The subspecies problem in the Trident leaf-nosed bat, *Asellia tridens:* homomorphism in widely separated populations

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Abstract

Examined univariate and multivariate morphometric variation in populations of a desert bat, *Asellia tridens*, from most of its range in Africa and Asia. Morphometric and color variation in this species suggest that two distinct taxonomic groups exist. One of these represents at least two widely disjunct populations with a large intervening region occupied by the other morphologically distinct group. The existence of widely separated homomorphic populations may prove to be more common than previously believed in mammalian species with large ranges, and may cause difficulty in recognizing subspecies based on classical taxonomic criteria.

Introduction

The trident leaf-nosed bat, *Asellia tridens* (É. Geoffroy St.-Hilaire, 1813), is known from arid and semiarid regions from Pakistan and Afghanistan through Arabia to Morocco and Mauritania, and as far south as Somalia and Gambia (Corbet and Hill 1980). The infraspecific systematics of this species has been complicated by descriptions of several subspecies that were based on one or a few specimens, and by the generally patchy distribution of this species in desert valleys and oases, and near human habitation.

Understanding morphologic variation in this species is important for several reasons. First, *Asellia* is adapted to xeric conditions, but avoids the extremely arid and usually lifeless extremes in many parts of the Sahara and Arabian deserts. This results in disjunct populations, which may adapt to the specialized conditions of local habitats. Second, several subspecific designations have been based primarily on pelage color and small differences in size; thus, an understanding of how color relates to morphometric variation (and subspecific designations) is of critical importance in establishing the taxonomy of this or any other color-variable species. Third, size variation in this species is interesting because larger specimens are reported to be found in peripheral portions of its range (e.g., Afghanistan, southwestern Arabia, and southern Sudan), with smaller individuals occurring in the central (and major) portion of the range of the species (Kock 1969). Similar patterns of size variation occur in other North African desert mammals (Osborn and Helmy 1980; Qumsiyeh 1985), and it thus is of interest to document this quantitatively across the range of a widely distributed species like *A. tridens*. Such documentation allows evaluation of the relation of morphologic variation to recognized zoogeographic regions.

Previous studies of variation in *A. tridens* either did not utilize statistical methods or, at most, employed only univariate statistics (Harrison 1957, 1964; Kock 1969; DeBlase 1980). In none of these studies was sexual dimorphism considered, or controlled for, in the accompanying analyses of geographic variation. In order to comprehensively assess morphometric variation in *A. tridens*, we undertook a series of multivariate analyses that allowed us to determine the extent of overall variation between sexes and among geographic populations. We also evaluated the usefulness of pelage color to describe geographic groupings within *A. tridens*.

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Materials and methods

We recorded three external and 18 cranial measurements from 153 specimens from across most of the range of *A. tridens* (Fig. 1, Appendix I). In addition to the measurements listed in Appendix II, we recorded dorsal and ventral pelage color on these and additional specimens (Appendix I), by

