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Description of *Danio absconditus*, new species, and redescription of *Danio feegradei* (Teleostei: Cyprinidae), from the Rakhine Yoma hotspot in south-western Myanmar

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Abstract

Danio feegradei Hora is redescribed based on recently collected specimens from small coastal streams on the western slope of the Rakhine Yoma, ranging from the Thade River drainage southward to slightly north of Kyeintali. *Danio absconditus*, new species, is described from the Kyeintali Chaung and small coastal streams near Gwa, south of the range of *D. feegradei*. Both species are distinguished from other *Danio* by the presence of a dark, elongate or round spot at the base of the caudal fin and a cleithral marking composed of a small black spot margined by a much smaller orange spot. *Danio feegradei* is characterized by the colour pattern, with series of white spots along the otherwise dark side; *D. absconditus* by about 7–11 dark vertical bars on the abdominal side. Within *Danio,* the presence of a complete lateral line, cleithral spot, and 14 circumpeduncular scales is shared with *D. dangila* and similar species, but these character states may be plesiomorphic as suggested by the shared presence of cleithral spot and complete lateral line in *Devario* and *Betadevario*. In other *Danio* the cleithral spot is absent, the lateral line is short or absent, and the circumpeduncular scale count is lower (10–12). Twenty teleost species are reported from streams on the western slope of the Rakhine Yoma, all probably endemic. The parapatric distribution of *D. absconditus* and *D. feegradei* is unique within the genus, and may be partly explained by changes in eustatic sea levels.

Key words: colour pattern, freshwater fish, morphology, species discrimination, taxonomy

Introduction

Many recent papers have contributed to show that the short coastal streams of the western slope of the Rakhine Yoma mountain range in south-western Myanmar harbour a rich and highly endemic fish fauna (e.g., Britz, 2007, 2010; Conway & Kottelat, 2010; Kullander, 2015; Kullander & Fang, 2004, 2009a; Ng, 2004). Still, only a fraction of the region has been surveyed and many species await description. *Danio feegradei* is one component of this endemic fauna. It was described by Hora (1937) on the basis of a single specimen from road-side drains in Sandoway (now Thandwe). There are no later collections of *D. feegradei* reported, although it has become available in the ornamental fish trade (Cottle, 2010), and aquarium specimens have been used in phylogenetic analyses (e.g., Collins *et al.,* 2012; Tang *et al.*, 2010). Barman (1991) considered *D. feegradei* to be a synonym of *D. dangila* (Hamilton), but recent taxonomic papers consider it as valid (Fang Kullander, 2001; Kottelat, 2013). In this paper we provide a revised diagnosis of *D. feegradei,* demonstrating its distinctness on the basis of recent collections. We also present evidence that a similar, undescribed species, sharing unique colour-pattern characters, is present on the western slope of the Rakhine Yoma. The two species are almost overlapping in distribution, presenting a rare example of parapatry between putative sister species, further underlining the importance of the coast of western Myanmar as a hotspot for fish diversity.

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Material and methods

Specimens are kept in the fish collections of the Swedish Museum of Natural History, Stockholm (NRM), the Natural History Museum, London (BMNH), and the Zoological Survey of India, Kolkata (ZSI). Measurements were taken with digital callipers to a precision of 0.1 mm. Counts and measurements were made according to Fang (1997), except that the last unbranched ray in the dorsal and anal fins, which articulates with the same pterygiophore as the branched ray preceding it, is designated as a half-ray (½), and body depth is measured at the origin of the dorsal fin instead of at the origin of the pelvic fin. Colour-pattern terminology follows Fang (1998), with the modifications in Kullander (2015). When present, horizontal dark stripes and light interstripes 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. With the same method interstripes are termed I (between P and P+1) and I+*n* dorsally and I-*n* ventrally. The interstripe Ia is a short interstripe dividing the P stripe anteriorly. 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, and stripes on the dorsal fin correspondingly. Fin-ray counts from pectoral and, pelvic fins were obtained directly from the specimens under a dissection microscope and with transmitted light. Fin-ray counts from the dorsal, anal, and 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). Values in parentheses after a count represent the frequency of that count. Statistics were calculated using SYSTAT v. 13 (Systat Software, 2009), except that the principal component analysis (PCA) of measurements was made using a separate procedure for component shearing, partialling out multivariate size residues from the second and further components as described by Humphries *et al*. (1981). The PCA was made with log-transformed measurement data to tenth of a millimetre in a covariance matrix, and without rotation.

Comparative material. Material of *Danio* Hamilton listed in Fang (1998), Kullander (2012, 2015), Kullander & Fang (2009 a, b), and Kullander *et al.* (2009).

Danio feegradei Hora, 1937

(Figs. 1–4)

Material examined. All from Myanmar, Rakhine State. BMNH 2011.3.24.7–28, 17, 28.0–57.5 mm SL; NRM 66246, 5, 39.3–50.0 mm SL. South stream Daung Chaung, 18°2'17"N, 94°30′26″E. 1 Dec 2009, R. Britz.—BMNH 2015.3.3.7–58, 52, 25.1–45.3 mm SL. Delmound Chaung,18°46′42″N, 94°17′6″E. 27 Nov 2009, R. Britz.—BMNH 2015.3.3.59, 1, 28.7 mm SL. Chaung Ma Gyi Chaung Leldee village, 18°35′7″N, 94°22′11″E. 28 Nov 2009, R. Britz.—BMNH 2015.3.3.60–99, 38, 29.5–51.6 mm SL; BMNH 2015.3.3.171–177, 7, 55.7–67.5 mm SL. Three different sites along Thandwe Chaung, 18°24′33″N, 94°28′46″E. 29 Nov 2009, R. Britz.—BMNH 2015.3.3.100–128, 29, 20.2–38.8 mm SL. Ka Din Lay Chaung, 18°18′39″N, 94°27′51″E. 30 Nov 2009, R. Britz.—BMNH 2015.3.3.138–144, 7, 29.6–39.2. North stream Kyauk Tan village, 18°2′40″N, 94°29′39″E. 1 Dec 2009, R. Britz.—NRM 45660, 1, 22.8 mm SL. Thade River drainage: Yan Khaw Chaung, ca 4 km on logging road from Gwetauk village, 23 km on road Taunggok-Pyay, 18°47′48″N, 94°21′46″E. 21 Mar 1998, S. O. Kullander & R. Britz.—ZSI F. 12477/1. Holotype, 37.2 mm SL, Sandoway (=Thandwe). Jun–Aug 1936, E. S. Feegrade (Photograph only).

