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Revision of *Centropyge fisheri* (SNYDER, 1904) (Teleostei, Pomacanthidae)

Revision von *Centropyge fisheri* (SNYDER, 1904) (Teleostei, Pomacanthidae)

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Summary: The taxonomy of the marine pygmy angelfish *Centropyge* (*Xiphypops*) *fisheri* (SNYDER, 1904), a species widespread in the Indo-Pacific, is revised. The three taxa *C. caudoxanthorus* SHEN, 1973, *C. flavicauda* FRASER-BRUNNER, 1933 and *Holacanthus acanthops* NORMAN, 1922 are considered as synonyms of *C. fisheri* which is the nominal species of the *C.* (*X.*) *fisheri*-complex. The members of this complex differ from all the other *Centropyge* species by the combination of two or three stout spines on the ventral margin of the lacrymal bone and more than 20 gill rakers on the first outer gill arch. *C.* (*X.*) *fisheri* is distinguished from the closely related species *C. argi*, *C. aurantonotus* and *C. resplendens* by a different colouration of the caudal fin (translucent vs. blue or yellow).

Key words: Pomacanthidae, *Centroypyge, Xiphypops, C. fisheri, C. flavicauda, C. acanthops, C. caudoxanthorus, C. fisheri*-complex, taxonomy, body shape.

Zusammenfassung: Der Zwergkaiserfisch *Centropyge* (*Xiphypops*) *fisheri* (SNYDER, 1904) wird revidiert. Die Taxa *C. caudoxanthorus* SHEN, 1973, *C. flavicauda* FRASER-BRUNNER, 1933 and *Holacanthus acanthops* NORMAN, 1922 werden als Synonyme von *C. fisheri* betrachtet. Die im Indo-Pazifik weit verbreitete Art ist Namensgeber für den *C.* (*X.*) *fisheri*-Artenkomplex. Die Angehörigen dieses Artenkomplexes unterscheiden sich von allen übrigen *Centropyge*-Arten durch die Kombination von zwei oder drei kräftigen Dornen am ventralen Rand des Lacrimale und mehr als 20 Kiemenrechen auf dem äußeren Kiemenbogen. Von den nah verwandten Arten *C. argi*, *C. aurantonotus* and *C. resplendens* unterscheidet sich *C.* (*X.*) *fisheri* durch eine anders gefärbte Schwanzflosse (durchsichtig gegenüber gelb bzw. blau).

Schlüsselwörter: Pomacanthidae, *Centroypyge, Xiphypops, C. fisheri, C. flavicauda, C. acanthops, C. caudoxanthorus, C. fisheri*-Komplex, Taxonomie, Körperform.

1. Introduction

In 1904 SNYDER described the pygmy angelfish *Holacanthus fisheri* from the Hawaii Islands. Later JORDAN in JORDAN & JORDAN (1922) used this taxon as the type species for the new genus *Xiphypops* (often misspelled as *Xiphipops*, see ESCHMEYER 1990). At the same time NORMAN (1922) described *Holacanthus acanthops* from the east coast of South Africa. He distinguished the new taxon from *H. fisheri* on the basis of a different number of stout spines on the lacrymal bone. The next closely related species was *Centropyge flavicauda* described by FRASER-BRUNNER (1933) from the China Sea. This author placed the mentioned *Holacanthus* species in *Centropyge* and distinguished it from *C. acanthops* and *C. fisheri* by its flatter body. A further species concerned is *C. caudoxanthorus* SHEN, 1973 from Taiwan, which was diagnosed by a different colouration of the caudal fin. ALLEN (1979) synonymized *C. caudoxanthorus* with *C. flavicauda* without explaining his reasons.

During the last decades the taxonomy of these taxa was controversially discussed and changed several times. SMITH (1955) synonymised *acanthops* with *fisheri*. ALLEN (1979) and HEEMSTRA (1984) treated the three taxa *acanthops*, *fisheri* and *flavicauda* as valid within the genus *Centropyge*, mainly because of differences in their colour

patterns. RANDALL (1996) mentioned *C. flavicauda* as a possible synonym of *C. fisheri*.

Recently, specimens with an intermediate colour pattern between *acanthops* and *flavicauda* were discovered at the Maldives. This population was introduced as a possible hybrid between *C. acanthops* and *C. flavicauda* by SCHNEIDEWIND & DREXHAGE (2001). Further studies, however, showed that these specimens are no hybrids, but represent an intermediate colour morph (SCHNEIDEWIND 2004). Therefore it is suggested as a result of the new data that only one species (*C. fisheri*) should be recognised. The purpose of this paper is to clarify the taxonomic status of *C. fisheri* (SNYDER, 1904) and to show that *C. acanthops* (NORMAN, 1922), *C. flavicauda* FRASER-BRUNNER, 1933 and *C. caudoxanthorus* SHEN, 1973 are junior synonyms of *C. fisheri*.

2. Material and Methods

2.1. Material

Counts were taken from the following 15 specimens: *C. acanthops*, 4 specimens, 30.5 to 43.6 mm SL. C. "Red Head", MTD F 28143-28144, 2 specimens of 34.5 and 35.6 mm SL and 2 specimens (not catalogued) of 30.2 and 35.5 mm SL. *C. fisheri* 2 specimens of 42.8 and 44.5 mm SL. *C. flavicauda*, 5 specimens of 39.6 to 53.8 mm SL. The examined specimens were fixed in formalin, stored in 75% alcohol and deposited in the fish collection of the Museum für Tierkunde, Dresden (MTD F) and in the private collection of the authors.

The specimens are named according to the following rules (abbreviation in parentheses): *C. acanthops* (ACA) all specimens from the east coast of Africa and Mauritius; *C. fisheri* (FIS) specimens from Hawaii and Johnston Island, *C. flavicauda* (FLA) all specimens from the Pacific (except for Hawaii and Johnston Island) and the eastern parts of Indic, *C.* sp. "Red Head" (RED) specimens from the Maldives. FISSP = all specimens of the groups ACA, FIS, FLA and RED. There is no group name for *caudoxanthorus* because this species is enclosed in FLA. Classification of genera and subgenera follows SCHINDLER (2003). The spelling of species names is according to SCHINDLER & SCHNEIDEWIND (2001).