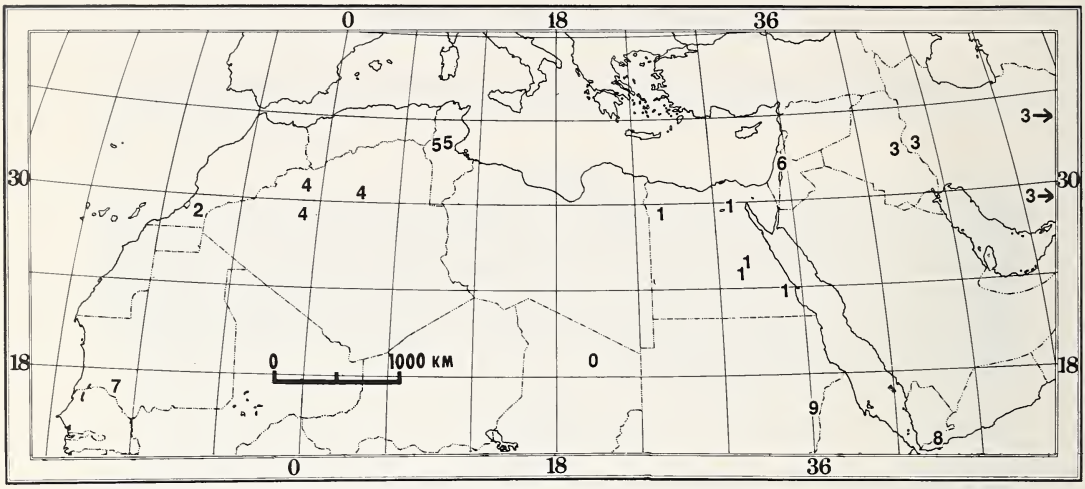

Fig. 1. Sample localities for *Asellia tridens*. Numbers refer to samples and groups used in this study. Two localities in Pakistan and Afghanistan are not shown here (outside boundaries) and are indicated by numerals with arrows

comparing specimens directly with the color standards of Ridgway (1912), updated by Smithe (1974, 1975). The data initially were subjected to a Principal Components Analysis (PCA) of the standardized character correlation matrix. PCA is an exploratory method involving no a priori assumptions concerning groups within the data set. The procedure allows ordination of individuals on a minimum number of axes accounting for a maximum amount of the data variance, in order to determine visually the groups that may occur within the overall sample. The significance of such groups then may be verified by appropriate statistical tests. The most appropriate test for this is a two-way (sex versus locality) Multivariate Analysis of Variance (MANOVA). This test recognizes and utilizes inter-character correlations in contrast to the analogous univariate statistics, which cannot test for multivariate differences (Willig et al. 1986). Because a significant sex-by-locality interaction effect was found in the two-way MANOVA, one-way MANOVA and Analyses of Variance (ANOVAs) were run to elucidate the manner in which sexual dimorphism differs between geographic groups. MANOVA utilizes only those specimens that have no missing data, and thus only 147 specimens were usable in multivariate analyses.

We used PCA again to search for subgroups within the two geographic groupings that were determined by the first analyses. Because sexual dimorphism had been demonstrated, each sex was treated separately in these analyses. Where a subgroup was found, MANOVA again was used to test its significance.

After ascertaining statistical significance of groups within the data, we used Canonical Discriminant Analysis (CDA) to define the differences among groups. CDA is a multivariate procedure that produces a discriminant function which maximizes the effects of those characters which differ most among groups.

Finally, we were concerned with the problem of several phenotypically intermediate specimens. We used classificatory Discriminant Function Analysis (DFA) to determine the closest affinities of these specimens.

Results

The principal Components Analysis of all specimens indicated two primary clusters, as defined by the projections of specimens onto Components I and II, which account for 38.4 and 12.0 percent of the total variation, respectively (Fig. 2). No other component or combination of components was found that showed clustering of specimens. The first cluster (group A) included specimens from Chad, Egypt, Algeria, Tunisia, People's Democratic Republic of Yemen, and Sudan (populations 0, 1, 4, 5, 8, and 9, respectively). The second cluster (group B) included specimens from Morocco, southwestern Asia, Palestine, and Mauritania (populations 2, 3, 6, and 7, respectively). We applied subsequent tests of geographic variation based on these two groups.

The two-way (group versus sex) MANOVA of these two phenotypic groups showed very high significance for both group and sex ($P < .001$), and also high significance for group-by-sex interaction ($.01 > P \geq .001$, see Table). Univariate ANOVAs indicated significant between-group differences in 19 of the 21 characters, between-sex differences in nine characters, and a significant interaction effect in seven characters. The one-way MANOVAs indicated highly significant sexual dimorphism in both groups A and B (Table). Of the 21 characters tested, the one-way ANOVAs indicated that 12 are significantly dimorphic in group A, whereas four are dimorphic in group B.