Diagnosis. Distinguished from all other species of *Danio* except *D. absconditus* by the presence of a large, elongate black spot at the base of the caudal fin (vs. absence; or minute and inconspicuous in *D. jaintianensis* (Dey), *D. choprae* Hora and *D. flagrans* Kullander; or small, round and margined by a lighter zone in *D. erythromicron* (Annandale)), a small black or grey cleithral spot and a light (orange in life) spot immediately above the cleithral spot (vs. absent; or present, large and not bordered by light spot in *D. assamila* Kullander, *D. catenatus* Kullander, *D. concatenatus* Kullander, *D. dangila*, and *D. sysphigmatus* Kullander; or minute, not separated from P stripe and not associated with light spot in *D. meghalayensis* Sen & Dey). Distinguished from all *Danio* except *D. absconditus*, *D. assamila, D. catenatus, D. concatenatus, D. dangila*, *D. meghalayensis* and *D. sysphigmatus* by the presence of a complete lateral line (*vs.* abbreviated or absent) and 14–16 circumpeduncular scales (vs. 10–12). Distinguished from *D. absconditus* by absence of dark vertical bars on abdominal sides (*vs.* presence of about 7–11 distinct dark bars), and presence of a dark area along the middle of the side, with two or three irregular horizontal rows of white dots (vs. absence of continuous dark area on anterior side and absence of white dots on the side).

Description. General body features and pigmentation are illustrated in Figures 1–3. Measurements are summarized in Table 1.

TABLE 1. Morphometry of *Danio feegradei*. Measurements are in per cent of standard length, except for standard length (in mm). SD, standard deviation; r, Pearson's correlation coefficient. Linear regression against SL calculated from measurements in mm, coefficients (a, b) .

	N	min	max	mean	SD	a	b	r
Standard length (mm)	17	28.0	57.5	44.7	8.8			
Body depth	17	27.3	31.2	28.9	1.2	0.670	0.273	0.974
Head length	17	23.0	26.9	24.5	1.2	1.999	0.198	0.990
Snout length	17	6.0	7.4	6.7	0.4	0.379	0.058	0.959
Head depth	17	16.0	18.7	17.4	0.9	1.252	0.145	0.966
Head width	17	12.9	14.9	13.8	0.6	0.596	0.124	0.978
Upper jaw length	17	9.2	11.1	10.0	0.6	0.983	0.077	0.984
Lower jaw length	17	10.8	13.2	11.9	0.7	1.288	0.089	0.982
Orbital diameter	17	6.6	9.3	8.0	0.8	1.442	0.046	0.944
Interorbital width	17	9.9	11.6	10.7	0.5	0.707	0.091	0.976
Caudal peduncle length	17	17.4	21.6	19.3	1.2	1.466	0.158	0.956
Caudal peduncle depth	17	11.8	14.2	13.2	0.6	-0532	0.145	0.984
Dorsal-fin base length	17	12.1	14.0	13.1	0.4	-0.356	0.139	0.992
Anal-fin base length	17	17.7	20.7	18.9	0.8	0.083	0.187	0.978
Predorsal length	17	58.4	62.9	61.0	1.3	0.617	0.595	0.996
Preanal length	17	63.8	67.2	65.5	1.1	-0.035	0.656	0.996
Prepelvic length	17	45.6	50.1	47.9	1.3	1.233	0.450	0.989
Pectoral-fin length	17	21.6	25.7	23.9	1.2	1.833	0.196	0.975
Pelvic-fin length	17	14.9	17.0	15.9	0.6	0.327	0.151	0.978
Rostral barbel length	17	13.7	18.0	15.4	1.2	-0.104	0.157	0.942
Maxillary barbel length	17	23.2	32.8	26.3	2.2	2.810	0.197	0.930

Body compressed, elongate, sexes isomorphic. Head laterally compressed, slightly deeper than wide. Snout short, obtuse, about equal to eye diameter. Mouth terminal, oblique in profile, jaws about equal in anterior extension or lower slightly projecting. Small bony knob at dentary symphysis, fitting into notch in upper jaw. Maxilla reaching slightly beyond vertical from anterior margin of orbit. Lower jaw ending anteriorly at about upper 1/3 of eye¸ posteriorly below about middle of orbit. Lower jaw with anterior lateral lobe margined with sharp, pointed tubercles; similar tubercles also distributed over anterior portion of dentary in varying number and density. Rostral barbel long, reaching to or very slightly beyond preopercular margin; maxillary barbel long, reaching slightly beyond posterior margin of pectoral-fin base, to about 1/3 of length of pectoral fin.

Lateral line complete, comprising 34 (4), 35 (5), 36 (8) scales; descending anteriorly for about 6 scales, posteriorly paralleling ventral profile. Median predorsal scales 16 (1), 17 (6), 18 (9), 20 (1). Scales in transverse series from dorsal-fin origin to pelvic-fin origin ½6+1+1½ (17); scales below lateral line not much smaller than above. Prepelvic scales rounded, about 17–19 along midline; pelvic-fin bases covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14 (13), 15 (3), 16 (1). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii.8½ (22); anal-fin rays iii.12½ (9), iii.13½ (13); pectoral-fin rays 1.9.i (1), i.9.ii (7), i.10.i (9); pelvic-fin rays i.7 (17). Principal caudal-fin rays 10+9 (22); procurrent caudal-fin rays dorsally 6 (1), 7 (2), 8 (15), 9 (4), ventrally 7 (4), 8 (15), 9 (1), 10 (2). Dorsal-fin origin at highest point of dorsum, slightly posterior to half distance from snout tip to caudal-fin base, and slightly anterior to vertical from anal-fin origin. Pectoral-fin origin slightly anterior to vertical through posterior margin of opercle; branched rays forming straight or slightly rounded margin, leading unbranched ray longest, not produced, not reaching insertion of unbranched pelvic-fin ray.

Tubercles absent from pectoral fin. Pectoral-fin axial lobe well developed. Pelvic-fin origin situated slightly anterior to midbody, well anterior to dorsal-fin origin. Pelvic-fin margin subtruncate, leading unbranched ray or both leading unbranched ray and first branched ray longest, but not prolonged, reaching urogenital opening. Caudal fin moderately forked, lobe tips subacuminate, lower lobe appearing broader than upper.

Vertebrae 17+19=36 (4), 18+18=36 (10), 18+19=37 (8); predorsal vertebrae 14 (14), 15 (8); vertebrae contained within caudal peduncle 7 (6), 8 (13), 9 (2). Ceratobranchial 5 tooth formula 5,3,2-2,4,5 (NRM 55111, 45.2 mm SL).

FIGURE 1. *Danio feegradei.* BMNH 2011.3.24.7–28, 50.2 mm SL. Myanmar, Rakhine State, Daung Chaung.

FIGURE 2. *Danio feegradei.* Adult male in live coloration. Aquarium specimen, not preserved.

FIGURE 3. *Danio feegradei*. Adult female in live coloration. Aquarium specimen, not preserved.

FIGURE 4. *Danio feegradei*. Holotype, ZSI F. 12477/1, 37.2 mm SL. Myanmar, Rakhine state, Thandwe.

