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Morphological variation of skeletal characters in the bird family Carduelidae: I. General size and shape patterns in African canaries shown by principal component analyses

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Abstract. In 44 carduelid species, most of them from the Afrotropical region, size and shape patterns of 44 skeletal features were investigated by principal component analyses. Obviously, mainly size-differentiation enables species of southern African canaries to coexist in the same habitat, whereas for equally-sized sympatric species differentiation in beak shape seems to be important for competition efforts. Several functional complexes and subcomplexes are demonstrated by the principal components in contrasting measurements of skeletal characters:

1. The flying apparatus, consisting of pectoral girdle and forelimb features, is contrasted with the feeding and hindlimb locomotion apparatuses, composed by cranial, pelvic and hindlimb features.
2. The flying apparatus is subdivided into a "wing-supporting" system, constructed of wing bones, and an "engine-supporting" system, consisting of pectoral elements.
3. In the locomotory complex, the two subsets forelimb locomotion (flying) and hindlimb locomotion (hopping and perching) are opposed.
4. In beak dimensions, measurements of lengths are contrasted with measurements of depth and width, indicating a change from slender and long to blunt and broad bills.

Key words. Aves, Carduelidae, skeletal characters, size and shape variation, principal component analyses, sympatry, Afrotropis.

Introduction

This first paper in a series of coherent publications aims at an interpretation of morphological differentiations within a group of highly specialized seed-eating song-birds. General trends in the development of their morphological features are discussed in connection with sympatry in 10 South African species. This paper shall be understood as the basis for further discussions, where several other aspects will be considered.

Among the almost worldwide distributed 140 carduelid species only 33 occur within the Afrotropis. 27 form a rather closely related species-group commonly known as African canaries. Recent investigations revealed that these 27 species belong to 4 species-groups (*Ochrospiza*, *Dendrospiza*, *Crithagra* and *Serinus*) and 3 species are of uncertain affinities (*Pseudochloroptila totta*, *Serinops flaviventris* and *Alario alario*). 3 of the mentioned genera most probably radiated within the Afrotropis, whereas *Serinus canicollis* links Palearctic faunal elements with the Afrotropical ornithofauna (Nicolai 1960, van den Elzen 1985).

The classification of Wolters (1975—1982) is founded on cladistic principles. It sets up phylogenetic entities as taxonomic units which correspond to ethological results (Nicolai 1960, van den Elzen 1985). His nomenclature is therefore taken as a basis

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for our study. African canaries are spread almost over the whole continent. Together with waxbills, buntings, sparrows, partly weavers, widows and larks they form the stock of seed-eating Passeres within that faunal region. Carduelids are specialized in the consumption of various seeds and have evolved a complicated mechanism (Ziswiler 1965) to cut and open hard grains. Canaries have neither invaded the tropical rain forest as waxbills and weavers nor the barren country as larks did. Thus canaries show their dependence on certain food qualities and water. In general their distribution coincides with the presence of bushes or trees usable as nesting sites. A majority of species inhabits the mountainous regions from eastern to southern Africa predominantly covered with evergreen vegetation. 11 species concentrate in sympatric ranges around the Victoria basin in East Africa; in the southern Cape region of South Africa the ranges of up to 10 species touch or coincide (Hall & Moreau 1970).

Competition between species will be reduced if they avoid direct contact particularly within sympatric ranges. Separation is essential for species exploiting the same trophic niche, especially during the breeding season. Kear (1962) and Newton (1967, 1972) demonstrated ecological separation in European carduelid species, Skead (1960), Winterbottom (1973) and Milewsky (1978) in South African canaries. Carduelids have specialized on different food plants, seed sizes and feeding habits or exploit different strata of their common habitat; some use their legs freely as assistance in seed harvest, others collect grains from the ground with their beaks only.

Specialization often depends on morphological differentiation manifested in morphometric variation (Bock 1978, Burton 1984, Leisler 1972, 1980, 1980a). Character divergency is expected to be higher between sympatric than between allopatric species (Brown & Wilson 1956). It broadly may be explained as variation in size and shape, size being defined as the magnitude of a distinct character, shape as the proportional relation between characters (James 1982, Somers 1986). On the other hand unrelated species of the same habitat are shown to bear common features, convergencies, typical for their ecological niches (Niemi 1985, Wiens & Rotenberry 1980). (Numerical) Taxonomists see a third aspect. In their opinion similarities are due to a common ancestry, and overall similarity is an indication for phylogenetic relationship (Schnell 1970, 1970a, Sneath & Sokal 1973).

Thus three main causes are considered to be responsible for morphological variation: competition (Abbott 1977), functional constraints, and phylogeny (James 1982). Morphological evolutionary relationships therefore should best be studied in phylogenetically related species of equal adaptive zones: i. e. African canaries.

Statistical procedures

Principal component analysis is a nowadays widely accepted method to summarize raw (= original) data and to distinguish size and shape patterns (Jolicoeur & Mosimann 1960). For a better understanding we give a brief description of the methodological process (see also Wiley 1981).

Principal component analysis (in the following abbreviated as PCA) is a multivariate statistical technique employed to identify structural relationships among continuous or noncontinuous variables, in our case linear measurements of bones. Starting from correlation- or variance-covariance matrices PCA looks for linear combinations which allow to transform the raw data into a system of new coordinates (system of the so-called principal components = PCs). In contrast to the sometimes highly intercorrelated original data (= character correlations) the

new variables (PCs) are mutually uncorrelated. Furthermore, the PCs are scaled in descending succession of their percentage contributions, explaining total variance of the whole character set. In many studies on measurements of organisms almost 75 % of total variance or more are explained by the first two PCs. The new and number-reduced data set is determined by an array of coefficients, the eigenvector. Its eigenvalue represents the amount of total variance which is explained by the individual PC. When the coefficient values of the eigenvector are scaled in relation to the contribution of the PC's eigenvalue to the total variance, these coefficients are called character loadings. Finally the specimens of a sample (termed OTUs, abbreviation for operational taxonomic units) may be displayed by an ordination technique and plotted in the new coordinate system. The arrangement of OTUs can be interpreted according to the distributions of their characters along the PC axes.

Material

We took 44 skeletal measurements from 208 carduelid specimens originating from most parts of the family's distributional range. Bony elements were measured with dial calipers (H. Classen and R. van den Elzen).

The characters are listed in Table 1 and figured in the Appendix. In the following we list species examined, number of specimens per species and faunal regions of species: P stands for Palaearctic region, N for Nearctic, H for Holarctic, NT for Neotropical, AT for Afrotropical region.