Colour slides of 52 specimens (10 ACA, 5 RED, 7 FIS, 5 FLA, 6 *C. bispinosa*, 2 *C. ferrugata*, 5 *C. loriculus*, 6 *C. potteri*, 3 *C. nigriocellus*, 1 *C. joculator*, 1 *C. shepardi* and 1 *C. nahackyi*) from the collection of RANDALL and the authors were used to analyse the variation in body shape by mean of the method of geometric morphometrics. See SCHINDLER (2003) for comparative material and explanation.

The photos mentioned above and in addition two pictures of ACA and 4 of RED (provided by AEBI and HARGREAVES) were used for the analysis of colour differences (cf. Fig. 1) within FISSP.

2.2. Methods

2.2.1. Data acquirement

Meristic data and traditional measurements were collected followed the methods described in RANDALL & WASS (1974). Measurements were taken with dial callipers (recorded to the nearest of 0.1 mm) under a dissection mircroscope and given in relation to the standard length (SL). For geometric morphometrics (ROHLF & MARCUS 1993) Cartesian coordianates of 11 landmarks (LMs) were digitized (fig. 1) using the program tpsDig (ROHLF 2001). For further details of the data collection see SCHINDLER (2003). Distance measurements (Euclidean metric) between LMs were computed by using the program Kood_Mess.vbp (SCHINDLER unpublished) and given as per cent of the distance of LM1 and LM12.

The hexadecimal RGB colour code was picked and recorded with the computer program "FarbenSammler" (SCHINDLER 2004) on scanned colour slides.

2.2.2. Data analysis

The program "Relative warps" version 1.29 (ROHLF 2003) was used to perform a within variation analysis of shapes described by the landmarks (LM1 to 11). The method of relative warps (see BOOKSTEIN 1991) computes a consensus con-

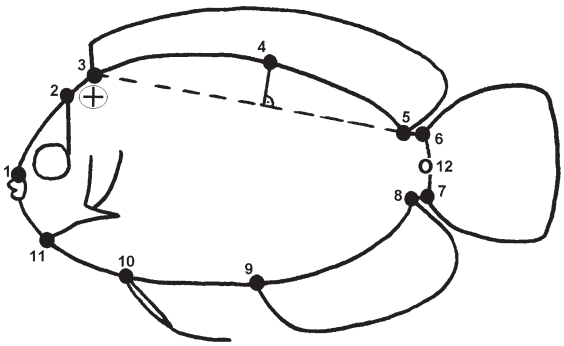

Fig. 1: Position of landmarks (1 to 12) and the area where the RGB-code was picked. 1 = anterior tip of head above upper jaw, 2 = intersection of a line drawn from the posterior eye margin with dorsal edge of head contour at presumed midsagittal line, 3 = anterior insertion of dorsal fin, 4 = intersection 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 brachiostegals with ventral margin of body contour, 12 = subsequently calculated as the arithmetic mean between the LM6 and LM7, + = area where the RGB-code was picked.

Abb. 1: Position der kritischen Punkte (1 bis 12) und der Region, in der der RGB-Code ermittelt wurde. 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, 12 = arithmetische Mitte zwischen den Punkten 6 und 7, + = Region, in der der RGB-Code erfaßt wurde.

figuration of landmarks using the generalized orthogonal least-squares Procrustes procedures described in ROHLF & SLICE (1990). Shape differences between the consensus landmark configuration and each individual specimen were obtained as represented by matrix of partial warp scores (BOOKSTEIN 1991). The relative warps scores were subsequently computed by a principal component analysis of the covariance matrix of these partial warps scores, with the alpha parameter set to zero to give equal weights to all partial warps at all spatial scales. The uniform shape component was included in the matrix of the partial warp scores. An informative example of relative warps analysis for morphometrics is given in ROHLF (1993). The statistical significance of group separations in measurements (Euclidean distance between LMs) was calculated with the parametric two sample t-test (see LOZAN & KAUSCH 1998).

The description and classification of colours is always somewhat problematic because it is affected by the individual subjective human colour vision and further weaknesses (ENDLER 1990). Therefore it is necessary to reduce subjective influence and to measure the differences in colouration with more objective criterions (ENDLER 1990). In this study the analysis of colouration is based on the picked RGB code. The colour code based on the primaries Red (R), Green (G) and Blue (B). Colour display monitors create different colours by additive mixtures of these three primaries (e. g. FOLEY et al. 1990, LEVKOWITZ 1997). For the calculation of the differences in the colouration the RGB code was transformed in its parts: red, green and blue. Subsequently, these values are used for the chromaticity diagram (HUNT 1987, see KÜPPERS 1981 for example) to observe the

ordination of specimens and groups of FISSP (see fig. 5).

3. Results

3.1. *Centropyge (Xiphypops) fisheri*

Holacanthus fisheri SNYDER, 1904: 532. Holotype: USNM 50881. Type locality: Oahu Island, Hawaii.
Synonyms:
Holacanthus acanthops NORMAN, 1922: 318. Holotype: BMNH 1922.1.13.38. Type locality: Durban, Natal, South Africa.
Centropyge flavicauda FRASER-BRUNNER, 1933: 597. Holotype: BMNH 1894.4.24.4. Type locality: Macclesfield Banks, China Sea.
Centropyge caudoxanthorus SHEN, 1973: 70. Holotype: NTU 72-11-23-001. Type locality: Ho-bi-hou, south-western tip of Taiwan.

3.2. Diagnosis

The nominal member of the *C. (X.) fisheri*-complex as diagnosed by SCHINDLER (2003, see 4.1. of this paper). *Centropyge (X.) fisheri* differs from the remaining members of this species complex in having an almost transparent (except for a dark anterior part of the dorsal- and ventral margin), slightly whitish to yellowish caudal fin *versus* a dark blue caudal fin in *C. argi* and *C. aurantonotus* or a bright yellow to orange caudal fin with a dark blue distal margin in *C. resplendens*.