Because of the sexual dimorphism and the geographic grouping, we considered four groups for further analyses (A males, A females, B males, and B females). Within these

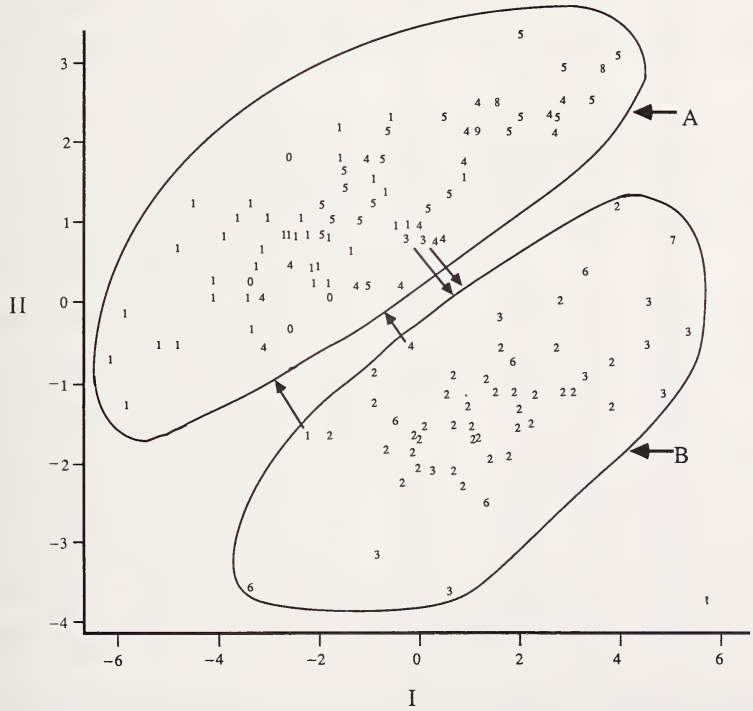

Fig. 2. Plot of *Asellia tridens* specimens on principal components I and II, accounting for 38.4 and 12.0 percent of the data variance, respectively. Numbers for specimens refer to locality groups as in Fig. 1. Arrows indicate four specimens of concern, that were determined by discriminant function analysis to be most similar to other specimens from their respective locality groupings

groups, additional PCAs suggested clusters only in group A females, in which the two Yemeni specimens differ in components I and II from those specimens from the remainder of group A localities. A MANOVA indicates that the difference is highly significant ($P < 0.005$), and the univariate ANOVAs show eight of the 21 characters to differ significantly.

Group means and standard errors for 21 characters in *Asellia tridens*

Also shown are *F*-values and significance levels[a] for 2-way MANOVA[b] and ANOVAs, and the same statictics for 1-way tests between sexes of each group separately. Characters are listed and described in Appendix II

