottawa [CNC]). Specimens were initially stored in 70% EtOH, then critical point-dried and point-mounted. Individuals for study were randomly selected from collections of specimens from each locality. Specimens were determined as *K. iridicolor*, *K. sulcifacies*, or "questionable," based on the combined sculpture and shape characters (described in the later section on taxonomic history). Questionable individuals were those with an "incorrect" combination of character states such as smooth face and high thoracic profile, or striate face and low thoracic profile.

After removal of specimens with missing values, the *K. sulcifacies*–Ecuador matrix was slightly less than full rank ($n = 28$). Stepwise discriminant analysis using a default acceptance level of 15% was used to eliminate 9 variables, leaving 19 variables which best expressed differences among populations. These 19 variables were used in all subsequent multivariate analyses. An independent test class was created for the discriminant analysis that included all specimens of questionable assignment.

To observe changes in morphology that may take place in different areas or seasons, a second independent data set was developed by measuring specimens from four different localities on Trinidad in the Curepe area (Santa Margarita Circular Road, St. George [St. Augustine], Moka Valley, and Maracas Valley). Twelve sampling dates are represented in these collections, providing a sporadic sample of monthly records from 1976 to 1978. 250 individuals were measured for the 19 variables which were selected after stepwise discriminant analysis on the initial data set.

Voucher specimens of material used in statistical analyses have been placed in the Texas A&M University Insect Collection as Voucher No. 596. Other specimens used in the statistical analyses are deposited in the CNC and BMNH. Material used in analyzing sympatry was borrowed from a number of museums. Locality information and depositions are available from the senior author upon request.

Measurements. Size and shape differences between species were characterized first by choosing 40 landmark points (black dots, Fig. 2) on the mesosoma, fore wing, and head. To the extent possible, these landmarks represent homologous locations (sensu Bookstein et al. 1985) and points that could be unambiguously observed on all specimens. Twenty eight distances between landmarks were measured to form our estimators of size and shape differentiation (Table 1 and Table 2). Approximately half of the measures pertain to the shape of the head and mesosoma (MS1–3, SC1–3, ME1–2, BSH, AXL, SCL, MSW, SCW, SOW, SIW, IOD, HDH, HDL, FWL, and FWW). Other measures estimate lengths of structures commonly used in discriminating other species of Eucharitidae (PSL, PTL, GSL, EYH, GNL, MVL, FL1, and SCP). Particularly for evaluating shapes of the mesosoma in profile (Fig. 2A), we attempted to derive sets of distances that covered the entire form (Humphries et al. 1981).

Specimens were measured using a Wild M5 stereomicroscope at 37.5× and 75× magnification. The image was superimposed on a Numonics 2200 digitizing tablet using a camera lucida attachment on the microscope. Reference coordinates were collected and converted to euclidean distance measures using programs developed by Marilyn Houck and Richard Strauss (both Texas Tech University).

Statistical Analyses. All morphometric analyses were performed using the statistical analysis system (SAS version 6.03) software (SAS Institute 1982, 1988). Multivariate and univariate normality were tested for the 28 variables in each of the four populations in the training data set. Questionable forms were not analyzed for multivariate normality because of low sample size (16) in relation to the number of variables. *K. sulcifacies*–Ecuador was the only group to fail multivariate normality; this group contained only 28 individuals after exclusion of individuals with missing data (one variable was dropped arbitrarily). Univariate statistics and results of normality tests for the 28 variables are summarized in Table 2. Univariate normality was rejected in 11 cases ($P < 0.05$), or ≈1.5 times the rate expected by chance alone. However, only mesoscutal width (MSW) was rejected in more than two populations (Table 2).

Principal components analysis (PCA) was performed on the variance–covariance matrix for the 19 remaining variables computed from the raw measurement data and from the logarithms (base 10) of the raw data. Six observations had missing data for one or more variables, leaving 212 observations available for the PCA. PCA was performed, in part, to observe the distribution of observations without the a priori constraints of assigning them to a particular population or

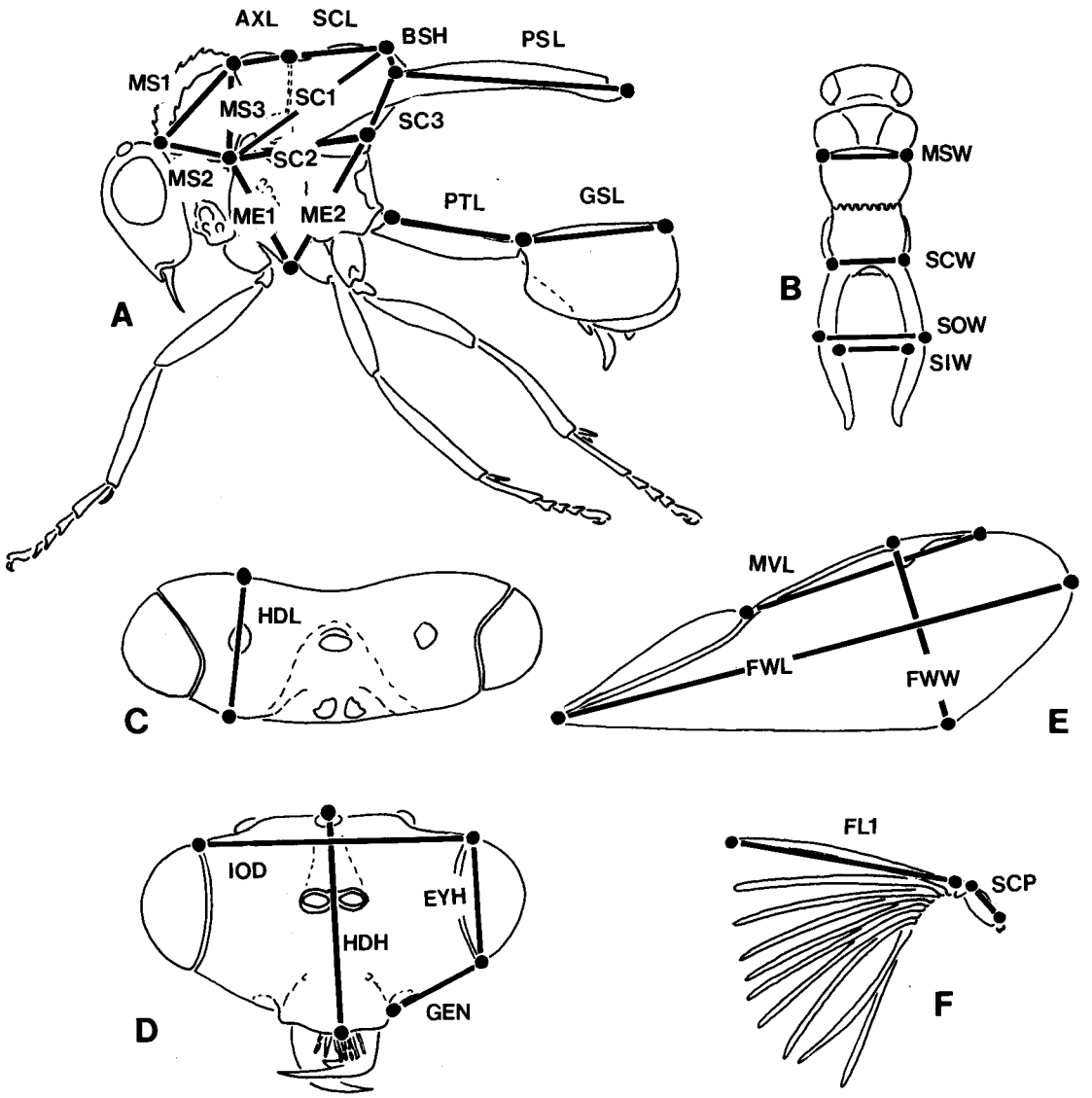


Fig. 2. Measurements of male *Kapala* spp. (see Table 1 for explanation of abbreviations). Dots are landmark points, the coordinates of which were recorded by digitizer; heavy lines are calculated distances. (A) Lateral view. (B) Dorsal view of head and mesosoma. (C) Dorsal view of head. (D) Frontal view of head. (E) Fore wing. (F) Antenna.

class, and also to determine the effects of size and shape on the distribution of scores along the first two principal component axes.