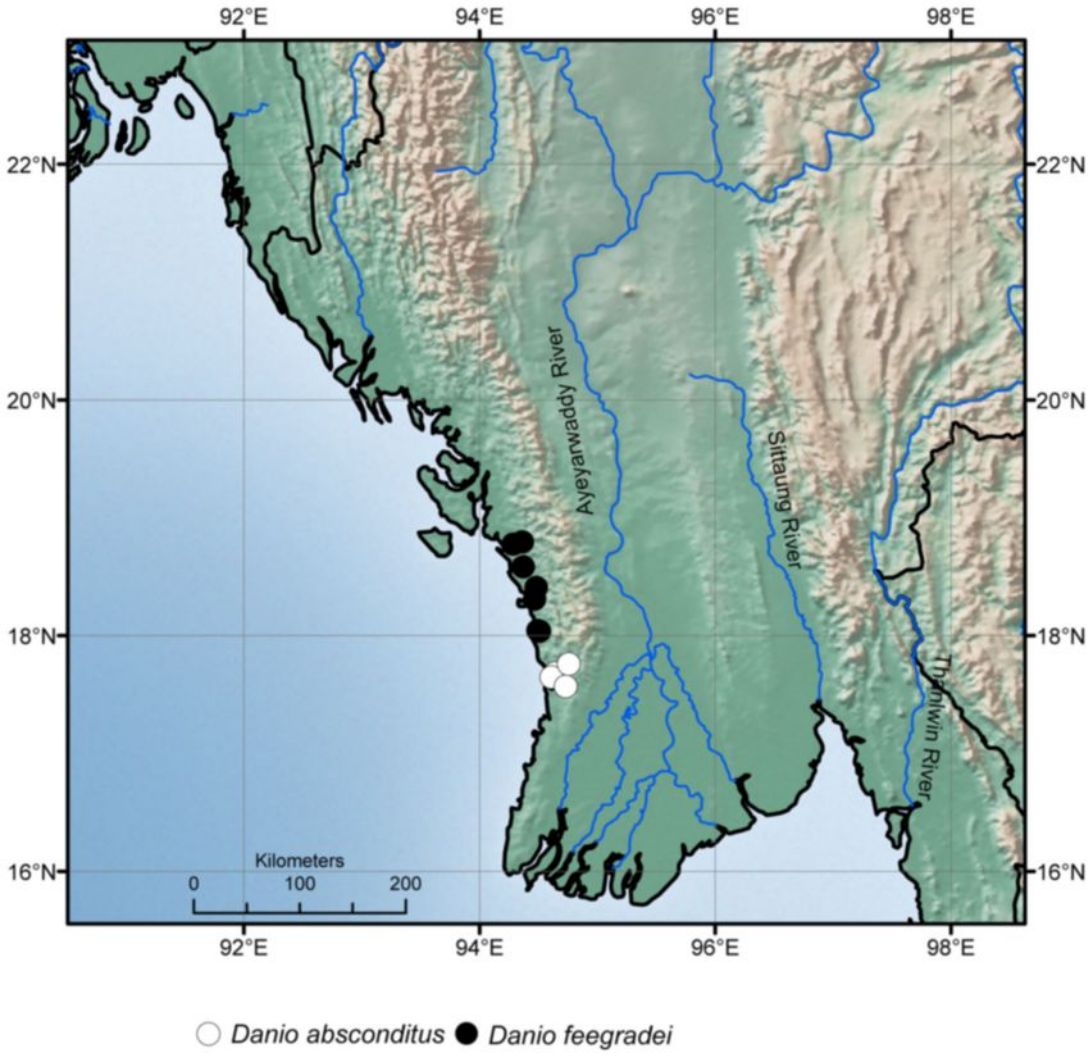

FIGURE 5. Map of southwestern part of Myanmar showing collecting localities of *Danio absconditus* and *D. feegradei*.

Colouration in preservative. Sexual dimorphism not observed. Dorsum above midaxis pale greyish. Dark-brown middorsal stripe anterior to dorsal fin, along dorsal-fin base and dorsal margin of caudal peduncle. Cleithral spot minute, black, margined anterodorsally by minute white or silvery spot. Blackish or dark brown P stripe from caudal-fin base anteriad to about middle of side, but vanishing in wide greyish or brownish area covering anterior side, between levels of midaxis and pectoral-fin base. P stripe margined dorsally by almost depigmented I stripe extending the length of the caudal peduncle, and continued on base of caudal fin; similar less distinct I-1 stripe posteriorly on caudal peduncle. On and slightly above P stripe forward, a row of about 8 to 15 small white or silvery spots, posteriorly round, anteriorly extended vertically; larger spots may have darkened borders resembling

rings with lighter centre. Similar series of light spots one scale row ventrally; some spots in this row with open lower margin to light abdomen; posterior spots above anal-fin base mostly very small, indistinct. Between upper and lower rows of light spots variable number of scattered small spots occasionally arranged in horizontal series. Abdomen unpigmented, yellowish white. Region immediately above anal fin and on lower half of caudal peduncle pale yellowish white, with sparse dark pigmentation. A black or dark-brown, slightly elongate spot at middle of caudal-fin base, bordered by lighter zones above and below. Caudal fin hyaline with faint dusky bands crossing upper and lower lobe, extending along middle rays. Dorsal fin dusky basally, with faint D stripe, distal half hyaline. Anal fin dusky basally, faint A stripe bordered distally by a thin white stripe, distal 1/3 of fin hyaline.

Colour in life (Figs. 2–3). Aquarium specimens: Epaxially dull olivaceous, grading to grey on dorsum; hypaxially pale slate grey with blue tinge, abdomen white. Interstripe I expressed as short rosy, almost pink stripe on caudal peduncle and adjacent caudal fin, anteriorly as rows of spaced oval spots. Similar spots along abdominal side in single principal row and several scattered. Bright orange spot close to cleithrum at interspace I level, bordered posteroventrally by small cleithral spot varying in intensity between black and grey. Dorsal fin hyaline, distal margin pale yellow. Anal fin hyaline, A stripe white in female, orange-red in male. Stripe across pelvic fin white in female, orange-red in male. Caudal fin with slightly elongate black spot at middle of base, bordered by light stripe above and below; lobe margins pale red in male. Pectoral fin pale yellow in male.

Type material. The holotype is presently in a poor state of preservation, partly covered by mould, fins damaged, and no remnants left of the colour pattern (Fig. 4). It is useless as a reference specimen for the species, but the detailed description and excellent drawings provided by Hora (1937) make the designation of a neotype unnecessary.

Geographical distribution (Fig. 5). *Danio feegradei* is known only from a small section of the western slope of the Rakhine Yoma, recorded from small coastal streams near Kyeintali north to the Thade River drainage.

Danio absconditus, new species

(Figs. 6–7)

Holotype. BMNH 2011.3.24.29, 51.7 mm SL. Comepyo Chaung, 17°40′57″N, 94°38′25″E, and Mway Tway Chaung, 17°38′53″N, 94°36′35″E. 3 Dec 2009, R. Britz.

Paratypes. All from Myanmar, Rakhine State. BMNH 2011.3.24.30-43, 14, 26.5–38.0 mm SL; NRM 66247, 5, 25.2–37.1 mm SL. Same data as holotype.—BMNH 2015.3.3.129-136, 8, 16.3-32.2 mm SL. Baw Di Chaung, Gwa Township, about 17°34′15″N, 94°43′47″E. 20 Jan 2005, Ya Htut Oo.—BMNH 2015.3.3.137, 1, 32.1 mm SL. Headstream of Kyeintali Chaung, Kyeintali Township, about 17°45′39″N, 94°45′23″E, 5 Mar 2006, Tin Win *et al.*

FIGURE 6. *Danio absconditus*. Holotype, BMNH 2011.3.24.29, 51.7 mm SL. Myanmar: Rakhine State, Comepyo Chaung.