	Group A[c]		Group B[d]		Two-way tests			Sexual Dimorphism	
Variable	Males	Females	Males	Females	Group	Sex	Interaction	Group A	Group B
MANOVA					58.29***	3.17***	2.25**	2.54**	2.92**
FAL	49.89 ±0.24	49.11 ±0.24	51.09 ±0.21	51.89 ±0.46	41.92***	0.50	6.92**	4.50*	2.93
MTC3	35.70 ±0.24	35.12 ±0.19	36.37 ±0.20	37.01 ±0.36	20.13***	0.57	5.68*	3.79	2.42
MTC4	29.50 ±0.23	29.23 ±0.19	30.58 ±0.16	30.79 ±0.53	27.02***	0.08	0.69	0.49	0.28
GLS	18.65 ±0.07	18.31 ±0.07	18.97 ±0.04	18.85 ±0.12	45.24***	12.68***	1.70	11.33**	1.38
CBL	16.47 ±0.07	16.08 ±0.06	16.15 ±0.04	16.00 ±0.12	7.72**	19.17***	2.36	17.54***	2.09
BBC	7.83 ±0.03	7.66 ±0.04	7.82 ±0.04	7.95 ±0.07	4.21*	1.13	8.27**	9.26**	2.09
IOC	2.33 ±0.02	2.36 ±0.02	2.47 ±0.02	2.55 ±0.09	29.90***	3.42	0.48	1.80	1.87
MASTB	8.69 ±0.03	8.61 ±0.03	7.10 ±0.03	7.12 ±0.20	962.14***	0.62	0.69	3.15	0.03
ZYGB	10.32 ±0.04	10.09 ±0.04	10.58 ±0.04	10.44 ±0.11	46.81***	12.71***	0.49	13.91***	1.78
RBCA	5.27 ±0.03	5.10 ±0.03	5.33 ±0.03	5.29 ±0.06	14.18***	13.02***	3.40	15.65***	0.39
RBMAX	7.33 ±0.03	7.25 ±0.03	7.47 ±0.03	7.51 ±0.05	29.39***	2.11	3.29	5.23*	0.37
PEW	2.26 ±0.01	2.24 ±0.01	2.29 ±0.02	2.37 ±0.03	8.27**	0.96	6.54*	0.62	5.49*
NASB	6.07 ±0.03	5.93 ±0.04	5.53 ±0.02	5.63 ±0.08	157.54***	1.36	7.07**	5.61*	2.57
PALL	3.66 ±0.04	3.78 ±0.05	3.70 ±0.03	3.57 ±0.11	0.99	0.29	5.11*	2.91	2.53
PPLL	8.53 ±0.04	8.36 ±0.04	8.61 ±0.03	8.54 ±0.11	11.81***	10.00**	1.23	10.64**	0.87
UTRL	6.76 ±0.02	6.62 ±0.03	6.87 ±0.02	6.74 ±0.03	29.49***	24.63***	0.04	12.85***	13.71***
UPMLM	5.06 ±0.02	5.04 ±0.03	5.28 ±0.02	5.19 ±0.05	55.43***	1.80	1.71	0.12	3.01
BRCD	5.36 ±0.03	5.29 ±0.03	5.37 ±0.02	5.29 ±0.05	0.27	5.68*	0.01	3.00	2.82
MANDL	12.19 ±0.06	11.97 ±0.04	12.40 ±0.03	12.20 ±0.09	27.99***	15.50***	0.08	9.16**	6.25*
MANDTR	7.81 ±0.04	7.66 ±0.04	7.92 ±0.03	7.69 ±0.08	10.69**	16.81***	0.81	6.85*	12.12***
CORH	5.02 ±0.06	4.91 ±0.03	5.23 ±0.04	5.37 ±0.09	32.64***	0.16	5.10*	2.73	2.52

[a] *, $0.05 > P \geq 0.01$; **, $0.01 > P \geq 0.001$; ***, $0.001 > P$. – [b] Using Wilks' criterion for calculation of exact F. – [c] Chad, Egypt, Algeria, Tunisia, Yemen, and Sudan (populations 0, 1, 4, 5, 8, and 9). N = 45 ♂♂, 45 ♀♀. – [d] Morocco, SW Asia, Palestine, and Mauritania (populations, 2, 3, 6, and 7). N = 49 ♂♂, 14 ♀♀.

The Canonical Discriminant Analysis of sexual dimorphism within the two geographical groups shows that there is considerable overlap of the sexes on canonical variate I in both groups (more so in group B). The CDA of geographic group differences, in contrast, indicates that, for either sex, a linear function may be constructed that entirely separates the two groups, the separation being more distinct in males. The same function for the females also successfully separates the two Yemeni specimens from the remaining group A females.

Classificatory Discriminant Function Analysis for morphometrically intermediate individuals was performed separately for each sex. In all cases this analysis indicated that the individuals in question are associated with the other specimens from their respective populations.

Discussion

Morphometric variation in *Asellia tridens*

Harrison (1957) observed that forearm measurements were larger and ears relatively smaller for specimens from Iraq and Yemen (which he referred to *A. t. murraiana*) than for those from Oman, Hofuf Oasis in Saudi Arabia, Sudan, and Egypt (which he referred to *A. t. tridens*). Although he included both males and females and provided no statistical tests of these differences, Harrison (1957) concluded that his data show that this species may migrate from Iraq to Yemen in the winter months. Gaisler et al. (1972) and Qumsiyeh (1985) found a slight difference between populations in northern and southern Egypt, but allocated all Egyptian material to the nominate subspecies. Kock (1969) suggested that size difference (especially forearm length) may be due to climatic (primarily temperature) differences.

All earlier studies listed above of *A. tridens* were limited to cursory examination of few specimens with at best univariate statistics. More importantly, these studies involved pooling of males and females into single samples, resulting in confusion of variation due to sexual differences with that due to geographic differences. Our results, based on specimens from most of the range of *A. tridens*, suggest that two distinct clusters occur (groups A and B), which are distinguished by morphometric analysis.