Canonical variates analysis (CVA) was used to evaluate particular variables for discrimination of classes in the training data and develop functions that could be used to classify new observations. The data matrix was analyzed using PROC DISCRIM in SAS (version 6.03) using the canonical option. The four populations excluding questionable forms, as discussed above, were treated as class variables in the analysis under the expectation that there would be differences between species or geographical populations of the same species. Homogeneity of the covariance matrices of the four classes was rejected ($P < 0.0001$, χ^2 723.8, 570 df); therefore, within-class covariance matrices were used.

The independent set of observations from Trinidad, the test class, were assigned scores for the first and second canonical variates using the TESTDATA option in the DISCRIM package. This procedure mean centers variables using the training data set and calculates the canonical scores of test data observations using the raw canonical coefficients. Observations for the test data could then be compared for correct classification with those of the original training classes.

Table 1. Description of distances measured for *Kapala* spp.

Abbreviation[a]	Character	Description[b]
MS1	Mesoscutum	Lateral diagonal from anterior lower margin of mesoscutum to dorsal margin at transscutal articulation (*tsa*).
MS2	Mesoscutum	Lateral length of mesoscutum along ventral margin.
MS3	Mesoscutum	Lateral height from posterior ventral margin to dorsal margin at *tsa*.
AXL	Axillar length	Dorsal length of axilla from *tsa* to scutoscutellar sulcus (*sss*).
*SCL	Scutellar length	Dorsal length of scutellum from *sss* to posterior arch between apical spines.
SC1	Scutellar shape	Lateral diagonal length of scutellum from arch to posterior ventral margin of mesoscutum.
*SC2	Scutellum	Lateral length along ventral margin from posterior ventral margin of mesoscutum to posterior ventral margin of scutellum at metanotum.
*SC3	Scutellum	Height of scutellum from posterior ventral margin of scutellum to arch between spines.
*BSH	Scutellum	Lateral height of arch from dorsal margin to dorsal base of spine.
PSL	Scutellum spine length	Lateral length of apical scutellar spines.
*ME1	Mesepimeron	Lateral diagonal length from posterior ventral margin of scutellum to ventral margin of mesepimeron.
*ME2	Mesepimeron	Lateral diagonal length from posterior ventral margin of mesoscutum to ventral margin of mesepimeron.
PTL	Petiole length	Dorsal length of petiole from flange at base to apex.
GLS	Tergite 1 length	Dorsal length of tergite from base at petiole to medial cleavage at apex.
MSW	Mesoscutal width	Dorsal width across mesoscutum at *tsa*.
SCW	Scutellar width	Width of scutellum at base of spines and between axillular carinae.
SOW	Scutellar spine outer width	Maximum outer width of spines.
SIW	Scutellar spine inner width	Minimum separation of spines measured at same point as SOW.
HDL	Head length	Dorsal length measured across posterior ocellus.
HDH	Head height	Height measured from dorsal margin of median ocellus to median apex of clypeus.
IOD	Interocular distance	Distance between eyes measured across dorsal margin of eyes.
*EYH	Eye height	Vertical height of eye.
*GEN	Gena length	Length measured from ventral margin of eye to base of mandibles.
FL1	Flagellomere 1 length	Length of ramus of FI from dorsal margin at pedicel to apex.
SCP	Scape length	Measured across dorsal margin.
FWL	Forewing length	Length of wing from apex of humeral plate to apex of wing.
FWW	Forewing width	Maximum width of wing measured at perpendicular to forewing margin at distal margin of stigmal vein.
MVL	Marginal vein length	Length from apex of costal cell to apex of postmarginal vein.

[a] *, Deleted from analyses after stepwise discriminant procedure.
[b] Length measures are illustrated in Fig. 2.

The purpose of applying the discriminant functions to an independent group of observations was to observe the performance of the functions on a set of data that were not used to construct them, and to observe the possible effects of date and locality of collection on the morphological form in the two recognized species.

The SAS data sets and a list of locality information for all specimens examined in this study are available from the authors upon request.

Geographical Distribution. Individuals of *Kapala* from South and Central America were separated by sex, species, and date of collection for each locality. Specimens of questionable identity were not included as part of the calculations; they accounted for only 1.2% (49/4,112) of the total number of specimens. Sympatry refers to different taxa that occupy the same geographical distribution. A more restricted definition, which we term here "strict sympatry," means that specimens have both a spatial and temporal overlap of distribution. Therefore, specimens collected at the same locality and on the same date were considered as strictly sympatric and complete congruence of all label information is required. Specimens that differed in collection by only 1 d were not considered strictly sympatric. This decreased the number of possible areas of sympatry in areas such as Panama, where both species were collected in a large number of small collections (one or two individuals) and the chances of collecting both forms together was small. The percentage of *K. sulcifacies* of the total number of *K. sulcifacies* + *K. iridicolor* was determined for all collections and for each collection in which the species were found to be strictly sympatric (Table 5). Additionally, the percentage of females of *K. sulcifacies* of the total number of females belonging to the two species was calculated for all of the collections where the males were determined to be strictly sympatric.

Results

Taxonomic History. *Kapala* is currently in a state of taxonomic confusion and very few morphotypes can be correctly assigned to previously described species based on the original descriptions. Examination of the type material of *Lirata iridicolor* Cameron (1904: 60–61) and *Lirata sulcifacies* Cameron (1904: 61) enabled correct identification of the species used in this study,

Table 2. Univariate statistics for variables used in morphometric analyses of training data set, including specimens of questionable allocation

