Description of *Danio flagrans*, and redescription of *D. choprae*, two closely related species from the Ayeyarwaddy River drainage in northern Myanmar (Teleostei: Cyprinidae)

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Danio flagrans, new species, is described from headwaters of the Mali Hka River in the vicinity of Putao in northern Myanmar. It is distinguished from *D. choprae* by longer barbels, longer caudal peduncle, shorter anal-fin base, more caudal vertebrae, fewer anal-fin rays, short vs. usually absent lateral line, details of the colour pattern, and mitochondrial DNA sequences. The two species share a unique colour pattern combining dark vertical bars anteriorly on the side with dark horizontal stripes postabdominally, and brilliant red or orange interstripes anteriorly and posteriorly on the side. Pointed tubercles on the infraorbital bones are observed in both species, but were found to be mostly present and prominent in *D. choprae* and mostly absent in *D. flagrans*, and are considered as possibly being seasonal in expression. *Danio choprae* is known from three localities along the Mogaung Chaung southwest of Myitkyina.

Introduction

The cyprinid fish genus *Danio* includes 16 valid species in South and South East Asia (Fang Kullander, 2001; Kullander et al., 2009; Kullander & Fang, 2009a,b). Ten valid species have been reported from Myanmar, including *D. aesculapii* Kullander & Fang, 2009, *D. albolineatus* (Blyth, 1860), *D. choprae* Hora, 1928, *D. erythromicron* (Annandale, 1918), *D. feegradei* Hora, 1937, *D. kyathit* Fang, 1998, *D. margaritatus* (Roberts, 2007), *D. nigrofasciatus* (Day, 1870), *D. quagga* Kullander, Liao & Fang, 2009, and *D. tinwini* Kullander & Fang, 2009 (Kullander et al., 2009; Kullander & Fang, 2009a–b).

Species of *Danio* have species specific colour patterns, commonly in the form of horizontal stripes, more rarely light or dark spots, or vertical bars. *Danio choprae,* described from near Myitkyina on the Ayeyarwaddy River in northern Myanmar is remarkable for its distinctive colour pattern of dark vertical bars combined with striking red horizontal interstripes giving it the name glowlight danio in the aquarium hobby (Cottle, 2010). Specimens identified as *D. choprae* or as a similar species have been reported from Putao, much further north in the Ayeyarwaddy River drainage (Kullander et al., 2009; Cottle, 2010). Glowlight danios from Putao were recently introduced in the aquarium hobby as *Danio* cf. *choprae* (Cottle, 2010). Morphological and DNA analyses of samples of glowlight danios from

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Putao show that they represent a distinct species. The description of the new species and a redescription of *D. choprae* form the objectives of the present paper.

Material and methods

Specimens are kept in the fish collections of the Swedish Museum of Natural History, Stockholm (NRM), the Natural History Museum in London (BMNH), and the Zoological Survey of India in Kolkata (ZSI). Measurements were taken with digital callipers to a precision of 0.1 mm. Counts and measurements were made according to Fang (1997a). Colour pattern terminology follows Fang (1998). Horizontal dark stripes are identified by alphanumeric annotations: the P stripe is the dark stripe along the middle of the side, those above are numbered P+1, P+2, those below P-1, P-2, P-3; stripes on the anal fin are numbered with the middle one the A stripe, the proximal stripe A+1, and the distal stripe A-1. The term interstripe, used by Quigley et al. (2005) for xanthophore-rich areas between dark melanophore-rich stripes, is adopted here, but without numbering. Fin-ray counts from pectoral, pelvic, dorsal and anal fins were obtained directly from the specimens under a dissection microscope and with throughfalling light. Fin-ray counts from the caudal fin and vertebral counts were taken from X-radiographs made with a Philips MG-105 low voltage X-ray unit and Kodak X-Omat V plates. Abdominal vertebrae counts include the Weberian apparatus (assumed to contain four centra). Sexes were separated by the presence in males vs. absence in females of tubercles on the pectoral fin. When adults of both sexes are present in the same sample this is a reliable criterion correlated with fuller abdomen in females; in samples of adults in which pectoral-fin tubercles are consistently absent, thickened interradial tissue may indicate males, but otherwise sex is recorded as indeterminable if no other sex dimorphism is present. Statistics were calculated using IBM Statistics v. 20 (IBM, 2011). Photographs of morphological detail were taken with a Leica M165C stereo microscope with motor stand, Leica DFC450 camera, and composed with Leica Application Suite 4.0 multifocus montage software. DNA sequences of *D. choprae* and *D. flagrans* were downloaded from GenBank. Only cytochrome *b* (*D. choprae*: Gen-Bank accession numbers EF452740, HM224264;

D. flagrans: EU241421), and rhodopsin (*D. choprae*: HM223904, JQ614128−614130; *D. flagrans*: EU 241356, JQ614112−614113) gene sequences were available for both species. Alignment using the ClustalW algorithm, and calculation of nucleotide divergence as uncorrected p distance was made in the Geneious computer software (Drummond et al., 2009).

Danio choprae Hora, 1928
(Figs. 1a–b)

Material examined. Myanmar: Kachin State: Ayeyarwaddy River basin: Mogaung River drainage: BMNH 2011.3.25.5-22, 20 (4 males, 22.1−25.2 mm SL, 14 females, 23.2−29.7 mm SL); Mogaung area; U Tin Win, Feb 2007. – BMNH 2012.7.23.148−203, 56 (28 examined, 7 males 18.7−22.0 mm SL, 19 females, 16.7−23.0 mm SL); small stream and pond south of Mogaung, 25°15.583' N 96°57.374' E, 145 masl; R. Britz, O. Crimmen and local fishermen, 23 Feb 2011. – NRM 52001, 76 (41 males, 25.0−29.0 mm SL; 35 females, 24.3−30.7 mm SL); hill stream around Kamaing; Hla Ku & Mg Nyo, 17 May 2004. – NRM 51965, 2, not measured; hill stream around Kamaing; U Tin Win, 31 Oct 2004. – ZSI F10811/1, 1, 22.0 mm SL; holotype of *D. choprae* (photograph only); small rocky stream round about Kamaing; B. N. Chopra, 23−30 Dec 1926. Aquarium specimens: NRM 50141−50143, 3, cleared and stained; NRM 48378, 1, tissue sample; NRM 48377, 6, not measured; 2002. – NRM 51832, 1, not measured; 2004.

Diagnosis. *Danio choprae* is similar to *D. flagrans* in general colour pattern with several vertical bars on abdominal sides, followed by postabdominal P and P+1 stripes, distinct P+2 stripe anterior to dorsal fin, and red interstripes between middorsal and P+2 stripes, and between P and P+1 stripes; and presence of well-developed tubercles on infraorbital ossicles. It is distinguished from *D. flagrans* by slightly deeper body (26.6−31.6 % SL vs. 22.5−26.6 % SL), shorter caudal peduncle (16.1−19.1 % SL vs. 20.5−24.7 % SL), longer anal-fin base (19.2−23.9 % SL vs. 14.2−18.3 % SL), shorter rostral barbel (5.9−10.1 % SL vs. 10.3−18.7 % SL), not reaching posterior margin of orbit in adults (vs. reaching caudally beyond preopercular margin); shorter maxillary barbels not reaching to pectoral-fin base in adults (vs. reaching to below pectoral-fin base), lateral line almost always absent, occasionally on up to three scales (vs. almost always present, on up to seven scales), fewer vertebrae contained in caudal peduncle (6−8 vs. 9−10), more anal-fin rays (12½−

Fig 1. a, *Danio choprae*, NRM 52100, 28.3 mm SL, adult male; Myanmar: Kachin State: Kamaing; right side, reversed; **b,** *D. choprae*, NRM 52100, 24.3 mm SL, adult female; Myanmar: Kachin State: Kamaing; right side, reversed; **c,** *D. flagrans*, NRM 62257, holotype, 24.2 mm SL, adult female; Myanmar: Kachin State: Nan Hto Chaung; **d,** *D. flagrans*, BMNH 2012.7.23.1-147, paratype, 31.3 mm SL, adult probable male; Myanmar: Kachin State: Londont Chaung.