Diagnosis. Distinguished from all other species of *Danio* except *D. feegradei* by the presence of a prominent elongate or round black spot at the base of the caudal fin (vs. absence; or minute and inconspicuous in *D. jaintianensis*, *D. choprae* and *D. flagrans*; or small, round and margined by a light zone in *D. erythromicron*), a small black or grey cleithral spot and a light (orange in life) spot immediately above cleithral spot (vs. absence; or present, large and not bordered by light spot in *D. assamila, catenatus, D. concatenatus, D. dangila*, *D.*

sysphigmatus; or minute, not separated from P stripe and not associated with light spot in *D. meghalayensis*). Distinguished from all *Danio* except *D. feegradei*, *D. assamila, catenatus, D. concatenatus, D. dangila*, *D. meghalayensis* and *D. sysphigmatus* by complete lateral line (vs. abbreviated or absent) and 14 circumpeduncular scales (vs. 10–12). Distinguished from *D. feegradei* by presence of about 7–11 distinct dark vertical stripes on abdominal sides (vs. absence), and absence of light dots along middle of side (vs. presence).

Description. General body features and pigmentation are illustrated in Figures 6–7. Measurements are summarized in Table 2. Counts from the holotype are marked with an asterisk (*).

TABLE 2. Morphometry of *Danio absconditus*. Measurements are in per cent of standard length, except for standard length (in mm). HT= Holotype. SD, standard deviation; r, Pearson's correlation coefficient. Linear regression against SL calculated from measurements in mm.

	N	HT	min	max	mean	SD	a	b	r
Standard length (mm)	12	51.7	29.1	51.7	35.2	6.0			
Body depth	12	28.8	26.1	30.6	28.9	1.3	-0.168	0.294	0.975
Head length	12	23.0	23.0	26.3	25.0	0.9	1.866	0.196	0.988
Snout length	12	5.8	5.8	6.6	6.3	0.3	0.379	0.052	0.970
Head depth	12	17.6	17.5	19.7	18.7	0.9	1.267	0.150	0.969
Head width	12	12.2	12.2	14.3	13.2	0.6	1.104	0.100	0.983
Upper jaw length	12	9.1	9.1	11.2	10.4	0.7	1.177	0.070	0.912
Lower jaw length	12	10.6	10.6	13.0	12.2	0.7	1.353	0.083	0.947
Orbital diameter	12	7.5	7.5	10.0	9.2	0.6	1.448	0.050	0.942
Interorbital width	12	9.9	9.9	10.9	10.3	0.3	0.489	0.089	0.989
Caudal peduncle length	12	17.6	17.6	20.7	18.8	0.9	0.968	0.160	0.957
Caudal peduncle depth	12	12.6	11.6	13.9	12.7	0.6	0.119	0.124	0.969
Dorsal-fin base length	12	13.0	12.8	14.6	13.3	0.5	0.447	0120	0.981
Anal-fin base length	12	21.9	19.9	23.0	21.4	0.8	-0.403	0.226	0.979
Predorsal length	12	58.6	58.6	61.3	59.9	0.8	1.398	0.302	0.999
Preanal length	12	63.4	63.0	64.6	63.8	0.5	0.178	0.632	0.999
Prepelvic length	12	45.5	45.5	48.6	46.5	0.8	0.669	0.446	0.995
Pectoral-fin length	12	22.4	22.4	26.0	24.2	1.0	1.770	0.191	0.983
Pelvic-fin length	12	15.1	14.3	16.2	15.3	0.5	0.320	0.144	0.981
Rostral barbel length	12	16.2	16.2	18.6	17.4	0.8	0.971	0.146	0.967
Maxillary barbel length	12	23.2	23.2	33.3	29.3	2.5	5.154	0.134	0.812

Body compressed, elongate. Sexes isomorphic. Head laterally compressed, slightly deeper than wide. Snout short, obtuse, about equal to eye diameter. Mouth terminal, oblique in profile, jaws about equal in anterior extension or lower slightly projecting. Small bony knob at dentary symphysis fitting into notch in upper jaw. Maxilla reaching to slightly beyond vertical from anterior margin of orbit. Lower jaw ending anteriorly at about upper 1/3 of eye, posteriorly below about middle of orbit. Lower jaw with anterior lateral lobe margined with sharp, pointed tubercles, similar tubercles also distributed over anterior portion of dentary in varying number and density. Rostral barbel long, reaching to slightly beyond preopercular margin; maxillary barbel long, reaching slightly beyond posterior margin of pectoral-fin base.

Lateral line complete, comprising 34 (2), 35* (9), 36 (1) scales; descending anteriorly for about 6–7 scales, posteriorly paralleling ventral profile. Median predorsal scales 15 (1), 17 (5), 18* (6). Scales in transverse series from dorsal-fin origin to pelvic-fin origin ½6+1+1½* (12); scales below lateral line not much smaller than above. Prepelvic scales rounded, about 15 scales along prepelvic midline; pelvic-fin bases covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14* (12). Pelvic axillary scale present. A row of scales along anal-fin base.

FIGURE 7. *Danio absconditus*. One of the types, living individual photographed immediately after capture. Myanmar: Rakhine State, Comepyo Chaung.

Dorsal-fin rays ii.7½ (2), ii.8½* (17), iii.8½ (2); anal-fin rays iii.13½ (5), iii.14½* (14), iii.15½ (1); pectoral-fin rays i.9 (1), i.10* (10), i.11 (1), plus 1–2 minute unbranched ventral rays; pelvic-fin rays i.7* (12). Principal caudal-fin rays 9+9 (1), 10+9* (17); procurrent caudal-fin rays dorsally 6* (2), 7 (8), 8 (8), ventrally 7 (8), 8* (10). Dorsal-fin origin at highest point of dorsum, slightly posterior to half distance from snout tip to caudal-fin base, and slightly anterior to vertical from anal-fin origin. Pectoral-fin origin at slightly anterior to vertical through posterior margin of opercle; branched rays forming straight or slightly rounded margin, leading unbranched ray longest, reaching slightly beyond insertion of unbranched pelvic-fin ray. Tubercles absent from pectoral fin. Pectoral-fin axial lobe well developed. Pelvic-fin origin situated slightly anterior to midbody, well anterior to dorsal-fin origin. Pelvic-fin margin subtruncate, leading unbranched ray slightly prolonged, reaching beyond rest of fin, to urogenital opening or shorter. Caudal fin moderately forked, lobe tips subacuminate, lower lobe appearing broader than upper.

Vertebrae 17+18=35 (6), 17+19=36* (10), 17+20=37 (1), 18+18=36 (1), 18+19=37 (2); predorsal vertebrae 13 (3), 14* (16), 14 (1); vertebrae contained within caudal peduncle 6 (1), 7* (15), 8 (4). Ceratobranchial 5 tooth formula 5,4,2-2,4,5 (NRM 66247, 37.1 mm SL).