<i>Serinus pusillus</i>	n = 6 P	<i>Ochrospiza reichenowi</i>	n = 7 AT
<i>Serinus serinus</i>	n = 7 P	<i>Ochrospiza atrogularis</i>	n = 6 AT
<i>Serinus syriacus</i>	n = 7 P	<i>Ochrospiza leucopygia</i>	n = 5 AT
<i>Serinus citrinella</i>	n = 5 P	<i>Ochrospiza xanthopygia</i>	n = 6 AT
<i>Serinus canaria</i>	n = 1 P	<i>Ochrospiza mozambica</i>	n = 8 AT
<i>Serinus canicollis</i>	n = 8 AT	<i>Ochrospiza dorsostriata</i>	n = 6 AT
<i>Alario alario</i>	n = 17 AT	<i>Linurgus olivaceus</i>	n = 2 AT
<i>Pseudochloroptila totta</i>	n = 10 AT	<i>Chloris chloris</i>	n = 5 P
<i>Dendrospiza hyposticta</i>	n = 6 AT	<i>Chloris spinoides</i>	n = 1 P
<i>Dendrospiza scotops</i>	n = 6 AT	<i>Chloris sinica</i>	n = 1 P
<i>Dendrospiza capistrata</i>	n = 1 AT	<i>Carduelis carduelis</i>	n = 9 P
<i>Dendrospiza koliensis</i>	n = 2 AT	<i>Spinus spinus</i>	n = 4 P
<i>Crithagra gularis</i>	n = 6 AT	<i>Spinus barbatus</i>	n = 2 NT
<i>Crithagra tristriata</i>	n = 2 AT	<i>Spinus cucullatus</i>	n = 6 NT
<i>Crithagra mennelli</i>	n = 1 AT	<i>Acanthis flammea</i>	n = 6 H
<i>Crithagra leucoptera</i>	n = 1 AT	<i>Linaria cannabina</i>	n = 2 P
<i>Crithagra burtoni</i>	n = 1 AT	<i>Leucosticte arctoa</i>	n = 1 H
<i>Crithagra striolata</i>	n = 4 AT	<i>Erythrura erythrura</i>	n = 1 P
<i>Crithagra albogularis</i>	n = 7 AT	<i>Erythrura mexicana</i>	n = 1 N
<i>Crithagra sulphurata</i>	n = 7 AT	<i>Uragus sibiricus</i>	n = 1 P
<i>Crithagra donaldsoni buchani</i>	n = 7 AT	<i>Procarduelis vinacea</i>	n = 1 P
<i>Serinops flaviventris</i>	n = 5 AT	<i>Coccothraustes coccothraustes</i>	n = 6 P

and 4 hybrids: *Ochrospiza dorsostriata* x *O. mozambica* (n = 2), *O. mozambica* x *O. atrogularis* (n = 1) and *Serinus serinus* x *S. canaria* (n = 1). Afrotropical carduelids are represented in 131 specimens and 24 species, outnumbering Palaearctic members (57 specimens, 15 species), Holarctic (7 specimens of 2 species), Nearctic (1 specimen in 1 species) and Neotropical (8 specimens, 2 species) members. Skeletons were taken both from captive birds and fieldcollected specimens. Within our sample only *Spinus cucullatus* and *Acanthis flammea* are regularly reared in captivity and can show divergencies due to domestication.—Measurements of domesticated *Serinus canaria* were disregarded because in this species morphological changes occurred with the creation of new races.

Characters originally were achieved to comprehend three functional complexes (1–3): feeding (1) and locomotion (2–3), the last represented by two locomotory systems — flying (2) and hopping-clinging (3). An R-analysis (correlation between characters over all species) nevertheless revealed highly significant correlations ($p < 0.001$) between feeding and hindlimb locomotion apparatus (Fig. 1, UPGMA-clustering).

Table 1: PCA of 44 skeletal characters in 44 carduelid species. l = length, w = width, d = depth. Extreme values in bold types.

Character number and name	PC I ₁ coefficients	PC II ₁	F I ₁ squared character loadings	F II ₁
Feeding apparatus				
Head				
1 Mandible, pars symphysialis	0.15	−0.08	0.77	0.01
2 Mandible, Dentale l	0.16	−0.07	0.87	0.01
3 Mandible, pars caudalis l	0.15	−0.15	0.84	0.04
4 Mandible, Dentale d	0.15	−0.07	0.84	0.01
5 Mandible, pars caudalis d	0.16	−0.02	0.92	0.00
6 Skull, w	0.16	−0.16	0.90	0.05
7 Interorbital, max w	0.16	−0.07	0.91	0.01
8 Interorbital, min w	0.14	0.11	0.73	0.02
9 Postorbital w	0.16	−0.00	0.88	0.00
10 Internasal w	0.16	0.00	0.87	0.00
11 Premaxilla l	0.16	−0.07	0.90	0.01
12 Postorbital l	0.16	−0.11	0.92	0.02
13 Quadratojugale l	0.16	−0.13	0.87	0.03
14 Orbital w	0.16	−0.15	0.90	0.04
15 Skull d	0.16	−0.13	0.92	0.03
16 Skull l	0.16	−0.11	0.94	0.02
17 Palatinum w	0.14	0.05	0.69	0.01
18 Pterygoid l	0.15	−0.05	0.79	0.00
19 Processus orbitalis quadrati	0.16	−0.05	0.89	0.00
20 Premaxilla d	0.16	−0.00	0.91	0.00
Walking apparatus				
Pelvic girdle				
21 Synsacrum l	0.16	−0.02	0.89	0.00
22 Synsacrum w	0.15	−0.03	0.79	0.00
23 Synsacrum d	0.13	−0.19	0.61	0.06
24 Synsacrum distal l	0.15	−0.16	0.76	0.05
Leg				
25 Femur l	0.16	−0.14	0.90	0.04
26 Femur w	0.15	−0.08	0.81	0.01
27 Tibiotarsus l	0.16	−0.12	0.87	0.02
28 Tibiotarsus w	0.15	−0.09	0.79	0.01
29 Tarsometatarsus l	0.15	−0.15	0.79	0.04
30 Tarsometatarsus w	0.08	−0.06	0.25	0.01
Flying apparatus				
Pectoral girdle				
31 Sternum l	0.16	0.20	0.88	0.10
32 Keel d	0.14	0.38	0.66	0.26
33 Keel l	0.15	0.29	0.78	0.15
34 Sternum distal w	0.14	0.00	0.70	0.00
35 Sternum d	0.14	0.30	0.74	0.16
36 Coracoid l	0.16	0.10	0.92	0.02
37 Hypocleidium l	0.11	0.42	0.44	0.33
38 Scapula l	0.16	0.16	0.88	0.05
Wing				
39 Humerus l	0.16	0.01	0.90	0.00
40 Humerus distal end w	0.14	0.01	0.74	0.00
41 Ulna l	0.16	0.14	0.87	0.04
42 Ulna w	0.13	0.17	0.64	0.05
43 Carpometacarpus l	0.15	0.23	0.81	0.10
44 Carpometacarpus w	0.15	0.08	0.83	0.01
Percentage of variance explained	80.6 %	4.11 %		
Cumulative variance		84.71 %		
Eigenvalue	35.50	1.81		