3.3. Description

Refer to figure 2 for general aspects and to figure 3 for images of preopercle and lachrymal bones. Body relatively flat and elongate (body depth 2.02 to 2.21, mean 2.14 times in SL), strongly compressed laterally; dorsal contour more arched than ventral one. In frontal aspect with slightly keeled nape and somewhat flat chest. Caudal peduncle longer than high. Head short (head length 2.98 to 3.48, mean 3.22 times in SL) and moderately deep. Snout shorter than interorbital width. Orbit situated below forehead contour, interorbital area convex. Mouth terminal, wider than high and wider than snout length. Jaw teeth slender, very elongate, slightly curved inward terminally, close-set, flexible, tricuspid (central cusp longer than lateral cusps); about 65 teeth in outer row in upper and in the lower jaw 55 respectively. A large, elongate horizontal spine at ventro-caudal corner of preopercle, another much smaller spine on anteroventral margin of preopercle and 12 to 18 much smaller spines on upper caudal margin of preopercle. Anteroventral margin of preorbital with 2 very stout spines, in larger specimens (> 45 mm SL) sometimes with an additional third smaller spine. Dorsal fin with XIV spines (except for one specimen of FLA with XV and one specimen of group RED with XIII) and 16 soft rays. Anal fin with III spines and 16 or 17 soft rays. Pectoral fin with 16 soft rays. Pelvic fin rays I, 5 (except for an atypical specimen of group RED with I, 4). Lateral line scales 33 to 36. Dorsal and anal fin scaled (except for distal margin of anterior spinous part). Anterior part of caudal fin scaled. Pectoral fin without scales. Caudal fin rounded in small specimens (< 35 mm SL) and subtruncate in larger specimens. Soft part of dorsal and anal fin rounded. Dorsal fin spines progressively longer posterior (last spine usually more than 3 times longer than the first spine), soft rays longer than spines. Pectoral fin slightly pointed, reaching a vertical above origin of anal fin. Pelvic fin pointed, elongate; filamentous tips reaching spinous part of anal fin.

3.4. Colouration

The colour pattern of FISSP is well documented in recently published books and articles (e. g. ALLEN et al. 1998, SCHNEIDEWIND 1999, 2004, DEBELIUS & KUITER 2003, ENDOH 2003). These references are recommended for general characters and confirmation. There is a considerable geographic variation in the colour pattern (particularly in the hue of the nape and back) of *C. fisheri* (ACA, FIS, FLA, RED). This is why each concerned group is separately mentioned. However, there is also a variation within one population, and the following descriptions can give only a rough impression of the average typical pattern. For quan-

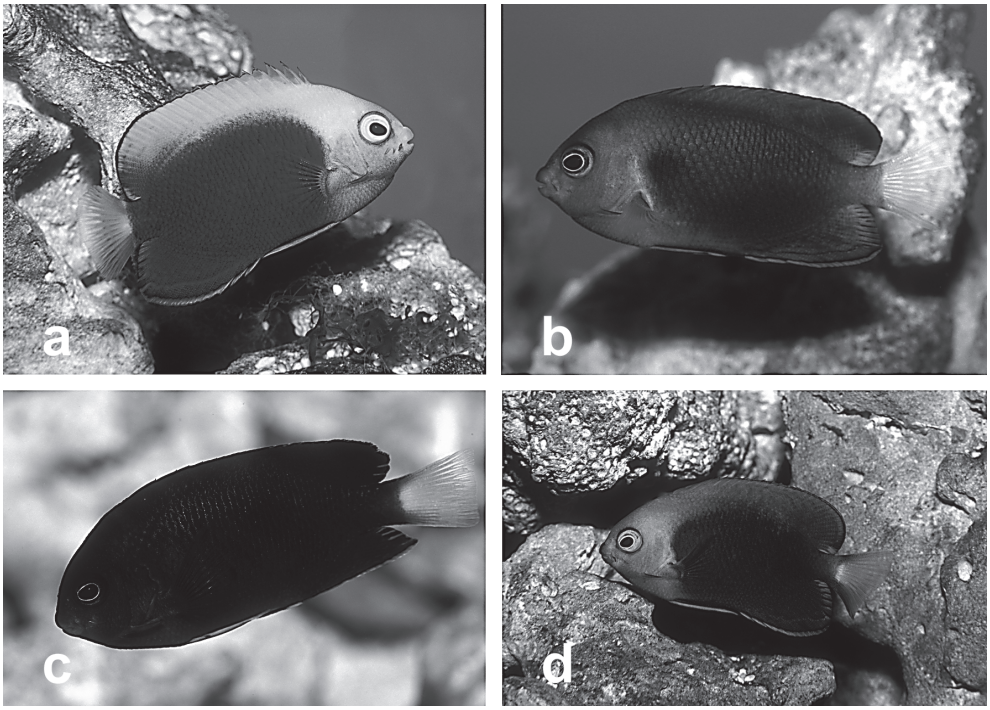

Fig. 2 a-d: Representative specimens of *Centropyge* (*Xiphypops*) *fisheri*. **a** = ACA (Kenia), **b** = FIS (Hawaii), **c** = FLA (Bali), **d** = RED (Maldives).
Abb. 2 a-d: Repräsentative Exemplare von *Centropyge* (*Xiphypops*) *fisheri*. **a** = ACA (Kenia), **b** = FIS (Hawaii), **c** = FLA (Bali), **d** = RED (Maldives).