13½, rarely 11½ branched rays vs. 9½–11½), anal-fin base dark (vs. light); and black streak usually present on lower lobe of caudal fin (vs. absent). It is distinguished from all other species of *Danio* by characters in combination: rostral barbel present (absent in *D. erythromicron*, *D. margaritatus*, *D. nigrofasciatus*, *D. tinwini*, variable in *D. rerio*); mandibular barbel present (absent in *D. erythromicron* and *D. margaritatus*); lateral line abbreviated or absent (complete in *D. dangila*, *D. feegradei*, *D. meghalayensis*; absent in *D. erythromicron*, *D. margaritatus*, *D. nigrofasciatus*, *D. rerio*, *D. tinwini*), colour pattern consisting of vertical bars or spots anteriorly on side, horizontal stripes posteriorly on side (only vertical bars in *D. erythromicron*; light spots on dark ground in *D dangila* and *D. margaritatus*; dark spots on light ground in *D. kyathit* and *D. tinwini*; horizontal stripes only in *D. rerio*, *D. jaintianensis*, *D. quagga*, *D. meghalayensis*, *D. nigrofasciatus*, *D. kerri*, *D. albolineatus*, *D. roseus*; bars anteriorly, two horizontal rows of spots posteriorly in *D. aesculapii*); branched dorsal-fin rays 7½ (6½ in *D. aesculapii* and *D. tinwini*); circumpeduncular scale rows 10 (12 in *D. aescu-* *lapii*, *D. albolineatus*, *D. erythromicron*, *D. kerri*; 14 in *D. dangila*, *D. feegradei*, *D. meghalayensis*).

Description. General body features and pigmentation are illustrated in Fig. 1a–b. Measurement data are summarized in Table 1.

Body compressed, males elongate (body depth 26.6–30.4 % SL), females only slightly deeper (body depth at origin of dorsal fin 26.8–31.6 % SL), but with deep and wide abdomen. Head compressed, slightly deeper than wide. Snout short, obtuse, shorter than eye diameter. Mouth terminal, oblique in profile, jaws about equal in anterior extension. Small bony knob at dentary symphysis fitting into vomerine notch. Maxilla reaching to slightly beyond vertical from anterior margin of orbit. Lower jaw ending anteriorly at about middle of eye. Lower jaw with anterior lateral lobe with numerous pointed tubercles; lower jaw lateroventral margin with 1–2 (small specimens to about 20 mm SL) or 2–3 (specimens about 25–30 mm SL) dense rows of pointed tubercles (Fig. 2). Small and few tubercles present in single row on adocular margin of in-

Table 1. Morphometry of *Danio choprae* and *D. flagrans*. SD, standard deviation. Values separating the two species are highlighted in boldface H, holotype of *D. flagrans*; also included in range values.

	D. choprae				D. flagrans				
	N	range	mean	SD	N	H	range	mean	SD
Standard length (mm)	20	19.8–29.9	23.9	3.6	21	24.2	18.4–33.0	25.3	4.8
Total length (mm)	20	25.8–38.6	31.6	4.4	20	31.5	26.2–43.3	33.8	6.0
In percent of standard length									
Body depth	20	**26.6–31.6**	28.6	1.4	21	26.5	**22.5–26.5**	24.9	0.9
Head length	20	23.3–27.3	24.5	0.9	21	25.6	23.5–26.8	25.1	1.0
Snout length	20	5.2–7.1	6.3	0.4	21	5.8	5.5–6.7	6.2	0.3
Head depth	20	17.2–19.8	18.6	0.7	21	17.8	16.6–19.6	18.1	0.7
Head width	20	13.3–15.2	14.2	0.6	21	13.2	12.6–15.5	13.9	0.5
Upper jaw length	20	8–6–10.6	9.4	0.6	21	9.9	8.7–10.9	10.0	0.5
Lower jaw length	20	9.9–13.1	11.3	0.8	21	12.0	11.1–13.0	12.0	0.4
Orbital diameter	20	8.0–9.9	9.0	0.5	21	8.7	7.7–9.8	8.7	0.5
Interorbital width	20	10.7–13.1	11.7	0.6	21	10.3	10.3–11.9	11.1	0.4
Caudal peduncle length	20	**16.1–19.1**	17.7	0.8	21	21.5	**20.5–24.7**	22.2	1.2
Caudal peduncle depth	20	11.8–15.1	13.6	0.9	21	12.0	11.4–13.3	12.2	0.5
Dorsal-fin base length	20	10.3–13.8	12.0	0.8	21	12.8	9.8–12.8	11.3	0.9
Anal-fin base length	20	**19.2–23.9**	21.3	1.3	21	16.5	**14.2–18.3**	16.2	1.1
Predorsal length	20	60.3–66.7	63.7	1.9	21	62.8	57.6–63.3	61.1	1.6
Preanal length	20	59.6–65.8	62.7	1.7	21	62.8	59.3–64.4	62.2	1.4
Prepelvic length	20	44.1–49.4	46.8	1.7	21	48.8	44.7–49.1	46.8	1.2
Pectoral-fin length	20	20.1–27.8	22.8	1.9	20	22.3	20.9–25.9	22.9	1.3
Pelvic-fin length	20	13.3–18.1	15.5	1.4	21	15.3	13.8–17.1	15.2	1.0
Rostral barbel length	20	**5.9–10.1**	8.2	1.1	21	14.1	**10.3–18.7**	14.7	3.1
Maxillary barbel length	20	9.3–15.7	13.2	1.5	21	17.4	14.2–23.1	18.4	2.7

terorbitals 2 and 3 in some small males and females 19–22 mm SL), otherwise absent; in larger specimens absent or very few in females, in males strongly developed large and small tubercles mixed, present along adocular margin of infraorbitals 2, 3, 4, and 5 (Fig. 3), adjacent to orbit dorsally and caudally, over dorsal part of opercle, and, much smaller and uniform in size, scattered over top of head and snout. Rostral barbel short, not reaching to middle of orbit in smallest specimens (16.7 mm SL), beyond middle but not to posterior margin of orbit in adults; maxillary barbel short, not reaching to pectoral-fin base.

Lateral line represented by one and three pored scales respectively in two specimens (Fig. 4), absent in 18; about 28–30 scales in a row representing expected lateral line course. Scales in a row along middle of side 29 (6), 30 (8), 31 (4). Median predorsal scales 15 (3), 16 (13), 17 (1), 18 (1). Horizontal scale rows 7 (19) between dorsal-fin origin and pelvic-fin insertion. Circumpeduncular scale rows 10 at middle, 12 posteriorly (10). A row of scales along anal-fin base.

Dorsal-fin rays ii.7½ (20); anal-fin rays iii.11½ (2), iii.12½ (12), iii.13½ (2); pectoral-fin rays i.10 (4), i.11 (16); pelvic-fin rays i.6 (20). Principal caudal-fin rays 10 + 9 (14); procurrent caudal-fin rays dorsally 6 (5), 7 (9), ventrally 6 (11), 7 (2), 8 (1). Dorsal fin inserted at highest point of dorsum, at about ⅗ distance from head to caudal-fin base, at about vertical from anal-fin origin. Pectoral-fin with truncate margin; insertion at about vertical through posterior margin of opercle; extending almost to pelvic-fin insertion. Pectoral-fin axial lobe well developed. Bands of minute tubercles present on lateral aspect of unbranched and first three branched rays of pectoral fin; smallest male with tubercles 18.7 mm SL. Pelvic-fin origin situated at about middle of body, well anterior to dorsal-fin origin; pelvic fin reaching to or almost to anal-fin origin. Pelvic axillary scale present. Caudal fin forked, lobes with rounded tips, upper lobe slightly longer than lower lobe. Vertebrae 15 + 18 = 33 (1), 16 + 16 = 32 (1), 16 + 17 = 33 (1), 16 + 18 = 34 (3); predorsal vertebrae 13 (2), 14 (10), 15 (2); vertebrae contained within caudal peduncle 6 (1), 7 (12), 8 (1). Pharyngeal bone (Fig. 5a) with tooth formula 2,3,5–5,3,2.

