

Analysis of body shape in species of *Centropyge* (Teleostei: Perciformes: Pomacanthidae)

Analyse der Körperform der Arten der Gattung *Centropyge* (Teleostei:
Perciformes: Pomacanthidae)

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Summary: The variation in body shape (lateral body outline) of Pygmy Angelfishes is analysed by means of geometric morphometrics. There is a significant ($p < 0.05$) divergence in body shape in the two subgenera *Xiphypops* and *Centropyge*. Within the subgenus *Xiphypops* the *C. (X.) fisheri*-complex differs from the remaining species of the subgenus by a more flat body and longer caudal peduncle. Body shapes in the subgenus *Centropyge* are more heterogeneous. *Centropyge (C.) aurantia*, *C. (C.) colini* and *C. (C.) narcosis* have a deeper and rounder body compared to the others. *Paracentropyge* are also deep bodied species, but significantly differ ($p < 0.01$) in this character only from *Xiphypops*. The body form and other morphological characters of *Centropyge flavivectoralis* are more similar to those of *Centropyge* than of *Xiphypops* species. Therefore this species is transferred from the subgenus *Xiphypops* to the subgenus *Centropyge*.

Key words: Pomacanthidae, *Centropyge*, *Xiphypops*, *Paracentropyge*, *Centropyge flavivectoralis*, *Centropyge-(Xiphypops)-fisheri*-complex, body shape, geometric morphometrics.

Zusammenfassung: Die Körperform (seitlicher Körperumriss) der Zwergkaiserfische wird mit Hilfe der geometrischen Morphometrie untersucht. Zwischen den taxonomischen Einheiten existieren erkennbare Unterschiede in der Körperform. Die zwei Untergattungen *Centropyge* und *Xiphypops* lassen sich anhand dieses Merkmals signifikant ($p < 0,05$) unterscheiden. Innerhalb der Untergattung *Xiphypops* kann der *C. (X.) fisheri*-Komplex aufgrund der Körperform abgetrennt werden. Die Mitglieder dieses Artenkomplexes unterscheiden sich durch einen flacheren Körper und einen längeren Schwanzstiel von den übrigen Angehörigen der Untergattung. Die Untergattung *Centropyge* zeigt sich heterogener in der Körperform. *Centropyge (C.) aurantia*, *C. (C.) colini* und *C. (C.) narcosis* besitzen einen höheren Körperbau. *Paracentropyge*-Arten zeigen ebenfalls einen hohen Körper, unterscheiden sich jedoch in dieser Merkmalsausprägung nur gegenüber den Arten der Untergattung *Xiphypops* signifikant ($p < 0,01$). *Centropyge flavivectoralis* ist den Angehörigen der Untergattung *Centropyge* in der Körperform und in weiteren morphologischen Merkmalen ähnlicher als denen der Untergattung *Xiphypops*. Deshalb wird diese Art von der Untergattung *Xiphypops* in die Untergattung *Centropyge* überführt.

Schlüsselwörter: Pomacanthidae, *Centropyge*, *Xiphypops*, *Paracentropyge*, *Centropyge flavivectoralis*, *Centropyge-(Xiphypops)-fisheri*-Komplex, Körperform, geometrische Morphometrie.

1. Introduction

The pygmy angelfishes of the pomacanthid genus *Centropyge* KAUP, 1860 are small (total length 10 cm on average), colourful tropical reef fishes. The genus includes about 30 species (ALLEN et al. 1998, SCHNEIDEWIND 1999). In his review of the family ALLEN (1979) recognized two subgenera: *Centropyge* (type species *Holacanthus tibicen* Cuvier, 1831) and *Xiphypops* JORDAN, 1903 (type

species *Holacanthus fisheri* SNYDER, 1904). SMITH (1955) elevated *Xiphypops* to generic rank. As a result of comparative osteological studies SHEN & LIU (1978) also treated *Xiphypops* and *Centropyge* as separate genera. More recently *Xiphypops* again was regarded as a subgenus (KISHIMOTO et al. 1996, CHUNG & WOO 1998). Other authors (e.g. FRASER-BRUNNER 1933, PYLE & RANDALL 1992) considered *Xiphypops* as synonym to *Centropyge*. BURGESS (1991) described two further

genera, *Paracentropyge* with *Holacanthus multifasciatus* SMITH & RADCLIFFE, 1911 and *Sumireyakko* with *Holacanthus venustus* YASUDA & TOMINAGA, 1969 as type species. The two taxa (*Paracentropyge* and *Sumireyakko*) were shortly after revised as synonyms of *Centropyge* by PYLE & RANDALL (1992). Presently, ALLEN et al. (1998), SCHNEIDEWIND (1999) and NAKABO (2000, after ESCHMEYER 2002) consider *Paracentropyge* as a possibly valid genus with the three species *P. multifasciata*, *P. boylei* and *P. venusta*. In addition, there is evidence that *Paracentropyge* is a non-monophyletic group (see CHUNG & WOO 1998). In this study *Paracentropyge* is recognized as group name in order to check differences in body shape between this unit with *Centropyge* and its subgenera *Centropyge* and *Xiphypops*. Comparative studies by KISHIMOTO et al. (1996) and CHUNG & WOO (1998) suggested that *Centropyge* and *Xiphypops* are valid subgenera of *Centropyge*.