Of special interest is the highly significant sex-by-group interaction effect in the MANOVA (Table). In univariate ANOVA, a difference of either direction or degree may cause an interaction effect among treatments; i.e., a different group may be larger, or the same group may be larger to greater or lesser extent. In the multivariate case, a third possibility (not associated with the other two) exists that may also cause an interaction effect. This is a difference in intercorrelation among characters. In the example of *A. tridens*, both group A and group B are highly dimorphic sexually, but the expression of dimorphism is quite different in the two groups. Group A is dimorphic for 12 of the 21 characters examined (males larger in all 12), whereas group B is dimorphic for only four (males larger in three, females in one).

The Canonical Discriminant Analysis indicates that males are more geographically variable than are females. However, this sex-related difference in variability is not expressed as a greater or lesser degree of overall dimorphism in one or the other geographic group (the MANOVA F-values for sexual dimorphism are essentially equal, see Table). Rather, the greater male plasticity appears to reflect a higher correlation among characters in group A than in group B (allowing a greater number of significant between-sex ANOVAs without a concomitant increase in MANOVA significance level). Thus, the species's morphology may be more severely constrained in the environment occupied by group A bats than in those of group B. Group A males are simply larger than females in

most characters, whereas group B bats exhibit a more complex suite of between-sex differences; many of these are not significant by a univariate test, but together combine for significant multivariate difference.

Systematic value of color in *Asellia tridens*

In many parts of its range, *A. tridens* is dimorphic in color with red individuals occurring among the "normal" gray or pale-colored individuals (Harrison 1957, 1964; Attallah 1978). Harrison (1957) stated that the red phase is not found in *A. t. murraiana*. However, we observed dichromatism in series of specimens from Assa, Morocco; Niger; Benni Abbes, Algeria; Mauritania; Afghanistan; and Iran. These data agree with the finding of Kock (1969) that presence or absence of the red phase is not useful as a systematic character.

Most specimens of the morphometrically defined group A are pale in color. A typical specimen has a dorsal coloration of smoke gray with bases even a paler smoke gray (no. 44 in Smithe's [1975] colors), and ventrally is pale pinkish buff. A specimen from Dandara temple (type locality of *A. t. tridens*) has a whitish ventrum and dorsal fur with glaucous tips and pearl gray bases. Specimens from Kassala, Sudan, also are pale in color with ventral hairs and bases of dorsal hairs pearl gray, tips glaucous, and membranes pale in color. Although specimens from group A are variable in color, all exhibit overall pale coloration similar to that described for *A. t. tridens* and *A. t. pallida*.

Bases of hairs in specimens from Iran (group B) range from smoke gray to drab gray (colors of Smithe 1974, 1975) and the membranes are darker in color than in Egyptian specimens. The two specimens examined from Pakistan are even darker than those from Iran. Color in southwestern Asian specimens is noticeably darker than in those from Saharan populations discussed above as group A, suggesting that there are two groups distinguished by color, with the mountain form (group B) being darker. It should be noted, however, that a series from Palestine includes pale, dark, and intermediate specimens, and that specimens from Yemen (which cluster with group A) have dark coloration overall (ventrum and bases of dorsal hairs being drab in color with tips olive brown). This suggests that color represents a local adaptation, and does not correspond completely with the morphometric groupings, thus limiting its value for systematic studies in this species.

Relationship of color and morphometric variation to the named subspecies of *Asellia tridens*

Geographic variation in mammals traditionally has been understood in light of discrete groupings termed subspecies (Lidicker 1962; Wilson and Brown 1953). Here we discuss, and relate the results of our multivariate analyses to, the named subspecies of *Asellia tridens*.

A. t. tridens (É. Geoffroy St.-Hilaire, 1813). The type locality of the nominate subspecies is from the Valley of the Kings and Dandara, Egypt (É. Geoffroy St.-Hilaire 1818). All our specimens from Egypt (populations numbered 1) including those from the type locality are small in size and pale in coloration, and are included in the morphologically defined group A. We recommend that the name *A. t. tridens* be applied to all populations represented in group A.