The linear measurements of the raw data matrix were logarithmically transformed for allometric reasons (Morrison 1976, Mosiman & James 1979). We performed three separate PCAs, one based on a correlation matrix, one on Spearman's rank correlation and one on a variance-covariance matrix. Whereas in a variance-covariance matrix each character differently contributes to the total variance of the whole character set, in a correlation matrix the contributions of the characters are always equally weighted. Spearman's rank correlation was performed to compare a parameterfree method with procedures dealing with normal distributions. The results proved to be very similar to those of the product-moment-correlation procedure (Table 1). Results presented in this paper are based on PCAs of correlation matrices.

For our study a statistical package was written in Amiga-Basic by H. L. Nemeschkal. It integrates the raw data input, transformations, PCA (Hotelling's iterative procedure), line printing and plotting. The program was prepared for a Commodore-Amiga-1000 and tested on that computer. Raw data matrices and PCA-plottings are partly stored in Bonn and partly in Vienna.

General patterns in carduelid morphology

PCA of the whole character set

We interpret the first principal component (PC I) mainly as a size factor in accordance with similar studies (Grant 1986, Leisler 1977, 1980, Niemi 1985, Somers 1986, Wiens & Rotenberry 1980). All coefficients are of positive sign and to a large extent equally high-loaded except tarsometatarsus width. Second PC (PC II) is best described as a factor opposing in a general trend the pectoral girdle as well as forelimb features to a complex consisting of the pelvic girdle, hindlimb and cranial features. In a sequence of pronounced increase tendencies, the character lengths of ulna and scapula, of ulna width, sternum length and depth, carpometacarpus, keel, hypocleidium lengths and keel depth are spread in positive direction along the PC II axis, as indicated by the high values of their character loadings with positive signs. Inversely the loadings of cranial, pelvic and hindlimb features indicate a trend to diminish shown by their character loadings with high values of reverse signs. This suggests a possible determination of the different complexes as units caused by functional constraints, namely feeding and walking apparatuses on the one hand, and flying apparatus on the other hand.

Fig. 2 shows a cluster composed of all Afrotropical species-groups combined within the whole carduelid sample. African representatives are generally of smaller size and exhibit less accentuated pectoral features than expected when we assume a random dispersal of size patterns over all geographic regions.

For example none of the species or genera living in Africa south of the Sahara reaches the size of grosbeaks, represented by *Coccothraustes coccothraustes* (Fig. 2, *C. c.*)

In Fig. 3, size arrangements of species-groups (= genera) exhibit greater size similarities between congeneric species than between genera. Similarly sized genera (mainly *Ochrospiza* and *Dendrospiza*, partly *Crithagra* including *Serinops*) diverge on the PC II axis, indicating that species of equal size are separated by different shape. In allocating the morphological characters of genera (= species-groups) to their main habitats we may assume that in general living in open country is correlated with a stronger flying apparatus, and living in forest or shrubby environments with leg elements proportionally longer than wing elements and/or a shallower pectoral girdle.

Ochrospiza, inhabitant of open and arid countrysides comprising the Sahel in northern and western Africa, the savanna from eastern to southern Africa and the Namib-