Most species of *Centropyge* are very similar or even identical in meristic characters (number of spines of fin rays and number of scales in longitudinal series). In most cases traditional morphometric measurements neither reveal any significant differences. Some authors separated species by body proportions (e. g. FRASER-BRUNNER 1933, KOSAKI 1989, PYLE 1990) even though there was a broad overlapping in measurements. On the other hand there are some species within the genus, which have a relatively high, more rounded body (e. g. *C. aurantia*, *C. colini*). The main diagnostic character of *Paracentropyge* is also the relative high body in comparison to the majority of *Centropyge* (BURGESS 1991, ALLEN et al. 1998). However, a comprehensive analysis of the differences in body shape in these groups has not been done yet. In the following study the variation in body shape (lateral body outline) in *Centropyge* and *Paracentropyge* is analysed by means of geometric morphometric methods (BOOKSTEIN 1991, ROHLF & MARCUS 1993) in order to check if there are taxonomically qualified differences between the groups mentioned. Since morphological characters may also be a result of evolutionary pressure, body morphology may also be susceptible to functional constraints. However, a discussion of adaptations in function

Tab. 1: Species and number of specimens of analysed Pygmy Angelfishes (Classification of genera and subgenera after ALLEN et al. [1998]).

Tab. 1: Liste der Arten und die Zahl der untersuchten Exemplare der Zwergkaiserfische (Klassifikation der Gattungen und Untergattungen nach ALLEN et al. [1998]).

Genus	Subgenus	Species	n		
<i>Centropyge</i>	<i>Centropyge</i>	<i>aurantia</i>	5		
		<i>bicolor</i>	2		
		<i>colini</i>	5		
		<i>eibli</i>	5		
		<i>flavissima</i>	5		
		<i>heraldi</i>	2		
		<i>heraldi</i> "woodbeadi" ¹⁾	3		
		<i>multispinis</i>	4		
		<i>narcosis</i>	2		
		<i>nox</i>	2		
		<i>tibicen</i>	2		
		<i>vrolikii</i>	1		
		<i>Centropyge</i>	<i>Xiphypops</i>	<i>acanthops</i>	5
				<i>argi</i>	1
				<i>aurantonotus</i>	3
<i>bispinosa</i>	4				
<i>debelius</i>	2				
<i>ferrugata</i>	3				
<i>fisheri</i>	4				
<i>flavicauda</i>	3				
<i>hotumatua</i>	2				
<i>interrupta</i>	4				
<i>joculator</i>	2				
<i>loriculus</i>	3				
<i>multicolor</i>	4				
<i>nabackyi</i>	2				
<i>nigriocellus</i>	2				
<i>potteri</i>	4				
<i>resplendens</i>	2				
<i>shepardii</i>	2				
spec. "Red Head" ²⁾	2				
<i>Centropyge</i>	<i>Xiphypops</i> ³⁾	<i>flavipectoralis</i>	3		
		<i>boylei</i>	1		
<i>Paracentropyge</i> ⁴⁾		<i>multifasciata</i>	3		
		<i>venusta</i>	3		

¹⁾ *Centropyge woodbeadi* is recognized as a synonym of *C. (C.) heraldi* by RANDALL & CARLSON (2000).

²⁾ "Red Head" was introduced by SCHNEIDEWIND & DREXHAGE (2001) for a possible hybrid between *C. acanthops* and *C. flavicauda*.

³⁾ Species transferred to subgenus *Centropyge* (see text).

⁴⁾ Possibly not monophyletic entity (CHUNG & WOO 1998).

nal morphology of different body forms is not within the scope of the paper since all pygmy angelfishes are living in the same habitat and have similar behaviour.

2. Material and Methods

2.1. Material

Photos of 102 specimens were used (Tab. 1) to analyse the variation in the body shape of pygmy angelfishes. The majority of them are from SCHNEIDEWIND's collection of colour slides, a few from the author's collection. Some of the depicted specimens were kept in an aquarium for approximately half a year. In rare species figures of type specimens published in the original descriptions were also used to collect data. Particular attention was given to the fact, that in photos the median plane of the fish was parallel to the focal plane of the camera. The position of a specimen in relation to the center of the photo did not affect the usefulness of the picture (HARDER 1994). Only photos of adult specimens were used. The relative size of the depicted specimen was without significance for data analysis, because of using defined baseline (see 2.2.).

Classification of genera and subgenera follows ALLEN et al. (1998). The spelling of species names is according to SCHINDLER & SCHNEIDEWIND (2001). The determination of specimens is based on comparison with colour photos in ALLEN (1979), SCHNEIDEWIND (1999) and STEENE (1977).