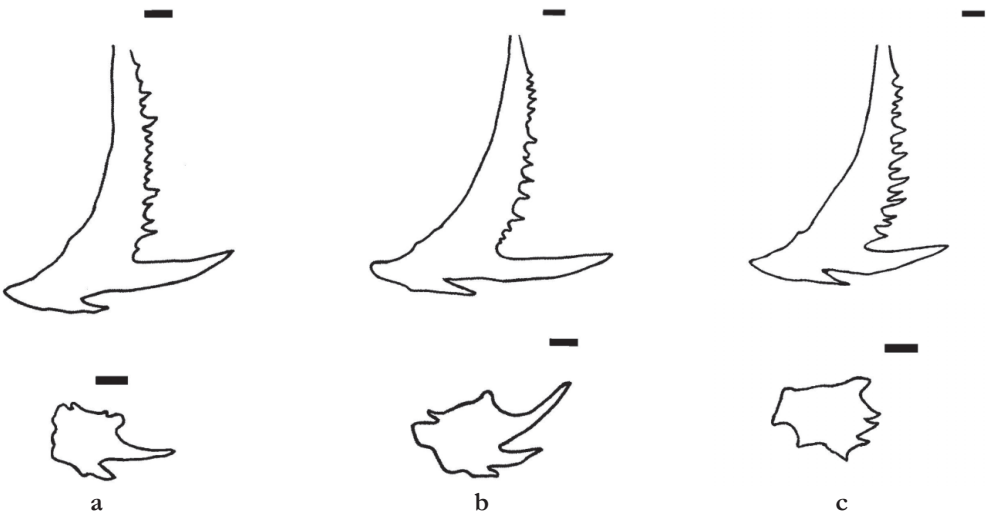

Fig. 3 a-c: Representative examples of the preopercle (above) and the lachrymal bone (below) of *C.* (*X.*) *fisheri* (**a** = FLA, **b** = ACA) and *C.* (*X.*) *loriculus* (**c**). Bar = approx. 1 mm.
Abb. 3 a-c: Repräsentative Beispiele für den Praeoperculum (oben) und das Lacrimale (unten) von *C.* (*X.*) *fisheri* (**a** = FLA, **b** = ACA) und *C.* (*X.*) *loriculus* (**c**). Balken = ca. 1 mm.

titative comparison of nape colour see figure 5. ACA: Snout, anterior part of head, nape and back yellow to light orange. Body dark blackish blue with a black patch above pectoral fin. Dorsal fin yellow to orange with blue margin. Caudal fin yellowish, anterior ventral and dorsal margin dark blue to blackish, posterior part colourless and transparent. Anal fin dark blue with light blue margin. Pelvic fin blue, first spin light blue. Pectoral fin with yellowish base, posterior part colourless and transparent.

FIS: Snout, head, nape and back light to dark orange or light brownish. Body brownish, dark, anterior part lighter, bluish patch above pectoral fin. Dorsal fin coloured like nape. Caudal fin yellowish, anterior part of ventral and dorsal dark. Edge of pelvic and anal fins light blue. Pectoral fin yellowish.

FLA: Snout, nape and anterior part of back dark, almost black or dark brownish. Body very dark blue or blackish, black patch above pectoral fin. Dorsal fin dark blue to blackish. Caudal fin colourless, anterior part yellowish with black ventral and dorsal margin. Pelvic and anal fin blackish with light blue margin. Pectoral fin yellowish or colourless.

RED: Snout, head, nape and back light orange to reddish brown. Body blackish with very dark patch above pectoral fin. Anterior part of dorsal fin reddish orange to brown, posterior part darker brown. Caudal fin colourless or whitish, with dark ventral and dorsal margins. Anal fin dark, edge light blue. Pelvic fin brown. Pectoral fin yellowish at base.

3.5. Distribution

The species *C. fisheri* in the here used sense is very widespread in the Indo-Pacific: from the Gulf of Aden and Oman along the East African coast to South Africa and Madagascar, the Seychelles, Mauritius and the Chagos Archipelago through the Maldives, Indonesia, the Philippines to the Tuamotu archipelago, north-eastward to the Johnston Atoll and Hawaii, northward up to Ogasawara Island, southward through the Coral Sea down to New South Wales (ALLEN et al. 1998, SCHNEIDEWIND 1999).

4. Discussion

4.1. *Centropyge* (*Xiphypops*) *fisheri* species complex

Centropyge fisheri is the type species of *Xiphypops* JORDAN. Members of the subgenus *Xiphypops* differ from the nominal subgenus *Centropyge* KAUP (type species *Holacanthus tibicen*) by several osteological and anatomical features (SHEN & LIU 1978, KISHIMOTO et al. 1996). Both (*Centropyge* and *Xiphypops*) are treated as valid subgenera of the genus *Centropyge* (e. g. KISHIMOTO et al. 1996, ALLEN et al. 1998, CHUNG & WOO 1998). Within the subgenus *Xiphypops, C.* (*X.*) *fisheri* and the closely related species *C.* (*X.*) *argi*, *C.* (*X.*) *aurantonotus* and *C.* (*X.*) *resplendens* (all three from the Atlantic) form a divergent species complex. The members differ from all the others species of the subgenera *Centropyge* and *Xiphypops* by the presence of two or three very stout, comparatively long spines on the ventral margin of the lacrymal bone (Fig. 3) and a more slender body (SCHINDLER 2003, see tab. 1 and fig. 4).

Centropyge (*X.*) *nigriocellus* also has two stout spines on the lacrymal bone and seems to be closely related to this species complex. However, it differs by a lower number of gill rakers on the first outer gill arch (up to 18 in *nigriocellus versus* 20 or more in the *C. fisheri* complex; PYLE pers. comm.), an unusual pattern of two dark blotches (one at the pectoral fin base and another at the posterior basis of the dorsal fin *versus* no such blotches; see e. g. ALLEN et al. 1998, SCHNEIDEWIND 1999), no dark patch above the pectoral fin, and a slightly different body shape (SCHINDLER 2003). This is why we do not include *C. nigriocellus* in the *C. fisheri* complex.