Coloration in preservative (Fig. 1a–b)**.** Sexual dimorphism absent in colour pattern. Ground colour whitish to pale yellowish. Dark markings brownish to greyish. Head dorsally greyish or brownish, on sides light with sparse pigment dots. Dorsum light brownish with dark brown scale margins and dark brown middorsal stripe anterior to dorsal fin; scale row adjacent to middorsal stripe conspicuously lighter. Next to it scales bearing narrow brownish P+2 stripe from near gill cleft caudad, merging with P+1 stripe below about dorsal fin base, or absorbed by general brownish colour of dorsal part of caudal peduncle. Sides anteriorly diffusely pigmented. P stripe continuous or anteriorly as a row of dark spots, originating at about level of dorsal-fin insertion, extending caudad to dorsal half of caudal-fin base; caudally indistinctly differentiated from dark pigmentation of dorsal part of caudal peduncle; continued as a narrow blackish streak along dorsal lobe of caudal fin. Ground colour of caudal peduncle and adjacent side ventral to P+1 stripe contrastingly pale. Anteriorly on side, from about level of tip of pectoral fin caudad on abdominal side and adjacent postabdominal side, a row of dark brown vertical bars reaching from level of P+1 stripe ventrad to level of pectoral fin. Vertical bars variable in degree of intensity, width, height, and number; expression similar in males and females, and present from smallest sizes (16.7 mm SL), except one small male 18.7 mm SL in which bars absent. Bar number frequency in males (N = 42, 18.7–28.6 mm SL)/females (N = 48, 16.7–30.7 mm SL): 0 (1/0), 3 (4/2), 4 (5/10), 5 (9/14), 6 (10/14), 7 (10/6), 8 (2/1), 9 (1/1). Vertical bars usually gradually shorter postabdominally and continued by continuous dark, narrow P stripe immediately below mid-axis of caudal peduncle, ending usually as a small dark spot at caudal-fin base. Interstripe between P and P+1 stripes devoid of pigmentation, contrasting whitish to yellowish, extending onto caudal-fin base. Lower part of caudal peduncle with sparse pigmentation. Abdomen whitish to greyish, without dark pigment, below pectoral-fin level. Pectoral fin with sparse pigment spots; pelvic fin hyaline. Dorsal fin lightly pigmented basally; blackish stripe from middle of first ray obliquely across fin to tips of posterior rays; distal to black stripe white. Anal fin hyaline, except for wide grey stripe along scaled base. Caudal fin hyaline except for black stripe along middle of upper lobe, dorsal margin whitish; and usually grey or blackish stripe along middle of lower lobe, ventral margin whitish.

Colour in life. Based on a photograph of a freshly collected live specimen (Fig. 6) and obser-

Fig. 2. *Danio choprae*, NRM 52001, adult male, 27.0 mm SL; ventral aspect of head showing pointed tubercles ventrolaterally and tuberculate lateral process ventrolaterally on lower jaw. Infraorbital tubercles partly visible lateral to rostral barbels.
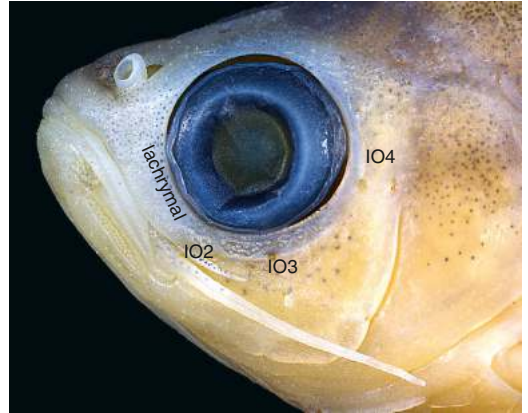

Fig. 3. *Danio choprae*, NRM 52001, adult male, 27.0 mm SL; lateral aspect of head, showing tubercles on infraorbital bones. Lachrymal and infraorbitals 2–4 labelled.

Fig. 4. *Danio choprae*, NRM 52001, adult female, 29.9 mm SL; lateral aspect of region of gill opening, showing lateral line scales.

Fig. 5. a, *Danio choprae*, NRM 52001, 26.5 mm SL; left pharyngeal bone in ventromedial aspect; **b,** *D. flagrans*, NRM 41270, 21.9 mm SL; right pharyngeal bone in ventromedial aspect, lateral margin damaged and one medial tooth lost during preparation.

vations on aquarium specimens: Interstripe between middorsal dark stripe and P+2 stripe anterior to dorsal fin orange, continued lighter to caudal-fin base. Interstripe between P+1 and P stripe bright orange or red postabdominally; pale yellowish interstripe between P+1 and P+2 stripes anteriorly on side. Dorsal fin with orange submarginal stripe distal to black transverse stripe. Dorsal and ventral margins of caudal fin yellow or orange. Anal fin with white or yellow stripe immediately distal to black A stripe. *Danio choprae* was included and illustrated in analyses of colour patterns in *Danio* by Parichy (2006, 2007) and Quigley et al. (2004, 2005).

Fig. 6. *Danio choprae*, BMNH 2012.7.23.148–203, specimen not individually labelled; Myanmar: Kachin State: south of Mogaung; right side, reversed. Photographed alive immediately upon capture. Photograph by Ralf Britz.

Geographical distribution (Figs. 7–8). *Danio choprae* is known only from near Kamaing and Mogaung in the Mogaung Chaung drainage, which is a tributary to the Ayeyarwaddy River entering it a little downstream from Myitkyina (Hora, 1928; Prashad & Mukerji, 1929; present
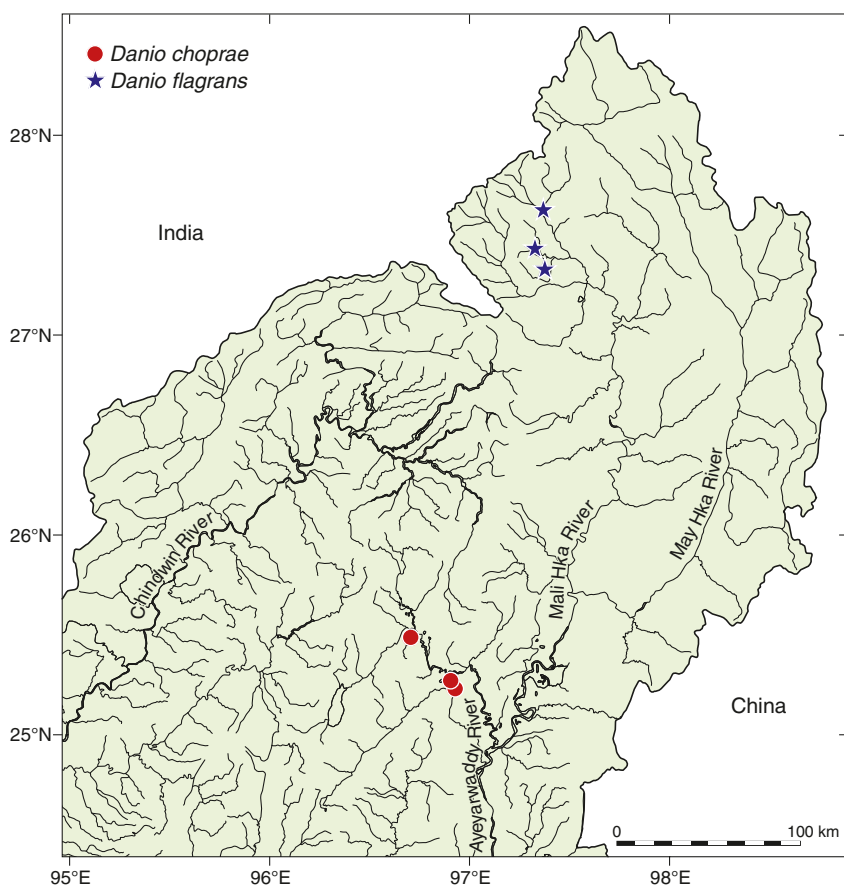

Fig. 7. Northern part of Myanmar showing collecting localities of *Danio choprae* and *D. flagrans*.