2. 2. Methods

2. 2. 1. Data acquirement

The colour slides of the specimens were projected on white paper to draw the critical points (landmarks). Subsequently these were scanned and stored as computer files. For each specimen Cartesian coordinates of 11 landmarks (LMs) were digitized (Fig. 1) using tpsDig (ROHLF 2001). The two dimensional coordinates are described by values for the x-axis and the y-axis,

representing the horizontal line (body length axis) and the vertical line (body depth axis) respectively. The raw landmark coordinates were translated into shape-coordinates (BOOKSTEIN 1991) by rotation and scaling relative to the unit baseline. The baseline is defined by LM1 and LM6 (Fig. 1) as endpoints. These endpoints get the coordinates (0,0) and (1,0), respectively. Using the Unigraph program by MARCUS (1993), the raw coordinates were rotated onto the baseline and divided by the baseline length to yield a set of Bookstein-shape-coordinates (BSCs) (SCHAEFER 1997). All subsequent analyses were based on these BSCs except the coordinates of the endpoints (LM1 and LM6) of baseline. BSCs represent a size-free description of body shape for each specimen (SCHAEFER 1997, MORAES et al. 2000). This method is particularly suited to distinguish differences in shape, if shape variation is small and baseline reasonable (DOUGLAS et al. 2001). Both assumptions are valid here. The coordinates are much more useful than traditional measurements, because the body form can be studied by a graphical display of its LMs (ROHLF & MARCUS 1993).

Traditional distance measurements (Euclidean distance) between two homologous landmarks are computed with the program Kood_Mess.vbp (SCHINDLER unpubl.).

2.2.2. Data analysis

Principal component analyses (PCA) with the correlation matrix between BSCs were applied to reduce dimensionality of data (PCs) (FADDA & CORTI 2000). Canonical variate analyses (CVA) were performed with BSCs to test the hypothesis of groups separation on the axes (CVs) of the greatest variation among units (SCHAEFER 1997, MORAES et al. 2000). The program MV-Nutshell (WRIGHT 1994) was used for the PCA and the CVA. The statistical significance of group separations was calculated with the nonparametric Kruskal-Wallis test (H-Test) and with a multiple pairwise comparison rank test, according to the procedure described in LOZAN & KAUSCH (1998), using the program H-skalk.bas (SCHINDLER unpubl.).

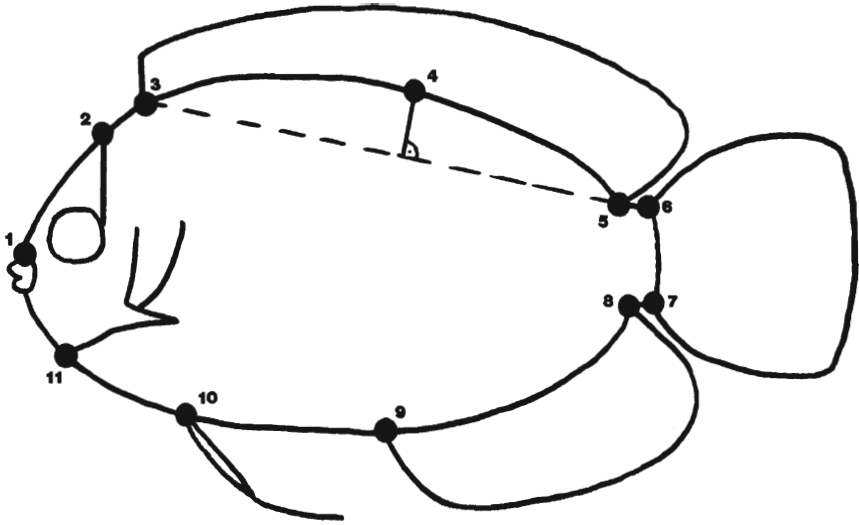


Fig. 1: Position of 11 landmarks used to define lateral body shape. (1) anterior tip of head above upper jaw, (2) intersection of a line drawn from the posterior eye margin with dorsal edge of head contour at presumed midsagittal line, (3) anterior insertion of dorsal fin, (4) intersection of a line drawn from the middle of the presumed axis between LM3 and LM5 to the body outline, (5) posterior insertion of dorsal fin, (6) dorsal insertion of caudal fin, (7) ventral insertion of caudal fin, (8) posterior insertion of anal fin, (9) anterior insertion of anal fin, (10) anterior insertion of pelvic fin, (11) intersection of branchiostegals with ventral margin of body contour.

Abb. 1: Position der elf kritischen Punkte zur Darstellung der Körperform. (1) vordere Spitze des Kopfes über dem Oberkiefer, (2) Schnittpunkt der Linie vom hinterem Rand des Auges mit der dorsalen Kontur des Kopfes entlang der mittleren Sagittallinie, (3) vorderer Ansatz der Rückenflosse, (4) Schnittpunkt einer Linie, die vom Mittelpunkt einer gedachten Achse zwischen den Punkten LM3 und LM5 zum dorsalem Rand des Körperumrisses führt, (5) hinterer Ansatz der Rückenflosse, (6) dorsaler Ansatz der Schwanzflosse, (7) ventraler Ansatz der Schwanzflosse, (8) hinterer Ansatz der Afterflosse, (9) vorderer Ansatz der Afterflosse, (10) vorderer Ansatz der Bauchflosse, (11) Schnittpunkt der Kiemenhautstrahlen mit der ventralen Kontur des Körperumrisses.