Colouration in preservative. Sexual dimorphism not observed. Ground colour pale beige, lighter abdominally. Dorsum light brownish with dark-brown middorsal stripe anterior to dorsal fin, along dorsal-fin base and dorsal margin of caudal peduncle greyish. Cleithral spot not discernible. Dark brown, narrow P stripe from caudal fin base anteriad to about root of caudal peduncle, margined dorsally on half or all of caudal peduncle by almost pigment-free interstripe I. P stripe continued on middle of side by dark brown line marking lateral septum. On abdominal side, between head and vertical from anal-fin origin, usually 7, but up to 10 brown vertical bars from midaxis ventrad to about level of pectoral-fin base, each bar of about equal thickness or narrowing ventrally; bars vertical and regular in most specimens, occasionally slanting or interrupted. Middle of caudal-fin base with dark-brown or black spot of about pupil diameter, round or slightly extended horizontally, margined above and below by lighter zones.

Colour in life. A specimen photographed close upon capture (Fig. 7) has markings similar to preserved specimens, but also shows distinctly a small, blackish cleithral spot, and anterodorsal to it a minute yellow or orange spot. Distal half of dorsal fin pale reddish. Caudal-fin lobes each crossed by a broad reddish stripe. A white stripe running distal to A stripe. Vertical bars on abdominal side, and P stripe blackish. Light, pale reddish or pinkish stripe bordering P stripe on middle of caudal peduncle. Caudal spot deep black.

Etymology. *Absconditus* is a Latin adjective meaning disguised, secret or hidden. Its application here is inspired both by the colour pattern, which strongly resembles that of barred species of *Devario* Bleeker and the relatively late discovery and recognition of the species.

Geographical distribution (Fig. 5). *Danio absconditus* is known only from a small part of the western slope of the Rakhine Yoma, where it has been collected from headwaters of small coastal streams near Gwa, and headwaters of the Kyeintali Chaung.

Comparative morphometry

The size ranges of the material available of *D. feegradei* and *D. absconditus* are only partially overlapping. Most problematic is that only one large adult of *D. absconditus* is available for study. Biplot analyses of measurements plotted against standard length do not show any sharp differences between the two species. A comparison with other *Danio* with a cleithral spot, using data from Kullander (2015) shows that *D. feegradei* and *D. absconditus* are more similar to *D. meghalayensis* than to the chain danios *D. assamila, D. catenatus*, *D. concatenatus*, *D. dangila*, and *D. sysphigmatus* (Table 3, Fig. 8). *Danio feegradei* and *D. absconditus* share with *D. meghalayensis* a shorter dorsal-fin base, pelvic and pectoral fins, and longer caudal peduncle (Fig. 9 a–h) but *D. meghalayensis* has a much shorter maxillary barbel (Fig. 9f). Together with *D. catenatus* they also have somewhat shorter anal-fin base compared to other chain danios (Fig. 9h), which is balanced by the somewhat longer caudal peduncle (Figs. 9a, c). The shorter fin bases may relate to the lower number of dorsal- and anal-fin rays, but there is also a difference in relative growth of the dorsal-fin base length. In *D. absconditus* and *D. feegradei* relative growth is isometric, in *D. meghalayensis* negatively allometric, and in remaining species variable but on the whole positively allometric (Fig. 9g). *Danio feegradei* has a shorter anal-fin base than *D. absconditus* (17.7–20.7 % SL vs. 19.9–23.0% SL; Fig. 9h), similar to *D. meghalayensis*. This condition corresponds to the difference in the modal number of branched anal-fin rays, 13½ in *D. feegradei,* 11½ in *D. meghalayensis*, and 14½ in *D. absconditus,* the latter similar to chain danios. Size allometry is masked by individual variation in anal-fin base length (Fig. 9h).

TABLE 3. Component loadings from Principal Component Analysis of morphometric data from *Danio absconditus* (N=12), *D. feegradei* (N=17), *D. meghalayensis* (N=5), and chain danios (*D. assamila* (N=6), *D. catenatus* (N=15), *D. concatenatus* (N=9), *D. dangila* (N=8), *D. sysphigmatus* (N=11)). The three highest loadings for each component II-IV are highlighted in boldface.

	PC I	PC II	Sheared PC II	PC III	Sheared PC III	PC IV	Sheared PC IV
Standard length	0.229	-0.145	-0.117	0.033	0.027	-0.161	-0.16
Body depth	0.250	-0.012	0.017	**0.390**	**0.383**	0.335	0.336
Head length	0.193	-0.066	-0.043	-0.048	-0.053	0.054	0.055
Snout length	0.225	-0.004	0.022	-0.254	-0.260	**0.350**	**0.351**
Head depth	0.181	-0.155	-0.132	0.113	0.108	-0.039	-0.038
Head width	0.213	-0.168	-0.141	-0.109	-0.115	0.067	0.069
Upper jaw length	0.179	-0.095	-0.073	-0.090	-0.094	0.056	0.057
Lower jaw length	0.177	-0.080	-0.058	-0.179	-0.184	-0.024	-0.023
Orbital diameter	0.144	-0.002	0.015	0.246	0.243	0.083	0.083
Interorbital width	0.226	0.014	0.04	-0.089	-0.095	0.223	0.225
Caudal peduncle length	0.146	**-0.582**	**-0.558**	-0.162	-0.166	**-0.421**	**-0.420**
Caudal peduncle depth	0.242	-0.246	-0.215	0.145	0.139	0.031	0.032
Dorsal-fin base length	0.340	**0.471**	**0.504**	-0.177	-0.186	**-0.627**	**-0.624**
Anal-fin base length	0.276	0.229	0.258	**0.663**	**0.656**	-0.179	-0.177
Predorsal length	0.225	-0.164	-0.136	0.035	0.03	0.001	0.003
Preanal length	0.241	-0.127	-0.097	-0.021	-0.028	-0.034	-0.032
Prepelvic length	0.230	-0.126	-0.098	-0.013	-0.019	0.084	0.085
Pectoral-fin length	0.259	**0.331**	**0.357**	-0.206	-0.212	0.140	0.141
Pelvic-fin length	0.290	0.255	0.285	**-0.292**	**-0.299**	0.198	0.200
Eigenvalue	1.0077	0.0302	NA	0.0084	NA	0.0049	NA
Cumulative variance (%)	94.20%	97.00%	NA	97.80%	NA	98.30%	NA