4.2. Synonyms

4.2.1. Notes on *Centropyge caudoxanthorus* SHEN, 1973

SHEN (1973) reported *C. fisheri* and *C. caudoxanthorus* from the most south-western tip of Taiwan (to be suspected as syntopic). He distinguished the new taxon *C. caudoxanthorus* (based

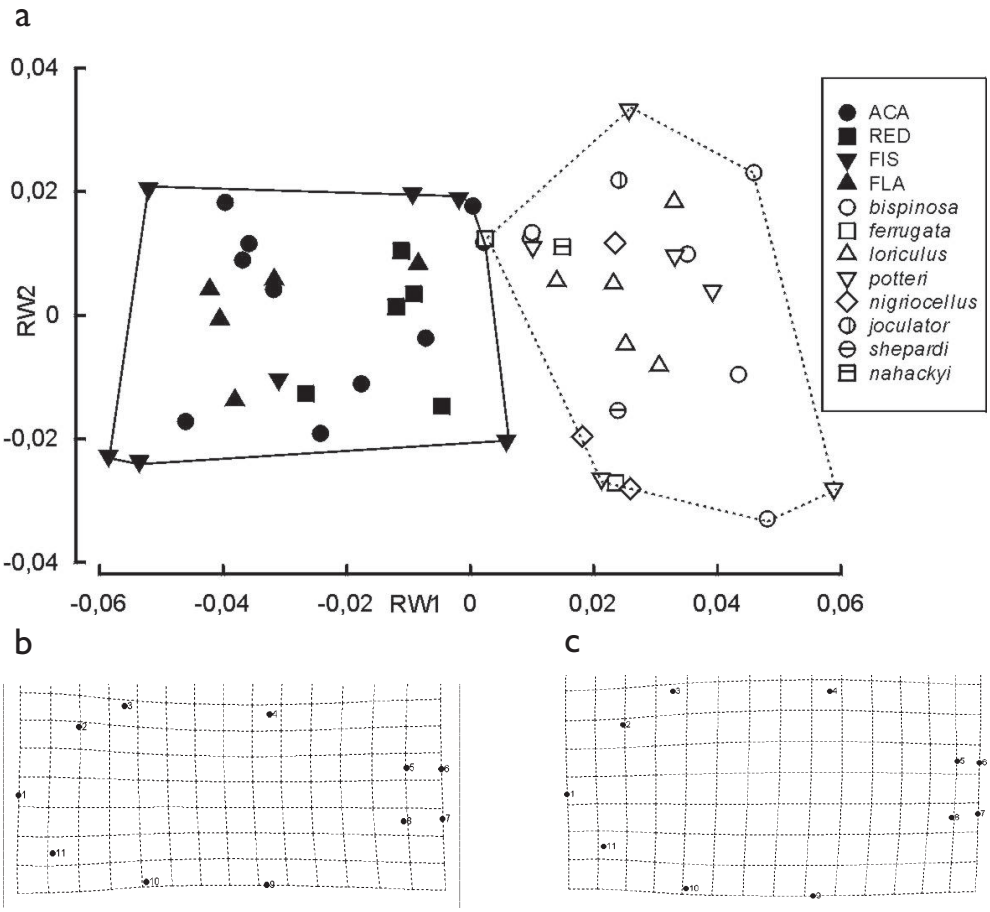

Fig. 4 a-c: Projection of relative warp 1 *versus* RW2 scores of *C.* (*X.*) *fisheri* (filled symbols), and selected species of remaining *Xiphypops* from the Indo-Pacific (**a**). Representative splines of the lowest RW1 value with the averaged RW2 value (**b**) and of the highest RW1 value with the averaged RW2 value (**c**). ACA = *acanthops*, FIS = *fisheri*, RED = "Red Head", FLA = *flavicauda*.

Abb. 4 a-c: Auftragung der Score-Werte von RW1 und RW2 von *C.* (*X.*) *fisheri* (ausgefüllte Symbole) und ausgewählten Arten der übrigen *Xiphypops* aus dem Indo-Pazifik (**a**). Repräsentative Splines (**b**) geringster RW1-Wert und mittlerer RW2-Wert und (**c**) höchster RW1-Wert mit mittleren RW2 Wert. ACA = *acanthops*, FIS = *fisheri*, RED = "Red Head", FLA = *flavicauda*.

only on the type specimen) on the single diagnostic character of a uniformly coloured caudal fin (*versus* the outer rays dark and a middle ray yellow). However, this character is variable in FISSP, even within one population. There are specimens with an elongate dark area on the ventral and dorsal border of the caudal fin and others without such dark rays or only at the most anterior base of outer caudal-fin rays (see e. g. figures in ALLEN et al. 1998, SCHNEIDEWIND 1999, DEBELIUS & KUITER 2003). This is why we are following ALLEN (1979) who synonymised *caudoxanthorus* with *flavicauda* and treated both as identical taxonomic entities.

4.2.2. Notes on *Centropyge flavicauda* FRASER-BRUNNER, 1933

The taxon *C. flavicauda* was diagnosed on a more elongate body form (based only on the single type specimen), different colour pattern (pale brown in *C. fisheri* with a conspicuous large black

Tab. 1: Selected distance measurements in percents of dLM1-12. Values are given for *Centropyge* (*X.*) *fisheri* (groups ACA, FIS, FLA and RED) and some remaining species of the subgenus *Xiphypops* (see fig. 4 for list of the compared specimens) from the Indo-Pacific. Range = lowest and highest value, mean = arithmetic mean, sd = standard deviation. Significance levels are Bonferroni adjusted for 10 comparisons, * = $p < 0.01$, ** = $p < 0.001$.

Tab. 1: Ausgewählte Distanzwerte in Prozent von dLM1-12. Gegeben sind die Werte für *Centropyge* (*X.*) *fisheri* (Gruppen ACA, FIS, FLA and RED) und einigen übrigen Arten der Untergattung *Xiphypops* (Auflistung der verglichenen Exemplare siehe Abb. 4) aus dem Indo-Pazifik. Range = niedrigster und höchster Wert, mean = arithmetischer Mittelwert, sd = Standardabweichung. Signifikanzniveaus sind mit der Bonferroni-Methode (für zehn Vergleiche) adjustiert, * = $p < 0{,}01$, ** = $p < 0{,}001$.