Variable[a]	Trinidad			Ecuador	
	K. iridicolor	*K. sulcifacies*	Questionable	*K. iridicolor*	*K. sulcifacies*
MS1	0.70 (0.11,50)	0.85 (0.10,79)	0.74 (0.11,17)	0.71 (0.08,50)	0.89 (0.08,29)
	0.41–0.91	0.64–1.07	0.55–0.92	0.50–0.88	0.72–1.09
MS2	0.64 (0.09,50)	0.69 (0.08,79)	0.62 (0.07,17)	0.65 (0.06,50)	0.69 (0.06,29)
	0.42–0.83	0.55–0.93	0.48–0.75	0.48–0.80	0.57–0.83
MS3	0.66 (0.10,50)$^{+}$	0.86 (0.10,79)	0.76 (0.11,17)	0.68 (0.07,50)	0.88 (0.08,29)
	0.39–0.88	0l.66–1.15	0.57–0.97	0.46–0.84	0.72–1.07
AXL	0.38 (0.05,50)	0.42 (0.05,79)	0.37 (0.05,17)	0.36 (0.03,50)	0.41 (0.04,29)
	0.25–0.48	0.32–0.57	0.30–0.46	0.28–0.43	0.34–0.49
*SCL	0.61 (0.11,50)	0.52 (0.07,79)	0.45 (0.06,17)	0.58 (0.06,50)	0.53 (0.05,29)
	0.31–0.82	0.39–0.68	0.35–0.57	0.40–0.72	0.42–0.60
SC1	1.14 (0.17,50)	1.16 (0.13,79)	1.02 (0.15,17)	1.09 (0.10,50)	1.17 (0.11,29)
	0.65–1.47	0.91–1.49	0.81–1.25	0.78–1.28	0.96–1.39
*SC2	0.77 (0.11,50)	0.83 (0.09,79)$^{+}$	0.74 (0.09,17)	0.74 (0.06,50)	0.83 (0.08,29)
	0.48–0.97	0.63–1.04	0.60–0.88	0.59–0.87	0.70–1.03
*SC3	0.57 (0.09,50)	0.62 (0.08,79)	0.55 (0.09,17)	0.55 (0.06,50)	0.64 (0.06,29)
	0.28–0.75	0.48–0.85	0.39–0.72	0.39–0.69	0.53–0.77
*BSH	0.19 (0.04,50)	0.23 (0.03,79)	0.21 (0.04,17)	0.17 (0.03,50)	0.22 (0.03,29)
	0.10–0.28	0.16–0.33	0.14–0.28	0.12–0.24	0.16–0.27
PSL	1.40 (0.18,50)	1.60 (0.15,79)	1.45 (0.22,17)	1.24 (0.15,50)	1.64 (0.10,29)
	0.79–1.73	1.25–2.08	0.13–1.91	0.94–1.50	1.47–1.82
*ME1	0.93 (0.13,50)	1.00 (0.10,79)	0.89 (0.10,17)	0.90 (0.07,50)	1.00 (0.08,28)
	0.57–1.17	0.83–1.26	0.74–1.04	0.69–1.05	0.85–1.21
*ME2	0.72 (0.09,50)	0.77 (0.08,79)	0.70 (0.09,17)	0.70 (0.05,50)$^{++}$	0.77 (0.06,28)
	0.46–0.89	0.58–0.96	0.58–0.86	0.61–0.85	0.63–0.90
PTL	0.68 (0.08,50)	0.86 (0.08,79)	0.78 (0.09,17)	0.72 (0.06,50)	0.90 (0.07,29)
	0.50–0.86	0.64–1.07	0.63–0.92	0.59–0.92	0.76–1.05
GSL	0.86 (0.13,50)	0.97 (0.10,79)$^{+}$	0.89 (0.10,17)	0.81 (0.07,50)	0.95 (0.08,29)
	0.52–1.16	0.73–1.19	0.71–1.10	0.65–1.04	0.77–1.14
MSW	1.05 (0.14,50)$^{++}$	1.13 (0.11,79)	1.02 (0.11,17)	0.99 (0.08,50)$^{+}$	1.11 (0.10,29)
	0.69–1.31	0.96–1.42	0.87–1.23	0.79–1.15	0.92–1.31
SCW	0.60 (0.10,50)	0.66 (0.08,79)	0.58 (0.09,17)	0.54 (0.06,50)$^{+}$	0.64 (0.07,29)
	0.33–0.81	0.51–0.89	0.43–0.73	0.40–0.67	0.52–0.79
SOW	0.76 (0.13,50)	0.98 (0.13,79)	0.83 (0.14,17)	0.68 (0.07,50)	0.96 (0.10,29)
	0.39–1.04	0.75–1.34	0.56–1.05	0.49–0.84	0.77–1.26
SIW	0.50 (0.08,50)	0.69 (0.09,79)$^{++}$	0.58 (0.10,17)	0.52 (0.07,50)	0.69 (0.06,29)
	0.25–0.65	0.50–0.94	0.37–0.76	0.36–0.66	0.56–0.83
HDL	0.45 (0.05,50)	0.42 (0.04,79)	0.40 (0.04,17)	0.42 (0.03,50)	0.42 (0.03,29)
	0.33–0.55	0.36–0.56	0.34–0.48	0.37–0.47	0.35–0.48
HDH	0.89 (0.09,50)	0.92 (0.07,79)	0.86 (0.08,17)	0.88 (0.05,50)	0.91 (0.05,29)
	0.64–1.08	0.77–1.08	0.75–1.01	0.75–1.00	0.81–1.02
IOD	0.94 (0.10,50)	1.03 (0.08,79)	0.96 (0.09,17)	0.91 (0.06,50)	1.03 (0.06,29)
	0.69–1.13	0.86–1.20	0.83–1.14	0.77–1.04	0.89–1.16
*EYH	0.44 (0.05,50)$^{+}$	0.45 (0.03,79)	0.42 (0.04,17)	0.43 (0.03,50)	0.44 (0.03,29)
	0.31–0.55	0.38–0.51	0.34–0.51	0.38–0.51	0.40–0.50
*GEN	0.37 (0.04,50)$^{++}$	0.42 (0.03,79)	0.38 (0.04,17)	0.39 (0.03,50)	0.43 (0.03,29)
	0.25–0.44	0.34–0.52	0.33–0.48	0.32–0.48	0.38–0.49
FL1	1.04 (0.12,50)	1.42 (0.12,79)	1.32 (0.15,16)	1.08 (0.08,49)	1.42 (0.09,29)
	0.65–1.25	1.10–1.73	1.00–1.51	0.86–1.30	1.24–1.61
SEP	0.24 (0.03,50)	0.24 (0.03,79)$^{++}$	0.23 (0.03,17)	0.22 (0.02,50)	0.24 (0.02,29)
	0.16–0.29	0.19–0.30	0.18–0.27	0.17–0.27	0.21–0.29
*FWL	2.63 (0.31,47)	2.81 (0.24,74)	2.60 (0.26,16)	2.62 (0.18,50)	2.94 (0.22,29)
	1.75–3.17	2.34–3.41	2.15–3.13	2.16–3.03	2.47–3.47
FWW	1.05 (0.12,46)	1.16 (0.10,76)	1.07 (0.10,17)	1.10 (0.08,50)	1.22 (0.09,29)
	0.77–1.25	0.95–1.40	0.92–1.29	0.89–1.24	1.01–1.40
MVL	0.98 (0.13,50)	1.00 (0.08,79)	0.95 (0.09,17)	0.99 (0.08,50)	1.11 (0.09,29)
	0.58–1.27	0.82–1.22	0.81–1.15	0.86–1.24	0.91–1.31

Values are means (STD, *n*)/range in millimeters. $^{+}$, Reject univariate normality, ($P \leq 0.05$, Kolmogorov-Smirnov D); $^{++}$, reject univariate normality, ($P \leq 0.01$, Kolmogorov-Smirnov D).

[a] See Table 1 for definitions. *, Deleted from analyses after stepwise discrimination procedure.

and these species are here transferred to the genus *Kapala* (new combinations). Further, *Lirata fulvicornis* Cameron (1904: 61) and *Lirata nigriventris* Cameron (1904: 61–62) are treated here as junior synonyms of *Kapala sulcifacies* (Cameron) (new synonymies). Cameron (1904) described these four species from Nicaragua based on earlier collections by C. F. Baker. Each of the species was based on a single specimen and all are housed in the BMNH. Additional material bearing the same locality data and Cameron's determination labels is located in the Cornell University collection. Cameron explicitly stated that his descriptions were based on single

specimens and the Cornell material cannot be considered part of the type series.

K. iridicolor and *K. sulcifacies* are distinguished from other species of *Kapala* by the following combination of character states: antennal flagellum testaceous, ramus of male first flagellomere elongate (exceeding head height), female flagellum serrate, facial striae (if present) moderately separated and not continuing onto supraclypeal area (Fig. 1D), mesoscutum dorsally rounded in frontal view (not bilobed medially, and dorsal lateral corners not sharply produced), striae of scutellum moderately separated, scutellar spines relatively narrow with striae roughly parallel along length, propodeal disk colliculate to smooth and medially flattened, upper mesepisternum smooth or with very weak irregular striae, and femora light testaceous. Individuals of *K. iridicolor* are recognized by the following character states: smooth face, frons slightly swollen lateral to scrobes cavity (Fig. 1C), mesoscutum with low lateral profile (Fig. 1A), lateral lobes of mesoscutum usually densely hairy, and scutellum elongate (Fig. 1A). Individuals of *K. sulcifacies* are recognized by the following: striate face, frons flat lateral to scrobes cavity (Fig. 1D), mesoscutum with strongly elevated lateral profile (Fig. 1B), lateral lobes sparsely hairy, and scutellum less produced (Fig. 1B). Females and males share the same distinguishing characteristics, except that females have a more robust mesosoma, and the facial striae are usually less pronounced in *K. sulcifacies* females.

Some geographical variation occurs within populations that is most apparent in the shape of the scutellar spines. The apex of the scutellar spines are broad and strongly emarginate in specimens from Trinidad and are gradually narrowed to a fine point in specimens from Ecuador. Both morphotypes are present and particularly well represented in collections from Ecuador and Trinidad, and these form excellent study populations for examining morphological variation. Most adults could be easily assigned to a particular morphotype, but a small proportion of individuals that had either different combinations of character states (i.e., striate face and low profile) or intermediate character states and therefore could not be confidently assigned.

Problems of assignment are apparent even in the original material available to Cameron, which contain all of the variation discussed in this study attributed to either specific or geographical differences. The four species recognized by Cameron came from two localities in Nicaragua (Chinandega and Managua). The holotype male of *K. sulcifacies* fits the description of this species and has the apex of the spines broadly excavated, which is typical of the Central American, Colombian, and Trinidadian populations. The holotype female of *K. iridicolor* matches females from the Ecuador population but lacks the bulging frons and distinct low profile of the mesoscutum which are characteristic of this species. However, the type is otherwise morphologically closer to *K. iridicolor* and is associated with *K. iridicolor* males at the same locality. Including the Cornell material, 17 males and 9 females were available for examination by Cameron. Of these, four males that were identified by Cameron as *K. iridicolor* or *K. fulvicornis* could be classified as intermediate forms with a bulging frons and low profile mesosoma but a striate face. Nicaragua and Honduras are the northern limits for *K. iridicolor;* we found a larger number of intermediate forms from this region than in more southern localities. This may account for the large amount of variation in the small amount of material available to Cameron.