Fig. 8. Part of collecting site of *Danio choprae* (BMNH 2012.7.23.148–203). Myanmar: Kachin State: pool south of Mogaung, 23 February 2011. The water was clear before work. Photograph by Ralf Britz.

paper). The locality yielding BMNH 2012.7.23.145-209 included a larger pool-like water body, about 30 m wide and 30–50 cm deep at the foot of a hill, and a small trickle (30 cm wide and 20 cm deep) emerging from the pool and meandering through grass land; pH 7.6, water temperature 24.8 °C, conductivity 11 µS·cm^{-1}, water clear, substrate mud, no aquatic vegetation.

Danio flagrans, new species
(Fig. 1c–d)

Holotype. NRM 62257, female, 24.2 mm SL; Myanmar: Kachin State: Ayeyarwaddy River drainage: Nan Hto Chaung in Putao, about 1 mile from 46th regiment, close to rice mill; S. O. Kullander & R. Britz, 27 March 1998.

Paratypes. All from Myanmar: Kachin State: headwaters of the Ayeyarwaddy River near Putao. BMNH 2012.7.23.1–147, 147, 12.9–32.1 mm SL; Londont Chaung, 27°37.600'N 97°22.102'E, 560 m asl; R. Britz, O. Crimmen and local fisher-men, 16 Feb 2011. – BMNH 2012.7.23.204–208, 5, 16.5–22.6 mm SL; unnamed stream, a tributary of Nam Plet Chaung. 27°25.989'N 97°19.652'E, 416 m asl; R. Britz, O. Crimmen and local fishermen, 20 Feb 2011. – NRM 40928, 10, 15.3–22.0 mm SL; NRM 41270, 9, 16.3–22.4 mm SL; NRM 41671, 1, not measured; same data as holotype.

Diagnosis. *Danio flagrans* is similar to *D. choprae* in general colour pattern with several vertical bars on abdominal sides, followed by postabdominal P and P+1 stripes, distinct P+2 stripe anterior to dorsal fin, and red interstripes between middorsal and P+2 stripes, and between P and P+1 stripes; and presence of well-developed tubercles on infraorbital ossicles. It is distinguished from *D. choprae* by slightly more slender body (22.5–26.6 % SL vs. 26.6–31.6% SL), longer caudal peduncle (20.5–24.7 % SL vs. 16.1–19.1 % SL), shorter anal-fin base (14.2–18.3 % SL vs. 19.2–23.9 % SL), longer rostral barbel (10.3–18.7 % SL vs. 5.9–10.1 % SL), reaching caudally beyond preopercular margin in adults (vs. not reaching posterior margin of orbit); longer maxillary barbel

reaching to below pectoral-fin base in adults (vs. not reaching to pectoral-fin base), lateral line almost always present, on up to seven scales (vs. almost always absent, occasionally on up to three scales), more vertebrae contained in caudal peduncle (9–10 vs. 6–8), fewer anal-fin rays (9½–11½ branched rays vs. 12½–13½, rarely 11½), anal-fin base hyaline (vs. anal-fin base dark), and black streak absent from lower lobe of caudal fin (vs. usually present). It is distinguished from all other species of *Danio* by characters in combination: rostral barbel present (absent in *D. erythromicron*, *D. margaritatus*, *D. nigrofasciatus*, *D. tinwini*, variable in *D. rerio*); mandibular barbel present (absent in *D. erythromicron* and *D. margaritatus*); lateral line abbreviated, rarely absent (complete in *D. dangila*, *D. feegradei*, *D. meghalayensis*; absent in *D. erythromicron*, *D. margaritatus*, *D. nigrofasciatus*, *D. rerio*, *D. tinwini*); colour pattern consisting of vertical bars or spots anteriorly on side, horizontal stripes posteriorly on side (only vertical bars in *D. erythromicron*; light spots on dark ground in *D dangila* and *D. margaritatus*; dark spots on light ground in *D. kyathit* and *D. tinwini*; horizontal stripes only in *D. rerio*, *D. jaintianensis*, *D. quagga*, *D. meghalayensis*, *D. nigrofasciatus*, *D. kerri*, *D. albolineatus*, *D. roseus*; bars anteriorly, two horizontal rows of spots posteriorly in *D. aesculapii*); branched dorsal-fin rays 7½ (6½ in *D. aesculapii* and *D. tinwini*); circumpeduncular scale rows 10 (12 in *D. aesculapii*, *D. albolineatus*, *D. erythromicron*, *D. kerri*; 14 in *D. dangila*, *D. feegradei*, *D. meghalayensis*).

Description. General body features and pigmentation are illustrated in Figures 1c–d. Measurements are summarized in Table 1.

Body compressed, elongate (body depth 22.5–26.5 % SL), sexes isomorphic. Head laterally compressed, slightly deeper than wide. Snout short, obtuse, shorter than eye diameter. Mouth terminal, oblique in profile, jaws about equal in anterior extension. Small bony knob at dentary symphysis fitting into vomerine notch. Maxilla reaching to slightly beyond vertical from anterior margin of orbit. Lower jaw ending anteriorly at about upper ⅓ of eye. Lower jaw with anterior lateral lobe with pointed tubercles; lower jaw lateroventral margin with 1–2 (small specimens to about 20 mm SL) or 2–3 (specimens about 25–30 mm SL) dense rows of pointed tubercles, occasionally absent. In measurement series three specimens (21.4, 26.8, 33.0 mm SL)

recorded with minute tubercles in single row on adocular margin of interorbitals 2 and 3, otherwise absent, 21.4 mm SL specimen also with minute tubercles in region of interorbital 5 and on top of head adjacent to orbit. Rostral barbel long, reaching to posterior margin of orbit or slightly beyond in small specimens about 20 mm SL, to beyond preopercular margin or even to opercular margin in large specimens about 30 mm SL and larger; maxillary barbel long, reaching almost to pectoral-fin base in small specimens about 20 mm SL, to or slightly beyond posterior margin of pectoral-fin base in large specimens about 30 mm and larger.

Scales abraded from predorsal region and posterior part of body in several specimens, so that accurate counts could not be made. Lateral line absent in two specimens, otherwise represented by 2 (1), 3 (3), 4 (4), 5 (9), 7 (1) pored scales; about 29–32 scales in a row representing expected lateral line course. Scales in a row along middle of side 29 (3), 30 (3), 31 (5), 32 (6). Median predorsal scales 15 (4), 16 (6), 17 (10). Body lateral scale rows 7 (20) between dorsal-fin origin and pelvic-fin insertion. Circumpeduncular scale rows 10 at middle, 12 posteriorly (18). A row of scales along anal-fin base.

Dorsal-fin rays ii.6½ (1), ii.7½ (27), ii.8½ (1); anal-fin rays iii.9½ (2), iii.10½ (25), iii.11½ (2); pectoral-fin rays i.10 (12), i.11 (9); pelvic-fin rays i.6 (21). Principal caudal-fin rays 8+9 (1), 10+9 (14); procurrent caudal-fin rays dorsally 5 (1), 6 (8), 7 (2), ventrally 6 (6), 7 (2), 5 (3). Dorsal fin inserted at highest point of dorsum, at about ⅗ distance from head to caudal-fin base, slightly anterior to vertical from anal-fin origin. Pectoral-fin with truncate margin; insertion at about vertical through posterior margin of opercle; extending almost to pelvic-fin insertion. Pectoral-fin axial lobe well developed. Bands of minute tubercles present on lateral aspect of first two branched rays of pectoral fin in one specimen 21.4 mm SL (NRM 40928); pectoral-fin tubercles absent in all other specimens; in three specimens 31.3, 28.7, 26.8 mm SL in measured series (BMNH 2012.7.23.1–147) thickened membrane between anterior pectoral-fin rays. Pelvic-fin origin situated at about middle of body, well anterior to dorsal-fin origin; pelvic fin reaching to or almost to anal-fin origin, usually slightly shorter. Pelvic axillary scale present. Caudal fin forked, lobes with rounded tips, lobes equal or upper lobe slightly longer than lower lobe.

Fig. 9. *Danio flagrans*, BMNH 2012.7.23.1–147, adult paratype, specimen not identified; Myanmar: Kachin State: Londont Chaung. Photographed in the field shortly after capture. Right side, reversed. Photograph by Ralf Britz.

