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Taxonomy of chain *Danio*, an Indo-Myanmar species assemblage, with descriptions of four new species (Teleostei: Cyprinidae)

Sven O. Kullander*

Danio dangila is widely distributed in the Ganga and lower Brahmaputra basins of India, Nepal and Bangladesh and distinguished by the cleithral spot in the shape of a short vertical stripe (vs. a round spot in all similar species). Four new species are described, similar to *D. dangila* but with round cleithral spot and each diagnosed by species specific colour pattern. *Danio assamila*, new species, is reported from the upper and middle Brahmaputra drainage in India. *Danio catenatus*, new species, and *D. concatenatus*, new species, occur in rivers of the western slope of the Rakhine Yoma, Myanmar. *Danio sysphigmatus*, new species, occurs in the Sittaung drainage and small coastal drainages in southeastern Myanmar. Those five species, collectively referred to as chain danios, make up a distinctive group within *Danio*, diagnosed by elevated number of unbranched dorsal-fin rays, long rostral and maxillary barbels, complete lateral line, presence of a prominent cleithral spot, horizontal stripes modified into series of rings formed by vertical bars between horizontal dark stripes, and pectoral and pelvic fins each with the unbranched first ray prolonged and reaching well beyond the rest of the fin. *Danio meghalayensis* is resurrected from the synonymy of *D. dangila*, with *D. deyi* as a probable junior synonym. *Danio meghalayensis* has a colour pattern similar to that of chain danios with vertical bars bridging parallel horizontal stripes but usually predominantly stripes instead of series of rings, a smaller cleithral spot and shorter barbels, and the unbranched ray in the pectoral and pelvic fins is not prolonged. *Danio meghalayensis* is known only from the Brahmaputra drainage in Meghalaya, India. The geographical distribution of the chain danios represents a unique pattern for the region, and may be explained by different climate and river drainage systems during the latest glacial period.

Introduction

The Asian cyprinid fish genus *Danio* was established by Hamilton (1822: 321) as a division of *Cyprinus*, and included originally ten species. Hamilton's descriptions are brief and general, and his species have since been recognized by the excellent illustrations, many of them in Hamilton (1822), others reproduced by M'Clelland (1839),

Gray (1830), and Hora (1929). Among the originally included species Bleeker (1863a: 204, 1863b: 264, 1863c: 29) selected *Cyprinus dangila* as type species of *Danio*. *Danio* was then for a long time confused with *Devario* Heckel (1843: 1015; type species *Cyprinus devario* Hamilton, 1822), species of which were generally assigned to *Danio*. After the description of *Brachydanio* by Weber & Beaufort (1916: 85; type species *Nuria albolineata* Blyth,

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1860), smaller species were generally referred to *Brachydanio*, and larger species kept in *Danio*. In his revision of *Danio* Barman (1991) lumped all *Brachydanio*, *Danio* and *Devario* in a single genus *Danio*. Fang (2001, 2003) showed that *Danio* and *Devario* are distinct taxa and synonymized *Brachydanio* with *Danio*. Primarily the variation in colour pattern and morphological reductions in smaller species inspired Roberts (2007) and Kottelat (2013) to recognize *Celestichthys* Roberts (2007) as a valid genus to which Kottelat (2013) referred *D. erythromicron* (Annandale), *D. margaritatus* (Roberts), *D. choprae* Hora, and *D. flagrans* Kullander. Kottelat (2013) also suggested re-erection of *Brachydanio* for other small species of *Danio*, leaving *Danio* monotypic with *D. dangila*. Previous and ongoing phylogenetic analyses strongly support a monophyletic *Danio* in the sense of Fang (2003), however, and I use the wider concept here. Up to and including the description of *D. flagrans* by Kullander (2012), *Danio* includes 17 valid species.

Danio dangila is a relatively little studied species which is also rare in collections, although reported from a wide area including northern India, Bangladesh, Nepal, and Myanmar (Talwar & Jhingran, 1991; Barman, 1991). It is one of the largest species in the genus, reaching nearly 90 mm body length in aquarium (NRM 57110), and has a characteristic colour pattern with dark horizontal stripes that anastomose to form series or a cloud of circles along the side. Among its putative synonyms are *D. meghalayensis* Sen and Dey (1985) and *D. deyi* Sen (in Sen & Dey, 1985) from Meghalaya (Fang, 2001; Kottelat, 2013). Analysis of collections from Myanmar identified as *D. dangila* show that they represent three distinct species, however, and at least two species are represented among *D. dangila* from India and Nepal. Recent material from Meghalaya shows that *D. meghalayensis* is a valid species with a distinctive colour pattern and morphology separating it from *D. dangila*. The objective of this paper is to describe the new taxa and provide diagnostic characters of *D. dangila* and *D. meghalayensis*.

Material and methods

Specimens are kept in the following collections: BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Fran-

cisco; CMK, collection of Maurice Kottelat, Delémont; KU, Biodiversity Institute, University of Kansas, Lawrence; NRM, Swedish Museum of Natural History, Stockholm; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor; USNM, United States National Museum of Natural History, Washington; ZMA Zoölogisch Museum, Amsterdam [now Naturalis Biodiversity Center, Leiden].

Measurements were taken with digital callipers to a precision of 0.1 mm. Counts and measurements were made according to Fang (1997). The count of lateral line scales excludes scales on the caudal fin. The terminal unbranched ray in the dorsal and anal fins, sharing base with the penultimate ray, is recorded as a half (½) ray. Fin-ray 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). 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. Preparations indicated as c&s were cleared and counterstained with Alcian Blue and Alizarin Red for cartilage and bone using the method of Taylor & Van Dyke (1985). In the descriptions an asterisk (*) marks counts from the holotype.

Colour pattern terminology follows Fang (1998), with modifications for special markings. Horizontal 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+3, 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. Interstripes are light horizontal zones between stripes. Interstripe I is the one between the P and P-1 stripes; remaining interstripes numbered I+1, etc. dorsally and I-1, etc. ventrally. A short anterior interstripe present in some species from the cleithrum to at most the middle of the side, and homologous with Interstripe I or I-1, is here named Ia.

Danio dangila (Hamilton, 1822)
(Figs. 1a–b)

Cyprinus dangila Hamilton, 1822: 321, 390. No types known; type locality mountain streams south from Mungger.

Perilampus reticulatus McClelland, 1839: 290, 397, pl. 45, fig. 1. New name for *Cyprinus dangila* Hamilton, 1822.

Material examined. Brahmaputra River drainage: BMNH 1889.2.1.1292, 1, 50.2 mm SL; India: West Bengal: Darjeeling; F. Day, no date. – CAS 128715, 2, 39.0–50.8 mm SL; India: West Bengal: Siliguri; G. E. Shaw & E. O. Shebbeare, no date. – CAS 141137, 10, 30.0–60.2 mm SL; India: West Bengal: Tista River drainage: Kalimpong Duars and Siliguri Terai; S. L. Hora, Nov 1938. **Ganga River drainage:** CAS 50240, 2, 43.2–58.5 mm SL; Nepal: Chitwan Valley: small streams rising in Churia Hills or Ranges and flowing north into [East] Rapti River; T. R. Roberts, 29 Apr 1975. – CAS 50338, 1, 60.6 mm SL; Nepal: Chitwan Valley: Rapti River drainage: Dudara River; T. R. Roberts, 1 April 1975. – KU 41371, 5, 28.3–47.2 mm SL; Nepal: Tanahun: Seti River at Khairentar; D. Edds, 16 Jun–15 Nov 1996. – UMMZ 243658, 1, 48.3 mm SL; India: West Bengal: Kartowoa River at barrage in Ambari, 104 m asl; Ng H. H., 14 Apr 2004. – ZMA 121.596, 1, 54.6 mm SL; India: Jharkand: Ganga River drainage: Parasnath Hill: Lili Nullah, 2500 ft. ASL; N. Annandale, Apr–May 1901. *Aquarium specimens:* NRM 49817 (tissue 1216), 1, 31.8 mm SL; NRM 49818 (tissue 1217), 1, 29.1 mm SL; Aquarium; R. Britz, 2002. – NRM 50197 (tissue 1398), 1, 40.2 mm SL; Aquarium; S. O. Kullander, 2004. – NRM 57110, 1, 88.5 mm SL; Aquarium, S. O. Kullander, 2007.

Diagnosis. *Danio dangila* is distinguished from all other species of *Danio* except *D. assamila*, *D. catenatus*, *D. concatenatus*, and *D. sysphigmatus* by produced first ray in pectoral and pelvic fins, large cleithral spot, and pattern of dark rings enclosing light interspaces on the side. Distinguished from those species by vertically extended cleithral spot (vs. round in all other species), absence of complete anterior interstripe Ia (vs. present in *D. assamila* and *D. concatenatus*), round rings in series along side, width of dark perimeter of about same width as diameter of light centre (vs. elongate in *D. assamila* and *D. sysphigmatus*, with narrower perimeter in *D. sysphigmatus*), ring pattern usually extending onto caudal peduncle (present on part of caudal peduncle in *D. catenatus* and *D. concatenatus*, absent in *D. assamila* and *D. sysphigmatus*), and lateral line scale count 32–34 (vs. 35–38 in *D. sysphigmatus*).

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

Body compressed, moderately elongate, no sexual dimorphism evident. Head compressed, slightly deeper than wide. Snout short, rounded, length about equal to eye diameter. Mouth terminal, oblique in profile, or lower jaw 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 slightly above level of middle of eye or close to level of upper orbital rim. Lower jaw with pointed anterior lateral lobe. Tubercles minute, present in two rows along lateral margin of dentary posterior to lateral lobe, and scattered anteriorly on lower jaw; absent from pectoral fin. Rostral barbel moderately long, reaching to slightly beyond preopercle, usually not to pectoral-fin base except in two specimens from Tista and Siliguri respectively. Maxillary barbel long, reaching past pectoral-fin base, up to middle or $\frac{3}{4}$ of pectoral fin.