Table 3. Eigenvalues and weights for the first two principal components, computed from the covariance matrix from log-transformed data

Variable	PCI	PCII
Eigenvalue	0.057	0.004
Proportion of Variance	0.800	0.067
SOW	0.36	−0.19
SIW	0.34	−0.34
MS3	0.30	−0.14
MS1	0.29	0.04
FL1	0.28	−0.38
SCW	0.26	0.23
PSL	0.24	−0.09
PTL	0.23	−0.25
AXL	0.22	0.19
GSL	0.21	0.00
MSW	0.21	0.21
SC1	0.19	0.36
MS2	0.18	0.24
IOD	0.17	0.06
SCP	0.16	0.24
FWW	0.16	0.08
MVL	0.13	0.18
HDH	0.12	0.19
HDL	0.09	0.40

Vectors are scaled so that sum of squares of elements in each vector is unity. Rows have been sorted on weights for first principal component separately.

Principal Component Analysis. The first two principal components computed from the log-transformed training data set accounted for 86.7% of the original variance. The third principal component accounted for 2.8% of the sample variance but did not contribute to a clear segregation of the different populations. The remaining principal components accounted for smaller proportions of the sample variance ranging from 1.8 to 0.0006% for the nineteenth. Eigenvalues and unitized eigenvectors for the first two components are shown in Table 3. The elements of each eigenvector have been scaled so that the sum of squares of all the elements in each vector is one. Therefore, the value of each element squared represents the proportion of variance that a variable contributes to the respective principal component (Neff & Marcus 1980).

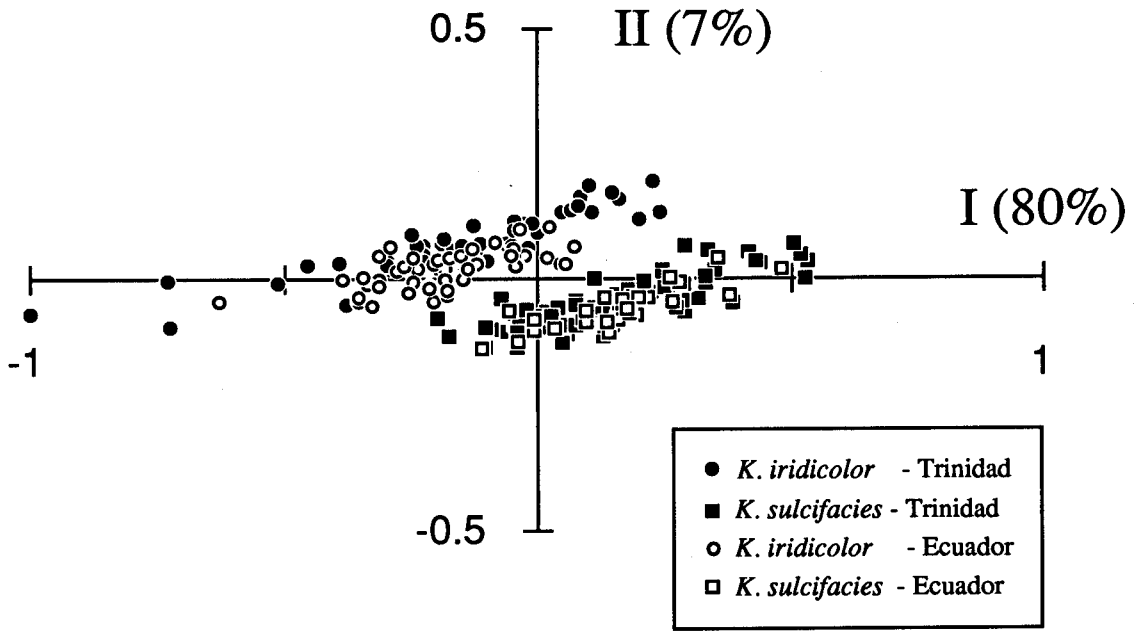


Fig. 3. Observations for training data set plotted on the first two principal components computed from the log-transformed data using 19 variables. The first principal component contains 80.0% of the sample variance, the second principal component contains 6.7%. Legend shows species and localities of four samples analyzed.

Principal components derived from log-transformed data yielded scores nearly identical to the untransformed data, suggesting that differences in the magnitude of variables did not have a strong influence on the principal component analysis. The log transformation resulted in increased weights for some variables which had relatively small mean values (SCP, HDL) and decreased the contribution of some variables with large mean values (FL1). However, the weights did not change drastically, and 8 of the 10 variables with the highest weights using untransformed data were among the 10 most highly weighted using the log-transformed data. Log transformations should equalize the contribution of numerically small and large variables to the principal components; therefore, the weights should be more representative of overall size and shape differences (Bookstein et al. 1985).

Observations of the training data set projected on the first two prinicipal components form two clusters congruent with species concepts based on the discrete measures listed earlier (Fig. 3). PCA did not reveal any differences between geographical populations of the two species. The two clusters of observations are both diagonal to the first two principal components (Fig. 3). This strongly suggests that these components, especially the first, are influenced by both overall size and shape differences (Jolicouer & Mosimann 1960, Humphries et al. 1981, Woolley & Browning 1987). The eigenvectors of the first principal component are all positive, suggesting that a size factor is involved with position along the first axis (Jolicouer & Mosimann 1960). In addition, we note that the long axis of the clusters appears more closely aligned to the first principal component than the second, suggesting that the first principal component contains a strong component of generalized size.

The oblique orientation of the two clusters to the first and second PCs makes isolation of variables associated with either size or shape differences difficult. However, two variables associated with height of the mesoscutum (MS1 and MS3) are strongly weighted on the first principal component, suggesting that *K. sulcifacies* does indeed have a taller mesoscutum. Additionally, SC1 is strongly weighted on the second PC, suggesting a proportionally longer scutellum in *K. iridicolor*. The strong positive weights for SOW and SIW on the first principal component indicate that the spines tend to be farther apart in *K. sulcifacies*. The strong positive weight for FL1 on the first principal component and strong negative weight for the same variable on the second principal component both reflect a longer antennal ramus in *K. sulcifacies* that is obvious even in univariate statistics (Table 2).

Canonical Variates Analysis. Observations of the four populations in the training data set are shown in Fig. 4 projected on the first and second canonical variates. Separation of the four populations along the first two canonical variates, using the 19 variables selected by stepwise discriminant analysis, was similar to the separation