3. Results

3.1. Geometric morphometrics

The scatter plot of PC1 against PC3 (Fig. 2) provided the best separation of specimens of the subgenus *Centropyge* from the subgenus *Xiphypops*. Furthermore, a species group related to *C. (X.) fisheri* was separated with higher PC1 scores against all others. On the left side of Fig. 1 (lower PC1 scores) the more deep bodied species *C. (C.) aurantia*, *C. (C.) narcosis* and *C. (C.) colini* together with members of *Paracentropyge* are separated from the remaining members of *Centropyge*. Near the centre of the scatter plot is a dense cluster in which *Xiphypops* and *Centropyge* overlap. No further spe-

cies unit was recognized. The results of H-Test (Tab. 2) show significant ($p < 0.05$) differences, particularly in y-axis. On PC1 scores there are significant ($p < 0.05$) differences between *Xiphypops* and *Centropyge* and between *Xiphypops* and *Paracentropyge* ($p < 0.01$). But there is no statistical difference between *Centropyge* and *Paracentropyge* in PC1 scores (Tab. 2).

A CVA with the three taxonomic units (*Centropyge*, *Xiphypops* and *Paracentropyge*) verifies the different body shape of the members of the two subgenera (Fig. 3). But *C. (X.) flavipectoralis* appears to diverge from the remaining *Xiphypops* and lies more closely to members of the subgenus *Centropyge*, although in the CVA this taxon was calculated as a member of the subgenus *Xi-*

Tab. 2: Results of multiple pairwise comparisons between taxonomic units. Not significantly ($p > 0.05$) different groups are included in parentheses. CEN = subgenus *Centropyge*, XIP = subgenus *Xiphipops* (except *fisheri*-complex), FIS = *C. (X.) fisheri*-complex, PAR = *Paracentropyge*.

Tab. 2: Ergebnisse der multiplen paarweisen Vergleiche der taxonomischen Einheiten. Signifikant nicht verschiedene Gruppen ($p > 0,05$) sind in einer Klammer zusammengefasst. CEN = Untergattung *Centropyge*, XIP = Untergattung *Xiphipops* (außer *fisheri*-Komplex), FIS = *C. (X.) fisheri*-Komplex, PAR = *Paracentropyge*.

Character	Groups
BSCs	
X2	(CEN, XIP, FIS, PAR)
Y2	(CEN, PAR)(XIP,FIS)
X3	(CEN, XIP, FIS, PAR)
Y3	(CEN, PAR)(XIP, FIS)
X4	(CEN, XIP, FIS, PAR)
Y4	(CEN, XIP)(CEN, PAR)(FIS)
X5	(CEN, XIP, PAR)(XIP, FIS, PAR)
Y5	(CEN, XIP, FIS, PAR)
X7	(CEN, XIP, PAR)(XIP, FIS, PAR)
Y7	(CEN, PAR)(XIP, PAR)(XIP,FIS)
X8	(CEN, XIP, FIS, PAR)
Y8	(CEN, PAR)(XIP, FIS)(XIP, PAR)
X9	(CEN, XIP, FIS, PAR)
Y9	(CEN, PAR)(CEN, XIP)(FIS)
X10	(CEN, XIP, FIS, PAR)
Y10	(CEN, XIP, PAR)(FIS)
X11	(CEN, PAR)(XIP, FIS, PAR)
Y11	(CEN, PAR)(XIP, FIS)
PC scores	
PC1	(CEN, PAR)(XIP)(FIS)
PC2	(CEN, XIP, FIS, PAR)
PC3	(CEN, XIP, FIS, PAR)
Distances measurements	
dLM3-LM8	(CEN, PAR)(XIP, FIS)
dLM3-LM9	(CEN, XIP)(CEN, PAR)(FIS)
dLM3-LM10	(CEN, XIP)(CEN, PAR)(FIS)
dLM5-LM7	(CEN, PAR)(CEN, XIP, FIS)

phypops. Consequently, *C. flavipectoralis* is not included in the subgenus *Xiphipops* for further analysis. *Paracentropyge* almost join the cluster of the subgenus *Centropyge*. The results of multiple pairwise comparison tests of CV1 scores show a significant ($p < 0.01$) separation of *C. (Xiphipops)* from *C. (Centropyge)* and *Paracentropyge*. While *Paracentropyge* is not statistically different ($p > 0.05$)

from the subgenus *Centropyge* in CV1 scores, *Paracentropyge* and the subgenus *Centropyge* separated ($p < 0.05$) in CV2 (Tab. 2).

The differences in body shape are illustrated in Fig. 6 using the arithmetic mean of each LMs based on BSCs. The main difference based on the displacement of LMs in the y-axis, with *Paracentropyge* as the most deep bodied form. A shifting of LM2 and LM3 in x-axis particularly in *Paracentropyge* is also visible. In addition, *Xiphipops* is more slender and has a slightly longer caudal peduncle. These results are reflected in statistical comparison of each BSC (Tab. 2).

The seven species related to *C. (X.) fisheri* (Fig. 2) are grouped against the remaining members of the subgenus in order to test differences in body shape diversity within *Xiphipops*. The seven species associated to *C. (X.) fisheri* are: *C. (X.) acanthops*, *C. (X.) argi*, *C. (X.) aurantonotus*, *C. (X.) fisheri*, *C. (X.) flavicauda*, *C. (X.) resplendens* and *C. (X.) spec. "Red Head"*. This group is called *C. (X.) fisheri*-complex. In Fig. 4 results of a CVA are presented. Based on the only extracted CV1 both groups are completely separate ($p < 0.01$). Apart from the *C. (X.) fisheri*-complex there is no further unambiguous cluster of specimens within the subgenus *Xiphipops*. The mean body shape of the *C. (X.) fisheri*-complex is less deep. This is reflected by uni-dimensional comparison of BSCs in significant separations ($p < 0.05$) of several values in y-axis (Y2, Y3, Y4, Y7, Y9, Y10). The difference in body shape between the *C. (X.) fisheri*-complex and the remaining members of the subgenus is shown in figure 7.