Lateral line complete, comprising 32(1), 33(3), 34(6) scales; descending anteriorly for about 6 scales from some of which pore absent, posteriorly paralleling ventral profile. Median predorsal scales 16(2), 17(4), 18(4). Scales in transverse series from dorsal-fin origin to pelvic-fin origin $\frac{1}{2}6+1+1$ (1), $\frac{1}{2}6+1+1\frac{1}{2}$ (1); below lateral line scales smaller than above. Prepelvic scales rounded, about 15–17 scales along prepelvic midline; pelvic-fin base covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14(9). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii.9 $\frac{1}{2}$ (5), ii.10 $\frac{1}{2}$ (12); anal-fin rays iii.12 $\frac{1}{2}$ (1), iii.13 $\frac{1}{2}$ (5), iii.14 $\frac{1}{2}$ (1), iii.15 $\frac{1}{2}$ (7), iii.16 $\frac{1}{2}$ (4); pectoral-fin rays i.10 (7), i.11 (2), plus 0–2 minute unbranched rays; pelvic-fin rays i.7 (10). Principal caudal-fin rays 10+9 (6); procurvent caudal-fin rays dorsally 6 (3), 7 (6), ventrally 6 (7), 7 (2). Dorsal fin inserted at highest point of dorsum, slightly posterior to half distance from snout tip to caudal-fin base, and distinctly anterior to vertical from anal-fin origin. Pectoral-fin insertion at about vertical through posterior margin of opercle; branched rays forming slightly rounded or truncate margin, leading unbranched ray prolonged beyond rest of fin, reaching to insertion of unbranched pelvic-fin ray or slightly beyond. Tubercles absent from pecto-

ral fin. Pectoral-fin axial lobe well developed. Pelvic-fin origin situated slightly anterior to midbody, well anterior to dorsal-fin origin. Pelvic-fin margin slightly rounded or truncate, leading unbranched ray slightly prolonged, reaching beyond rest of fin, to vent or anal-fin origin. Caudal fin slightly forked, lobes about equal, tips subacuminate.

Vertebrae 17+17=34 (1), 18+17=35 (8), 18+18=36 (5), 19+19=38 (1); predorsal vertebrae 13 (2), 14 (6); vertebrae contained within caudal peduncle 4 (1), 5 (3), 6 (4). Ceratobranchial 5 tooth formula 2,3,5-5,3,2.

Colouration in preservative (Figs. 1a–b). Sexual dimorphism absent in colour pattern. Ground colour fawn or dull white, markings absent from head and venter, except slight concentration of dark pigment adjacent to lower margin of orbit. Dorsal midline anterior and posterior to dorsal fin marked by narrow dark brown stripe. Cleithral spot dark brown or black, vertically extended, about as large as pupil or smaller, partially or entirely bordered by light zone.

Dark brown stripes P, P+1, P+2, P+3, P-1; P-2 stripe diffuse, brownish. P+3 stripe consisting of small brown spots in irregular row from above

upper end of gill cleft to below posterior part of dorsal-fin base. P+2 stripe irregular, partly fragmented, from close to cleithral spot caudad to slightly posterior to vertical from end of dorsal-fin base; anteriorly anastomizing in irregular ring pattern with P+1 stripe. P+1, P and P-1 stripes distinct on most or posterior part of caudal peduncle where forming straight parallel stripes, usually bridged by 1–3 dark rings; anteriorly anastomizing with adjacent stripes. Anterior to striped portions contributing to row of about 6–9 round dark brown rings enclosing Interstripe I. P-1 stripe distinct, narrow posteriorly, paralleling posterior parts of P and P+1 stripes, but ending in upward slant on basal scales of caudal fin; anterior to caudal peduncle anastomizing with lower branch of P stripe to form about 5–8 large round brown rings fragmenting interstripe I-1. Anterior side lacking anterior interstripe Ia, instead anterior horizontal stripes anastomizing irregularly to form cloud of dark-ringed light spots of different sizes. Posterior to that a few rings may form between the rows of rings between the major upper and lower rows of rings. P-2 stripe diffuse, may be more distinct posteriorly, straight, narrow, originating at pectoral-fin base, and before ending above posterior part of anal-fin

Table 1. Morphometry of *Danio dangila*. 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.

	N	min	max	mean	SD	a	b	r
Standard length (mm)	9	39.0	60.6	52.3	7.9			
Body depth	9	28.8	33.5	31.4	1.4	1.114	0.292	0.954
Head length	9	22.6	26.2	24.3	1.3	2.979	0.184	0.950
Snout length	9	6.0	7.9	6.9	0.5	0.809	0.053	0.886
Head depth	9	16.3	18.3	17.3	0.7	1.409	0.146	0.980
Head width	9	11.8	14.6	13.1	0.9	0.850	0.114	0.810
Upper jaw length	9	8.9	10.5	9.6	0.5	0.797	0.081	0.948
Lower jaw length	9	10.4	12.1	11.3	0.6	0.812	0.097	0.947
Orbital diameter	9	7.4	9.0	8.0	0.6	1.463	0.052	0.930
Interorbital width	9	10.4	11.4	11.1	0.4	0.444	0.102	0.975
Caudal peduncle length	9	12.1	17.1	14.8	1.6	-0.684	0.162	0.830
Caudal peduncle depth	9	11.8	13.8	12.9	0.7	-1.821	0.165	0.993
Dorsal-fin base length	9	16.7	20.9	18.4	1.3	0.243	0.179	0.963
Anal-fin base length	9	21.3	25.4	23.4	1.5	1.389	0.207	0.903
Predorsal length	9	56.1	62.3	59.2	1.9	1.747	0.557	0.980
Preanal length	9	64.4	69.2	67.0	1.7	-1.288	0.696	0.990
Prepelvic length	9	47.2	50.3	48.7	1.1	-1.444	0.515	0.992
Pectoral-fin length	8	25.3	30.1	27.8	1.9	-1.745	0.313	0.938
Pelvic-fin length	8	16.9	21.9	19.5	1.9	-3.250	0.258	0.940
Rostral barbel length	9	17.5	28.6	21.1	4.0	-3.074	0.271	0.697
Maxillary barbel length	9	25.3	36.4	30.8	3.7	4.122	0.228	0.706

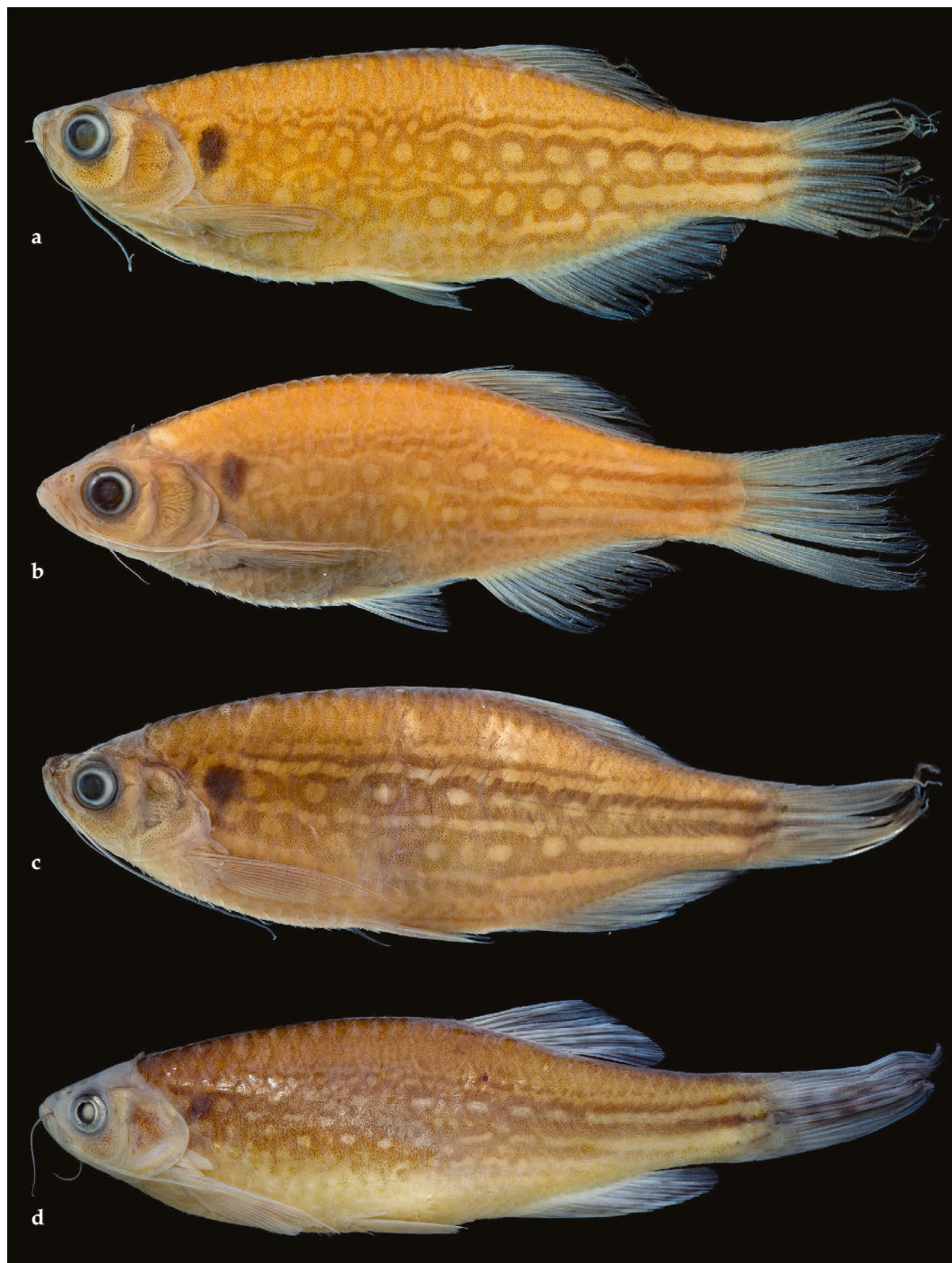


Fig. 1. **a**, *Danio dangila*, UMMZ 243658, 48.3 mm SL; India: Ganga River drainage: Ambari; **b**, *Danio dangila*, CAS 50240, 43.2 mm SL; Nepal: Ganga River drainage: Rapti River; **c**, *Danio assamila*, NRM 65571, holotype, 55.0 mm SL; India: Assam: Brahmaputra River drainage: Amguri; **d**, *Danio assamila*, NRM 51441, paratype, 57.3 mm SL; India: Assam: Brahmaputra River drainage: Nagaon, Lanka forest.

base; may be separated horizontally by light spots. Dorsal fin hyaline basally, with indistinct greyish median D stripe, distal half hyaline. Anal fin hyaline with indistinct greyish median A stripe and usually distinct A-1 stripe. Caudal fin dusky, lighter along middle and with distinct dark stripes continuing stripes P+1, P, and P-1.