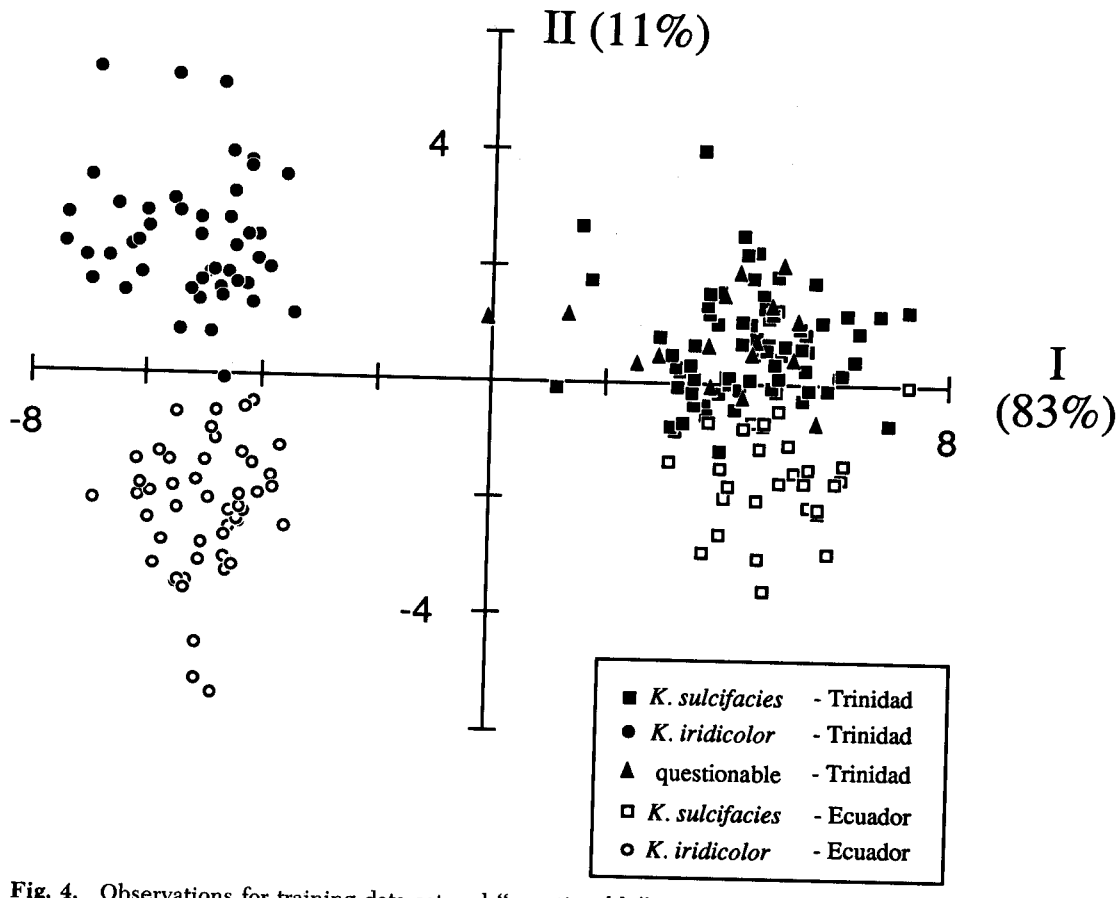


Fig. 4. Observations for training data set and "questionable" specimens plotted on the first two canonical variate axes computed from the untransformed data and 19 variables. Only *K. iridicolor* and *K. sulcifacies* that could be correctly allocated were used in construction of the canonical variate scores. Scores for questionable forms were computed using these same canonical variates (a posteriori classification). The first canonical variate accounts for 83.2% of the between-group variance and the second canonical variate accounts for 11.1%. Legend shows species and localities of four samples analyzed.

based on all 28, although clusters of observations were more concentrated in the former. Clear separation of the four populations is expected in canonical variate analysis because computations involve minimizing the within-group variance and maximizing the between-group variance to provide the most distinct separation of classes (Albrecht 1980, Campbell & Atchley 1981). However, addition of the "questionable" (Trinidad) class to the discriminant analysis did not alter the distribution of observations on the first two canonical variates, and the questionable observations were included within the *K. sulcifacies*–Trinidad cluster.

The first two canonical variates account for 94.3% of the between-groups variance. The raw, standardized, and total canonical structure coefficients are presented in Table 4. Standardized canonical coefficients are the products of the pooled within-class standard deviations and canonical vector coefficients for each variable. The standardized coefficients represent the amount of change in the canonical variate score for each change in the original variable by one standard deviation (Neff & Marcus 1980). Raw canonical coefficients can be applied directly to mean-centered raw data (or via constants as mentioned earlier) to calculate the canonical score for each individual. The total canonical structure values indicate the total-sample correlations between the original variables and the canonical structure scores.

The first canonical variate accounted for 83.2% of the between-group sample variance and essentially discriminates between species, regardless of locality. High positive standardized coefficients for MS1 and MS3 and strong negative coefficients for MS2 and SC1 (Table 4, Fig. 4), taken together, indicate a higher and narrower mesoscutum and shorter scutellum in *K. sulcifacies* as was seen in the PCA weights. Also congruent with PCA results were a strong positive

Table 4. Standardized, raw, and total canonical structure coefficients (CS) for the canonical variates analysis on the training data set

Variable	CVI coefficients			CVII coefficients		
	Raw	Standardized	Total CS	Raw	Standardized	Total CS
Proportion of Between-Group Variance		0.832			0.111	
MS3	18.94	2.53	0.75	0.35	0.05	−0.03
SOW	11.05	1.92	0.75	21.00	3.65	0.20
FL1	8.47	1.78	0.88	−3.16	−0.67	−0.04
IOD	15.87	1.49	0.59	7.68	−0.72	0.12
MS1	8.52	1.08	0.64	−10.42	−1.31	−0.03
PSL	2.61	0.57	0.67	2.55	0.55	0.26
AXL	0.35	0.02	0.47	0.77	0.04	0.19
GSL	−0.02	−0.03	0.56	5.95	0.72	0.17
SCP	−1.49	−0.04	0.31	22.07	0.60	0.32
SCW	−0.95	−0.09	0.45	3.12	0.30	0.32
MVL	−1.03	−0.10	0.24	−3.94	−0.40	−0.20
FWW	−0.02	−0.12	0.46	−5.77	−0.64	−0.21
PTL	−1.01	−0.12	0.76	−8.14	−0.93	−0.16
MSW	−2.56	−0.32	0.42	6.99	0.87	0.22
HDL	−17.32	−0.68	−0.15	−1.02	0.04	0.29
SIW	−6.16	−0.74	0.77	−19.36	−2.31	−0.04
HDH	−13.98	−0.98	0.26	−8.57	−0.60	0.07
MS2	−13.88	−1.07	0.29	−3.00	−0.23	−0.06
SC1	−18.65	−2.53	0.21	−3.04	−0.41	−0.12

Standardized coefficients are the amount that the canonical score will change for a change in the original variable of one standard deviation. The total CS values are the total–sample correlations between the original variables and CS scores. Rows have been sorted by the elements of the vector of coefficients for the first standardized canonical variate.

coefficient for SOW, indicating wider separation of scutellar spines in *K. sulcifacies*, and a strong positive coefficient for FL1 reflecting a longer antennal ramus in *K. sulcifacies*. Unique to the CVA results are strong positive coefficients for IOD and a negative coefficient for HDH, which together suggest a tendency toward a more strongly transverse head in frontal view in *K. sulcifacies*.

The second canonical variate represents 11.1% of the between-group sample variance and discriminates between localities; therefore, the standardized coefficients of particular variables on it provide insights into the influence of morphology on location alone. Specimens from Trinidad tend to have positive scores on the second CV (Fig. 4) and specimens from Ecuador almost without exception have negative scores. The

Table 5. Summary statistics for geographic distribution of *K. iridicolor* (KI) and *K. sulcifacies* (KS)

Parameters	Locations					
	Colombia	Costa Rica	Ecuador	Panama	Trinidad	Venezuela
			Males			
1. No. specimens, n.	161	150	729	112	2,349	21
2. No. collections, c.	41	65	30	68	139	8
3. Only KI present, c(n).	15 (26)	4 (4)	10 (20)	51 (95)	16 (24)	0
4. Only KS present, c(n).	14 (37)	60 (142)	7 (13)	16 (15)	64 (233)	6 (6)
5. Both KI and KS present (sympatric), c(n)/(KI:KS)	11 (98) (26:73)	1 (4) (2:2)	13 (696) (103:593)	1 (2) (1:1)	59 (2092) (1369:723)	2 (15) (8:7)
6. No. large collections in which n > 10.	5	0	9	1	38	0
7. No. large collections with both KI and KS.	4	0	9	0	35	0
8. % KS males in all collections.	82.4	96.0	15.7	14.3	68.2	66.7
9. % KS males in sympatric collections, mean (c)/range.	63.7 (11) 25.0–92.9	50.0 (1) —	19.6 (13) 2.6–69.2	50.0 (1) —	58.1 (59) 25.0–96.9	50.9 (2) 14.3–87.5
			Females			
10. No. specimens, n.	39	78	74	21	247	10
11. No. collections, c.	15	42	19	8	97	5
12. % KS females in all collections.	92.3	96.2	98.5	95.2	95.5	90.0
13. % KS females in collections with KI and KS males, mean (c, n)/range	100 (3, 13) 100	— —	91.1 (6, 58) 50–100	— —	99.4 (25, 120) 93.3–100	75.0 (2, 6) 50–100

Number of collections refers to total number of locations and dates sampled in a given country. Sympatry indicates strict sympatry, which was determined by congruence of all label information. Questionable forms, representing 1.2% of total number of specimens, were not included.

strong negative coefficient for PTL shown in Table 4 indicates that individuals of both species from Ecuador tend to have longer petioles. The negative coefficient for MS1 suggests that the higher mesoscutum in *K. sulcifacies* is confounded by a trend to a higher mesoscutum in specimens from Ecuador. The third canonical variate contains the remaining 5.7% of the variance. It provided good discrimination of *K. sulcifacies* specimens to locality, but interestingly, little discrimination of *K. iridicolor* to locality.

A posteriori classification of the calibration data was very successful: one specimen of *K. sulcifacies* from Trinidad was classified into the *K. sulcifacies*–Ecuador class. This is to be expected, of course, because the discriminant functions were constructed using these data. All of the specimens from Trinidad of questionable identity were classified into the *K. sulcifacies*–Trinidad class.