To evaluate the diversity of body shape in members of the subgenus *Centropyge*, a PCA with the specimens of this unit was performed (Fig. 5). At the first glance the scatter plot (Fig. 5) appears to have three distinct clusters. Closer examination reveals that the gap runs through the range of at least one species of species units. Thus, no unambiguous cluster of species could be validated. However, the deep bodied species *C. (C.) colini*, *C. (C.) narcosis* and particularly *C. (C.) aurantia* are separated from the others. This is reflected in statistical tests of BSCs and PCs scores (Tab. 3).

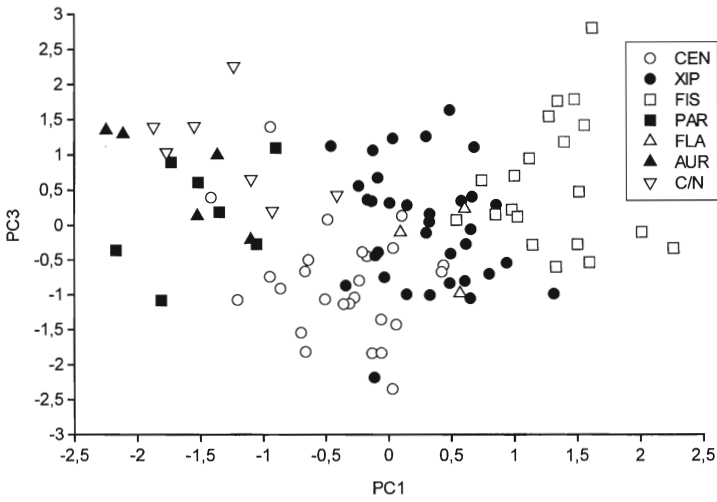


Fig. 2: Scatter plot of PC scores. CEN = subgenus *Centropyge*, XIP = subgenus *Xiphiypops* (except *fisheri*-complex), FIS = *C.-(Xiphiypops)-fisheri*-complex, PAR = *Paracentropyge*, FLA = *C. flavipectoralis*, AUR = *C. (C.) aurantia*, C/N = *C. (C.) colini* and *C. (C.) narcosis*.

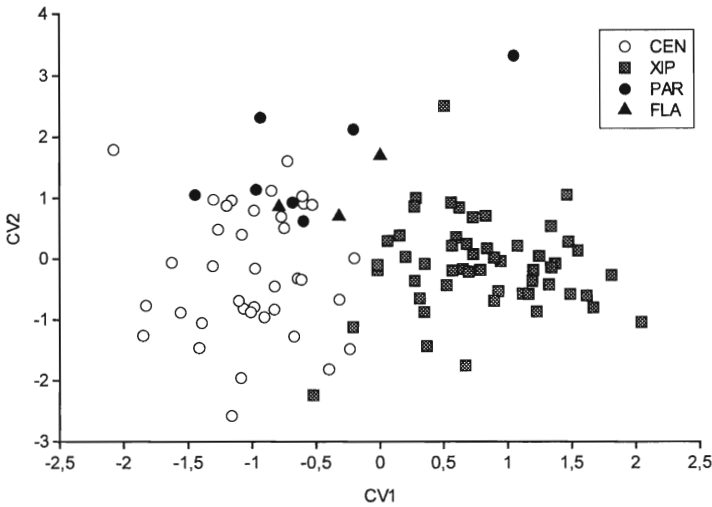


Abb. 2: Punktdiagramm der Hauptkomponentenwerte. CEN = Untergattung *Centropyge*, XIP = Untergattung *Xiphiypops* (except *fisheri*-complex), FIS = *C.-(Xiphiypops)-fisheri*-complex, PAR = *Paracentropyge*, FLA = *C. flavipectoralis*, AUR = *C. (C.) aurantia*, C/N = *C. (C.) colini* and *C. (C.) narcosis*.

Fig. 3: Scatter plot of CV scores of taxonomic groups. Refer to Fig. 2 for abbreviations of the groups.

Abb. 3: Punktdiagramm der CVA-Werte. Abkürzungen der Gruppennamen wie in Abb. 2.

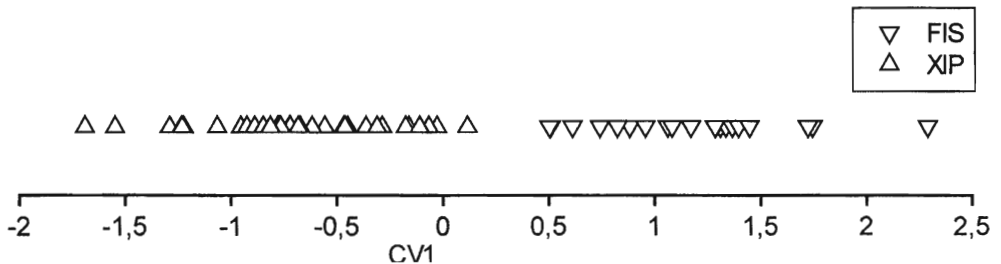


Fig. 4: Result of CVA between *C.-(X.) fisheri*-complex and remaining species of subgenus *Xiphiypops*. Refer to Fig. 2 for abbreviations of the groups.