Vertebrae 15 + 19 = 34 (1), 16 + 18 = 34 (13), 16 + 19 = 35 (1), 17 + 17 = 34 (1), 17 + 18 = 35 (1), 17 + 19 = 36 (1), 18 + 17 = 35 (1), last abdominal vertebra as counted here, with short or long haemal apophysis and articulating with long second anal-fin pterygiophore, succeeding vertebra with short haemal apophysis and inserted between two anal-fin pterygiophores; predorsal vertebrae 13 (2), 14 (14), 15 (2), 16 (1); contained within caudal peduncle 8 (1), 9 (11), 10 (7). Pharyngeal bone (Fig. 5b) with tooth formula 2,4,5–5,4,2.

Colouration in preservative. Sexual dimorphism absent in colour pattern. Ground colour whitish to pale yellowish. Dark markings brownish to greyish. Head dorsally pale brownish grey. Sides of head sparsely pigmented. Dorsum light brownish with dark brown middorsal stripe anterior to dorsal fin; scale row adjacent to middorsal stripe conspicuously lighter. Next to it, scales bearing narrow brownish P+2 stripe from near gill cleft caudad, merging with P+1 stripe below about dorsal fin base. Sides anteriorly diffusely pigmented, from about distal part of pectoral fin followed by a number of dark vertical bars or blotches, which continuous dorsally; extending from level of P+1 stripe level to about level of pectoral-fin base. Number of bars (excluding spots) in subsample of 38 specimens 19.3–26.2 mm SL, 2 (1), 3 (4), 4 (23), 5 (7), 6 (3), in subsample of 10 specimen 26.8–33.0 mm SL, 5 (6), 6 (3), 10 (1). Bars gradually shorter caudally and integrating with continuous P stripe above anal-fin base. Vertical bars developing from small spots ante-

riorly in stripes P+1 and P, spots coalescing vertically, but often disarranged in smaller spots mixed with bars. Specimens 20 mm SL and longer all possess vertical bars or blotches; specimens smaller show incipient spots or bars, but generally up to about 18 mm SL blotches absent and P and P+1 stripes extending uniform and distinctly separated by lighter stripe to close to head. P stripe narrow, extending onto caudal-fin base where usually ending in a small spot. Usually two dark spots above anal-fin base, frequently indistinct, representing P-2 stripe. P+1 stripe obsolete anteriorly on side, initiated as a few indistinct spots in transition abdominal to postabdominal region, and then continuous to caudal-fin base, but barely distinct from dark colour of dorsal part of caudal peduncle. Narrow interstripe between P and P+1 stripes contrastingly light.

Pectoral and pelvic fins hyaline. Dorsal fin hyaline with dark brown or blackish stripe from middle of anterior margin obliquely across rays to tip of posterior rays; beyond that stripe hyaline. Anal fin basally greyish; blackish stripe from middle of anterior margin caudad across rays to tip of posterior rays; distal to that stripe hyaline. Caudal fin hyaline or slightly pigmented; brown or black stripe along upper rays, dorsal margin white; ventral margin white. In juveniles smaller than 18 mm dark stripe on caudal fin absent, dark stripe in dorsal fin present but faint, A stripe distinct, occasionally absent.

Colour in life. A specimen from BMNH 2012.7.23.1–147 (Fig. 9) has interstripe between mid-

Fig. 10. Myanmar: Kachin State: Nan Hto Chaung near Putao, close to actual collecting site of holotype of *Danio flagrans*, 27 March 1998.

dorsal dark stripe and P+2 stripe anterior to dorsal fin bright orange. Interstripe between P+1 and P stripes bright orange postabdominally; weaker orange interstripe between P+1 and P+2 stripes anteriorly on side. Bright orange spots on iris. Dorsal fin with bright red submarginal stripe distal to black transverse stripe. Caudal fin dorsal margin red; ventral margin orange. Anal fin with orange stripe immediately distal to black A stripe. A much smaller specimen sampled in 1998 (NRM 40928 or 41270) did not show body markings, but orange or yellowish orange stripes present in dorsal, anal, and caudal fins.

Etymology. The specific name *flagrans* is a Latin participial adjective meaning flaming, blazing, burning, glowing, and is given with reference to the red to orange colour in living specimens, and with inspiration from the name glowlight danio applied on this species and *D. choprae*.

Geographical distribution and habitat (Figs. 7 and 10). *Danio flagrans* is so far known only from a few small streams in the upper Mali Hka river drainage, near Putao in northern Myanmar. The type locality was a very small stream, only about 50 cm wide, almost dry, and with no other fish present. This stream emptied in the somewhat larger Nan Hto, from which no *Danio* were obtained. The Londont Chaung (BMNH 2012.7.23.1–147) was a small stream, about 2 m wide and less than 1 m deep, with fast flowing cold water, no aquatic vegetation, lots of boulders and wood in the stream, substrate sand and gravel; water temperature 16.7 °C, pH 8.2, conductivity 93 µS·cm⁻¹. BMNH 2012.7.23.204–208 were collected in a stream up to 4 m wide and 2 m deep, clear cool water, with faster flowing parts but also deeper pools with slower water, no aquatic vegetation; water temperature 17 °C, pH 7.77, conductivity 55 µS·cm⁻¹.

Comparative morphometry
of *D. choprae* and *D. flagrans*

Proportional measurements of *D. choprae* and *D. flagrans* were compared with those of two other small species of *Danio*, for which measurement data were available (Kullander & Fang,

2009a,b), viz. *D. tinwini* and *D. aesculapii*, expecting that *Danio* species of the same small size would be informative about the direction of character transformation in the caudal peduncle and anal fin proportions. *Danio aesculapii* also has a colour pattern similar to *D. choprae* and *D. flagrans*, and *D. tinwini* was collected in the Mogaung River upstream of *D. choprae* localities. The principal component analysis shows *D. choprae* separated from *D. flagrans* + *D. aesculapii* on Component II and *D. tinwini* from the rest on Component III (Table 2; Fig. 11). Most of the variation is expressed in the length of the maxillary barbel, which is very short in *D. choprae* (9.3–15.7 % SL), and very long in *D. aesculapii* (16.8–19.0 %) and *D. flagrans* (14.2–23.1 %) (Fig. 12a). The rostral barbel was excluded from the PCA because it is absent in *D. tinwini*. It is relatively long in *D. aesculapii* and much longer in *D. flagrans* than in *D. choprae* (10.3–18.7 % SL vs. 5.9–10.1 in *D. choprae* (Fig. 12b). Remaining variation separating species the PCA and biplots, are above all caudal peduncle length and anal-fin base length, separating *D. flagrans* and *D. tinwini*, both with short anal-fin base, as well as *D. choprae* with short caudal peduncle and long anal-fin base, and *D. flagrans* with long caudal peduncle (Fig. 12c–e). Body depth is important in Component II, probably because of the deeper *D. choprae* and slender *D. flagrans* at larger sizes (Fig. 12f; 26.6–31.6 % SL in *D. choprae*, 23.1–27.2 in *D. aesculapii,* 23.0–30.3 in *D. tinwini*, and 22.5–26.5 in *D. flagrans*). Components III–IV also reflect dorsal-fin base length, which is short in *D. aesculapii* (7.7–10.4 % SL) and *D. tinwini* (8.9–9.2) compared with *D. choprae* (10.3–13.8) and *D. flagrans* (9.8–12.8).

Genetic comparison
of *Danio choprae* and *D. flagrans*

Complete or partial sequences of the mitochondrial cytochrome b, cytochrome c oxidase subunit I (COI), NADH dehydrogenase subunit 4 (ND4), 16S ribosomal RNA, and 12S ribosomal RNA genes, and parts of the nuclear recombination activating protein 1 (RAG1) and rhodopsin genes were used in various combinations in phyloge-

Table 2. Component loadings from Principal Component Analysis of morphometric data from *Danio choprae* (N = 20), *D. flagrans* (N = 20), *D. aesculapii* (N = 10; data from Kullander & Fang, 2009a), and *D. tinwini* (N = 10; data from Kullander & Fang, 2009b). Rostral barbel length was excluded because the rostral barbel is absent in *D. tinwini*. The four highest loadings for each component are highlighted in boldface.