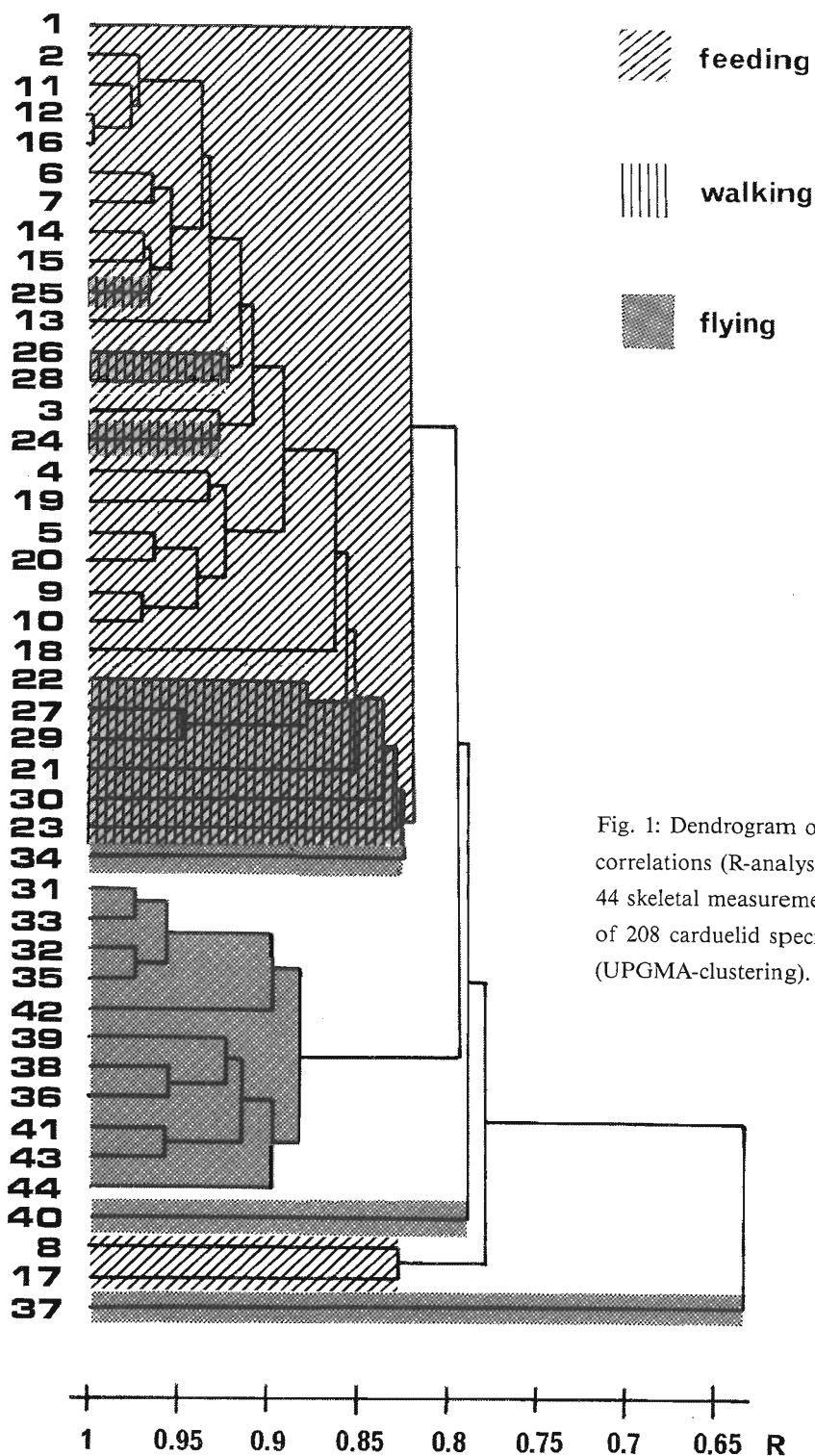


Fig. 1: Dendrogram of character correlations (R-analysis) between 44 skeletal measurements of 208 carduelid specimens (UPGMA-clustering).

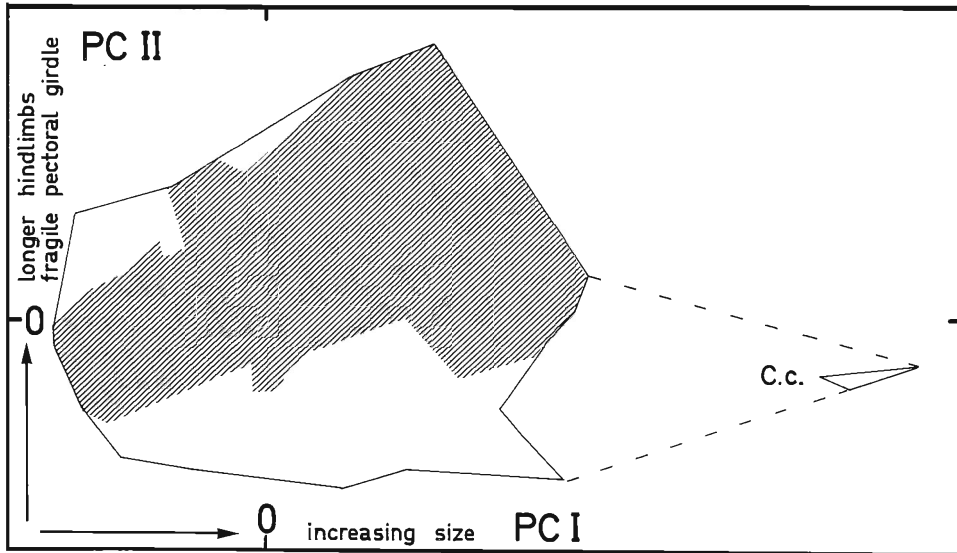


Fig. 2: PCA of 44 skeletal characters; morphological ranges of African canaries (shaded) within the whole sample of carduelids. *C. c.* = *Coccothraustes coccothraustes*.

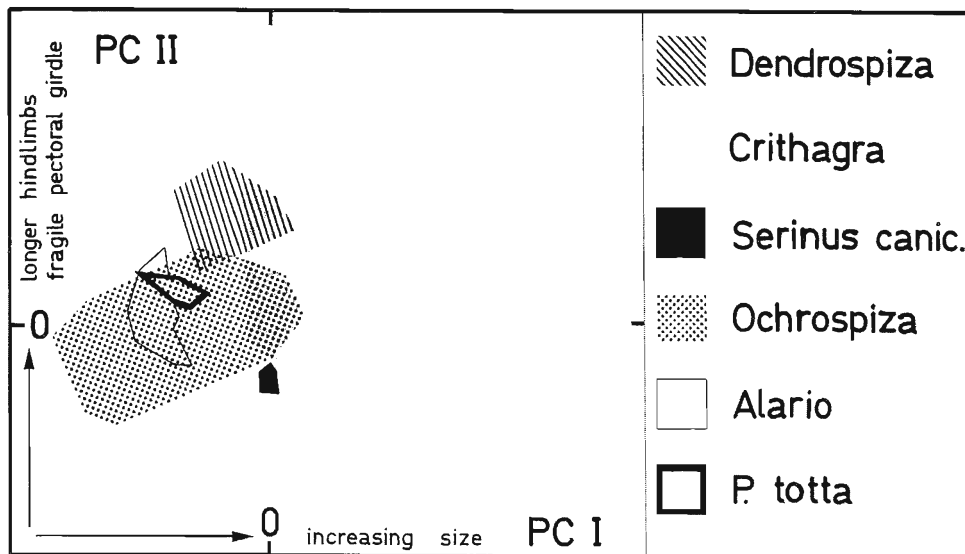


Fig. 3: PCA of 44 skeletal characters; morphological ranges of Afrotropical species-groups (= genera).

Desert in Namibia, forms the cluster of the smallest sized birds with a well-developed flying apparatus. Almost equally sized, but with accentuated cranial-hindlimb features, are members of the genus *Dendrospiza*. They live in woodland to forests along moun-

tain sides in eastern and southern Africa. Within the genus *Crithagra* (incl. *Serinus*) divergent tendencies impede an equal interpretation: The cluster arrangement displays the largest birds with the bulkiest bills as well as the largest birds with the longest hindlimbs, but birds with the strongest bills also tend to have pronounced pectoral elements, a trend visible in the European grosbeak as well. We interpret this phenomenon as a consequence of overall size, assuming that a heavier bird needs a stronger engine to fly.

The whole African group inhabits various environments, from the subdesert steppe to woodlands and from mountains to lowlands. Species with proportionally shorter wings, a fragile pectoral girdle and longer legs are shrub- or tree-dwelling species of East African mountains.

Serinus canicollis, as his Palaearctic congeners, belongs to the group of well-flying birds with relatively short legs and bills. It inhabits evergreen mountainous areas and gardens from Ethiopia to the Cape Province in southern Africa, preferring trees as breeding sites. *Alario alario*, a shrub-dwelling bird of the Karroo and Cape macchia, is small sized and exhibits greater diversity on the shape than on the size axis. In this analysis it completely falls within the cluster of *Ochrospiza* congeners and also overlaps with *Pseudochloroptila totta*.