Abb. 4: Ergebniss einer CVA zwischen dem *C.-(X.) fisheri*-Komplex mit den übrigen Arten der Untergattung *Xiphiypops*. Abkürzungen der Gruppennamen wie in Abb. 2.

Fig. 5: Scatter plot of PC scores within subgenus *Centropyge*. AUR = *C. (C.) aurantia*, C/N = *C. (C.) colini* and *C. (C.) narcosis*, EIB = *C. (C.) eibli*, F/H = *C. (C.) flavissima*, CEN = remain members of subgenus *Centropyge*.
Abb. 5: Punktdiagramm der Hauptkomponentenwerte innerhalb der Untergattung *Centropyge*. AUR = *C. (C.) aurantia*, C/N = *C. (C.) colini* and *C. (C.) narcosis*, EIB = *C. (C.) eibli*, FLA = *C. (C.) flavipectoralis*, CEN = übrige Arten der Untergattung *Centropyge*.

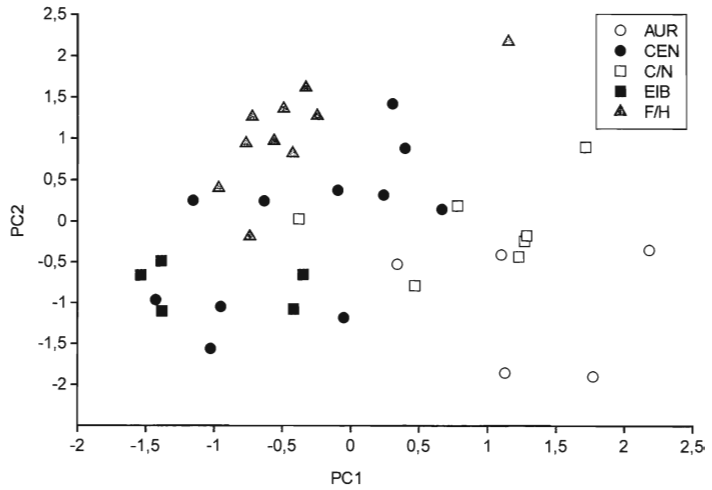


Fig. 6: Differences in Bookstein-coordinates between taxonomic units. CEN = *Centropyge*, XIP = *Xiphipops*, PAR = *Paracentropyge*.
Abb. 6: Unterschiede in den Bookstein-Koordinaten zwischen den taxonomischen Gruppen. CEN = *Centropyge*, XIP = *Xiphipops*, PAR = *Paracentropyge*.

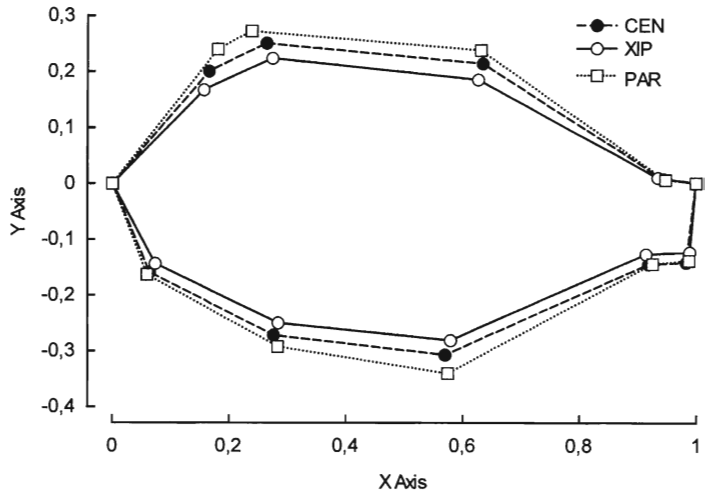
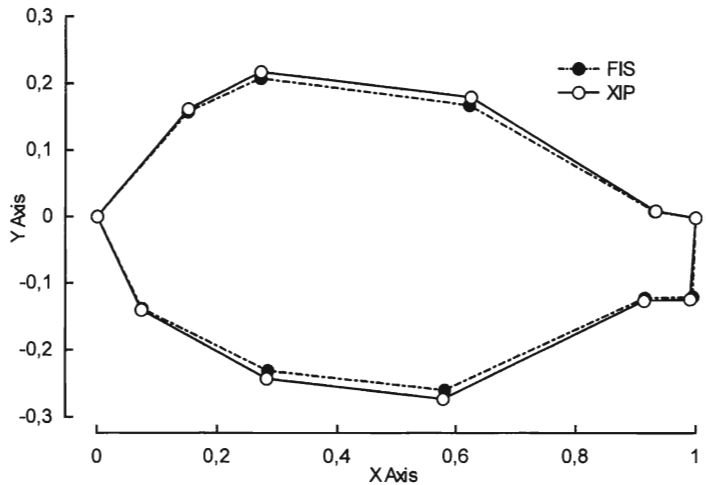


Fig. 7: Differences in Bookstein-coordinates between the *fisheri*-complex and remaining members of subgenus *Xiphipops*. FIS = *C.-(X.) fisheri*-complex, XIP = *Xiphipops* (except *fisheri*-complex).
Abb. 7: Unterschiede in den Bookstein-Koordinaten zwischen dem *fisheri*-Komplex und den übrigen Angehörigen der Untergattung *Xiphipops*. FIS = *C.-(X.) fisheri*-Komplex, XIP = *Xiphipops* (außer *fisheri*-complex).