Geographical distribution (Fig. 2). Ganga and adjacent Brahmaputra basin in Nepal, India, and Bangladesh. Literature records of probably correctly identified *D. dangila* suggest a wide distribution in the Ganga, lower Brahmaputra (Tista and Jumna Rivers), and Meghna basins: Barman (1988: Tripura, Armarpur, Gumti River, Meghna River basin), Sen (1992: Damodar River, West Bengal); Hamilton (1822: Munger). Barman (1991) reported *D. dangila* from the Bastar District (= Jagdalpur) in Madhya Pradesh, suggesting that the species is also present in the Godavari drainage.

Remarks. There is no known type material of *Danio dangila*. Hamilton (1822) based his work on field observations and drawings and did not preserve specimens (Hora, 1929). Hamilton related that he “found the *Dangila* among the rocks and stones which compose the bottom of several clear. [sic] mountain streams, south from Mungger”. Mungger must be Munger, in the present state of Bihar, in the Ganga main catchment. Consequently, specimens from the Ganga basin are here considered to represent *Danio dangila*. *Perilampus reticulatus* was proposed by M’Clelland (1839) as a new name for *D. dangila* and takes the same type material and type locality.

Most of the specimens reported here as *D. dangila* are in a poor state of preservation, but the colour pattern and barbel lengths can be made out from most specimens. All specimens were collected either in the Ganga basin or in the Tista basin, the latter a tributary to the lower Brahmaputra River. The only possible indication of heterogeneity in the material is that the specimens from the Seti River have slightly smaller and more numerous rings, about 9–10 in the upper row anterior to the caudal peduncle, whereas the remaining specimens have at most 7, but the classification of anterior circles as belonging to the rows or the scattered pattern may be ambiguous. Rapti and Seti specimens have less anal-fin rays than the other specimens here assigned to *D. dangila* (iii.12½–14½ vs. iii.15½–16½), and Rapti specimens may lack rings on caudal peduncle.

All specimens have a vertically extended humeral blotch, however, separating them from *D. assamila* and other species of *Danio*.

Most literature records of *D. dangila* in India are probably correctly identified. Records from Meghalaya (Yazdani, 1977), which may concern *D. meghalayensis* as well as *D. dangila* or potentially even *D. assamila*, need revision. Records from Arunachal Pradesh (e.g., Bagra et al., 2009) probably concern *D. assamila*.

Danio dangila may be the largest species in the genus. Barman (1991) reported the “largest specimen examined” to be 83 mm SL, and Sen (1985) reported the largest recorded specimen as “150 mm in length”. The largest aquarium specimen available is 88.5 mm SL (NRM 57110).

Barman (1987, 1991) considered *D. feegradei* Hora (1937) from Myanmar to be a synonym of *D. dangila*. Talwar & Jhingran (1991) synonymized both *D. feegradei* and *D. meghalayensis* with *D. dangila*. Fang (2001) referred both *D. meghalayensis* and *D. deyi* to the synonymy of *D. dangila*. *Danio feegradei* is a valid species (Kullander & Britz, in press). The status of *D. meghalayensis* and *D. deyi* is discussed below. Although the present analysis shows that the name *D. dangila* has been applied on several peripheral distinct species, and one may thus consider selecting a neotype to fix the application of the name to the species in the Ganga drainage. Both because no specimens are available from the type locality area, and because variation within the Indian range of distribution could not be addressed for reason of lack of access to specimens, it would be inopportune at this time to select a neotype.

Danio assamila, new species

(Figs 1c–d)

Holotype. NRM 65571, 55.0 mm SL; India: Assam: Brahmaputra River drainage: tributary of Dibru River, 2 km N of Digholtrang, Amguri (about 27°37'48" N 95°23'43" E); K. K. Lahkar, 20 Sep 1998.

Paratypes. All from India: Assam: Brahmaputra River drainage. CMK 5938, 1, 49.1 mm SL; Dibru River; H. Bleher, 9 Nov 1987. – NRM 42645 (tissue 1433), 1, 53.4 mm SL; Dibru River drainage, 10 km NNE of Digholtrang, Punijan; K. K. Lahkar, 30 Apr 1998. – NRM 42647, 6, 60.2–68.3 mm SL; NRM 46947, 1, not measured, c&s; NRM, 46953, 1, not

measured, c&s; NRM 46957, 1, not measured, c&s; same data as holotype. – NRM 51440 (tissue 7182), 1, 34.1 mm SL; NRM 51441. 2, 37.6–57.3 mm SL; Nagaon, Lanka forest; H. Bleher, 25 Feb 2009. – NRM 44998, 7, 31.0–40.8 mm SL; NRM 47422 (tissue 7185), not measured; NRM 47423 (tissue 7183), 1, not measured; Karbi Anglong: Silonijan Forest, stream near Barpathar; H. Bleher, 29 Feb 2009.

Diagnosis. *Danio assamila* is distinguished from all other species of *Danio* except *D. dangila*, *D. catenatus*, *D. concatenatus*, and *D. sysphigmatus* by produced first ray in pectoral and pelvic fins, large cleithral spot, and pattern of dark rings enclosing light interspaces on the side. Distinguished from those species by round or slightly oval cleithral spot (vs. vertically extended in *D. dangila*), anterior interstripe Ia usually present (vs. absent in *D. dangila*), rings in series along side elongate, width of dark perimeter of about same width as diameter of light centre or wider (vs. elongate, with narrower perimeter in *D. sysphigmatus*, round in other species), ring pattern not extending onto caudal peduncle (vs. present on part of caudal peduncle in *D. dangila*, *D. catenatus* and *D. concatenatus*), and lateral line scale count 32–34, rarely 36 (vs. 35–38 in *D. sysphigmatus*).

Description. General body features and pigmentation are illustrated in Figs. 1c–d. Measurement data are summarized in Table 2.

Body compressed, moderately elongate to moderately deep, no sexual dimorphism evident. Head compressed, slightly deeper than wide. Snout short, rounded, length about equal eye diameter. Mouth terminal, oblique in profile, jaws about equal in anterior extension or lower jaw slightly projecting. Small bony knob at dentary symphysis fitting into notch in upper jaw. Maxilla reaching to or slightly beyond vertical from anterior margin of orbit. Lower jaw ending anteriorly at about middle of eye or slightly higher. Lower jaw with pointed anterior lateral lobe. Tubercles absent from lower jaw and pectoral fin. Rostral barbel long, reaching to or, usually beyond base of leading pectoral-fin ray. Maxillary barbel long, reaching to middle or $\frac{1}{5}$ of pectoral fin.

Lateral line complete, comprising 32(1), 33*(4), 34(3), 36(1) scales; descending anteriorly for about 7 scales from some of which pore absent, posteriorly paralleling ventral profile. Median predorsal scales 16(5), 17(2), 18*(1). Scales in transverse series from dorsal-fin origin to pelvic-fin origin $\frac{1}{2}6+1+1\frac{1}{2}$ * (8), $\frac{1}{2}7+1+1\frac{1}{2}$ (1); below lateral line scales much smaller than above. Prepelvic scales

Table 2. Morphometry of *Danio assamila*. 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) given when ANOVA $p < 0.05$.

	N	min	max	mean	SD	a	b	r
Standard length (mm)	9	37.6	68.3	58.7	9.1			
Body depth	9	26.9	34.6	32.0	2.7	-5.839	0.422	0.969
Head length	9	21.9	24.2	23.1	0.8	1.422	0.206	0.979
Snout length	9	6.0	6.7	6.5	0.3	-0.145	0.067	0.984
Head depth	9	15.2	17.3	16.4	0.7	0.449	0.156	0.964
Head width	9	12.4	13.6	13.1	0.4	0.311	0.125	0.997
Upper jaw length	7	8.8	9.6	9.2	0.3	0.82	0.077	0.984
Lower jaw length	8	10.1	12.2	10.8	0.7	1.483	0.082	0.979
Orbital diameter	9	6.6	8.0	7.1	0.5	1.089	0.052	0.951
Interorbital width	9	10.1	11.3	10.9	0.4	-0.408	0.116	0.982
Caudal peduncle length	9	13.0	17.8	15.0	1.4	3.059	0.097	0.968
Caudal peduncle depth	9	11.7	14.8	13.6	1.2	-2.799	0.185	0.968
Dorsal-fin base length	9	14.4	20.2	18.0	1.7	-3.101	0.234	0.946
Anal-fin base length	9	18.6	24.8	22.8	2.0	-5.338	0.321	0.980
Predorsal length	9	58.2	61.1	60.3	0.9	-2.426	0.645	0.999
Preanal length	9	66.3	71.0	68.4	1.6	1.377	0.66	0.994
Prepelvic length	9	46.7	49.7	48.1	1.1	1.195	0.46	0.997
Pectoral-fin length	8	25.9	31.6	28.8	2.0	-3.081	0.342	0.955
Pelvic-fin length	9	16.5	22.7	19.8	2.1	-4.849	0.282	0.943
Rostral barbel length	5	15.2	22.7	19.6	3.6	-5.752	0.034	0.922
Maxillary barbel length	5	24.0	37.3	31.8	5.7	–	–	–