	C. (X.) fisheri (n = 27)			***Xiphypops*** (n = 25)			
distance	range	mean	sd	range	mean	sd	t-value
dLM1-3	30.5 - 38.2	33.82	2.00	33.2 - 40.6	36.48	1.85	4.98**
dLM1-9	58.4 - 67.2	63.15	2.25	60.4 - 68.7	64.87	2.04	2.87
dLM2-11	25.4 - 34.5	30.73	1.91	28.6 - 39.1	32.58	1.98	3.43
dLM3-8	69.3 - 75.0	72.15	1.53	71.1 - 78.2	74.78	2.02	5.3**
dLM3-9	49.4 - 61.8	56.13	2.54	59.8 - 67.2	62.15	1.95	9.53**
dLM3-10	39.9 - 48.7	44.06	2.30	48.1 - 53.6	50.63	1.43	12.24**
dLM4-9	38.0 - 48.8	43.68	2.83	47.4 - 59.1	51.60	2.75	10.23**
dLM5-6	5.6 - 9.3	7.42	0.86	4.1 - 9.9	6.18	1.35	3.97*
dLM5-9	40.1 - 48.4	44.77	1.89	44.9 - 53.8	48.60	2.60	6.12**
dLM6-7	11.0 - 13.4	12.02	0.54	12.4 - 15.4	13.45	0.82	7.51**

patch above pectoral fin *versus* dark brown, without conspicuous patch) and XV instead of XIV dorsal fin spines (Fraser-Brunner 1933). However, the body form is within the variation of *C. fisheri* (Fig. 4). The body colour is variable, too. There are specimens with a lighter, paler ground colour and other specimens with a darker pattern in both entities (FLA and FIS) (see e. g. figures in Schneidewind 1999, Debelius & Kuiter 2003). There is only an unambiguous separation in nape and back colour between FLA and ACA (fig. 5). The dark patch above the pectoral fin described as a diagnostic character by Fraser-Brunner (1933) is also present in *C. flavicauda*, but only visible in colour phases depending on the mood or in specimens with paler ground colour (see e. g. figures in Schneidewind 1999, Debelius & Kuiter 2003). One of the examined specimens has XV dorsal fin spines (from group FLA). The first anterior spine in this specimen is much smaller than usual. It is most likely that the count of XV dorsal fin spines is rare count in FISSP and that it is just a coincidence that Fraser-Brunner (1933) reported this number.

As none of the characters mentioned by Fraser-Brunner (1933) is different, *C. flavicauda* is synonymized with *C. fisheri*. Recently, Randall (1996) and Randall et al. (1997) also mentioned (but without further details) that both species are probably identical. Even Fraser-Brunner (1933) discussed the possibility that *C. flavicauda* represents a form (called subspecies in Fraser-Brunner) of *C. fisheri*.

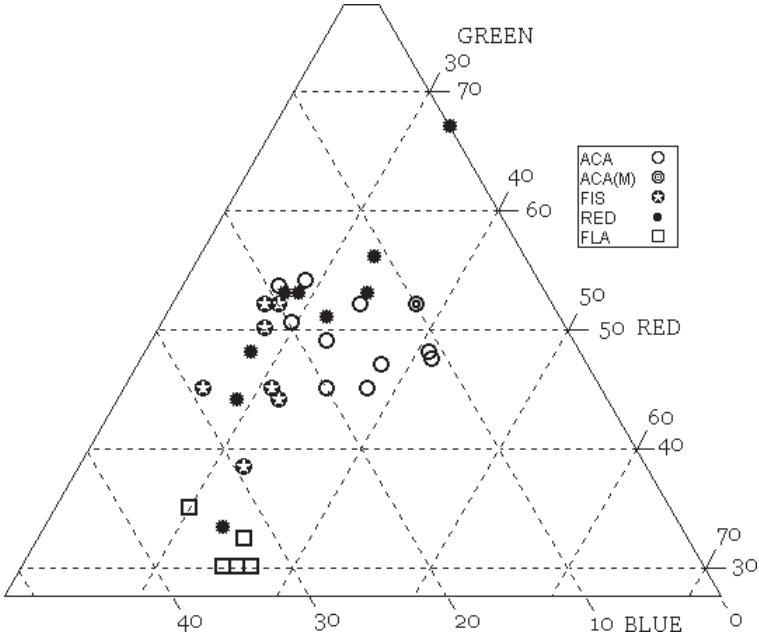

Fig. 5: Ternary plot for the RGB values (red + green + blue = 100%) of *C.* (*X.*) *fisheri.* ACA (M) = *acanthops* from Mauritius (abbreviations see fig. 4).
Abb. 5: Dreiecksdiagramm für die RGB-Werte (Rot + Grün + Blau = 100%) von *C.* (*X.*) *fisheri.* ACA(M) = *acanthops* von Mauritius (Abkürzungen siehe Abb. 4).

4.2.3. Notes on *Holacanthus acanthops* Norman, 1922

This taxon was described from the east coast of South Africa (Durban). Norman (1922) recognized the similarity and close relationship of the new taxon with *C. fisheri*. In the original description of *H. acanthops,* Norman (1922) distinguished *acanthops* from *H. fisheri* by only one stout spine on the preorbital (*versus* three in *fisheri*). Fraser-Brunner (1933) negated this character, because of variable number and ontogenetic change of stout spines, but added a round caudal fin (*versus* truncate) and the colour pattern of body (back and dorsal fin yellow in *acanthops versus* pale brown) as diagnostic characters. The majority of authors (e. g. Allen 1979, Heemstra 1984) followed this opinion and treated both as separate taxa. Smith (1955), however, recognized *H. acanthops* as a synonym of *C. fisheri*. The interpretation that *H. acanthops* is only a morph of *C. fisheri* gets strong support since Schneidewind & Drexhage (2001) introduced specimens of a population from the Maldives with an intermediate colour pattern (figs. 2, 5). First it was thought that these represent hybrids between *H. acanthops* and *C. flavicauda* (see Schneidewind & Drexhage 2001). But after further field observations by the underwater photographer J. Aebi (pers. comm.) and new imports of additional specimens from the Maldives it seems more likely that these specimens represent an intermediate self-sustaining population instead of being simply hybrids (Schneidewind 2004). The Maldive Islands are placed at the geographic border of the known distribution of *H. acanthops* and *C. flavicauda* (see e. g. Allen 1979, Schneidewind 1999). Therefore we conclude that there is a kind of east to west clinal variation from more dark brown populations to brownish-orange and yellowish ones and that within selected populations there is even much more variation in this character than previously thought (particularly in RED, see fig. 5). The dark patch above the pectoral fin (des-