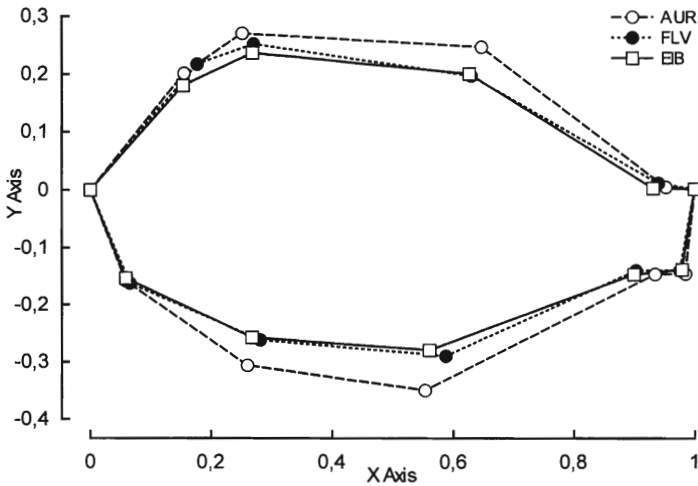


Fig. 8: Differences in Bookstein-coordinates between selected species of subgenus *Centropyge*. AUR = *C. (C.) aurantia*, F/H = *C. (C.) flavissima*, EIB = *C. (C.) eibli*.

Abb. 8: Unterschiede in den Bookstein-Koordinaten zwischen ausgewählten Arten der Untergattung *Centropyge*. AUR = *C. (C.) aurantia*, FLV = *C. (C.) flavissima*, EIB = *C. (C.) eibli*.

The differences in positions of LMs within the subgenus *Centropyge* are shown in Fig. 8 by using the mean configuration of three species representing extreme PC scores (Fig. 5). These three species are: *C. (C.) aurantia* (high PC1 and low PC2 scores), *C. (C.) eibli* (low PC1 and low PC2 scores) and *C. (C.) flavissima* (highest PC2 and averaged PC1 scores). The heterogeneity of the subgenus *Centropyge* is distinctly visible: *Centropyge (C.) aurantia* has the deepest, rather round body form and the shortest caudal peduncle, *C. (C.) flavissima* had shifted positions of LM2 and LM3 in y-axis and displaced LM9 on x-axis, while *C. (C.) eibli* seems to have a more or less ordinary body shape.

3.2. Distance measurements

Distances between LMs were also analysed to class preserved specimens into taxonomic units on the basis of traditional measurements. Only four (dLM3-LM8, dLM3-LM9, dLM3-LM10 and dLM5-LM9) of all the distances (d) between LMs (except for LM2 and LM4) are extracted which tolerably characterized taxonomic units (Tab. 2, 3). All are recommended for use in comparisons founded on distance measurements. But there is no distance measurement, which is sufficient to discriminate all the taxonomic units, and none depicts the general body shape. Most helpful for discriminations between taxo-

nomic samples is dLM3-LM10, which represents the body height.

4. Discussion

Despite their superficial morphological similarities, it is possible to reveal differences in body shape of the taxonomic groups of pygmy angelfishes studied. The differences between members of the subgenera *Centropyge* and *Xiphytops* are statistically significant (Tab. 2) and clearly visible (Fig. 2, 6). However, if the extremes (*C. (X.) fisheri*-complex and *C. (C.) aurantia*, *C. (C.) colini* and *C. (C.) narcosis*) are excluded the differences are less distinct. This is reflected in a continually dense cluster in centre of Fig. 2. However, both taxonomic groups (*Xiphytops* and *Centropyge*) are not only separated by their body shape. They are also characterized by differences in their osteology, behaviour and allozyme variation (SHEN & LIU 1978, MOYER 1989, CHUNG & WOO 1998). At first glance it seems reasonable, therefore, to raise them to generic level. But not all characters mentioned by SHEN & LIU (1978) to separate *Xiphytops* and *Centropyge* are valid for all species (KISHIMOTO et al. 1996). Thus, if the subgenera *Xiphytops* and *Centropyge* are not - from a more conservative point of view - lumped together in only a single taxon, it may even be possible that there are more than two evolutionary trends within the pygmy angelfishes. Therefore it seems to be

Tab. 3: Selected results of multiple pairwise comparisons between species and species units within the subgenus *Centropyge*. Not significantly ($p > 0.05$) different groups are included in paranthesis. AUR = *C. (C.) aurantia*, CEN = subgenus *Centropyge* (other than AUR, C/N, EIB, F/H), C/N = *C. (C.) colini* and *C. (C.) narcosis*, EIB = *C. (C.) eibli*, F/H = *C. (C.) flavissima* and *C. (C.) heraldi*.

Tab. 3: Ausgewählte Ergebnisse der multiplen paarweisen Vergleiche zwischen den Arten und Artengruppen innerhalb der Untergattung *Centropyge*. Signifikant nicht verschiedene Gruppen ($p > 0,05$) sind in einer Klammer zusammengefasst. AUR = *C. (C.) aurantia*, CEN = Untergattung *Centropyge* (außer AUR, C/N, EIB, F/H), C/N = *C. (C.) colini* und *C. (C.) narcosis*, EIB = *C. (C.) eibli*, F/H = *C. (C.) flavissima* und *C. (C.) heraldi*.