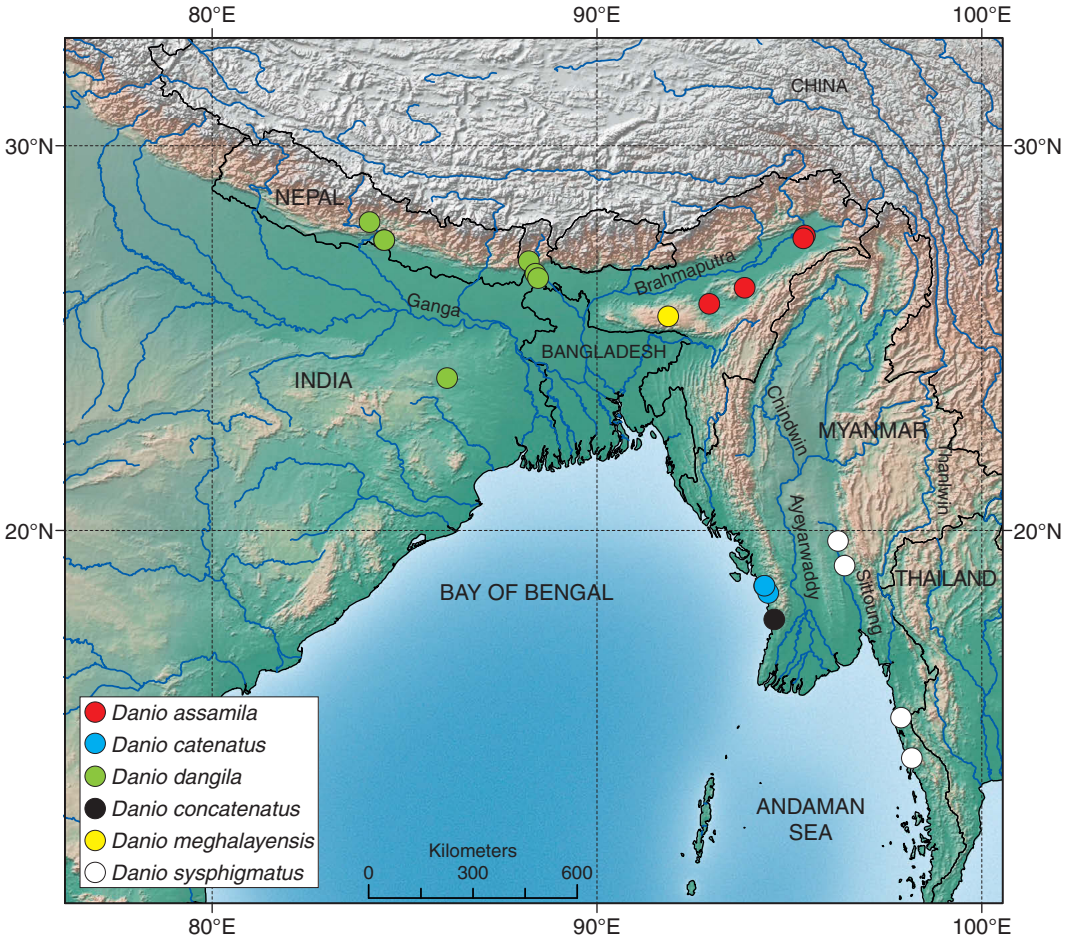


Fig. 2. Collecting sites of *Danio assamila*, *D. catenatus*, *D. concatenateus*, *D. dangila*, *D. meghalayensis*, and *D. sysphigmatus*.

elongate, about 14–17 scales along prepelvic midline; pelvic-fin base covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14* (9). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii.9½* (5), ii.10½* (4); anal-fin rays iii.12½ (1), iii.13½ (3), iii.14½* (4), iii.15½ (1); pectoral-fin rays i.10* (7), i.11 (1), plus 1–2 minute unbranched ventral rays; pelvic-fin rays i.7* (9). Principal caudal-fin rays 10+9* (7); procurrent caudal-fin rays dorsally 6* (1), 7 (5), ventrally 6* (4), 7 (2). Dorsal fin inserted at highest point of dorsum, slightly posterior to half distance from snout tip to caudal-fin base, and distinctly anterior to vertical from anal-fin origin. Pectoral-fin insertion at about vertical through posterior margin of opercle; branched rays forming slightly rounded

margin, leading unbranched ray prolonged beyond rest of fin, reaching beyond insertion of unbranched pelvic-fin ray, at most to near middle of pelvic fin. 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 slightly rounded or truncate, leading unbranched ray slightly prolonged, reaching beyond rest of fin, to base of first anal-fin ray or shorter. Caudal fin slightly forked, lobes about equal, lobe tips subacuminate.

Vertebrae 17+18 = 35 (1), 18+16 = 34 (1), 18+17 = 35 (2), 18+18 = 36* (1); predorsal vertebrae 14* (7); vertebrae contained within caudal peduncle 5* (6), 6 (1). Ceratobranchial 5 tooth formula 2,4,5–5,4,2.

Colouration in preservative. Sexual dimorphism absent in colour pattern. Ground colour fawn or dull whitish, markings absent from head and venter, except slight concentration of dark pigment adjacent to lower margin of orbit. Cleithral spot black, round, about as large as pupil, occasionally slightly ovate, narrower ventrally. Dorsal midline anterior and posterior to dorsal fin marked by narrow dark brown stripe.

Dark brown stripes P, P+1, P+2, P+3, P-1; P-2 stripe diffuse, brownish. P+3 stripe consisting of small brown spots in irregular row from above upper end of gill cleft to below middle or posterior part of dorsal-fin base.

P+2 stripe irregular, partly fragmented, from slightly dorsal to cleithral spot caudad to slightly posterior to vertical from end of dorsal-fin base or, fragmented, close to end of caudal peduncle. P+1 and P stripes distinct on caudal peduncle where forming straight parallel stripes ending on scaled base of caudal fin; anteriorly anastomizing, contributing to a row of about 6–8 elongate dark brown rings enclosing interstripe I. P-1 stripe distinct, narrow posteriorly, paralleling posterior parts of P and P+1 stripes, but ending in upward slant on basal scales of caudal fin; for most of extension anastomizing with lower branch of P stripe to form about 6–7 large brown rings fragmenting interstripe I-1; pattern irregular, with occasional absent ring parts.

Narrow interstripe Ia inserted between dorsal and ventral rows of rings, extending from below cleithral spot to about vertical from anterior anal-fin rays, occasionally with narrow brown stripes crossing from upper to lower horizontal row of rings.

P-2 stripe diffuse anteriorly, straight, narrow, originating at pectoral-fin base, and ending above posterior part of anal-fin base.

Dorsal fin hyaline basally, with indistinct greyish median D stripe, distal half hyaline. Anal fin hyaline with indistinct greyish median A stripe and usually distinct A-1 stripe. Caudal fin dusky, lighter along middle and with distinct dark stripes continuing stripes P+1, P, and P-1.

Geographical distribution (Fig. 2). *Danio assamila* occurs in left bank tributaries of the Brahmaputra River. The type series represents localities in the Dibru River and, streams on opposite sides of the Karbi Anlong Plateau. Some reports of *D. dangila* from Assam probably concerns this species, e.g., Ganesh ghat in Tezpur (Sen, 1985),

Bhareli (= Kameng) and Namdapha Rivers (Barman, 1991), possibly also records from Khasi Hills (Yazdani, 1977, 1985). Records of *D. dangila* from Arunachal Pradesh, e.g. Poma River (Bagra et al., 2009) are likely to concern *D. assamila*.

Etymology. The species epithet is a construction from the area of occurrence (Assam) and the ending in *dangila*, to be understood as ‘the *Danio dangila* of Assam’.

Danio catenatus, new species

(Fig. 3a)

Holotype. NRM 45661, 45.4 mm SL; Myanmar: Rakhine State: Kananmae Chaung, near Leldee village, by foot 45 min from Gwechaung village at km 18 on road Thandwe–Taunggok, 18°35'39"N 94°22'45"E; S. O. Kullander & R. Britz, 20 Mar 1998.

Paratypes. All from Myanmar, western slope of Rakhine State: NRM 40836, 20, 36.5–47.9 mm SL; NRM 41676, not measured (tissue); NRM 46966, 1, 34.8 mm SL (c&s); NRM 46967, 1, 60.6 mm SL (c&s); NRM 46968, 1, 48.7 mm SL (c&s); collected with holotype. – BMNH 2015.3.3.1–3, 3, 54.2–58.6 mm SL; three different sites along Thandwe Chaung (18°25'16"N 94°27'38"E; 18°24'32"N 94°28'45"E; 18°25'11"N 94°29'43"E); R. Britz, 29 Nov 2009. – BMNH 2015.3.3.4–6, 3, 44.0–49.6 mm SL; Kananmae Chaung near Leldee village; R. Britz, 28 Nov 2009.

Diagnosis. *Danio catenatus* is distinguished from all other species of *Danio* except *D. assamila*, *D. dangila*, *D. concatenatus*, and *D. sysphigmatus* by produced first ray in pectoral and pelvic fins, large cleithral spot, and pattern of dark rings including light interspaces on the side. Distinguished from those species by round cleithral spot (vs. vertically extended in *D. dangila*), absence of anterior interstripe Ia (vs. present in *D. assamila*, *D. concatenatus* and *D. sysphigmatus*), round rings in three series along side, width of dark perimeter of about same width as diameter of light centre (vs. elongate in *D. assamila* and *D. sysphigmatus*, with narrower perimeter in *D. sysphigmatus*; two series and variably round or elongate in *D. concatenatus*), ring pattern extending onto caudal peduncle (vs. not extending onto caudal peduncle in *D. assamila* or *D. sysphigmatus*, and some *D. dangila*).

Description. General body features and pigmentation are illustrated in Figure 3a. Measurements are summarized in Table 3.

Body compressed, elongate. No sexual dimorphism evident. Head laterally compressed, slightly deeper than wide. Snout short, rounded, shorter than eye diameter. Mouth terminal, oblique in profile, lower jaw slightly projecting. Small bony knob at dentary symphysis fitting into vomerine notch. Maxilla reaching slightly posterior to vertical from anterior margin of orbit. Lower jaw ending anteriorly at about level of middle of orbit. Lower jaw with sharp anterior lateral lobe with pointed tubercles along posterior margin followed by short series of pointed tubercles along lateral margin of dentary, occasionally tubercles absent or additionally a few scattered pointed tubercles on anterior surface of lower jaw. Rostral barbel moderately long, not reaching posterior margin of opercle or beyond insertion of leading pectoral-fin ray. Maxillary barbel long, reaching about middle or to almost end of branched rays of pectoral fin.

Lateral line complete, comprising 34(2), 35*(6), 36(7) scales; descending anteriorly for about 6–7 scales from some of which pore absent, posteriorly paralleling ventral profile. Median predorsal

scales 16(7), 17*(6), 18(1), 19(1). Scales in transverse series from dorsal-fin origin to pelvic-fin origin $\frac{1}{2}6+1+1\frac{1}{2}$ * (15); below lateral line scales much smaller than above. Prepelvic scales elongate, about 16–18 scales along prepelvic midline; pelvic fin bases covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14*(15). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii.9 $\frac{1}{2}$ (5), ii.10 $\frac{1}{2}$ * (18), ii.11 $\frac{1}{2}$ (1); anal-fin rays iii.14 $\frac{1}{2}$ * (17), iii.15 $\frac{1}{2}$ (7); pectoral-fin rays i.8 (2), i.9 (10), i.10* (3), plus 1–3 minute unbranched ventral rays; pelvic-fin rays i.7* (15). Principal caudal-fin rays 10+9 (22), 11+9 (1); procurrent caudal-fin rays dorsally 5(3), 6(20), ventrally 5(5), 6(16). Dorsal fin inserted 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 insertion at about vertical through posterior margin of opercle; branched rays forming straight or slightly rounded margin, leading unbranched ray slightly prolonged beyond rest of fin, reaching beyond insertion of unbranched pelvic-fin ray, at most to middle of pelvic fin. Tubercles absent from pectoral fin. Pectoral-fin axial lobe well developed. Pelvic-fin origin situated slightly

Table 3. Morphometry of *Danio catenatus*. 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.