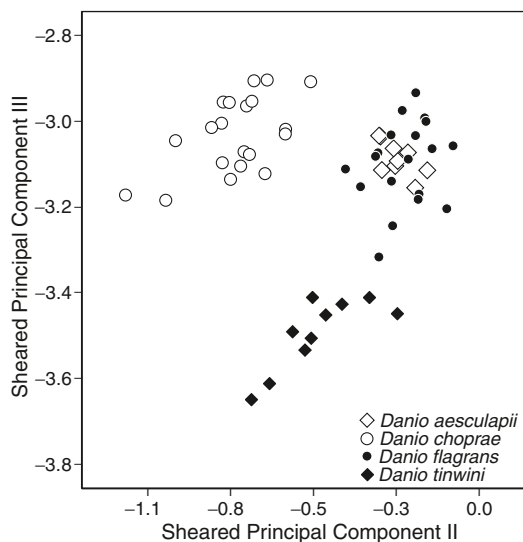|	PC I	PC II	Sheared PC II	PC III	Sheared PC III	PC IV	Sheared PC IV
Standard length	0.203	−0.016	−0.012	−0.189	−0.171	−0.042	−0.029
Body depth	0.210	**−0.259**	**−0.256**	−0.197	−0.179	−0.172	−0.158
Head length	0.185	0.037	0.040	−0.162	−0.147	−0.019	−0.007
Snout length	0.230	−0.008	−0.004	0.079	−0.097	0.000	0.015
Head depth	0.235	−0.110	−0.106	−0.020	−0.001	0.276	0.292
Head width	0.205	−0.053	−0.049	−0.061	−0.044	0.035	0.049
Upper jaw length	0.272	0.095	0.099	0.283	0.303	0.189	0.207
Lower jaw length	0.222	0.120	0.123	0.110	0.127	0.113	0.127
Orbital diameter	0.152	−0.014	−0.012	−0.087	−0.075	−0.105	−0.094
Interorbital width	0.215	−0.089	−0.085	0.038	0.055	0.079	0.093
Caudal peduncle length	0.173	**0.305**	**0.308**	**−0.424**	**−0.408**	**0.415**	**0.427**
Caudal peduncle depth	0.245	−0.218	−0.214	0.009	0.029	0.026	0.042
Dorsal-fin base length	0.306	−0.198	−0.193	**0.333**	**0.356**	**0.436**	**0.456**
Anal-fin base length	0.235	**−0.405**	**−0.401**	**0.345**	**0.362**	**−0.438**	**−0.422**
Predorsal length	0.215	−0.071	−0.067	−0.198	−0.179	−0.158	−0.143
Preanal length	0.201	−0.016	−0.012	−0.260	−0.243	−0.155	−0.142
Prepelvic length	0.191	−0.011	−0.007	−0.310	−0.293	−0.153	−0.140
Pectoral-fin length	0.153	0.086	0.088	−0.240	−0.226	−0.273	−0.262
Pelvic-fin length	0.220	−0.052	−0.049	−0.072	−0.054	0.136	0.151
Maxillary barbel length	0.322	**0.725**	**0.730**	**0.334**	**0.358**	**−0.324**	**−0.302**
Eigenvalue	0.5473	0.0642	N/A	0.0304	N/A	0.0125	N/A
% Variance	80.2 %	89.6 %	N/A	94.1 %	N/A	95.9 %	N/A

Fig. 11. Comparative morphometry of *Danio choprae* and *D. flagrans,* and similar species. Plot of scores from Principal Component Analysis of measurement data.

netic analyses of *Danio*, including *D. choprae* and / or *D. flagrans* by Collins et al. (2012), Fang et al. (2009), Mayden et al. (2007), Quigley et al. (2004), and Tang et al. (2010). Further COI sequences were used by Collins et al. (2012), but are not available from GenBank (searched 2012-08-29). All of those sequences seem to be based on aquarium specimens, except the *D. choprae* analysed by Fang et al. (2009), which is actually *D. flagrans* (NRM 41671). Collins et al. (2012) used the name *Danio* aff. *choprae* for *D. flagrans,* as verifiable from photos of voucher specimens uploaded to the BOLD database (BOLD Systems, 2012). The rhodopsin fragments show 0.3–0.8 % divergence between *D. choprae* and *D. flagrans,* 0–0.4 % divergence within *D. flagrans,* and 0–0.8 % within *D. choprae*. The overlapping 1130 base-pairs of the three cytochrome *b* sequences show 6.8–7.1 % divergence between *D. choprae* and *D. flagrans* and 0.8 % divergence between *D. choprae* samples. Collins et al. (2012) found an average divergence of 7.4 % between the species in COI and 0.5 % in rhodopsin, using the K2P model.

Discussion

Danio choprae was described by Hora (1928) from several specimens collected from "small rocky streams about Kamaing and Namma in the Myit-kyina District". The description is detailed and accompanied by an excellent drawing and measurement data for three specimens 20.5–21.0 mm SL. According to Hora the lateral line is absent. No mention is made of tubercles. Barbels are described and figured as being relatively short. Counts and proportional measurements agree with my referred material of *D. choprae*, and differ from those of *D. flagrans*, particularly the shorter caudal peduncle and the count of 13 branched anal-fin rays as reported by Hora. Fang Fang examined and photographed the holotype. According to her data, the specimen is approximately 22.0 mm SL, severely desiccated and overall pale brownish, the margins of the body translucent. No useful meristic or morphometric data or colour information could be obtained from it, but it also did not present any characters disagreeing with the present concept of *D. choprae*. According to the label data it was collected from a small rocky stream round about Kamaing, 23–30 December 1926.

  Danio choprae was implicitly named in honour of the collector of the type series, presented as "Dr. B. N. Chopra" in the original description (Hora, 1928). There is no indication of Dr. Chopra's gender in the original description, but Hora later used the spelling *choprai* (Hora, 1937) and explained that the original spelling was in error, from which one may conjecture that Dr. Chopra was a man, although this was not stated in either of the two papers. Notwithstanding, a change of ending of patronymic genitives only for reason of mismatch with the gender of the person from whose name the specific name is formed, is not permitted under the International Code of Zoological Nomenclature (International Commission for Zoological Nomenclature, 1999), and thus the original spelling must be maintained. Alternatively, in accordance with Article 3.1.1 of the Code, Chopra may be considered as a latinized name, for which the natural Latin genitive ending would be Choprae, regardless of the gender of the bearer of the name.

  Danio choprae and *D. flagrans* are similar in habitus and colour pattern, but differ in body proportions, and vertebral and anal-fin counts. *Danio flagrans* has a proportionally longer caudal