The Cape siskin, *P. totta*, is a bird of smaller size with slightly prolonged hindlimb features. It occupies the coastal mountain regions with shrubby vegetation in the southernmost parts of southern Africa, where it is sympatrical in range and to a great extent also in habitat with *Alario alario* and *Serinus canicollis*. As *Alario* the Cape siskin rarely stays in tree tops. It breeds in crevices of rocks or trees, *Alario* in shrubs and only *S. canicollis* regularly nests in tree tops.

PCA of the pectoral girdle

Since the pectoral girdle (as a sub-complex) mainly contributes to the forming of the shape axis, PC II, we analysed 13 measurements of the flying apparatus separately

Table 2: PCA of the flying apparatus.

Character number and name	PC I coefficients	PC II coefficients	F I squared character	F II loadings
31 Sternum l	0.29	0.01	0.96	0.00
32 Keel d	0.28	0.35	0.85	0.08
33 Keel l	0.29	0.17	0.92	0.02
35 Sternum d	0.28	0.21	0.88	0.03
36 Coracoid l	0.29	—0.10	0.92	0.01
37 Hypocleidium l	0.23	0.64	0.60	0.26
38 Scapula l	0.29	—0.08	0.93	0.00
39 Humerus l	0.28	— 0.35	0.86	0.08
40 Humerus distal end w	0.26	— 0.44	0.74	0.12
41 Ulna l	0.29	—0.17	0.93	0.02
42 Ulna w	0.26	0.03	0.73	0.00
43 Carpometacarpus l	0.29	—0.01	0.93	0.00
44 Carpometacarpus w	0.27	—0.19	0.83	0.02
Percentage of variance explained	85.31 %	4.87 %		
Cumulative variance		90.18 %		
Eigenvalue	11.09	0.63		

(Table 2): The first PC is a size axis again. In the second axis all characters of sternum and hypocleidium lengths (with positive signs) are opposed to a complex consisting of coracoid length, scapula length as well as measurements of the humerus.

A first interpretation leads to the assumption that the skeletal framework of a flying apparatus consists of two counter-developing subsets: On the one hand a “wing-supporting” system (mainly characterized by wing bones), on the other hand an “engine-supporting” system (mainly represented by pectoral features) for the insertion of the main pectoral muscles. We hope that the inclusion of wing feather proportions, wing loadings and weight data of the examined species will allow a reliable interpretation.

PCA of forelimb and hindlimb elements

In a next step we analysed 6 elements of forelimbs and hindlimbs for comparison of locomotory abilities. The results are compiled in Table 3. Leg and wing measurements diverge as indicated by PC II: Carduelidae have either relatively longer leg or longer wing elements as already indicated above by the PCA of the whole character set. Within the sample (not figured), *Ochrospiza* and *Serinus canicollis* possess longer wings and shorter legs than *Dendrospiza* and *Crithagra*. Further functionally and ecologically orientated detailed studies may elucidate these connections, because hindlimb dimensions are highly correlated with beak dimensions, and feet are used for handling food as well as for hopping and clinging. Therefore a satisfactory interpretation requires a higher amount of still unknown details on feeding behaviour.

Table 3: PCA of the locomotion complex (forelimb and hindlimb elements).

Character number and name	PC I coefficients	PC II coefficients	F I squared character	F II loadings
25 Femur I	0.41	−0.32	0.93	0.04
27 Tibiotarsus I	0.41	−0.33	0.94	0.04
29 Tarsometatarsus I	0.40	−0.49	0.88	0.08
39 Humerus I	0.42	0.14	0.94	0.01
41 Ulna I	0.41	0.44	0.91	0.07
43 Carpometacarpus I	0.39	0.58	0.84	0.12
Percentage of variance explained	90.83 %	5.88 %		
Cumulative variance		96.71 %		
Eigenvalue	5.45	0.35		

PCA of bill characters

Different food regimes and trophic competition are expected to bring about a variety of bill structures, because carduelids are birds of specialized feeding habits. The capacity to evolve significant changes in bill structures under selective constraints has already been proved by close relatives, the Hawaiian honeycreepers, Drepanidinae (Richards & Bock 1973), a subfamily of Carduelidae (Sibley & Ahlquist 1982). Even the Palearctic grosbeaks or crossbills can be cited as an illustration of an extreme beak design within the family (Fig. 4).

Table 4: PCA of the feeding apparatus (bill characters).

Character number and name	PC I coefficients	PC II coefficients	F I squared character loadings	F II squared character loadings
2 Mandible, Dentale l	0.41	0.03	0.41	0.00
3 Mandible, pars caudalis l	0.40	-0.61	0.40	0.07
9 Postorbital w	0.40	0.65	0.40	0.08
11 Premaxilla l	0.42	-0.10	0.42	0.00
12 Postorbital l	0.42	-0.26	0.42	0.01
20 Premaxilla d	0.41	0.35	0.41	0.02
Percentage of variance explained	92.03 %	3.27 %		
Cumulative variance		95.30 %		
Eigenvalue	5.52	0.20		

A PCA of six selected bill characters shows that African canaries are distributed regularly within the sample of small to medium sized carduelids (Fig. 5). The first PC explains the main part of total variance and serves as size axis again (Table 4). For bill measurements PC II opposes characters of width and depth (positive signs) to characters of length. Thus the proportional change proceeds from slender and long to thick and short bills.

Fig. 6 shows, that congeneric species form again distinct clusters. Genera are not much better separated than in the foregoing analysis of all characters combined. This time *Dendrospiza* and *Crithagra* (with *Serinus* included) overlap to a greater extent than in PCA of the whole character set. In *Crithagra* smaller-faced species are supposed to tend to more slender bills whereas relatively bigger-faced species have proportionally blunter bills, reflecting the great variety of diets taken in this genus, from small seed in *C. gularis* (see chapter on beak features) to fruit in most of the other species. *Alario* again lies within the cluster of *Ochrospiza* species. Both genera feed on small seed, *Ochrospiza* preferring monocotyledon (graminoid) seed, *Alario* dicotyledon seed. *Alario*'s bill is similar in shape to (but smaller than) that of *Serinus canicollis*, a specialist on Asteraceae. With respect to these characters *Pseudochloroptila totta* is absolutely outstanding and forms a cluster of its own. It feeds on graminoid seed and occasionally some arthropods.