	N	min	max	mean	SD	a	b	r
Standard length (mm)	15	37.7	47.9	43.6	2.6			
Body depth	15	28.2	30.2	29.2	0.6	-0.430	0.302	0.953
Head length	15	23.8	26.0	24.9	0.5	0.795	0.231	0.936
Snout length	15	6.5	7.2	6.9	0.2	0.409	0.060	0.827
Head depth	15	15.8	18.0	16.9	0.6	2.493	0.112	0.833
Head width	15	12.7	14.1	13.2	0.4	1.382	0.391	0.883
Upper jaw length	15	9.7	10.6	10.2	0.3	1.016	0.078	0.860
Lower jaw length	15	11.7	13.2	12.3	0.4	0.322	0.115	0.852
Orbital diameter	15	7.4	9.0	8.1	0.3	1.991	0.036	0.774
Interorbital width	15	10.7	11.9	11.3	0.3	0.788	0.095	0.887
Caudal peduncle length	15	15.2	18.1	16.6	0.9	-0.613	0.180	0.781
Caudal peduncle depth	15	11.8	13.3	12.4	0.5	-1.035	0.148	0.898
Dorsal-fin base length	15	16.4	19.8	17.9	0.9	-4.082	0.273	0.922
Anal-fin base length	15	19.6	22.8	21.6	0.9	0.032	0.215	0.832
Predorsal length	15	58.2	61.4	59.4	0.9	1.731	0.554	0.968
Preanal length	15	61.0	68.9	65.5	1.8	-5.592	0.784	0.946
Prepelvic length	15	46.4	48.9	47.5	0.8	1.130	0.449	0.961
Pectoral-fin length	15	27.0	31.8	29.6	1.1	0.652	0.281	0.825
Pelvic-fin length	15	16.7	21.2	18.7	1.1	1.186	0.159	0.654
Rostral barbel length	15	17.0	21.6	19.4	1.2	-5.261	0.315	0.876
Maxillary barbel length	15	31.9	36.3	34.1	1.1	-2.254	0.393	0.908

anterior to midbody, well anterior to dorsal-fin origin. Pelvic-fin margin rounded, leading unbranched ray slightly prolonged, reaching beyond rest of fin, to base of first anal-fin ray or shorter, occasionally slightly longer. Caudal fin slightly forked, lobes about equal, lobe tips subacuminate.

Vertebrae 18+18 = 36* (6), 18+19 = 37 (13), 18+20 = 38 (3), 19+19 = 38 (2); predorsal vertebrae 13 (4), 14 (20); vertebrae contained within caudal peduncle 5 (8), 6 (13), 7 (3). Ceratobranchial 5 tooth formula 2,3,5-5,3,2.

Colouration in preservative (Fig. 3a). Sexual dimorphism absent in colour pattern. Ground colour fawn or dull whitish, markings absent from head and venter, except slight concentration of dark pigment adjacent to lower margin of orbit. Dorsal midline anterior and posterior to dorsal fin marked by narrow dark brown stripe. Cleithral spot blackish, round, about as large as pupil in adults, relatively smaller in young specimens.

Dark brown stripes P, P+1, P+2, P+3, P-1; P-2 stripe diffuse, brownish, absent in young specimens. P+3 stripe consisting of small brown spots in irregular row from above upper end of gill cleft to below middle or posterior part of dorsal-fin base P+2 stripe irregular, partly fragmented, from spot slightly anterior and dorsal to cleithral spot caudad to slightly posterior to vertical from end of dorsal-fin base or close to end of caudal peduncle.

P+1 and P stripes distinct on all or posterior half of caudal peduncle where forming straight parallel stripes ending on scaled base of caudal fin; anteriorly, from middle of caudal peduncle rostrad anastomizing, contributing to a row of about 7-8 round or slightly elongate dark brown rings enclosing interstripe I, but pattern irregular. P-1 stripe more or less distinct, narrow or obsolete posteriorly, paralleling posterior parts of P and P+1 stripes, but ending in upward slant on basal scales of caudal fin; for most of extension anastomizing with P stripe, forming large brown round rings fragmenting interstripe I-1 into about 6-9 rings, but pattern irregular with occasional absent ring parts.

Interstripe Ia absent, but light spaces between dorsal and ventral ring series contribute to third row of light spots.

P-2 stripe diffuse, undulated, narrow, originating at pectoral-fin base, ending above posterior part of anal-fin base, disconnected from P-1 stripe or connecting to it at intervals, producing up to

four or five rings in vertical succession on middle of side.

Dorsal fin hyaline basally, with indistinct greyish proximal D-1 and wider median D stripe, distal half hyaline. Anal fin hyaline, basal dusky A+1 stripe present or (usually) absent; indistinct greyish median A stripe and wide dusky A-1 stripe. Caudal fin dusky, lighter along middle and with indistinct brown spots scattered over middle of fin; in several specimens also faint pattern of elongate brown spots continuing stripes P+1, P and P-1 at least basally.

Etymology. The species name *catenatus* is a Latin adjective meaning chained, and refers to the chain-like colour pattern on the sides.

Geographical distribution and habitat (Fig. 2). *Danio catenatus* is known only from two streams in the Thandwe Chaung drainage, which has its mouth slightly north of Thandwe on the western side of the Rakhine Yoma. The type locality was described and illustrated by Kullander & Fang (2009). It is a small clear water forest stream with bottom of pebbles, rock, and gravel. Among 21 associated species were *Danio aesculapii* and *Devario xyrops*. Day (1878: 596) reported *D. dangila* from hills above Akyab (= Sittwe) on the Rakhine coast, which may represent *D. catenatus*. Ahmed et al. (2013) listed and illustrated *D. dangila* from Cox's Bazar in Bangladesh, which look more similar to *D. catenatus* than to *D. dangila* by the spotted caudal fin.

***Danio concatenatus*, new species**
(Fig. 3b)

Holotype. BMNH 2011.3.24.50, 61.1 mm SL; Myanmar: Rakhine State: Comepyo Chaung near Gwa, 17°40'57" N 94°38'25" E; R. Britz, Dec 2009.

Paratypes. BMNH 2011.3.24.51-57, 7, 43.5-71.8 mm SL; BMNH 2011.3.24.84-85. 2, 48.9-62.6 mm SL; same data as holotype.

Diagnosis. *Danio concatenatus* is distinguished from all other species of *Danio* except *D. assamila*, *D. dangila*, *D. catenatus*, and *D. sysphigmatus* by produced first ray in pectoral and pelvic fins, large cleithral spot, and pattern of dark rings enclosing light interspaces on the side. It is distinguished from those species by round cleithral

spot (vs. vertically extended in *D. dangila*), presence (rarely absence) of anterior interstripe la (vs. absent in *D. dangila*, *D. catenatus*), round or slightly elongate rings in two series along side, width of dark perimeter of about same width as diameter of light centre (vs. elongate in *D. assamila* and *D. sysphigmatus*, with narrower perimeter in *D. sysphigmatus*; three rows anteriorly in *D. catenatus*), ring pattern usually not extending onto caudal peduncle (vs. extending onto caudal peduncle in *D. catenatus* and variably in *D. dangila*), and lateral line scale count 35–36 (vs. 32–34 in *D. dangila*, 32–34, rarely 36 in *D. assamila*).

Description. General body features and pigmentation are illustrated in Figure 3b. Measurements are summarized in Table 4.

Body compressed, elongate. No sexual dimorphism evident. Head laterally compressed, slightly deeper than wide. Snout short, rounded, slightly longer or shorter than eye diameter. Mouth terminal, oblique in profile, lower jaw slightly projecting. Small bony knob at dentary symphysis fitting into vomerine notch. Maxilla reaching slightly posterior to vertical from anterior margin of orbit. Lower jaw ending anteriorly at about level of middle of orbit. Lower jaw with

sharp anterior lateral lobe. Tubercles absent from lower jaw or pointed tubercles present along posterior margin of lobe, then usually followed by short series of pointed tubercles along lateral margin of dentary. Rostral barbel moderately long, not or barely reaching insertion of leading pectoral-fin ray. Maxillary barbel long, reaching about middle or to $\frac{2}{3}$ of branched rays of pectoral fin.

Lateral line complete, comprising 35* (5) or 36 (4) scales; descending anteriorly for about 6–7 scales from some of which pore absent, posteriorly paralleling ventral profile. Median predorsal scales 16 (5), 17* (4). Scales in transverse series from dorsal-fin origin to pelvic-fin origin $\frac{1}{2}6+1+1\frac{1}{2}$ * (7), $\frac{1}{2}7+1+1\frac{1}{2}$ (2); below lateral line scales much smaller than above. Prepelvic scales elongate, about 15–16 scales along prepelvic midline; pelvic-fin base covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14* (9). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii.10.5* (3), ii.11 $\frac{1}{2}$ (6); anal-fin rays iii.14 $\frac{1}{2}$ * (3), iii.15 $\frac{1}{2}$ (6); pectoral-fin rays i.10* (1), i.11 (6), i.12 (2), plus 1–2 minute unbranched ventral rays; pelvic-fin rays i.7* (9). Principal caudal-fin rays 10+9* (9); procurvent caudal-fin rays dorsally 6* (4), 7 (4), 8 (1), ven-

Table 4. Morphometry of *Danio concatenatus*. 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.