A. t. diluta Andersen, 1918. The type specimen is from El Golea, Algerian Sahara. Andersen (1918) referred other specimens from Biskra to this taxon, which he distinguished as being larger than *A. t. tridens*, with the pelage "conspicuously" pale. All our specimens referable to *A. t. diluta* are from Algeria (populations numbered 4). These

clearly are identifiable with group A, both morphometrically and by color, and we recommend that *A. t. diluta* be considered a synonym of *A. t. tridens*.

A. t. pallida Laurent, 1937. Described from Oued Tatta, Anti Atlas Mountains, Morocco, this subspecies is presumably a much paler form than *A. t. diluta*, with color reaching white ventrally and the membranes being pale. Brosset and Caubere (1960) referred specimens from Figuig (Morocco), Biskra, and El Golea (Algeria) to *A. t. diluta*. These specimens were darker than *pallida* as described by Laurent (1937), and Brosset and Caubere (1960) concluded that the specimens examined by Laurent (1937, 1942) either were bleached or represented an evolutionarily localized population. Our specimens from Morocco are from a locality only a few kilometers from the type locality of *A. t. pallida*, but are clearly referable to group B both morphometrically and by color (most specimens being much darker than those examined from Algeria). Because we have not examined the type material of *A. t. pallida*, we cannot determine the nomenclatorial status of populations currently referred to this name, or of our material from Morocco and Mauritania.

A. t. murraiana Anderson, 1881. Described from Karachi, Sind (now Pakistan), as a subspecies darker and larger, but with relatively smaller ears, than *A. t. tridens*. Specimens examined from Pakistan, Afghanistan, Iran, and Iraq (referred by all previous authors to *A. t. murraiana*) were identifiable with group B. This name would constitute the earliest available for populations included in group B.

A. t. italosomalica DeBeaux, 1931. This subspecies, from Somalia, was distinguished by its small size (DeBeaux 1931). We examined no specimens of this taxon and cannot comment on its status.

To summarize, within the populations of *Asellia tridens* examined, we recognized two groups based on multivariate analyses of morphologic variation. One group (A), to which the name *A. t. tridens* is applicable, has a wide range throughout the Sahara and Arabian deserts. The second group (B) includes at least two disjunct populations (separated geographically by group A). The southwestern Asian populations (3 and 6) clearly are referable to *A. t. murraiana*. Populations from northwest Africa (2 and 7, indistinguishable in our analyses from *A. t. murraiana*) pose a systematic problem.

Most authors would recognize geographically disjunct populations of a species that have "their own evolutionary tendencies" as distinct subspecies (Lidicker 1962). The northwestern African population of group B may fit this definition of a subspecies, but these specimens are morphologically indistinguishable from those of populations of *A. t. murraiana*. This homomorphism is not limited to overall size or even to a simple shape-related suite of characters. Rather, it includes similarity of geographic patterns of inter-character correlations across sexes. Thus, it is difficult to postulate from these data that the two populations are evolutionarily distinct entities. This evolutionary and nomenclatorial problem may perhaps be resolved by additional data, such at mitochondrial DNA or protein electrophoretic mobilities, which should further elucidate the evolutionary histories of these populations.

Our study of this desert-adapted bat demonstrates the value of multivariate morphometric analysis of specimens from the entire distribution of such a species. We believe that other studies utilizing such analyses on widely distributed species will document that the phenomenon of homomorphism in disjunct populations is more common than previously suspected in natural populations of mammals.

Appendix I

Specimens examined. The locality is given first followed by (in parentheses) the museum abbreviations (see Appendix II) and number of specimens examined:
Morocco: Agadir Prov., Assa Khetara (USNM 39 ♂♂).