Test Data. Of greater interest is the performance of the discriminant functions (canonical variates) on the observations in the test data set. Figure 5 shows data from several populations of both species from Trinidad (test data) projected onto the first two canonical variates constructed using the calibration data. These individuals fall into almost exactly the same locations as those in the calibration data, perhaps the only difference being more *K. sulcifacies* with negative scores on the second CV (however, this is also apparent in the calibration data; see Fig. 4). These results indicate that the morphological differences noted between species are consistent across several Trinidad localities and that specimens from Trinidad share a similar covariance structure. Classification of the test data using the discriminant functions developed from the calibration data were reasonably successful. All five observations assigned a questionable designation were assigned to the *K. sulcifacies*–Trinidad class. Of the 85 specimens determined as *K. iridicolor*, 7 were treated as misclassified and placed in the *K. iridicolor*–Ecuador class, indicating a morphology more like that of specimens from Ecuador. Of the 160 specimens determined as *K. sulcifacies*, 7 were treated as misclassified and placed into the *K. sulcifacies*–Ecuador populations. The good results obtained with the *K. sulcifacies* class indicate that the overlap of *K. sulcifacies*–Trinidad and *K. sulcifacies*–Ecuador seen in Fig. 4 is misleading. In fact, these two classes are quite distinct on the third canonical variate.

Although the morphological distinction between species and countries (Trinidad and Ecuador) appears to be very consistent in both the calibration and test data, there was no apparent pattern between localities in Trinidad (Fig. 5). We also found no apparent patterns when observations sorted by locality and month of collection were plotted on the first canonical variate axis, indicating that time of year has no effect on morphology.

Geographical Distribution. The distributional data for *K. sulcifacies* (KS) and *K. iridicolor* (KI) is summarized in Table 5 by the number of collections and specimens for six countries in South and Central America. The distribution of *K. sulcifacies* and *K. iridicolor* is illustrated in Fig. 6. Additional small collections were also recorded from Brazil (males, 5KS, 1KS-1KI in sympatry; female, 1KS), El Salvador (males, 8KS; females, 2KS), Honduras (males, 1KI), Nicaragua (females, 1KS, 2KI), Peru (males, 3KS; females, 2KS), Mexico (males, 5KS; females, 14KS), and Surinam (females, 1KS, 1KS) (see Fig. 7). These smaller collections indicate that the distributional overlap of both *K. sulcifacies* and *K. iridicolor* extend at least as far north as Honduras and as far south as Peru and Brazil. A few specimens from Arizona and northern Argentina that are slightly different in some features may be extremes in the distribution of *K. sulcifacies* and *K. iridicolor*, respectively, but are currently excluded from these species as recognized for this study. In Fig. 6, sympatry is presented in a broader sense without a restriction placed on the date of collection for determination of sympatry.

In total, 4,040 specimens were examined as part of this study (excluding those mentioned in the above paragraph), and of these, 3,991 are represented in the summary of information in Table 5. Individuals of questionable identity (26 males, 23 females) accounted for 1.2% of the total number of specimens and are not included in any of the following calculations. Individuals were distributed over a total of 291 separate collections of males and 186 collections of females for both species. The largest of the samples were usually collected by malaise trap, although collections excluding those from the BMNH, CNC, and FLA were mostly collected in sweep samples. The male-biased sex ratio (3,522 males: 469 females) may be attributed to the greater mobility of males in search of females. We assume that there is no bias toward the collection of either species. Of the collections of males, there were a number of samples in which *K. iridicolor* and *K. sulcifacies* were collected alone (Table 5, rows 3 and 4). The number of collections with males of both species, in strict sympatry, ranged from 1 in Costa Rica and Panama to 59 in Trinidad and represented a total of 2,907 specimens (Table 5, row 5), or 82.5% of all males collected. There is an obvious bias toward the collection of males of one species or the other in small collections as a result of sampling error. If only collections of more than 10 males are used (Table 5, row 6), the proportion of strictly sympatric collections increases dramatically (rows 6 and 7). The percentage of *K. sulcifacies* in all collections ranged from 14.3 in Panama to 96.0 in Costa Rica (Table 5, row 8). The percentage of *K. sulcifacies* that

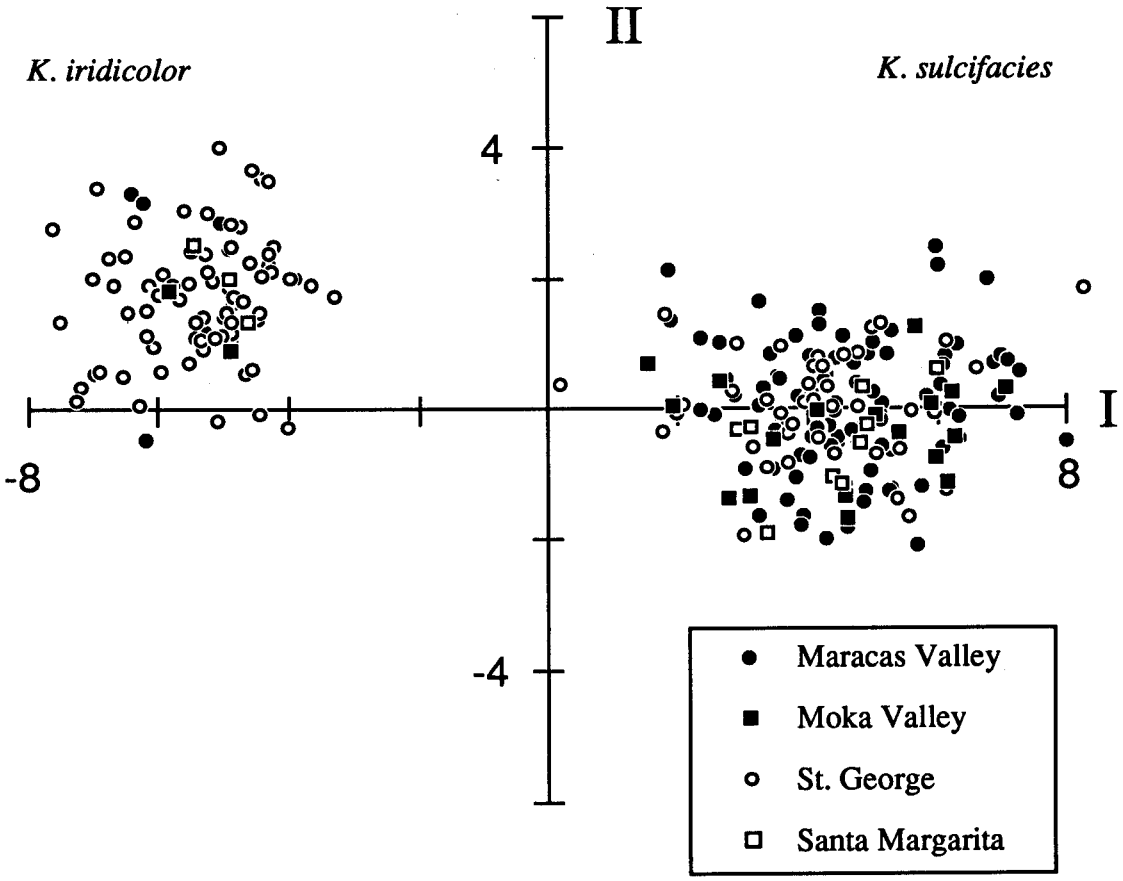


Fig. 5. Observations of *Kapala* spp. in Trinidad plotted on the first two canonical variates. Canonical scores obtained from application of discriminant functions from training data set. Legend shows four localities analyzed. Negative scores on the first canonical score belong to *K. iridicolor* and all positive scores to *K. sulcifacies*.

occurs in all collections of strictly sympatric males (Table 5, row 9) ranges from an unweighted average ($\Sigma p_i/N$) of 19.6 in Ecuador to 63.7 in Colombia. For all of the countries, the percentage of *K. sulcifacies* males was 55.5 (1955/3522) over all collections and 51.9 (1,509/2,907) in strict sympatry.