peduncle than *D. choprae* (Table 1; Fig. 12c–e) and more vertebrae contained within the caudal peduncle (usually 9–10 vs. usually 7). Caudal peduncle length is measured from the base of the last anal-fin ray to the middle of the caudal-fin base, and consequently correlated with the position of the anal-fin, and slightly with the depth of the caudal peduncle. *Danio flagrans* has modally 10 branched anal-fin rays, which is two or three less than in *D. choprae* with modally 12, occasionally 13 branched anal-fin rays. The longer caudal peduncle may thus reflect a shorter anal-fin base (Fig. 12d–e). *Danio flagrans* also has one more caudal vertebra, which also could explain a longer caudal peduncle. The depth of the caudal peduncle, and the preanal length in proportion to standard length is about the same in both species, and this at least indicates that the anterior position of the anal-fin base is the same in both species, but the anal-fin base is much shorter in *D. flagrans*. Consequently, the longer caudal peduncle of *D. flagrans* may be the result of both a shorter anal-fin base and development of one more vertebra in the caudal region, or either. In comparison with data from other species of *Danio* (*D. aesculapii*, *D. roseus*, *D. quagga*, *D. kyathit*, *D. tinwini*, and data from Fang, 1998, 2003), *D. flagrans* is within the lower range of anal-fin ray counts (9–14 branched rays in the genus), relatively short anal-fin base (14–24 % SL in the genus) and in the higher range of caudal peduncle lengths (14–23 % SL in the genus), whereas *D. choprae* has mid-range values for caudal peduncle lengths and is in the mid to upper range of anal-fin ray counts. In comparison with the small species in the comparative analysis (Fig. 12), *D. choprae* stands out as having a shorter caudal peduncle (16–19 % SL) relative to the others (18–25 % SL) and longer anal fin similar to large species of *Danio* (12–13 branched rays). It seems thus as if *D. choprae* maintains a long anal fin and short caudal peduncle, whereas the opposite is seen in *D. flagrans*, *D. tinwini*, and *D. aesculapii*. Because phylogenetic analyses show *D. flagrans* and *D. choprae* to be sister taxa and not closely related to *D. tinwini* or *D. aesculapii*, it seems likely that the evolutionary differentiation of these taxa includes the elongation of the caudal peduncle by reduction of the anal fin in *D. flagrans*.
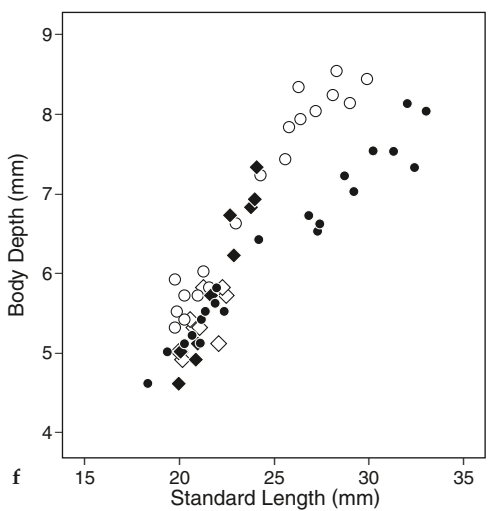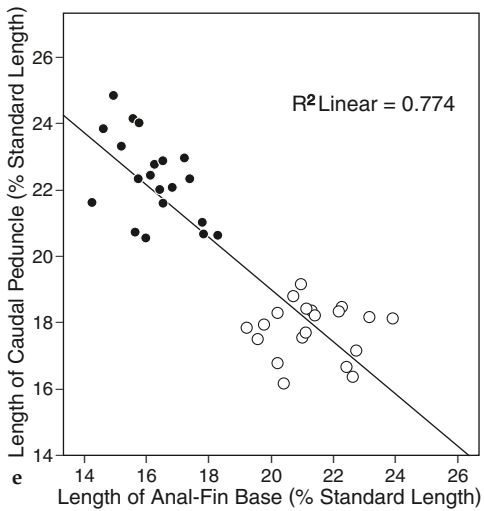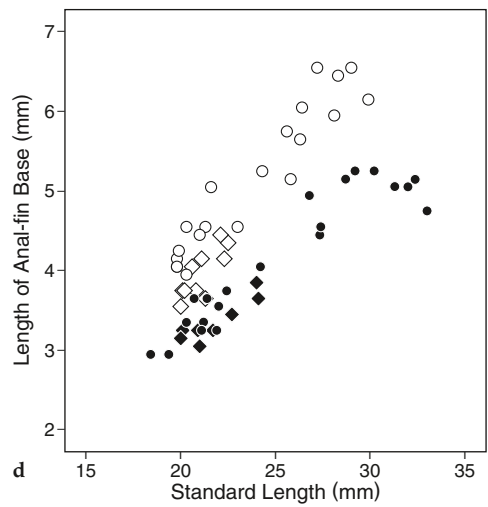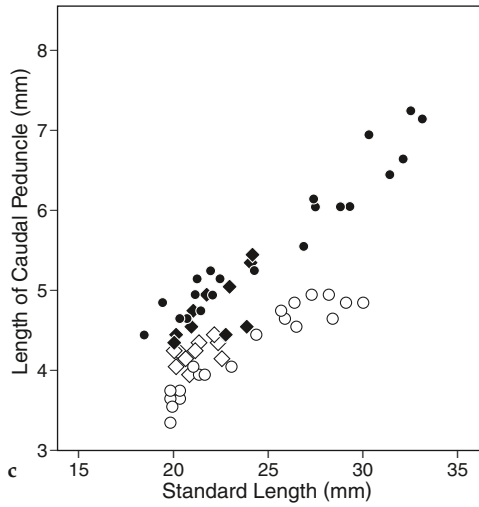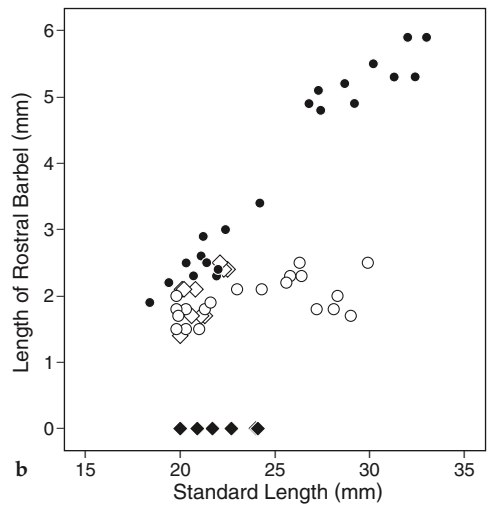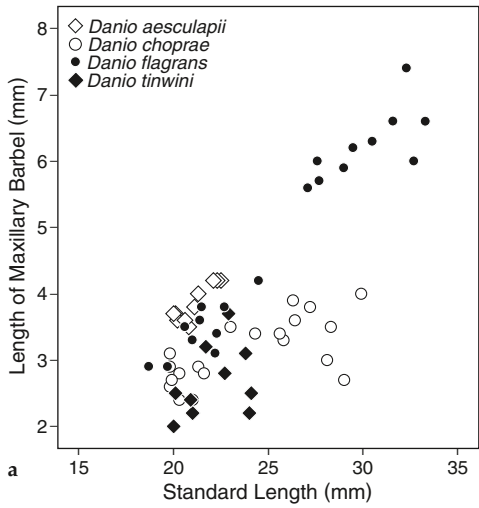
Both the rostral and maxillary barbels are longer in *D. flagrans* than in *D. choprae* when specimens of the same size are compared, but the difference becomes much more marked in large specimens (Figs. 12a–b). Not expressed in the PCA is the short lower jaw of *D. tinwini* (9.0–10.5 % SL) compared to the other species (*D. aesculapii* 11.0–12.0, *D. choprae* 9.9–13.1, *D. flagrans* 11.1–13.0).

In most specimens of *D. choprae* there are no perforated or tubed scales as reported by Hora (1928) for the type series, but in two specimens are present 1 and 3 perforated scales, respectively (Fig. 4). The presence of perforated scales was initially overlooked in *D. flagrans*, but in contrast to *D. choprae* there are almost always a few perforated scales anteriorly on the side in *D. flagrans*.

In both *D. choprae* and *D. flagrans* the circumpeduncular scale count is reported here as 10 as taken at about the middle of the peduncle, but actually on each side a horizontal scale row of two scales is inserted ventrally close to the caudal-fin base, giving a count of 12 if the count is taken too far back. If the middle row of scales dorsally on the caudal peduncle is taken as the first horizontal row, the extra scales are inserted between rows 5 and 6 on the same side, where row 6 is the middle row of scales ventrally on the caudal peduncle. Most of the smaller species of *Danio* have 10 circumpeduncular scale rows, but *D. aesculapii* was diagnosed with 12 rows (Kullander & Fang, 2009a). Re-examination of specimens in the type series of *D. aesculapii* confirms that there are 12 rows also close to the root of the caudal peduncle.

Tubercles on the lower jaw are reported from most species of *Danio*, and are better developed in males than in females. An elongated patch of tubercles is formed laterally on each dentary and in contact with a patch of tubercles on the mandibular lateral process (Fig. 2). In addition, isolated tubercles may be found anteriorly on the lower jaw. In both *D. choprae* and *D. flagrans* tubercles are found also on the distal tip of the

Fig. 12. Comparative morphometry of *Danio choprae*, *D. flagrans* and similar species. **a,** length of maxillary barbel ▷ plotted against Standard Length; **b,** length of rostral barbel plotted against Standard Length; **c,** length of caudal peduncle plotted against Standard Length; **d,** length of anal-fin base plotted against Standard Length; **e,** relation of length of caudal peduncle to length of anal fin base (in *D. choprae* and *D. flagrans* only); **f,** depth of body plotted against Standard Length.

lachrymal, and on infraorbitals 2, 3, and 4 close to the orbit, and to some extent on infraorbital 5, frontals, and opercle. In large males of *D. choprae* those sharp projections along the lower margin of the orbit are very impressive. The tubercles appear to be smaller and less numerous in females and both sexes of *D. flagrans*. In many specimens only shallow pits remain in place of all or several of the tubercles, but it is not clear if this reflects natural shedding or abrasion from handling of museum samples. In the NRM paratypes of *D. flagrans* infraorbital tubercles are present only in the largest male, and in the BMNH paratypes they are absent except in two specimens, one of which is a possible male with wide mandibular tubercle band, and thickened interradial pectoral-fin skin. In *D. flagrans,* however, the infraorbital tubercles are relatively small. Because the large BMNH series of *D. flagrans* does not contain any specimens with pectoral-fin tubercles, it seems possible that both infraorbital and pectoral fin tubercles are expressed only seasonally. In a BMNH few specimens, thickened interradial skin is present between pectoral-fin rays, probably representing a state in the development of the pectoral-fin tuberculation, and those specimens may be regarded as males. Three such specimens are included in the measurement series.