	N	min	max	mean	SD	a	b	r
Standard length (mm)	9	43.5	71.8	57.7	10.2			
Body depth	9	29.8	32.6	30.8	1.0	0.773	0.394	0.983
Head length	9	22.4	25.5	24.0	1.0	2.825	0.307	0.976
Snout length	9	6.5	7.6	7.0	0.3	0.380	0.065	0.966
Head depth	9	15.7	18.0	16.7	0.7	2.296	0.767	0.973
Head width	9	12.4	13.5	13.0	0.4	0.374	0.123	0.980
Upper jaw length	9	9.0	10.3	9.7	0.4	0.655	0.086	0.969
Lower jaw length	9	10.6	12.4	11.4	0.7	1.381	0.089	0.959
Orbital diameter	9	6.7	8.3	7.4	0.6	1.841	0.041	0.976
Interorbital width	9	10.5	11.7	11.1	0.4	0.904	0.095	0.985
Caudal peduncle length	9	14.3	15.7	15.1	0.5	0.134	0.149	0.977
Caudal peduncle depth	9	12.2	13.6	13.0	0.5	-0.023	0.131	0.983
Dorsal-fin base length	9	18.2	20.1	19.2	0.6	-0.737	0.205	0.990
Anal-fin base length	9	21.6	24.5	22.8	1.0	0.491	0.219	0.971
Predorsal length	9	58.9	61.4	59.8	0.9	-0.179	0.601	0.996
Preanal length	9	65.5	68.9	66.9	1.0	-0.433	0.676	0.997
Prepelvic length	9	46.6	48.5	47.7	0.7	0.661	0.465	0.996
Pectoral-fin length	9	25.7	29.9	27.5	1.3	3.049	0.220	0.985
Pelvic-fin length	9	17.6	19.7	18.7	0.7	1.048	0.168	0.977
Rostral barbel length	9	18.1	20.5	19.3	0.8	1.467	0.167	0.973
Maxillary barbel length	9	26.0	33.3	30.2	2.3	6.329	0.189	0.902



Fig. 3. a, *Danio catenatus*, NRM 45661, holotype, 45.4 mm SL; Myanmar: Rakhine State: Kananmae Chaung; b, *Danio concatenatus*, BMNH 2011.3.24:50, holotype, 61.1 mm SL; Myanmar: Rakhine State: Comepyo Chaung near Gwa; c, *Danio sypshigmatus*, NRM 65561, holotype, 63.3 mm SL; Myanmar: Mon State: Ale village at Malwe Mountain.

trally 5(1), 6*(4), 7(3), (1). Dorsal fin inserted 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 insertion at about vertical through posterior margin of opercle; branched rays forming straight or slightly rounded margin, leading unbranched ray slightly prolonged beyond rest of fin, 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 rounded or subtruncate, leading unbranched ray slightly prolonged, reaching beyond rest of fin, to base of first anal-fin ray or shorter. Caudal fin slightly forked, lobes about equal, lobe tips rounded.

Vertebrae 18+18=36 (4), 18+19=37 (4), 19+18=37* (1); predorsal vertebrae 13(1), 14*(8); vertebrae contained within caudal peduncle 5(7), 6*(2). Ceratobranchial 5 tooth formula 2,4,5-5,4,2.

Colouration in preservative (Fig. 3b). Ground colour fawn or dull whitish, markings absent from head and venter, except slight concentration of dark pigment adjacent to lower margin of orbit. Dorsal midline anterior and posterior to dorsal fin marked by narrow dark brown stripe. Cleithral spot blackish, round, about as large as pupil in adults, relatively smaller in young specimens.

Dark brown stripes P, P+1, P+2, P+3, P-1; P-2 stripe diffuse, brownish. P+3 stripe consisting of small brown spots in irregular row from above upper end of gill cleft to below middle or posterior part of dorsal-fin base. P+2 stripe irregular, partly fragmented, from spot slightly anterior and dorsal to cleithral spot caudad to slightly posterior to vertical from end of dorsal-fin base or close to end of caudal peduncle.

P+1 and P stripes distinct on all or posterior half of caudal peduncle where forming straight parallel stripes ending on scaled base of caudal fin; anteriorly, from middle or, usually, root of caudal peduncle rostrad anastomizing to form a row of up to 10 round or slightly elongate dark brown rings enclosing interstripe I, but pattern irregular.

P-1 stripe more or less distinct, narrow or obsolete posteriorly, paralleling posterior parts of P and P+1 stripes, but ending in upward slant on basal scales of caudal fin; for most of extension anastomizing with P stripe fragmenting interstripe I-1, forming about 6–9 large round or slightly elongate rings, but pattern irregular.

Continuous interstripe Ia between dorsal and ventral ring series straight, narrow.

P-2 stripe diffuse, straight, narrow, originating at pectoral-fin base, ending above posterior part of anal-fin base, disconnected from P-1 stripe.

Dorsal fin hyaline basally, with indistinct greyish wide median D stripe, distal half hyaline. Anal fin hyaline, basally dusky; indistinct greyish median A stripe present. Caudal fin dusky, lighter along middle and with indistinct brown spots scattered over middle of fin; in several specimens also faint pattern of elongate brown spots continuing stripes P+1, P and P-1 at least basally.

Etymology. The species name *concatenatus* is a Latin adjective meaning chained, and refers to the chain-like colour pattern on the sides.

Geographical distribution (Fig. 2). *Danio concatenatus* is known only from the type locality, a

small coastal stream near Gwa on the western slope of the Rakhine Yoma.

Danio sysphigmatus, new species

(Fig. 3c)

Holotype. NRM 65561. Adult male, 63.5 mm SL; Myanmar: Mon State: Ale village at foot of Malwe mountain (about 15°7'43"N 97°56'09"E; Tin Win, 4 Jan 2004.

Paratypes. All from Myanmar. NRM 51642, 7, 46.8–70.8 mm SL; same data as holotype. – BMNH 2011.3.24:89–93, 5, 35.4–51.9 mm SL; Naypyidaw Union Territory: Sittaung River drainage: Paung Laung Stream, Pyinmana Township; Tun Tun Oo, 15 Dec 2005. – BMNH 2011.3.25:1–4, 4, 44.7–61.9 mm SL; Tanintharyi Region: stream at Son-sinpya village, Dawei Township; Kyaw Zim, 7 Mar 2006. – USNM 44802, 1, 55.1 mm SL; Kayah State: NNE Toungoo, probably Sittaung River drainage: Biapo village, 900 m asl; L. Fea, 1885.

Diagnosis. *Danio sysphigmatus* is distinguished from all other species of *Danio* except *D. assamila*, *D. dangila*, *D. catenatus*, and *D. concatenatus* by produced first ray in pectoral and pelvic fins, large cleithral spot, and pattern of dark rings enclosing light interspaces on the side. It is distinguished from those species by round cleithral spot (vs. vertically extended in *D. dangila*), presence of anterior interstripe Ia (vs. absent in *D. dangila* and *D. catenatus*), round or, usually, slightly elongate rings in 1–2 series along side, width of dark perimeter narrower than diameter of light center (vs. rings clearly elongate in *D. assamila*; perimeter width equal to diameter of light center in *D. assamila*, *D. catenatus*, *D. concatenatus*, and *D. dangila*), ring pattern not extending onto caudal peduncle (vs. extending onto caudal peduncle in *D. catenatus*, *D. concatenatus* and occasionally *D. dangila*), and lateral line scale count 35–38 (vs. 32–34 in *D. dangila*, 32–34, rarely 36 in *D. assamila*).

Description. General body features and pigmentation are illustrated in Figure 3c. Measurements are summarized in Table 5.

Body compressed, elongate. No Sexual dimorphism evident. Head laterally compressed, slightly deeper than wide. Snout short, rounded, shorter than eye diameter. Mouth terminal, oblique in profile, lower jaw slightly projecting,

jaws about equal in anterior extension. Small bony knob at dentary symphysis fitting into vomerine notch. Maxilla reaching to vertical from anterior margin of orbit. Lower jaw ending anteriorly slightly below middle of orbit. Lower jaw with anterior lateral lobe with pointed tubercles along posterior margin followed by short series of pointed tubercle; a few scattered pointed tubercles on anterior surface of lower jaw. Rostral barbel long, reaching to or, usually, slightly beyond base of first pectoral-fin ray. Maxillary barbel long, reaching about middle or to almost end of branched rays of pectoral fin.

Lateral line complete, comprising 35(1), 36(4), 37*(6), 38(1) scales; descending anteriorly for about six scales from some of which pore absent, posteriorly paralleling ventral profile. Median predorsal scales 16(3), 17(6), 18*(2). Scales in transverse series from dorsal-fin origin to pelvic-fin origin $\frac{1}{2}6+1+1\frac{1}{2}$ (10), $\frac{1}{2}7+1+1\frac{1}{2}$ * (1); below lateral line scales much smaller than above. Prepelvic scales elongate, with subacuminate free tip. About 15–17 scales along prepelvic midline; pelvic-fin base covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14*(11). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii.10 $\frac{1}{2}$ * (8), ii.11 $\frac{1}{2}$ (3); anal-fin rays iii.14 $\frac{1}{2}$ * (2), iii.15 $\frac{1}{2}$ (8), iii.16 $\frac{1}{2}$ (2); pectoral-fin rays i.10* (10), i.11 (1), plus 0–2 minute unbranched ventral rays; pelvic-fin rays i.7* (8). Principal caudal-fin rays 10+9* (8); procurent caudal-fin rays dorsally 6*(5), 7(2), 8(1), ventrally 6*(5), 7(3). Dorsal fin inserted 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 insertion at about vertical through posterior margin of opercle; branched rays forming slightly rounded margin, leading unbranched ray slightly prolonged beyond rest of fin, reaching to or almost to insertion of unbranched pelvic-fin ray. Bands of minute tubercles present on dorsal aspect of first four or five branched rays, present or absent on leading unbranched fin ray, in four specimens 58.3–68.7 mm SL. Pectoral-fin axial lobe well developed. Pelvic-fin origin situated well anterior to midbody, well anterior to dorsal-fin origin. Pelvic-fin margin rounded, leading unbranched ray slightly prolonged, reaching beyond rest of fin, to base of first anal-fin ray or shorter. Caudal fin only slightly forked, lobes about equal, lobe tips rounded or subacuminate.

Vertebrae 18+19=37* (5), 18+20=38 (1), 19+18

Table 5. Morphometry of *Danio sypshigmatus*. 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) given when ANOVA $p < 0.05$.