Commonly bill dimensions are set in relation to food size (Grant 1986, Schluter & Grant 1984, Schoener 1965). Abbott, Abbott & Grant (1975) suggest that small-billed individuals of Galapagos finches can handle both small and large seed, whereas larger billed individuals can better handle large seed. For several species of African canaries a correlation of bill dimensions with food size is indicated by Classen (1983). Bowman (1961) divided feeding functions of the bills of Galapagos finches into 3 classes: probing, tip-biting and base-crushing. Ziswiler (1965) quotes 5 functional categories: plucking, probing, depositing, cutting and husking. Slender bills are better capable to pluck small seed, large and broad ones to crush hard seed. A general analysis of the bill shape function was given by Bock (1966); for carduelids a functional analysis of beak design and jaw muscles is in preparation (H. Classen).

Patterns of sympatric South African species

A survey of the whole arrangement of OTU-clusters causes difficulties, because several ranges of species and/or genera coincide. This overlap may have different reasons of

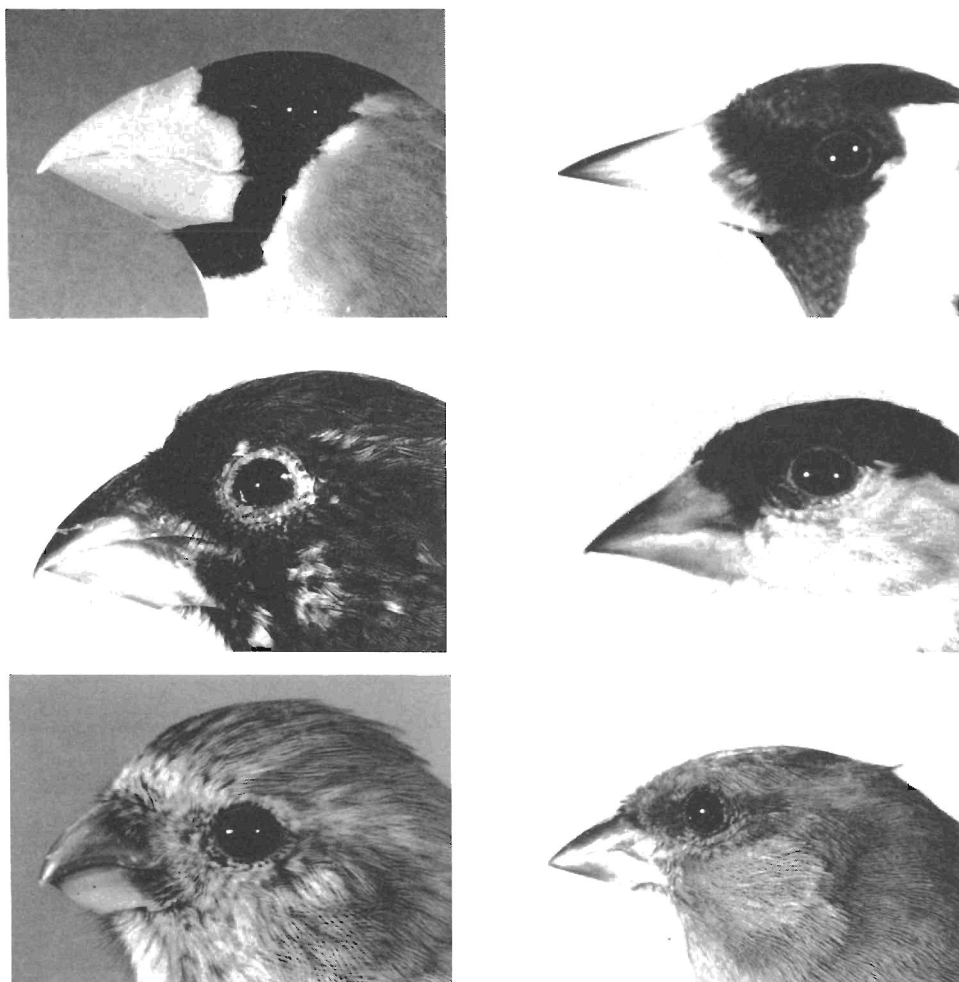


Fig. 4: Bill design in carduelids: left side — *Uragus sibiricus* (bottom); *Crithagra burtoni* (middle); *Eophona personata* — thick billed species; right side — *Serinus canicollis* (bottom); *Spinus yarellii* (middle); *Carduelis carduelis* — long and slender billed species. Photos: H. Classen.

which we enumerate relatedness and convergencies of OTUs as the most important. To extricate logical arrays we started with the comparison of species of sympatric ranges and/or identical habitats, emphasizing on overall size and shape of bill features.

Sympatry frequently occurs among African canaries. Several species inhabit the same environment and feed in guilds the composition of which may vary regionally.

We plotted 10 South African species of at least partly sympatric ranges (Table 5) to exhibit their possible morphological differences.

These species were chosen on several grounds: 1. A majority of our material is represented by South African species. 2. Studies of their ecology and behaviour provide sufficient support for an interpretation of their morphology. 3. One of the primary

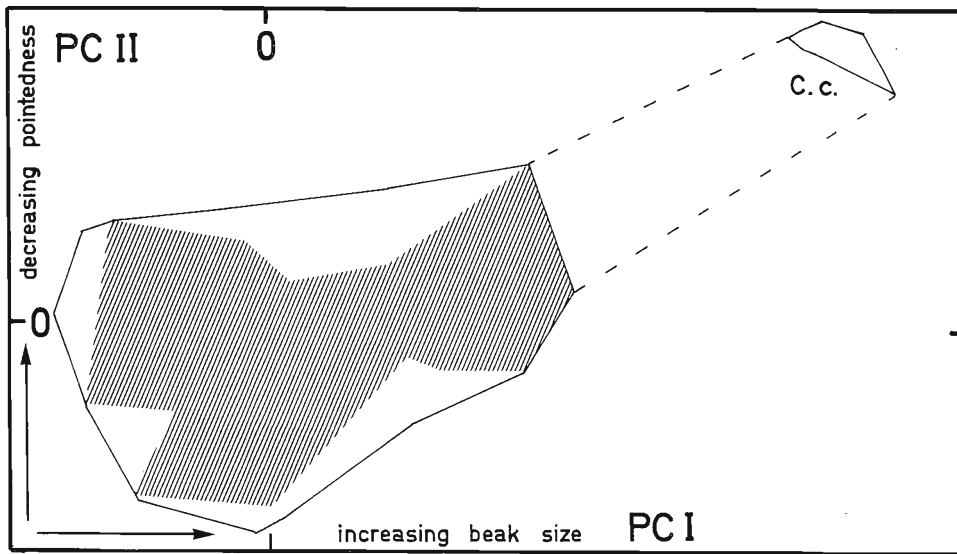


Fig. 5: PCA of 6 bill characters; morphological ranges of African canaries (shaded) within the whole sample of carduelids. C. c. = *Coccythraustes coccythraustes*.