Infraorbital tuberculation appears not to have been observed in danionine cyprinids before. Only *D. choprae* and *D. flagrans* are known to develop the very conspicuous tubercles illustrated in Figure 3. Infraorbital tubercles (restricted to infraorbitals 2, 3, occasionally 4) were observed also in males of *D. albolineatus*, *D. kerri*, *D. feegradei*, *D. margaritatus*, *D. meghalayensis*, *D. nigrofasciatus*, *D. quagga*, *D. roseus*, and *D. tinwini*. In the smaller species, however, they are very small and arranged in a single series, restricted to infraorbitals 2, 3, occasionally 4. In the larger species, they are minute and components of groups of scattered tubercles over much of the head. Infraorbital tubercles were not observed in males of *D. aesculapii*, *D. dangila*, *D. erythromicron*, *D. kyathit*, or *D. rerio*. As the infraorbital tubercles were absent in a large number of *D. flagrans*, it is obvious, however, that larger series of specimens of the latter five species may be needed to confirm absence. In alcohol specimens of both *D. choprae* and *D. flagrans* infraorbital 2 is very short and flexible, giving the impression that it may not be ossified, but it is ossified in a cleared and stained specimen of *D. choprae*.

The colour patterns of *D. flagrans* and *D. choprae* are strikingly similar, and also similar to that of *D. aesculapii* from the western slope of the Rakhine Yoma. In *D. flagrans* the P+1 and P stripes are present in small juveniles from 13 mm SL and a gradual transition to a pattern of blotches or bars anteriorly on the side can be observed at a little shorter than 20 mm SL, whereby the P+1 and P stripes break up into spots eventually meeting to form a vertical bars. Already the smallest *D. choprae* available, 19 mm SL, possess vertical bars, but it seems likely that the same bar ontogeny is present in that species. In *D. choprae* the bars tend to be better defined and more separated, whereas in *D. flagrans* they may be wider and often appear in a pattern of irregular blotches. The largest *D. flagrans* have up to about 10 bars, but otherwise 4–5 bars seem to be prevalent in medium sized specimens of both species. The P+2 stripe tends to be better developed in *D. flagrans,* and the light stripe between it and the middorsal stripe tends to contrast more. The caudal-fin pigmentation differs in that the lower black stripe present in most *D. choprae* is absent in *D. flagrans*, and where *D. choprae* has a dark band covering the inner half of the anal fin, *D. flagrans* has a typical A stripe across the middle of the fin. In both species the precise pattern of dark markings varies considerably, each individual having its proper pattern, and thus there are extremes of each species approaching the modal of the other species. In *Danio aesculapii* horizontal stripes are absent, but the pattern of vertical bars on the abdominal sides is apparently homologous to that in *D. flagrans* and *D. choprae*. In *D. aesculapii* dark spots continuing the bars postabdominally represent fragmented P+1 and P stripes (Kullander & Fang, 2009a), distinguishing it from *D. choprae* and *D. flagrans* in which the P+1 and P stripes are continuous at least posteriorly. *Danio aesculapii* does not show any red markings on the body in life. *Danio flagrans* and *D. choprae* share a red or orange interstripe between the P+1 and P stripes, and between the predorsal stripe and anterior part of the P+2 stripe. In other striped species of *Danio* the light interstripe between the P+1 and P+1 stripes is simply pale or yellowish, and it is only in *D. roseus* and *D. albolineatus* that it is red, from pink to bright red. The combination of a red median and a red dorsal interstripe is unique to *D. choprae* and *D. flagrans.*

The shared elaborate colour pattern of *D. flagrans* and *D. choprae* suggests a close phyloge-

netic relationship, further supported by the presence of well-developed tubercles on the infraorbital ossicles. *Danio flagrans* was recovered in a clade containing *D. margaritatus* and *D. erythromicron* by Fang et al. (2009) and Pramod et al. (2010) based on cytochrome *b* and rhodopsin. Tang et al. (2010) included the cytochrome *b* and rhodopsin data from Fang et al. (2009), but also reported the same two genes, RAG1, and cytochrome *c* oxidase I (COI), from a second specimen, probably representing the true *D. choprae.* Their two *D. choprae* come out as sister taxa, and form the sister clade to *D. erythromicron* and *D. margaritatus*. The latter two were found to be sister species also by morphological characters by Conway et al. (2008). *Danio erythromicron* shares the barred colour pattern with *D. flagrans* and *D. choprae*, but in this species there is sexual dimorphism, and horizontal markings are absent. Males have relatively broad dark bars, similar to bars in *D. flagrans* and *D. choprae*, but extending postabdominally; females possess approximately the double number of narrow vertical bars. The close phylogenetic relationship of *D. choprae* and *D. flagrans* with *D. erythromicron* suggests a transitional state of the colour pattern in the former two, from the usually striped colour pattern in danionines, to the exclusively barred colour pattern in *D. erythromicron*. *Danio margaritatus* has a unique body colour pattern, dark with numerous small white spots in irregular horizontal rows on the side (Conway et al., 2008), which then stands out as autapomorphic in an otherwise barred clade. The colour pattern of *D. choprae* and *D. flagrans* also provides a very striking parallel to that of several species of *Devario* in which there is a series of dark vertical bars on the anterior side, followed by a postabdominal dark P stripe with light dorsal border, most marked in, i. e., *D. maetaengensis* (Fang, 1997), and *D. shanensis* (Hora, 1928), but also expressed in *D. apopyris* (Fang & Kottelat, 1999), *D. interruptus* (Day, 1869) and *D. apogon* (Chu, 1981) (images in Fang, 1997b, 2000; Fang & Kottelat, 1999). All these species of *Devario* occur only east of the localities of *D. choprae* and *D. flagrans*. Phylogenetic analyses including both *Danio* and *Devario* (Fang et al., 2009; Pramod et al. 2010; Tang et al. 2010) do not indicate that this similarity in colour pattern is explained by shared recent ancestry, but must have evolved in parallel within each genus.

Despite a similar colour pattern, *D. aesculapii* did not cluster with *D. choprae* and *D. flagrans* in molecular analyses, but instead with *D. nigrofasciatus*, *D. kyathit* and undescribed species (Fang et al., 2009, as *D.* "snakeskin", cytochrome *b*; Pramod et al., 2010), or positioned basal to other *Danio* except *D. dangila* (Kullander et al., 2009, rhodopsin), or a clade including *D. rerio*, *D. kyathit*, *D. nigrofasciatus*, and undescribed species (Tang et al., 2010, as *D.* "Panther" and *D. aesculapii*).

Comparative material. *Danio albolineatus*, NRM 37308; *D. dangila*, NRM 51441; *D. erythromicron*, NRM 51629; *D. feegradei*, NRM 55111; *D. jaintianensis*, NRM 60762; *D. kerri*, NRM 36414; *D. kyathit*, NRM 50496; *D. margaritatus*, NRM 55113; *D. meghalayensis*, UMMZ 243666; *D. nigrofasciatus*, NRM 51630*; D. rerio*, NRM 40446; *D. roseus*, NRM 44799; and material of *D. aesculapii*, *D. kyathit*, *D. quagga*, and *D. tinwini* already listed in Fang (1998), Kullander & Fang (2009a,b), and Kullander et al. (2009).

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