	N	min	max	mean	SD	a	b	r
Standard length (mm)	12	44.7	70.8	58.7	8.9			
Body depth	12	26.2	31.4	28.8	1.6	2.581	0.243	0.911
Head length	12	21.1	24.8	23.1	1.1	3.195	0.163	0.980
Snout length	12	5.7	7.3	6.4	0.4	0.860	0.049	0.920
Head depth	12	14.2	19.0	16.2	1.2	2.681	0.116	0.857
Head width	12	12.1	14.3	13.2	0.7	0.574	0.122	0.908
Upper jaw length	12	8.3	10.0	9.1	0.6	1.842	0.059	0.919
Lower jaw length	12	9.9	12.0	11.0	0.7	2.094	0.073	0.887
Orbital diameter	12	6.5	8.5	7.5	0.7	2.442	0.033	0.876
Interorbital width	12	9.5	11.2	10.3	0.5	1.534	0.077	0.945
Caudal peduncle length	12	13.5	17.0	15.5	1.1	0.131	0.152	0.865
Caudal peduncle depth	12	11.6	13.5	12.8	0.5	0.984	0.110	0.946
Dorsal-fin base length	12	16.8	19.4	18.5	0.8	-1.976	0.219	0.993
Anal-fin base length	12	21.6	24.9	23.1	1.3	-2.193	0.269	0.962
Predorsal length	12	56.4	61.5	59.1	1.3	-0.373	0.598	0.986
Preanal length	12	62.7	70.6	65.6	2.3	5.656	0.558	0.976
Prepelvic length	12	44.4	49.9	47.0	2.1	6.669	0.353	0.978
Pectoral-fin length	11	23.4	31.9	27.6	2.7	6.396	0.167	0.710
Pelvic-fin length	12	16.9	21.9	19.0	1.8	5.612	0.092	0.851
Rostral barbel length	12	18.5	29.8	22.1	3.4	–	–	–
Maxillary barbel length	12	28.7	42.7	33.6	4.0	10.91	0.146	0.553

=37 (2); predorsal vertebrae 14* (8); vertebrae contained within caudal peduncle 5 (2), 6* (5), 7 (1). Ceratobranchial 5 tooth formula 2,3,5-5,3,2.

Colouration in preservative (Fig. 3c). Sexual dimorphism absent in colour pattern. Ground colour fawn or dull whitish, markings absent from head and venter, except slight concentration of dark pigment adjacent to lower margin of orbit. Dorsal midline anterior and posterior to dorsal fin marked by narrow dark brown stripe. Cleithral spot black, round, about as large as pupil.

Dark brown stripes P, P+1, P+2, P+3, P-1; P-2 stripe diffuse, brownish. P+3 stripe consisting of small brown spots in irregular row from above upper end of gill cleft to below middle or posterior part of dorsal-fin base.

P+2 stripe irregular, partly fragmented, from spot slightly anterior and dorsal to cleithral spot caudad to slightly posterior to vertical from end of dorsal-fin base or close to end of caudal peduncle.

P+1 and P stripes distinct on caudal peduncle where forming straight parallel stripes ending on scaled base of caudal fin; anteriorly anastomizing to form a row of elongate dark brown rings enclosing interstripe I and occasionally part of I+1.

Approximately 6-8 rings representing interstripe I, but pattern irregular, with a narrow interstripe Ia inserted between dorsal and ventral (occasionally absent) rows of rings, extending from below cleithral spot to about vertical from anal-fin origin.

P-1 stripe more or less distinct, narrow posteriorly, paralleling posterior parts of P and P+1 stripes, but ending in upward slant on basal scales of caudal fin; for most of extension anastomizing with stripe P forming about 4-7 large brown rings fragmenting interstripe I-1, but pattern irregular, with occasional absent ring parts.

P-2 stripe diffuse, straight, narrow, originating at pectoral-fin base, and ending above posterior part of anal-fin base.

Dorsal fin hyaline basally, with indistinct greyish median D stripe, distal half hyaline. Anal fin hyaline with indistinct greyish median A stripe. Caudal fin dusky, lighter along middle and with indistinct brown spots, either a few elongate spots posterior to stripes P+1, P and P-1, or several elongate spots scattered over middle half of fin; smaller specimens with three distinct straight dark stripes on caudal fin, continuing stripes P+1, P and P-1.

Etymology. The species name, *sysphigmatus*, is an adjective based on the Greek adjective σύσφιγματος, meaning chained, and refers to the chain-like colour pattern on the sides.

Geographical distribution and habitat (Fig. 2). *Danio sysphigmatus* has been collected from scattered localities in the Sittaung drainage and coastal rivers along the Thanintharyi coast.

Remarks. Vinciguerra (1890) reported *Danio dangila* collected by Fea in 1885 in a Karen village in Kayah State NNE Taungoo, and named by him Biapó (“paese del Carin Biapó”). It is probably in the Sittaung drainage but the exact locality seems not to be recorded. A specimen from that collection examined (USNM 44802) is in a poor state of preservation, but the now much faded colour pattern, long barbels and produced pectoral and pelvic fin rays is consistent with characters observed in *D. catenatus*, *D. concatenatus*, *D. dangila*, and *D. sysphigmatus*, and given the locality it seems likely that the specimen represents *D. sysphigmatus*.

Danio meghalayensis Sen & Dey, 1985

(Figs. 4a-b)

Danio meghalayensis Sen & Dey, 1985: 62, fig. 2.

Holotype repository not stated; type locality a hill stream at Barapani, Meghalaya.

Danio deyi Sen in Sen & Dey, 1985: 61, fig. 1. Holotype repository not stated; type locality Umroi stream, Khasi hills, Meghalaya, India.

Material examined. BMNH 1934.10.17:51-53, 3, 38.9-41.4 mm SL; Bengal; K. N. Das, no date. - NRM 60877, 4 32.6-38.4 mm SL; aquarium. - NRM 66231, 3, 46.2-50.2 mm SL; aquarium. - UMMZ 243666, 2, 46.5-50.5 mm SL; India: Brahmaputra River drainage: Eastern Khasi Hills: Umshing River; Ng H. H., 21 April 2004.

Diagnosis. *Danio meghalayensis* is similar to *D. dangila*, *D. assamila*, *D. catenatus*, *D. concatenatus*, *D. sysphigmatus* and *D. feegradei* in presence of cleithral spot (usually difficult to discern at anterior end of P stripe), complete lateral line, and circumpeduncular scales 14 (vs. 12 or less in other *Danio*). It differs from those species by absence (vs. presence) of elongated unbranched ray in pectoral and pelvic fins, rostral barbel not reaching beyond gill cover margin, maxillary



Fig. 4. *Danio meghalayensis*, UMMZ 243666; India: Khasi Hills: Umshing River; a, 50.5 mm SL; b, 46.5 mm SL.

barbel not reaching beyond pectoral-fin base (vs. much longer), absence or multiple rows of round or slightly elongate rings on side (vs. presence), branched anal-fin rays $10\frac{1}{2}$ – $12\frac{1}{2}$ (vs. $13\frac{1}{2}$ – $16\frac{1}{2}$); from all except *D. feegradei* by branched anal-fin count branched dorsal-fin rays $8\frac{1}{2}$ (vs. $9\frac{1}{2}$ – $10\frac{1}{2}$); different from *D. feegradei* in presence of horizontal stripes along side, P, P+1 and P-1 stripes distinct, occasionally P and P+1 stripes anastomosing (vs. absence).

Description. Based on wild specimens. General body features and pigmentation are illustrated in Figs. 4a–b. Measurements are summarized in Table 6.

Body compressed, elongate. No sexual dimorphism evident. Head laterally compressed, slightly deeper than wide. Snout short, rounded, approximately as long as eye diameter. Mouth terminal, oblique in profile, lower jaw slightly projecting, jaws about equal in anterior extension. 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 middle of orbit or slightly above. Lower jaw with blunt anterior lateral lobe without tubercles; pointed tubercles present to varying degrees at anterior surface of

lower jaw. Rostral barbel short, reaching only slightly posterior to preopercular margin. Maxillary barbel short, reaching to base of first pectoral-fin ray or slightly shorter.

Lateral line complete, comprising 34 (1), 35 (2) scales, number uncertain in two with many scales lost; descending anteriorly for about six scales from some of which pore absent, posteriorly paralleling ventral profile. Median predorsal scales 17 (1), 18 (3), 19 (1). Scales in transverse series from dorsal-fin origin to pelvic-fin origin $\frac{1}{2}6+1+1\frac{1}{2}$ (5); below lateral line scales much smaller than above. Prepelvic scales elongate. About 14–15 scales along prepelvic midline; pelvic fin bases covered by overlapping scales arranged in three rows. Circumpeduncular scale rows 14 (5). Pelvic axillary scale present. A row of scales along anal-fin base.

Dorsal-fin rays ii. $10\frac{1}{2}$ (8), ii. $8\frac{1}{2}$ (5); anal-fin rays iii. $9\frac{1}{2}$ (1), iii. $10\frac{1}{2}$ (1), iii. $11\frac{1}{2}$ (3); pectoral-fin rays i.9.i (1), i.10.i (4); pelvic-fin rays i.7 (5). Principal caudal-fin rays dorsally 6 (2), 7 (3), ventrally 5 (1), 6 (4). Dorsal fin inserted at highest point of dorsum, distinctly posterior to half distance from snout tip to caudal-fin base, and slightly anterior to vertical from anal-fin origin. Pectoral-fin insertion at about vertical through posterior margin of

opercle; branched rays forming slightly rounded margin, leading unbranched ray only little longer than remaining, reaching to or slightly beyond base of unbranched pelvic-fin ray. Bands of minute tubercles present on dorsal aspect of leading unbranched ray and first four branched rays, in four specimens, 58.9–50.5 mm SL. Pectoral-fin axial lobe well developed. Pelvic-fin origin situated at about midbody, well anterior to dorsal-fin origin. Pelvic-fin margin truncate, leading unbranched ray not prolonged, fin reaching urogenital opening. Caudal fin only slightly forked, lobes about equal, lobe tips rounded.

Vertebrae 17+18 = 35 (2), 18+17 = 35 (1), 18+18 = 36 (2); predorsal vertebrae 14(2), 15(3); vertebrae contained within caudal peduncle 7(2), 8(3). Ceratobranchial 5 tooth formula 2,4,5–5,4,2 in aquarium specimen 46.2 mm SL.

Colouration in preservative. In UMMZ 243666 (Figs. 4a–b) ground colour fawn, markings absent from head and venter except intense dark brown pigmentation around orbit. Cleithral spot blackish, smaller than pupil, not separate from P+1 and P stripes. Dark brown stripes P, P+1, P+2, P-1; P-2 stripe diffuse, brownish. P stripe from cleithral spot to middle of caudal-fin base where

continued narrow along middle caudal-fin rays; entire, but with lighter areas anteriorly.