Algeria: El Golea (BMNH 1 ♀, FMNH 1 ♂, 1 ♀), Bechar (ROM 1 ♀), Beni Abbes (CM 1 ♀, 9 ♂♂; SMNS 3 ♀♀).
Mauritania: Sahel Saranna, 3 km s Aleq (USNM 2♂♂ 1 ♀).
Tunisia: 4 km s Redeyf (ELC 3♀♀, 4 ♂♂), 12 km n Tozour (ELC 8 ♂♂, 8 ♀♀).
Chad: Ouniang Kabir (USNM 3♀♀, 1♂).
Egypt: Red Sea Gov., Bir Abraq (FMNM 1 ♀, USNM 1 ♀), Qena Gov., Qena (FMNH 1♀), Qena Gov., Dandara Temple (SMNS 1 ♀, CM 11♂♂, 11 ♀♀), Qena Gov., Luxor (CM 3 ♀♀, 11 ♂♂), Western Desert Gov., Siwa (FMNH 1 ♀), Sinai Gov., Sinai, (USNM 2♀♀), Giza Gov., Saqqara (SMNS 1♀).
Sudan: Kassala (USNM 1 ♂).
Yemen: Lahej (USNM 2 ♀♀).
Palestine: Coastal Prov, Tel Aviv-Jaffa (TAU 2 ♀♀, 1 ♂), Jordan Valley Prov., Yarmouk, near Jordan Bridge (TAU 1 ♀), Jordan Valley Prov., Wadi Ashak, Chama el Malah, near Mehola (TAU 2 ♂♂).
Iraq: Baghdad Liwa, Baghdad (UCONN 1 ♀, FMNH 2 ♀♀, 2 ♂♂).
Iran: Lurestan, Dehloran (FMNH 1 ♀, 3 ♂♂); Shuh or Susa (ROM 2 ♀♀).
Afghanistan: Dilaram (FMNH 1 ♂, 1 ♀).
Pakistan: Baluchistan, Panjgur (FMNH 2 ♀♀).

Appendix II

List of abbreviations

Museums: BMNH – British Museum of Natural History; CM – Carnegie Museum of Natural History, Pittsburgh; ELC – E.L. Cockrum Collection, Tucson, Arizona; FMNH – Field Museum of Natural History, Chicago; ROM – Royal Ontario Museum, Toronto, Ontario; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany; TAU – Tel Aviv University, Zoology Dept. Museum; USNM – National Museum of Natural History, Washington, D.C.; UCONN – University of Connecticut Museum of Natural History, Storrs.

Measurements: FAL – forearm length; MTC3 – third metacarpal length; MTC4 – fourth metacarpal length; GLS – greatest length of the skull; CBL – condylobasal length (from occipital condyles to anterior alveolar margin of canine); BBC – breadth of braincase (taken at base of zygomatic arch); IOC – interorbital constriction; MASTB – mastoid breadth; ZYGB – zygomatic breadth (maximum breadth of zygomatic arches); RBCA – rostral breadth at canine alveolars; RBMAX – rostral breadth (maximum breadth taken on outside margins of maxilla); PEW – palatal emargination width (maximum); NASB – nasal breadth (maximum); PALL – palatal length (from posterior margin of palate to ventral tip of foramen magnum); PPLL – post-palatal length (from posterior margin of palate to ventral tip of foramen magnum); UTRL – upper toothrow length from canine to last molar; UPMLM – upper toothrow length from premolar to last molar; BRCD – braincase depth (taken externally but excluding sagittal crest); MANDL – mandible length; MANDTR – mandibular toothrow length from anterior margin of canine to last molar; CORH – coronoid height (maximum height of coronoid process of mandible).

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Zusammenfassung

Die Unterarten-Problematik bei der Dreizack-Blattnase, Asellia tridens: Homomorphie in räumlich weit getrennten Populationen

Morphometrische Unterschiede in verschiedenen Populationen der wüstenbewohnenden Fledermaus *A. tridens* wurden vom überwiegenden Teil des Verbreitungsgebietes in Asien und Afrika mittels uni- und multivariater Statistik untersucht. Diese Daten und Unterschiede in der Färbung legen die Existenz zweier verschiedener taxonomischer Gruppen nahe. Das Vorhandensein homomorpher, jedoch räumlich weit getrennter Populationen scheint üblicher zu sein als früher angenommen wurde. Diese Tatsache erschwert die Erkennung von Subspecies anhand klassischer taxonomischer Kriterien.

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