cribed above, see 4.2.2) is also present in *H. acanthops* (see Schneidewind 1999, Debelius & Kuiter 2003), however, it is not always visible. The diagnostic character of a round caudal fin in *acanthops versus* a more truncate caudal fin in *C. fisheri* and *C. flavicauda* is based only on the fact that the single specimen of *H. acanthops* examined by Fraser-Brunner (1933) has a total length of only 36 mm. The subtruncate to almost truncate caudal fin shape develops only during later ontological stages and there is a slight variation in this character within FISSP. Even Norman (1922) mentioned a subtruncate caudal fin shape in his description.

As neither the colour pattern nor the caudal fin or body shape (see above and fig. 2, 4, and 5) can be interpreted as convincing diagnostic characters, *acanthops* is synonymised with *fisheri*. For pictures and further discussion of the Maldivian population see Schneidewind (2004).

4.3. Species limits of *C.* (*X.*) *fisheri*

Centropyge (*X.*) *fisheri* – in the sense used herein – has a widespread distribution in the Indo-Pacific. However, such a vast indo-pacific distribution with the development of local colour forms is not unusual and has been described for several tropical reef fishes even within the family Pomacanthidae. Particularly, *C. bispinosa, Pomacanthus imperator* and *Pygoplites diacanthus* show colour forms within their occurrence and/or a remarkable variation in this character within one population. Such a distribution pattern with local colour forms is also known in species of the closely related family Chaetodontidae (*Chaetodon kleinii, C. octofasciatus*) and other Perciformes (e. g. *Paracanthurus hepatus, Anthias squamipinnis*).

All formally recognized species (*H. acanthops, C. caudoxanthorus, C. fisheri, C. flavicauda*) have most similar teeth, mouth, gill raker and body shape. They have an identical social behaviour and occupy the same ecological niche (Schneidewind 1999, 2004). Without further evidence none of the species formerly recognised as separate can be interpreted as an independent evolutionary lineage. This is why we conclude that all represent only one evolutionary species (in the sense of Wiley 1978), which has to be named *Centropyge* (*Xiphypops*) *fisheri* after the oldest available taxon.

Maybe it seems surprising to include *H. acanthops* in the taxon *C. fisheri*. But according to the above mentioned arguments *H. acanthops* represents only a colour form of *C. fisheri* (figs. 2, 5; see Schneidewind 2004). Nevertheless, the taxonomic treatment of such colour forms in pygmy angelfishes is not without subjectivities (Moyer 1989). Based on extensive field observations, Moyer (1989) already discussed the possibility of the identity of *C. flavicauda, C. fisheri* and *C. acanthops*. Furthermore, the hybridization between ACA, FLA and FIS in an aquarium is well documented (Frische 1999). And recently published photos of the brood of *C. fisheri* from Hawaii (Baensch 2003) showed that some specimens are not distinguishable by colour from specimens from the Maldives. Therefore, the colour of nape and back is a weak character for species discrimination within the here discussed taxa.

Centropyge fisheri differs from all other species of *Centropyge sensu lato* (except for *C. nigriocellus*, see 4.1.) from the Indo-Pacific by the presence of two or three stout spines on the preorbital (fig. 3) and a more slender body (Schindler 2003, tab. 1 and fig. 5). The closely related species *C. argi*, *C. aurantonotus* and *C. resplendens* from the Atlantic have a similar body form and body colouration (Schindler 2003), but differ significantly by the dark blue coloured caudal fin in *C. argi* and *C. aurantonotus* and the bright yellow caudal fin with blue margin in *C. resplendens*.

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6. Literature

ALLEN, G. R. 1979. Falter- und Kaiserfische. Band 2. Mergus-Verlag, Melle.

ALLEN, G. R., R. STEENE, & M. ALLEN. 1998. A guide to Angelfishes & Butterflyfishes. Odyssey Publishing, Perth.

BAENSCH, F. 2003. Die Zucht von drei Zwergkaiserfischen: *Centropyge flavissimus, C. loriculus* und *Centropyge fisheri*. Aquaristik Fachmagazin 34, 80-84.

BOOKSTEIN, F. L. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge Univ. Press. New York.

BURGESS, W. E. 1991. Two new genera of angel fishes, family Pomacanthidae. Trop. Fish Hobb. 39, 68-70.

CHUNG, K. C., & N. Y. S. WOO. 1998. Phylogenetic relationships of the Pomacanthidae (Pisces: Teleostei) inferred from allozyme variation. J. Zool. 246, 215-231.

DEBELIUS, H., & R. H. KUITER. 2003. Kaiserfische. Verlag Eugen Ulmer, Stuttgart.

ENDLER, J. A. 1990. On measurement and classification of colour in studies of animal colour patterns. Biol. J. Linnean Soc. 41, 315-352.

ENDOH, K. 2003. Angelfishes of the world. Aqualife, Tokyo.

ESCHMEYER, W. N. 1990. Catalog of the genera of recent fishes. California Academy of Science, San Francisco.

FOLEY, J. D., A. VAN DAM, S. K. FEINER, & J. F. HUGHES. 1990. Computer graphics principles and practice. Addison Wesley, Reading.

FRASER-BRUNNER, A. 1933. A revision of the chaetodont fishes of the subfamily Pomacanthinae. Proc. Zool. Soc. London 103, 543-599.

FRISCHE, J. 1999. Erfolgreiche Nachzuchten im Meerwasseraquarium. Bede-Verlag, Ruhmannsfelden.

HEEMSTRA, P. C. 1984. *Apolemichthys kingi*, a new species of angelfish (Pomacanthidae) from South Africa, with comments on the classification of angelfishes and a checklist of Pomacanthids of the Western Indian Ocean. Spec. Publ. Smith. Inst. Ichthyol. 35, 1-17.