Character	Gruppen
BSCs	
Y3	(AUR, CEN, C/N, F/H)(CEN, EIB, C/N, F/H)
Y4	(AUR, CEN, EIB)(AUR, C/N, EIB)(CEN, EIB, F/H)
Y9	(AUR, CEN, C/N)(CEN, C/N, EIB, F/H)
PC scores	
PC1	(AUR, CEN, C/N, F/H)(EIB, CEN, C/N, F/H)
PC2	(AUR, CEN, C/N, F/H)(AUR, CEN, C/N, EIB)
PC3	(AUR, C/N, EIB)(AUR, CEN, EIB, F/H)
Distances measurements	
dLM3-LM8	(AUR, CEN, EIB, F/H)(AUR, C/N)
dLM3-LM9	(AUR, CEN, C/N, F/H)(CEN, EIB, F/H)
dLM3-LM10	(AUR, C/N)(CEN, C/N, EIB, F/H)

best not to change their current systematic status (cf. CHUNG & WOO 1998) till a thorough phylogenetic analysis is available.

Within *Xiphipops* the *C. (X.) fisheri*-complex is a divergent group. It is distinctly separated in body shape (Fig. 7). In addition this species complex differs in distance measurements (dLM3-LM10 41-48% of base-line length in the *C. (X.) fisheri*-complex vs. 47-52% in other *Xiphipops* and dLM3-

LM9 52-58% vs. 57-64%). Further on, all species of the *C. (X.) fisheri*-complex have two or three very stiff spines on the ventral margin of the lacrymal bone (KISHIMOTO et al. 1996, pers. observ.) instead of three or more less stiff spines (this character has not been checked in all species) as in most of the remaining species of *Xiphipops* (e. g. *C. (X.) loriculus*, *C. (X.) shepardi*). *Centropyge (X.) nigriocellus*, for example, has a few stiff spines and therefore seems to be closely related to the *C. (X.) fisheri*-complex. The results of body shape analyses, however, did not reveal another species group within *Xiphipops*. But this may be caused by the small sample size for each species.

Species of the subgenus *Centropyge* are more heterogeneous in their body shape. *Centropyge (C.) aurantia* and *C. (C.) colini* are most deep and more round bodied, but not necessary closely related. The two bright yellow coloured species *C. (C.) flavissima* and *C. (C.) heraldi* seem to be more rather closely related to each other, for both are characterised by a relative strong displacement of LM2 and LM3 (Fig. 8). But this has to be checked on the basis of more specimens.

Centropyge flavipectoralis RANDALL & KLAUSEWITZ, 1977 was included in the subgenus *Xiphipops* by ALLEN (1979) and ALLEN et al. (1998), although the closely related species *C. multispinis* was transferred from the subgenus *Xiphipops* to the subgenus *Centropyge* by KISHIMOTO et al. (1996) mainly because of osteological features. MOYER (1989) believes that *C. flavipectoralis* represents a colour morph of *C. multispinis*. *Centropyge flavipectoralis* clustered more to the specimens of subgenus *Centropyge* than to *Xiphipops* in body shape analysis (Fig. 3). As *C. flavipectoralis* share all characters (see RANDALL & KLAUSEWITZ 1977, ALLEN 1979) with *Centropyge* rather than *Xiphipops* (e.g. total gill rakers < 20 in *C. flavipectoralis* vs. minimally 20 in *Xiphipops*, ventro-posterior margin of lacrymal bone with 4-9 small spinules vs. 1-3 spines, some spinules), this species is transferred from the subgenus *Xiphipops* to the subgenus *Centropyge*.

An important diagnostic feature of *Paracentropyge* is the relatively deep body (BURGESS 1991). But in this study the body shape is not confirmed as a significantly distinguishing feature to separate *Paracentropyge* from all the other taxo-

onomic units. In this aspect species of *Paracentropyge* differ significantly ($p < 0.01$) only from members of *Xiphypops* (dLM3-LM10 >55% of the baseline length in *Paracentropyge* vs. <53% in *Xiphypops*). An analysis of the allozyme variation provided evidence that *Paracentropyge* (with *C. multifasciatus*) is a synonym of *Centropyge* and that the type species of *Sumireyakko* (*H. venustus*) is a member of *Holacanthus* (see CHUNG & WOO 1998). However, any revision of the systematic position of the pygmy angelfishes should not be based on a single character complex, but should include a comparison of several distinguishing features (e. g. osteology, morphology, behaviour etc.).

In this analysis the method of geometric morphometrics (ROHLF & MARCUS 1993) proved to be an effective tool to analyse the body shapes of fishes. In contrast to the use of traditional measurements it was possible to define different units within the pygmy angelfishes. These units can be separated statistically on the basis of the discrimination of the taxonomic groups. The differences in body shape of pygmy angelfishes described above correlated with results in osteology (KISHIMOTO et al. 1996) and allozyme variation (CHUNG & WOO 1998). Thus, differences in the body shape at least partly represent the results of phylogenetic history, instead of only environmental factors.

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