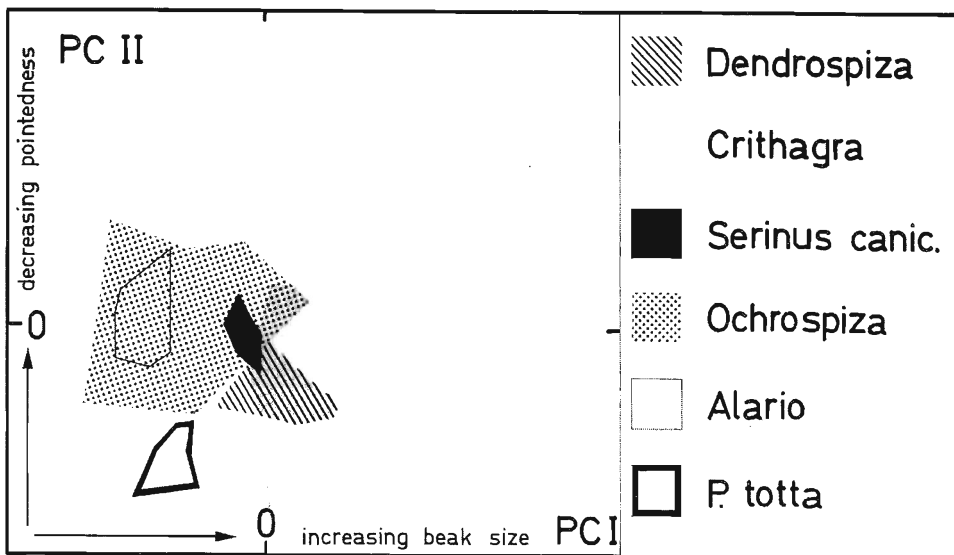


Fig. 6: PCA of 6 bill characters; morphological ranges of Afrotropical species-groups (= genera).

areas of Afrotropical plant species is situated in southern Africa (Wickens 1976). The distributional ranges of *D. scotops*, *A. alario* and *O. atrogularis* contact only marginally with all others, whereas the geographical ranges of the remainder and of *A. alario* with *O. atrogularis* broadly overlap. Distinct ecological separation is found between

Table 5: Sympatry in South African canaries; + = fully sympatric ranges, $\pm$ = small zones of overlapping ranges, — = allopatric ranges.

<i>S. flaviventris</i>	$\pm$	●	●	●					
<i>C. leucoptera</i>	—	+	●	●					
<i>C. sulphurata</i>	+	$\pm$	+	●					
<i>C. albogularis</i>	—	+	+	$\pm$	●				
<i>C. gularis</i>	+	$\pm$	+	+	$\pm$	●			
<i>O. atrogularis</i>	$\pm$	$\pm$	—	$\pm$	+	$\pm$	●		
<i>A. alario</i>	—	$\pm$	—	—	$\pm$	—	+	●	
<i>S. canicollis</i>	+	$\pm$	+	+	+	+	$\pm$	$\pm$	●
<i>P. totta</i>	—	+	+	+	+	+	—	$\pm$	+
	<i>D. scotops</i>	<i>S. flaviventris</i>	<i>C. leucoptera</i>	<i>C. sulphurata</i>	<i>C. albogularis</i>	<i>C. gularis</i>	<i>O. atrogularis</i>	<i>A. alario</i>	<i>S. canicollis</i>

P. totta, *S. flaviventris* and all 3 *Crithagras*, *D. scotops* and *S. canicollis* in habitat choice; between *P. totta*, *S. flaviventris* and all *Crithagras*, between *C. leucoptera* and *C. sulphurata*, between *S. canicollis*, *O. atrogularis* and the remainder in food preferences. *C. leucoptera*, *S. canicollis*, *O. atrogularis* and *P. totta* are specialized on distinct food plants (plant families). In food size, *C. sulphurata* prefer the largest, and *A. alario*, *O. atrogularis* and *P. totta* the smallest grains (Milewsky 1978).

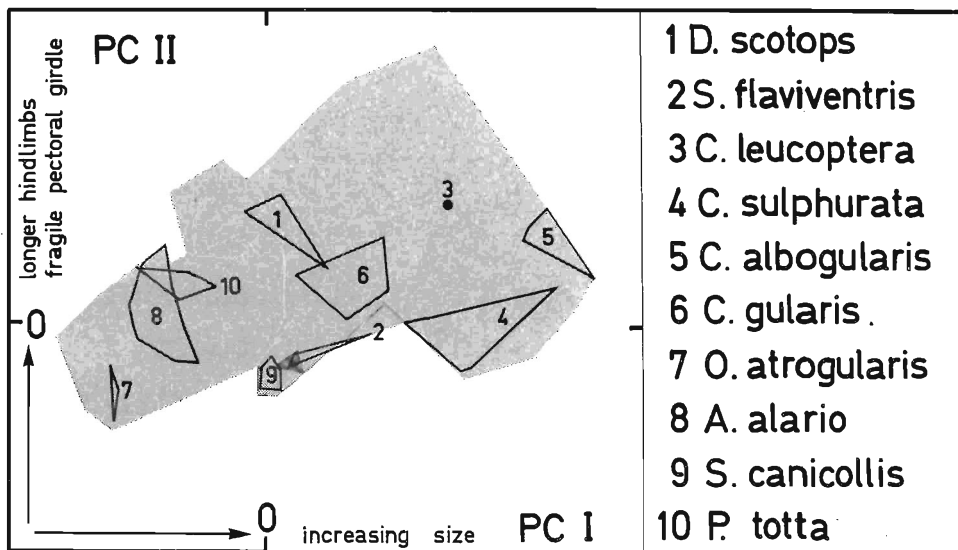


Fig. 7: PCA of 44 skeletal characters; general size and shape patterns in 10 (at least partly) sympatric South African canaries.

General size and shape patterns

The score arrangements of these 10 representatives within the whole sample of Afrotropical species along the PCs are shown in Fig. 7. *Ochrospiza atrogularis*, the smallest and best-flying species, prefers the open country; it is typical for its congeners and feeds both on the ground and in shrubby vegetation, but nests preferably in trees.