HUNT, R. W. G. 1987. Measuring Colour. Ellis Horwood Ltd., Chichester.

JORDAN, D. S., & E. K. JORDAN. 1922. A list of the fishes of Hawaii, with notes and descriptions of new species. Mem. Carnegie Mus. 10, 1-92.

KISHIMOTO, H., S. HIOKI and K. SUZUKI. 1996. Transfer of *Centropyge multispinis* (Teleostei; Pomacanthidae) from subgenus *Xiphypops* to subgenus *Centropyge*. Ichthyol. Res. 43, 153-159.

KÜPPERS, H. 1981. Die Logik der Farbe. 2nd edition. Verlag Callway, München.

LEVKOWITZ, H. 1997. Color theory and modelling for computer graphics, visualization, and multimedia applications. Kluwer Academic Publishers, Boston.

LOZAN, J. L., & H. KAUSCH. 1998. Angewandte Statistik für Naturwissenschaftler. Parey Studientexte 74. Blackwell Wissenschafts-Verlag, Berlin.

MOYER, J. T. 1989. On the blinding nature of experience. How many species of pygmy marine angelfishes are there? Trop. Fish Hobb. 37, 86-96.

NORMAN, J. R. 1922. Three new fishes from Zululand and Natal, collected by Mr. H. W. BELL MARLEY. Ann. Mag. Nat. Hist. 9, 318-319.

RANDALL, J. E. 1996. Shore Fishes of Hawai´i. Natural World Press,Vida.

RANDALL, J. E., I. IDA, K. KATO, R. L. PYLE, & J. L. EARLE. 1997. Annotated checklist of the inshore fishes of the Ogasawara Islands. Nat. Sci. Mus. Tokyo Monogr. No. 11, 1-74.

RANDALL, J. E., & R. C. WASS. 1974. Two new pomacanthid fishes of the genus *Centropyge* from Oceania. Jap. J. Ichthyol. 21, 137-144.

ROHLF, F. J. 1993. Relative warp analysis and an example of its application to mosquito wings, pp. 131-159. In: Contributions to Morphometrics (MARCUS, L. F., E. BELLO, A. GARCIA-VALDECASAS, eds.). Museo Nacional de Ciencias Naturales (CSIC) Vol. 8, Madrid.

ROHLF, F. J. 2001. tpsDig. Version 1.29. SUNY at Stony Brook. Computer program.

ROHLF, F.J. 2003. TPSRELW: Relative warps analysis. Version 1.29. Dept. of Ecology and Evolution, State University of New York, Stony Brook.

ROHLF, F. J., & L. F. MARCUS. 1993. A revolution in morphometrics. Trends Ecol. Evol. 8, 129-132.

ROHLF, F. J., & D. E. SLICE. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Zool. 39, 40-59.

SCHINDLER, I. 2003. Analysis of body shape in species of *Centropyge*. Z. Fischk. 6, 37-47.

SCHINDLER, I. 2004. FarbenSammler. Version 1. Computer program. IS-Online-Publ. No. 8.

SCHINDLER, I., & F. SCHNEIDEWIND. 2001. Zur richtigen Schreibweise der Artnamen von *Centropyge* und *Paracentropyge*. Aquar. Terr. Z. (DATZ) 54 (11), 14-15.

SCHNEIDEWIND, F. 1999. Kaiserfische. Tetra Verlag, Bissendorf.

SCHNEIDEWIND, F. 2004. Noch einmal *Centropyge* sp. „Rotkopf" von den Malediven. Aquar. Terr. Z. (DATZ) 57 (5), 22-27.

SCHNEIDEWIND, F., & K. DREXHAGE. 2001. Ein weiterer Hybride unter den Zwergkaisern. Aquar. Terr. Z. (DATZ) 54 (1), 12-13.

SHEN, S. C. 1973. Ecological and morphological study on fish-fauna from the waters around Taiwan and its adjacent islands. 3. Study on the chaetodont fishes (Chaetodontidae) with description of a new species and its distribution. Rep. Inst. Fish. Biol. 3, 1-75.

SHEN, S. C., & C. S. LIU. 1978. Clarification of the genera of the Angelfishes (Family Pomacanthidae). Acta Oceanogr. Taiwanica Sci. Rep. Nat. Taiwan Univers. 1978, 57-77.

SMITH, J.L.B. 1955. The fishes of the family Pomacanthidae in the Western Indian Ocean. Ann. Mag. Nat. Hist. 8, 377-384.

SNYDER, J.O. 1904. A catalogue of the shore fishes collected by the steamer "Albatross" about the Hawaiian Islands in 1902. Bull. U. S. Fish Comm., 513-538

WILEY, E. O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 27, 17-26.

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Appendix

Since the genus name *Centropyge* is treated as feminine (instead of masculine) (ESCHMEYER 1990), the specific names *nigriocellus* and *loriculus* are sometimes erroneously misspelled as *nigriocella* and *loricula* (e. g. ALLEN et al. 1998, SCHNEIDEWIND 1999). However, the species epithets are nouns or at least have to be treated as nouns (Art. 31.2.2. ICZN). Thus, the original spelling must be retained (Art. 31.2.1. ICZN) and the valid names are *Centropyge nigriocellus* and *C. loriculus* (see SCHINDLER & SCHNEIDEWIND 2001). ICZN = International Code for the Zoological Nomenclature.

Note added in proof

During the proof of this article RICHARD PYLE's DPh thesis was presented: "A systematic treatment of the Reef-Fish Family Pomacanthidae (Pisces: Perciformes)", University of Hawai'i, Honolulu. In chapter 2 of his unpublished work, he gives a revision of genus *Centropyge*. Like us, he synonymised *C. flavicauda* with *C. fisheri*. The *Centropyge* specimens from the Maldives are part of his *C. fisheri* taxon and he does not accept the intermediate character of this population. This is why he regards *C. acanthops* as a distinct taxon. Since he does not give any new evidence, we still treat *C. acanthops* as a synonym of *C. fisheri* (see discussion above).