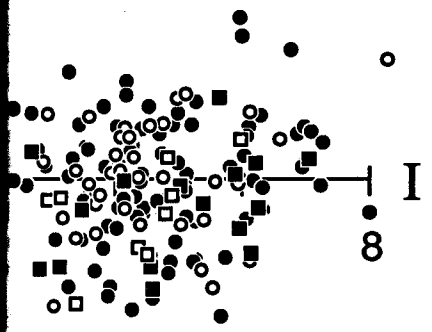
The number of females represented in the samples is low, and in many cases females were not collected in association with males. Whenever females were collected with males from an independent (pure species) sample of males of either species, they almost always belonged to *K. sulcifacies*. The percentage of females of *K. sulcifacies* in all collections ranged from 86.5 in Ecuador to 95.5 in Trinidad. The percentage of female *K. sulcifacies* in strictly sympatric collections of males ranged from 75.0 in Venezuela to 100 in Colombia (Table 5, row 13). Given the relatively low percentage of *K. sulcifacies* males in strictly sympatric collections from Ecuador (Table 5, row 9), the percentage of *K. sulcifacies* females in sympatric collections from Ecuador is unexpectedly high.

Both species were found ovipositing on *Cordia macrostachya* (Trinidad) and *Gossypium hirsutum* (Nicaragua) at localities where the two species were found in strict sympatry. J.M.H. observed both species in Trinidad ovipositing in flower buds of *Cordia* separated by <3 m. The only other known host plants are *Cordia cana* (Costa Rica) for *K. iridicolor* and "a flowering asclepiad-like cactus" (Nicaragua) for *K. sulcifacies*. Thus, there appear to be only minimal differences between the two in the use of host plants.

Discussion

The morphometric analyses show a strong morphological distinction between *K. iridicolor* and *K. sulcifacies* with no intermediate forms, supporting the notion of two distinct species that are reproductively isolated. Specimens of questionable assignment were allocated to *K. sulcifacies* by the discriminant functions. Generally, questionable forms are rare and morphometric analyses supported the discrete characters that

K. sulcifacies



- Maracas Valley
- Moka Valley
- St. George
- Santa Margarita

st two canonical variates. Canonical scores set. Legend shows four localities analyzed. nd all positive scores to *K. sulcifacies*.

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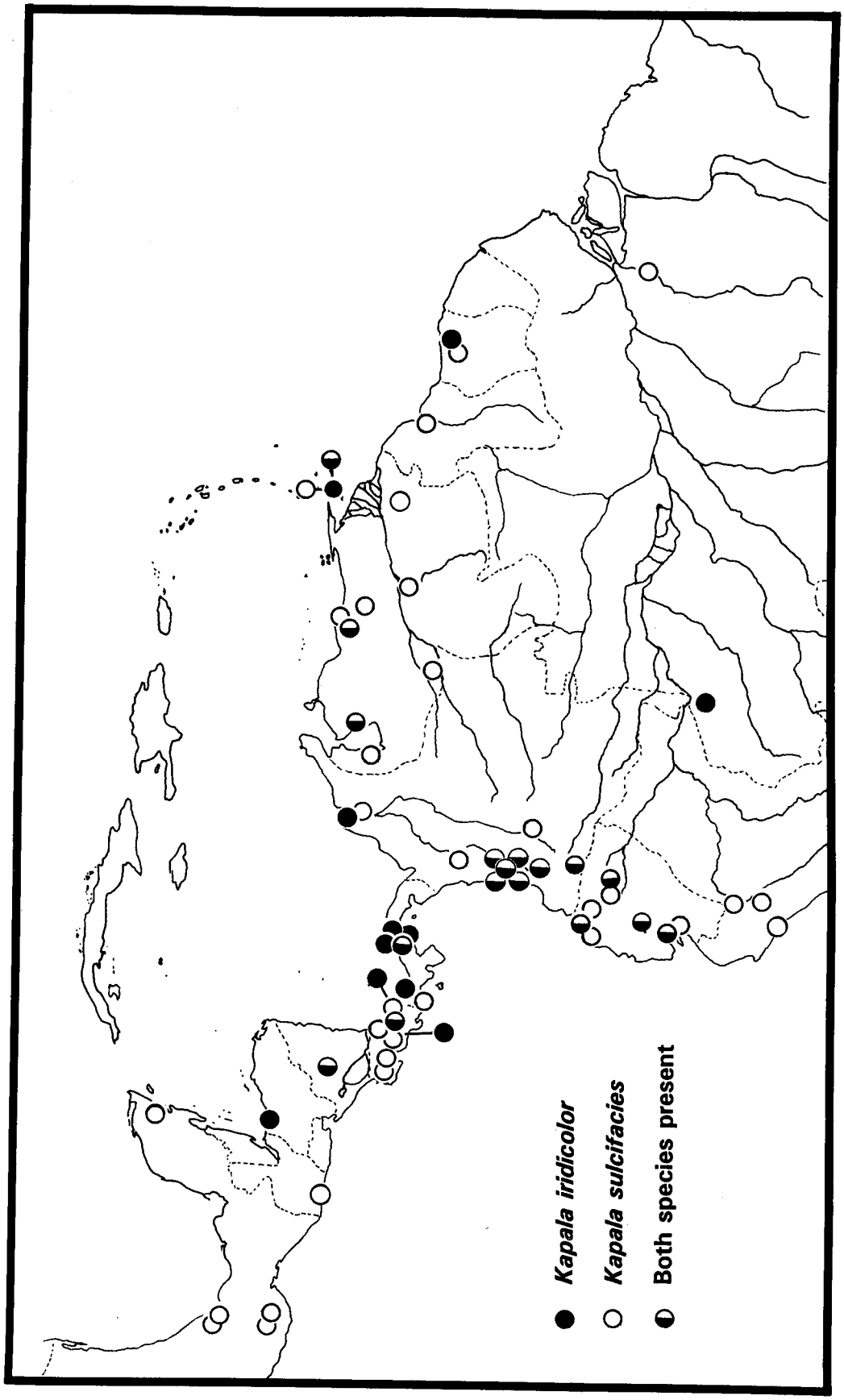
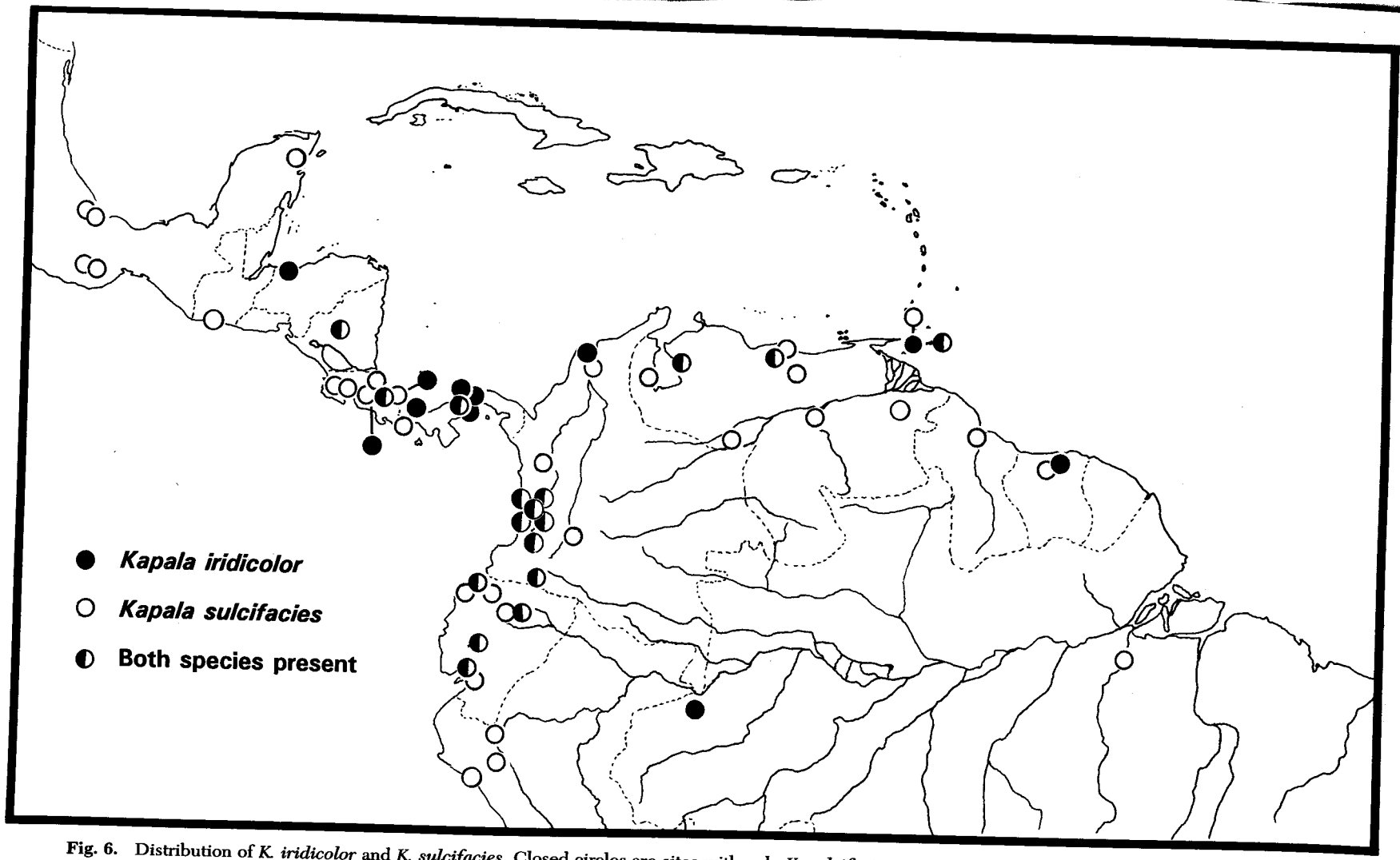