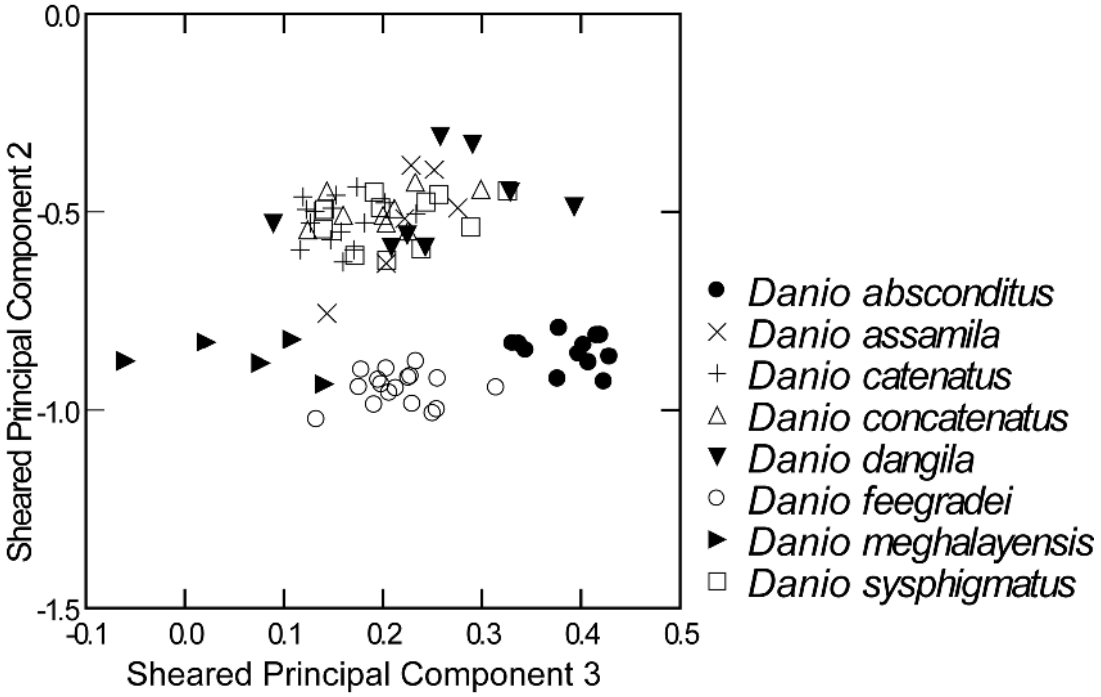

FIGURE 8. Principal Component Analysis of pooled morphometric data from *Danio absconditus, D. feegradei, D. meghalayensis*, and chain danios (*D. assamila, D. catenatus, D. concatenatus, dangila*, and *D. sysphigmatus*).

Discussion

Contrasting with a relatively conservative morphology, species of *Danio* exhibit considerable variation in colour pattern, including almost uniform colour in *D. roseus* (Fang & Kottelat, 2000), rich pattern of dark spots (e.g., *D. kyathit* Fang, *D. tinwini* Kullander & Fang), dark circles (e.g., *D. dangila*), several horizontal stripes (e.g., *D. rerio* (Hamilton)), a combination of dark spots and stripes (*D. nigrofasciatus* (Day)), light dots on dark background (*D. margaritatus* (Roberts)), or dark vertical bars (e.g., *D. choprae* Hora). In this they parallel the variation among species of *Devario.* The earlier synonymy of the two genera was probably much influenced by the similarities in colour pattern. The two species described in this paper share elements with *Devario* Heckel and *Betadevario* Pramod, Fang, Rema Devi, Liao, Indra, Jameela Beevi & Kullander, but also present colour-pattern elements indicating that they are sister species. *Danio feegradei* is similar in colour pattern to *Devario devario* (Hamilton) from India, Bangladesh, and Nepal. In *D. devario* the sides are also dark and adorned by round or slightly vertically extended white or silvery spots. *Danio absconditus* is characterized by dark vertical bars on the abdominal side, characteristic of several species of *Devario* from the Shan and Yunnan plateaus, e.g., *D. jayarami* (Barman) and *D. maetaengensis* (Fang) (Fang, 2000). The similarity to *Devario* and *Betadevario* is further enhanced by the presence in both *D. feegradei* and *D. absconditus* of a small cleithral spot, characteristic of *Devario* and *Betadevario* but much smaller than in those genera. A large cleithral spot is present in the chain danios, *D. dangila, D. assamila, D. catenatus, D. concatenatus,* and *D. sysphigmatus*.

None of the *Devario* mentioned above occur in western Myanmar, which excludes options of mimicry to explain the similarity across genera in colour pattern. Only one species of *Devario* is recorded from coastal streams in Rakhine State, viz. *D. xyrops* Fang & Kullander (2009b), which is sympatric with *D. feegradei* and probably with *D. absconditus* as well, but has a different colour pattern, with two dark blotches on the side. Three additional species of *Danio* are recorded from Rakhine coastal streams. *Danio aesculapii* Kullander & Fang is sympatric and syntopic with both *D. feegradei* and *D. absconditus*. It is a very small species with a colour pattern in preservative somewhat resembling that of *D. absconditus*, with irregular short vertical marks along the side, but in life with silvery reflections quite unlike *D. absconditus* (Kullander & Fang, 2009a). *Danio catenatus* and *D. concatenatus* are large species with a complex pattern of dark rings enclosing light interspaces (Kullander, 2015). The former is sympatric with *D. feegradei*, the latter with *D. absconditus.* It seems thus that the distribution of the different standard colour patterns available to *Danio* and *Devario* may be more discriminating than mimetic.