The neighbouring clusters unite three species-pairs: *Alario alario* with *Pseudochloroptila totta* in size and shape, *Dendrospiza scotops* with *Serinus canicollis* and *Serinus flaviventris* with *Crithagra gularis* in size only. *D. scotops* and *S. canicollis* are birds of mountain and forest environments. Their shape differences are greater than those between *Serinus flaviventris* and *Crithagra gularis*, two species with partly overlapping distributional ranges (Table 5). In our sample *Crithagra leucoptera* is only represented by a single individual. Nevertheless, its overall size seems to be equal to that of *Crithagra sulphurata*, but its shape is different. Both meet in the same environment, but food items as well as food size differ significantly (Milewsky 1978). The congeneric *C. albogularis* is shaped similarly to *D. scotops* and *C. leucoptera*, but considerably larger.

In general the 10 species cluster almost regularly upon the size axis (PC I). Distributions along the shape axis will show, if we compare our examples with the whole set of African canaries, that emphasis is laid rather on pectoral elements than on characters of the hindlimbs.

Beak features

Beak characters separate species arrays in a different manner. Again, PC I as the size divides species to a greater amount than the shape axis. The general arrangement assumes exclusion of a per chance distribution (Fig. 8).

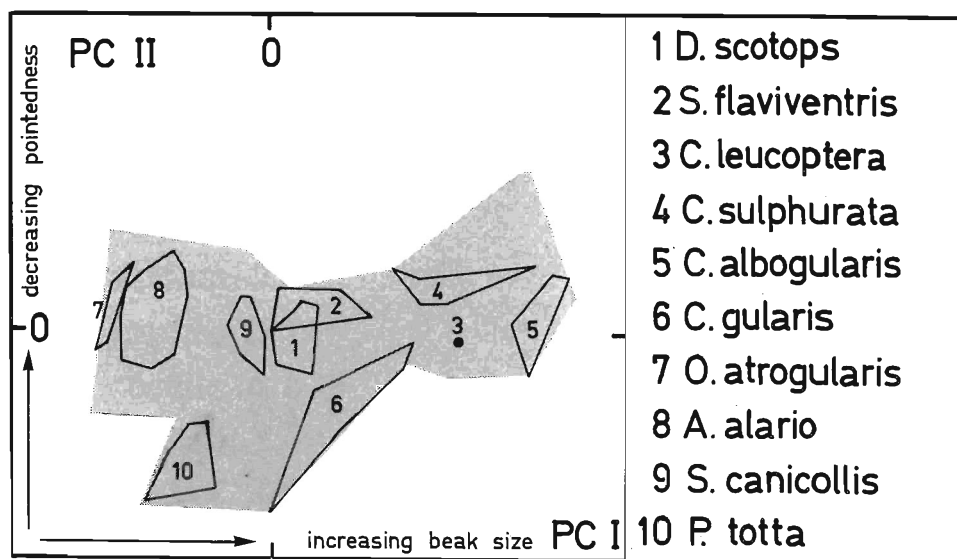


Fig. 8: PCA of 6 bill characters; patterns in 10 (at least partly) sympatric South African canaries.

Also in beak dimensions *O. atrogularis* remains the smallest species, its bill is neither pointed nor blunt. In increasing bill size it is followed by *A. alario*, which has the most similarly shaped bill, by *S. canicollis*, *D. scotops* (overlapping with *S. flaviventris*), *C. sulphurata*, *C. leucoptera* and *C. albogularis*. *P. totta*, of equal size as and similar in overall proportions to *A. alario*, is separated drastically from that species in bill features. A high amount of variation in bill shape is found in *C. gularis*. In size between *D. scotops*, *S. flaviventris* and *C. sulphurata*, it exhibits bill features reaching from the slender bills of *P. totta* to the blunt bills of *D. scotops*. For a better understanding we resume the classification of beak, body and food dimensions in three size classes (Table 6).

Table 6: Classification of body size, bill size and food size in 10 partly sympatric South African canaries; + = large, $\pm$ = medium, — = small.

Species	Body size	Bill size	Food size
<i>D. scotops</i>	$\pm$	$\pm$	$\pm$
<i>S. flaviventris</i>	$\pm$	$\pm$	+
<i>C. leucoptera</i>	+	+	+
<i>C. sulphurata</i>	+	+	+
<i>C. albogularis</i>	+	+	+
<i>C. gularis</i>	+	$\pm$	$\pm$
<i>O. atrogularis</i>	—	—	—
<i>A. alario</i>	—	—	—
<i>S. canicollis</i>	$\pm$	$\pm$	—
<i>P. totta</i>	—	—	—

Species of similar size and/or identical bill proportions are either allopatric or overlap only marginally in distributional range. In our study *D. scotops* together with *C. gularis*, and *P. totta* with *A. alario* form two equally sized pairs. *D. scotops* and *S. flaviventris* are of equal bill shape. Species-pairs of both similar size and bill shape are never formed by sympatric congeners, as far as demonstrated by our sample. We conclude from our analysis that mainly size differentiation enables South African canaries to coexist in the same habitat and sometimes even in the same guild. For equally-sized sympatric species only, beak differentiation seems to be essential for competition constraints.

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Zusammenfassung

Wir untersuchten Größen- und Gestaltmuster von 44 Cardueliden-Arten (208 Individuen), überwiegend afrotropischer Herkunft, mit Hilfe der Hauptkomponentenanalyse. Die Materialgrundlage bildeten jeweils 44 Meßstrecken am Skelett. Bei den 10 untersuchten südafrikanischen Girlitzarten reichen offenbar schon Größenunterschiede aus, um einen Lebensraum gemeinsam bewohnen zu können. Sympatrische Arten annähernd gleicher Allgemeingröße zeigen starke

Unterschiede in der Schnabelgestalt. Durch Merkmalskontrastierung weisen die Hauptkomponenten verschiedene Funktionskreise aus:

1. Der Flugapparat besteht aus Elementen des Schultergürtels und der Vorderextremitäten. Er ist sowohl dem Funktionskreis Nahrungserwerb als auch dem Funktionskreis Laufen gegenübergestellt, die sich aus Merkmalen von Kopf-, Beckenregion und Beinmaßen zusammensetzen.
2. Der Flugapparat seinerseits ist wiederum in zwei Funktionskreise unterteilt. Vorderarmknochen bilden das Manövriersystem, Elemente des Brustkorbes das Antriebssystem.
3. Im Funktionskreis Fortbewegung sind Fliegen und Laufen voneinander entkoppelt.
4. Von den Schnabelmerkmalen sind Längenmaße den Höhen- und Breitenmaßen opponiert. Die Hauptkomponenten weisen auf gegenläufige Entwicklung von schlanken, spitzen Schnäbeln zu stumpfen, kegelförmigen Schnäbeln hin.

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Appendix. Definitions of the 44 skeletal measurements used in this study.