Fig. 6. Distribution of *K. iridicolor* and *K. sulcifacies*. Closed circles are sites with only *K. sulcifacies*, open circles are sites with only *K. iridicolor*, half-filled circles are localities where both species are present. Sympatry is interpreted in the broad sense and requires the presence of the two species at the same locality but not necessarily the same date. Points represent summaries of collections at each locality. Individuals of questionable allocation are not represented.



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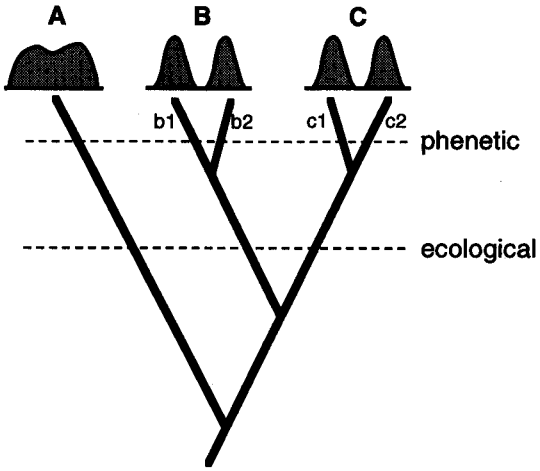

Fig. 7. Hypothetical relationship among three "species" of *Kapala* that express phenotypic polymorphism. Distributions represent frequency of phenotypes at any particular locality. Dashed lines represent two levels of recognition based on different criteria to infer reproductive isolation. Lowercase letters refer to additional species recognized using phenetic criteria.

were used to separate the two species; therefore, discriminant functions are not usually necessary for separation of the two species. There is a geographical separation of populations in each of the species along the second canonical variate that may indicate a pattern of clinal variation across South America. This variation was not apparent in the first few principal components. The geographic differentiation is correlated between the two species based on a similar magnitude of change in location on the second canonical variate. This suggests that similar shape differences are involved in both species.

Interestingly, although there is a strong morphological separation of populations, the problem of almost complete sympatry still exists. Of 53 collections with >10 specimens, 48 contained both species in strict sympatry. This may be because both species use the same host resources with regard to either the plant or ant. These two species are morphologically quite distinct from other *Kapala* species and may be closely related, if not sister species. Other pairs of closely related species of *Kapala* express similar morphotypes that also occur in sympatry. These pairs of species differ only slightly from each other in the length and coloration of the male antennae, degree of serration of the female antennae, striation of the mesosoma, or different spine morphology. In only one undescribed species pair from Costa Rica (in J.M.H. collection) is the low profile and bulging frons correlated with the smooth face. In most other cases, the face is striate in both morphotypes. *Kapala* sp. nr. *cuprea* Cameron (Paraguay; in Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina) exhibits a full range of intermediate morphological types between a low and high profile mesosoma.

Environmental factors as causative agents for the morphological differences are discounted by the fact that different populations of *Kapala* from Trinidad express no differences attributed to either locality or date. However, a correlation of morphotypes with the host ant being attacked (either species or caste) still remains a strong possibility for observed differences within a locality. This would allow for a single species with two forms that are host-dependent, and geographic differences may be correlated with the host species. If this were the case, we would expect a similar ratio of morphotypes in males and females, but this does not occur.

There is another interpretation of the presence of two distinct morphotypes. The phenotypic separation may be a genetic polymorphism within a single species (or group of species, each with two variant forms) (West-Eberhard 1989). There is a strong bias toward the females of *K. sulcifacies* and almost complete absence of female *K. iridicolor* at localities where the two are sympatric. The males of each species are commonly collected in approximately equal numbers when found in sympatry (Table 5, row 9). The overall proportion of females at sympatric localities is 9:1 and males occur in a ratio of ≈1:1 (within a broad range of 2.2–92.9% over the entire geographical range). Importantly, the proportion of females of *K. sulcifacies* is always high and is not correlated with the proportion of males (Table 5, rows 8 and 12). These ratios suggest that the differences between the two phenotypes could be related to one or more linked dominant genes. Thus, a recessive allele(s) would produce the smooth face–low mesoscutum phenotype of *K. iridicolor*. Such a phenotype would be expressed in all haploid males that possess this genotype but would be expressed only in diploid females with a homozygous recessive genotype. However, this would not necessarily explain the presence of intermediate forms.

Phylogenetic affinities among the above-mentioned species are currently unresolved in *Kapala*. Relationships presented in Fig. 7 are what we would regard as a plausible hypothesis under the minimal assumption that *B* and *C* are reproductively isolated and not merely extreme variants of a single species. Species *A* is representative of *K.* sp. nr. *cuprea*, which has a broad range of phenotypes that can occur in sympatry. *K. iridicolor* and *K. sulcifacies* are represented by branches *b1* and *b2* such that *B* is composed of the two phenotypes that occur in sympatry. Finally, group *C* represents a sister species that has similar distinct phenotypes occurring in sympatry such that *c1* and *c2* have similar corresponding phenotypes in *B*. Basing our inference of reproductive barriers using only phenetic concepts would result in the recognition of five

species (*A, b1, b2, c1, c2*). However, if the two phenotypes expressed in *B* or *C* were a polymorphism within a species, then only three species (*A, B, C*) are recognized, and there would be no reproductive barriers between *b1* and *b2* or *c1* and *c2*. If this is true, the occurrence of phenotype pairs may have a phylogenetic component which arose in the ancestor of *B* and *C*, and smooth and striate forms *within* several species are more closely related.

Phenotypic polymorphism has been shown for a number of organisms and may be based on *conditional* mechanisms which are dependent on the environmental conditions, or *allelic-switch* mechanisms which are dependent on alleles present at one or more switch loci (West-Eberhard 1989). Either mechanism may result in two or more phenotypes of one species occuring in temporal and spatial sympatry. Initially, assortative mating between phenotypes during mating would not occur; however, sympatric speciation could result from a continued accumulation of differences (West-Eberhard 1989).

We are continually presented with the problem of recognizing interbreeding members of a species based only on phenetic measures. In this example, the distinct morphological separation of the two forms in sympatry argues for their recognition as distinct species, and we elect to retain the two species names for the moment. However, the occurrence of both morphotypes in almost complete sympatry and of similar morphotype pairs in closely related species suggests that this is a polymorphism within a species. The hypothesis that these represent a single species can be addressed only by future genetic or biological studies of these very puzzling animals.

Acknowledgments

We thank G. J. Umphrey (University of Western Ontario), F. Ronquist (Lund University, Sweden), and W. B. Smith (Texas A&M University) for their comments on earlier drafts of the manuscript. Marilyn Houck (Texas Tech University, Lubbock) provided the digitizing software. Mike Rose and John Huff (Texas A&M University) provided valuable assistance in making the digitizing equipment operable. Greg Zolnerowich and Karen Bell (Texas A&M University) tolerated the incessant beeping during its operation. We also thank the curators of numerous museums who made material available, and collectors who persist in collecting long series of specimens. This work was supported in part by an NSF BSR 8914680 grant to J.B.W. and J.M.H., and an NSERC Postgraduate Fellowship to J.M.H. while at Carleton University, Ottawa. This is contribution no. 14 of the Center for Biosystematics and Biodiversity, Texas A&M University.

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Received for publication 16 October 1992; accepted 5 April 1993.