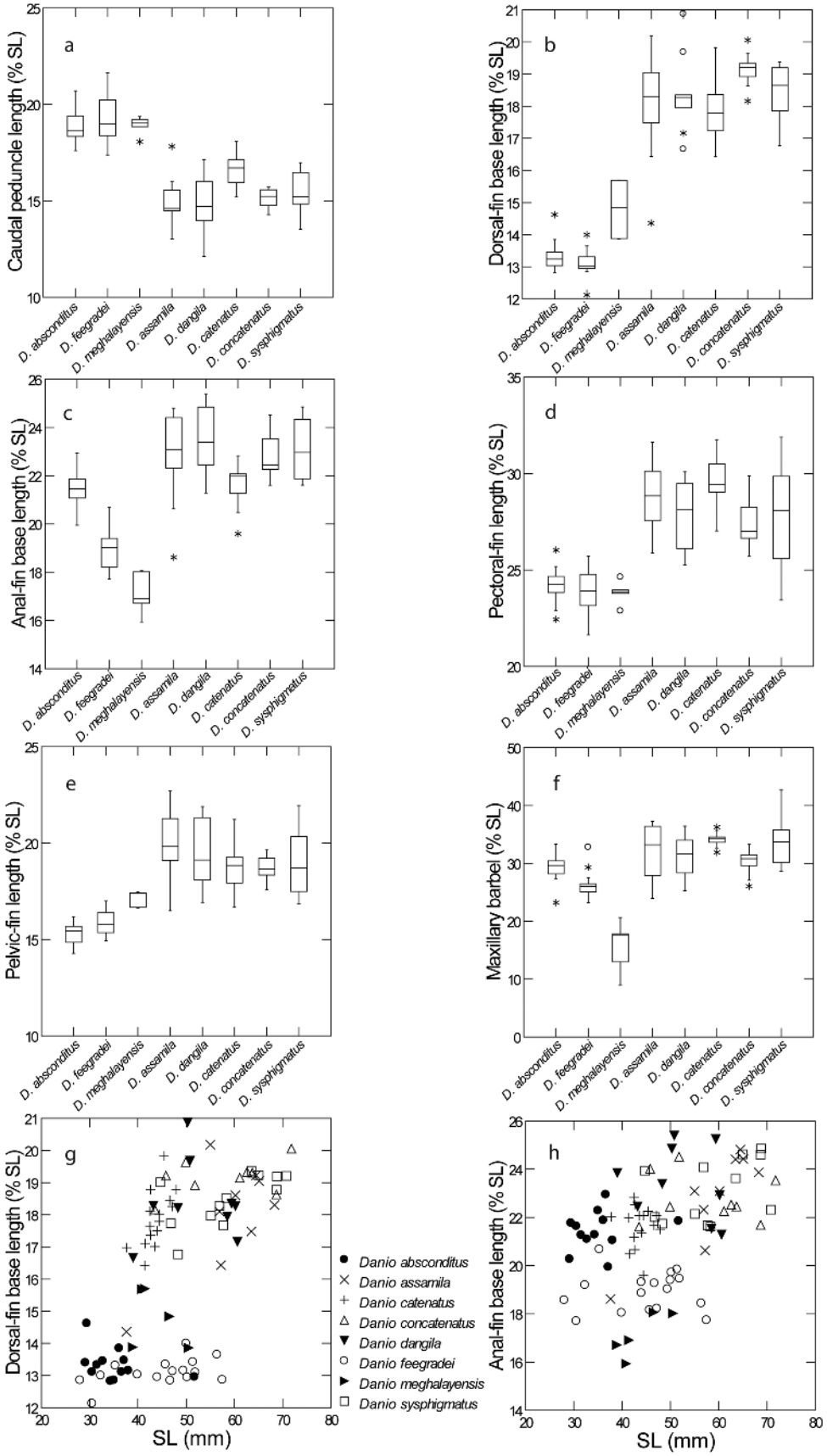

FIGURE 9. Comparative morphometric analysis of *Danio absconditus, D. feegradei, D. meghalayensis*, and chain danios (*D. assamila, D. catenatus, D. concatenatus, dangila*, and *D. sysphigmatus*). a–d, box-and-whisker plots of proportional measurements (as per cents of standard length; e-f, proportional measurements (per cents of standard length) plotted against standard length, exposing differences in size allometry.

Danio absconditus and *D. feegradei* share a distinct dark-brown or black spot at the base of the caudal fin with *D. erythromicron*, a minute species endemic to Inle Lake in eastern Myanmar. In *D. erythromicron* this spot is ringed with light, and has the appearance of an ocellar marking. In *D. absconditus* and *D. feegradei*, the contrast between the light areas above and below the dark caudal spot is not striking, but it nevertheless has a rudimentary appearance of an ocellar marking. Also *D. jaintianensis* from the Shillong Plateau in Meghalaya and *D. flagrans* and *D. choprae* from the Ayeyarwaddy River system in Myanmar present a minute black spot at the caudal-fin base, terminating the P stripe. In those species, however, the spot is very small and often difficult to distinguish. The caudal spot in *D. absconditus* and *D. feegradei* is here considered a synapomorphy which, taken together with the identity of the two species in almost all other regards, suggests a sister species relationship. The presence in *D. absconditus* and *D. feegradei* of a complete lateral line and cleithral spot, and elevated number of circumpeduncular scales (14), is shared with chain danios and *D. meghalayensis*, but also with species of *Devario* (12–16 circumpeduncular scales) and *Betadevario* (12–14 circumpeduncular scales), suggesting that those may be plesiomorphic within *Danio*. In other *Danio* the lateral line is absent or represented by only a few perforated scales; a cleithral spot is absent, and the circumpeduncular scale count is lower (10–12). Chain danios are characterized by the elaborate colour pattern forming series of dark rings along the side, prolonged unbranched rays in the pectoral and pelvic fins, and somewhat elevated number of dorsal-fin rays (9½–11½ vs. 7½–8½ in *D. feegradei* and *D. absconditus*). *Danio meghalayensis* also has a somewhat short dorsal fin, with 8½ branched rays (Kullander, 2015). *Danio absconditus* and *D. feegradei* are more similar to *D. meghalayensis* than to chain danios in the morphometric comparison (Fig. 9), and the two clusters seem to differ in the patterns of size allometry, particularly in the length of the dorsal-fin base, which shows a slight relative size allometry in chain danios, but also considerable individual variation that possibly reflects sex dimorphism. Variation in size allometry has not been studied comparatively in danios, but may be phylogenetically significant. Unfortunately, the size range of some of the material available is limited. As an example, only one large adult of *D. absconditus* has been available for study. Aquarium observations and preserved material suggest that at least *D. dangila* can reach very large sizes (for a *Danio*) whereas *D. feegradei* and *D. meghalayensis* do not seem to far exceed the size reported here; aquarium observations are not available for the other chain danios. It may be that large size requires shape adjustments, and a relatively longer dorsal-fin base may be a consequence of altered function of the dorsal fin in large specimens.

In the molecular phylogeny of Tang *et al*. (2010), *D. feegradei* is sister taxon to remaining *Danio*. In the analysis of Collins *et al*. (2012) it is sister to *D. rerio* in a clade sister to *D. dangila* and similar species based on the mitochondrial COI fragment, and sister to remaining *Danio* based on the nuclear rhodopsin fragment. There are no published DNA sequences of *D. absconditus*. The presence of a cleithral spot, complete lateral line, and 14 circumpeduncular scales, shared with devarionins, also suggest a basal phylogenetic position of *D. feegradei* and *D. absconditus.*

Although we report measurements as ratios here, both in Tables 1–2 and in Figure 9, most ratio measurements are not diagnostic because of size allomety. The interesting exception is the dorsal-fin base length which almost separates *D. absconditus* and *D. feegradei* from chain danios. It reflects the near isometry in *D. absconditus* and *D. feegradei*, which means that they keep about the same ratio (13–14%) between about 30 and 60 mm SL, whereas in the group of chain danios, the ratio is size dependent, between about 17 and 19% in the same SL range. Table 4 summarizes the proportional ratios of the measurements suggested by the PCA, and the barbel lengths, which mainly indicate a separation between the chain danios and the rest. The barbels were excluded from the PCA because of individual variability and frequently missing values. It may be impossible to decide if very short barbels are damaged or naturally short, and thus the lower values for barbel lengths may be underestimates. They are recorded, however, unless clearly broken. As apparent from the ratio data, chain danios tend to have longer barbels, which is also obvious as in these species the maxillary barbel reaches well beyond the pectoral-fin base. Barbels in *D. meghalayensis* are consistently short; in *D. absconditus* and *D. feegradei* they are long but not reaching much posterior to the base of the pectoral fin.

Aquarium specimens examined of *D. dangila, D. meghalayensis* and *D. feegradei* include males with well-developed tubercles on the pectoral fin (Kullander, 2015), a male character recorded in most *Danio* species and shared with *Devario.* No such tubercles were found in wild chain danios, *D. meghalayensis*(Kullander, 2015), *D. feegradei* or *D. absconditus* .This may be an indication that the presence of pectoral tubercles is seasonal. They are also quite delicate and easily lost from old museum specimens, and abrasion may to some extent explain their absence from wild specimens in this study.

TABLE 4. Comparative morphometry of species of *Danio* with a cleithral spot and complete lateral line, limited to measurements showing non-overlapping or minimal overlap between two or more species. Measurements are in per cent of standard length.

	absconditus	*feegradei*	*meghalayensis*	*dangila*
Caudal peduncle length	17.6–20.7	17.4–21.6	18.1–19.4	12.1–17.1
Dorsal-fin base length	12.8–14.6	12.1–14.0	13.9–15.7	16.7–20.9
Anal-fin base length	19.9–23.0	17.7–20.7	15.9–18.1	21.3–25.4
Pectoral-fin length	22.4–26.0	21.6–25.7	22.9–24.6	25.3–30.1
Pelvic-fin length	14.3–16.2	14.9–17.0	16.6–17.5	16.9–21.9
Rostral barbel length	16.2–18.6	13.7–18.0	9.6–17.0	17.5–28.6
Maxillary barbel length	23.2–33.3	23.2.32.8	9.0–20.6	25.3–32.8

continued.

	assamila	*catenatus*	*concatenatus*	*sysphigmatus*
Caudal peduncle length	13.0–17.8	15.2–18.1	14.3–15.7	13.5–17.0
Dorsal-fin base length	14.4–20.2	16.4–19.8	18.2–20.1	16.8–19.4
Anal-fin base length	18.6–24.8	19.6–22.8	21.6–24.5	21.6–24.9
Pectoral-fin length	25.9–31.6	27.0–31.8	25.7–29.9	23.4–31.9
Pelvic-fin length	16.5–22.7	16.7–21.2	17.6–19.7	16.9–21.9
Rostral barbel length	15.2–22.7	17.0–21.6	18.1–20.5	18.5–29.8
Maxillary barbel length	24.0–37.3	31.9–36.3	26.0–33.3	28.7–42.7

Twenty species of teleosts are already known only from streams on the western slope of the Rakhine Yoma, while most of the area is still unexplored: *Akysis vespertinus* Ng, *Batasio elongatus* Ng, *Channa pulchra* Britz, *Danio absconditus*, *D. aesculapii, D. catenatus, D. concatenatus*, *D. feegradei*, *Devario xyrops, Garra vittatula* Kullander & Fang, *G. rakhinica* Kullander & Fang, *G. flavatra* Kullander & Fang, *G. nigricollis* Kullander & Fang, *G. propulvinus* Kullander & Fang, *Hara spinulus* Ng & Kottelat, *Macrognathus pavo* Britz, *Psilorhynchus melissa* Conway & Kottelat, *P. pavimentatus* Conway & Kottelat, *Schistura hypsiura* Bohlen, Ŝlechtová & Udomritthiruj and *Systomus binduchitra* (Hora).

Judging from the close similarity of *Devario anomalus* Conway, Mayden & Tang from westernmost coastal Bangladesh and *D. xyrops* from western Rakhine Yoma, which share a unique colour pattern (Fang & Kullander, 2009), there is at least one indication that this fauna may be more related to that of eastern Bangladesh, or alternatively that the particular area of endemism extends into eastern Bangladesh, which is still little explored. Another potential pattern is the separation of southern and northern taxa within the Rakhine Yoma, as particularly well exemplified by *Danio absconditus* and *D. feegradei*, but also indicated by *D. catenatus* and *D. concatenatus* (Kullander, 2015). More inventories are needed, but observations so far suggest that the present endemism may reflect earlier lower ocean levels during glacial periods when current coastal rivers east of the Jumna may have been headwaters of one or more now submerged river systems, possibly including an extension of the present Kaladan River. Sea-level regression during the latest glacial maximum centred at 21,000 years BP was at most between 120 and 135 m (Clark & Mix, 2002; Voris, 2000). Because the relief is rather step along the coast of the Rakhine Yoma, however, any such river extensions would still have been relatively short. The ichthyofauna of the Kaladan is still not well known, but would then be expected to have species related to endemics in the western Rakhine Yoma. Under a scenario depending on a glacial period, however, the present-day Kaladan River would have been colder and at a relatively higher altitude with more passage barriers, and perhaps with a different fauna. A potential example of a common history is *Batasio convexirostrum* Darshan, Anganthoibi & Vishwanath, 2011 from the lower Kaladan, which is somewhat similar to *B. elongatus* from the Rakhine coast south of the Kaladan; but on the other hand, species of *Batasio* tend to be similar and the original description of *B. convexirostrum* does not contain any relationship analysis. The Rakhine Yoma emerged along with the rest of the Indo-Burman range in the Miocene as a consequence of major thrust from the Indian plate (Bender, 1983). At that time it was a

seismically active region with considerable volcanism, but became accessible to freshwater fishes in the Late Neogene. Aside from the Kaladan River there are no major drainages on the Rakhine coast, and the fish distribution was probably largely mediated since the Pliocene between smaller streams by stream capture following stream erosion. So far, there are no records of species found on both sides of the range, suggesting that displacement by stream capture may be rare, but on the other hand, only a small part of the Rakhine Yoma has been surveyed for fishes. The probable relationship with *D. meghalayensis* and the chain danios, which are most diverse in Indian highlands, suggest again that the Western Rakhine may be a component of the Naga Hills and Shillong Plateau hill-stream fish fauna more than that of central or northern Myanmar. A major component of the described endemism consists of species of *Garra* Hamilton, which are specialized hill stream fishes (Kullander & Fang, 2004) with considerable diversity of species from further north along the Indo-Myanmar Range.

Danio includes 23 valid species in South and South East Asia (Fang Kullander, 2001; Kullander, 2012, 2015). Fifteen valid species have already been reported from Myanmar, including *D. aesculapii, D. catenatus* and *D. concatenatus* also from the coast of Rakhine state*, D. albolineatus* (Blyth)*, D. choprae, D. erythromicron, D. feegradei , D. flagrans*, *D. kyathit*, *D. margaritatus, D. nigrofasciatus, D. quagga* Kullander, Liao & Fang, *D. roseus*, *D. sysphigmatus,* and *D. tinwini.* Only five species are known from west of Myanmar (*D. rerio, D. jaintianensis, D. assamila, D. dangila*, *D. meghalayensis*), and only four from east of Myanmar (*D. kerri* Smith, *D. pulcher* Smith*, D. tweediei* Brittan, *D. roseus*). Only one Myanmar species has a wide distribution, viz., *D. roseus*, which is found over most of northern Myanmar and adjacent China, Laos, and Thailand (pers. obs.). *Danio* species so far described have allopatric or overlapping distributions, and this extends also to sister species. In Myanmar the species pair *Danio flagrans* and *D. choprae* are mutually exclusive in the Ayeyarwaddy drainage (Kullander, 2012), and along the southern coasts the closely related *D. catenatus, D. concatenatus* and *D. sysphigmatus* have allopatric distributions (Kullander, 2015). The sister taxa *D. erythromicron* and *D. margaritatus* occupy different lakes in the Shan limestone karst region (Roberts, 2007; pers. obs.). Parapatry, i.e., abutting distributions as in *D. absconditus* and *D. feegradei*, have not been observed before in the genus. A main reason for that may be lack of collection coverage, and more cases likely exist in the region. Parapatric sister species are of interest because they have the potential for hybridisation and introgression and may mark very precise barriers for dispersal and/or speciation. In the case of *D. feegradei* and *D. absconditus* each species is present in several coastal streams and there is no obvious physical structure in the transitional region that may explain the complementary distribution. They have, however, been isolated for a long time, resulting in highly disparate colour patterns. It may be that the two taxa are headwater descendants of a species inhabiting a now submerged river or extension of the Kaladan River along the Rakhine coast, as outlined above, but there is no geological support for such an extension, and the taxonomic and geographical sampling density of the Rakhine Yoma is still too incomplete to point to a well substantiated pattern of fish distribution.

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