P+1 stripe originating in cleithral spot, narrower than P stripe, terminating on upper half of caudal peduncle, but extended narrowly on caudal fin. P and P+1 stripes anteriorly connected by 2–6 vertical bars fragmenting interstripe I, into large light elongate blotches

P+2 stripe much narrower than P+1 stripe, expressed as series of small spots, posteriorly partly contiguous, first blotch above cleithral spot, stripe terminating slightly posterior to vertical from dorsal-fin base.

P-1 stripe originating at pectoral axilla, about as wide as P+1 stripe, to end of anal-fin base, continued narrower on lower side of caudal peduncle and extended as series of elongate spots on caudal fin.

P-2 stripe diffuse, partly interrupted, from beneath pectoral-fin base to about middle of anal-fin base.

Dorsal fin with wide brownish D stripe across middle rays, base and distal margin hyaline. Anal fin proximally hyaline; dark indistinct A and A-1 stripes present; distal margin hyaline. Caudal fin dusky with three dark stripes or fragments of stripes extending stripes P+1, P, and P-1. Light

Table 6. Morphometry of *Danio meghalayensis* 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) given when ANOVA $p < 0.05$.

	N	min	max	mean	SD	a	b	r
Standard length (mm)	5	38.9	50.5	43.6	4.8			
Body depth	5	22.1	25.8	24.6	1.5	-1.249	0.275	0.911
Head length	5	23.2	24.6	23.8	0.6	0.957	0.216	0.976
Snout length	5	5.9	6.8	6.4	0.3	1.256	0.035	0.930
Head depth	5	17.0	18.8	17.9	0.7	0.865	0.159	0.935
Head width	5	12.9	14.0	13.3	0.4	-0.065	0.135	0.967
Upper jaw length	5	9.7	10.3	10.0	0.3	0.265	0.094	0.969
Lower jaw length	5	11.1	13.2	11.8	0.9	-1.151	0.102	0.767
Orbital diameter	5	6.8	8.2	7.5	0.6	-1.151	0.102	0.919
Interorbital width	5	9.5	10.3	9.9	0.3	1.332	0.068	0.998
Caudal peduncle length	5	18.1	19.4	18.9	0.5	0.358	0.181	0.967
Caudal peduncle depth	5	12.0	13.3	12.7	0.5	0.018	0.127	0.942
Dorsal-fin base length	5	13.9	15.7	14.8	0.9	–	–	0.832
Anal-fin base length	5	15.9	18.1	17.1	0.9	-3.190	0.245	0.985
Predorsal length	5	56.0	62.2	59.5	2.7	2.061	0.547	0.917
Preanal length	5	62.2	68.1	65.2	2.1	-6.990	0.184	0.990
Prepelvic length	5	44.5	49.1	46.4	1.8	-5.498	0.591	0.981
Pectoral-fin length	5	22.9	24.6	23.8	0.6	-0.751	0.256	0.981
Pelvic-fin length	5	16.6	17.5	17.1	0.4	0.799	0.153	0.974
Rostral barbel length	5	9.6	17.0	13.2	3.5	–	–	0.623
Maxillary barbel length	5	9.0	20.6	15.6	4.6	–	–	0.863

interstripes I, I+1, I+2, I-1, and I-2 present. Interstripes I and I-1 similar in width to P and P-1 stripes, widening slightly on caudal peduncle, where I-1 wider than P-1. Interstripes I+1 and I+2 diffuse, only slightly lighter than P+2 stripe, and darker than interstripe I.

Remarks. The BMNH specimens are in a poor state of preservation, having suffered from dissection and loss of scales, and have had one or more fins removed. In one specimen the dorsal fin is cut away at the base and the dorsal fin count is obtainable only from the x-ray. The BMNH specimens are labelled only as Bengal, which is a large area which on present-day maps covers much of easternmost India and Bangladesh. It excludes Meghalaya, but Meghalayan rivers drain to Assam and Bengal. Seven aquarium specimens examined have dorsal-fin count ii.8½ (7), anal fin counts iii.10½ (1), iii.11½ (4), iii.12½ (2), lateral line scales 34 (2), 35 (5).

The descriptions of *Danio deyi* and *D. meghalayensis* (Sen & Dey, 1985) are very general and the accompanying illustrations insufficient for identification. *Danio meghalayensis* was synonymized with *D. dangila* by Talwar & Jhingran (1991), Fang (1991) and Kottelat (2013). *Danio deyi* was synonymized with the catch-all taxon *Devario aequipinnatus* (McClelland) by Talwar & Jhingran (1991) and with *D. dangila* by Fang (2001) and Kottelat (2013). Neither author provided arguments for the synonymization and at least Fang did not have access to specimens. Barman (1991) did not mention these species. *Danio deyi* is unlikely to be the same as *Devario aequipinnatus* as it is depicted with rostral and mandibular barbels, whereas in *Devario* barbels are absent or very short. Specimens from Meghalaya now studied (UMMZ 243666) show at least that there is a distinct species of *Danio* in Meghalaya, which resembles the description of *D. meghalayensis*, and which consequently is identified with that name here. Whether *D. deyi* is a distinct species or the juvenile of *D. meghalayensis* remains to investigate. The two names are here considered as validly published. It is noteworthy, however, that each description starts with the heading "Material" and it is not indicated to which species the material or following data belongs, except in the final Etymology section. Although holotype and paratypes are listed for both species, no repository or voucher number is given. As first reviser I select *D. meghalayensis* to have priority over *D. deyi*

whenever the two are considered to be the same species.

There is no mention of barbels in the original descriptions, but the drawings show two (fig. 1A) or a single (fig. 2A) relatively short barbel, not reaching to the base of the pectoral fin. That character and the absence of rings in the colour pattern must exclude identity with *D. dangila* or *D. assamila*. The closest match for both *D. deyi* and *D. meghalayensis* is the species here identified as *D. meghalayensis*. The colour pattern of the specimen in Fig. 4b, and in the drawing of *D. meghalayensis* in Sen & Dey (1985: fig. 2A), with several thin dark stripes resembles that of the specimen of *Devario fraseri* Hora (in Hora & Mukerji, 1935: fig. 3). Specimens from the type locality area identified as *D. fraseri* (BMNH 1938.2.22:25-31), however, possess a pattern of relatively wide lateral stripes as in most striped *Devario*, and by the presence of a supraorbital groove and rudimentary barbels they clearly represent a species of *Devario*.

The specimens of *D. meghalayensis* reported here differ in meristics from data presented in the original description for *D. meghalayensis* and *D. deyi*, for which are reported respectively iii.7-9, and iii.9 dorsal-fin rays (vs. ii.8½), ii.12-13, and ii.11-12 anal-fin rays (vs. iii.9½-11½), i.6 pelvic-fin rays (vs. i.7), 7/3, and 5½/3½ scales in transverse series (vs. ½6+1+1½), 14 and 12 circumpectuncular scales (vs.14).

Das & Biswas (2008) illustrate their account of *Danio rerio* from the Brahmaputra with an image of a *D. meghalayensis*. With the horizontal stripes *D. meghalayensis* bears a certain similarity to *D. rerio*.

Morphometric comparison

Proportional measurements of *D. assamila*, *D. catenatus*, *D. concatenatus*, *D. dangila*, and *D. sysphigmatus* overlap (Tables 1-5). *Danio meghalayensis* (Table 6) is distinct in lesser body depth (22.1-25.8 % SL vs. 26.2-34.6), shorter anal-fin base (15.9-18.1 % SL vs. 18.6-37.3), shorter pectoral fin (22.9-24.6 % SL vs. 23.4-31.9 %), and shorter maxillary barbel (9-20.6 % SL vs. 24.0-42.7). Principal component analysis of measurement data (Table 6; Fig. 5) shows mainly considerable individual variation, especially in caudal peduncle length, but also separates *D. meghalayensis* from *D. assamila*, *D. catenatus*, *D. concatenatus*,

D. dangila, and *D. sysphigmatus*, with most variability in body depth, pectoral-fin length, anal-fin base length, and also reflecting the somewhat shorter dorsal-fin base and pelvic fin in *D. meghalayensis*.

Discussion

In most phylogenetic analyses *Danio dangila* (and/or *Danio* cf. *dangila*) is resolved as the sister group of remaining *Danio* (Conway et al., 2008; Fang, 2003; Fang et al. 2009; Mayden et al., 2007; Pramod et al., 2010; Quigley et al., 2002, 2004; Tang et al., 2010), but *D. feegradei* is more basal in Collins et al. (2012), and *D. dangila* and *D. feegradei* a clade sister to remaining *Danio* in McCluskey & Postlethwait (2015). In Fang's (2003) analysis *D. dangila* and *D. catenatus* (as *D. aff. dangila*) separated from remaining *Danio* by having the state of 8–10 instead of the more common state of 6–7 branched dorsal-fin rays among danionines. I find a range of 9½–11½, with 10½ dominant in *D. assamila*, *D. catenatus*, *D. concatenatus*, *D. dangila*, and *D. sysphigmatus*. All other *Danio* have 8½ or less, including *D. meghalayensis* which shares components of

the unique colour pattern of chain danios. In Fang (2003) and Pramod et al. (2010) the cleithral spot is coded as absent in *D. dangila* and *D. catenatus*, although it is clearly present. Correcting the matrix, however, does not change the tree. The cleithral spot is a prominent marking in all *Devavario*, *Betadevario*, *Chela*, and *Laubuka*. It is present but small in *D. meghalayensis* and *D. feegradei*, but absent in all other *Danio*, as well as in *Microdevavario* and *Microrasbora*.

Danio meghalayensis was not included in morphological analyses (Fang, 2003; Pramod et al., 2010) because it was believed to be a synonym of *D. dangila*, and no material was available. A close relationship to the chained *Danio* is nevertheless manifest in shared anastomosing lateral stripes and available DNA information. In a study of barcode sequences from aquarium specimens, Collins et al. (2012) included *D. dangila* (RC0122–0123, RC0344–0348, as *D. dangila*), *D. assamila* (RC0343, as *D. cf. dangila*), *D. concatenatus* (RC0561, RC0563–0564, as *D. aff. dangila*), *D. sysphigmatus* (RC0560, RC0562, as *D. aff. dangila*) and *D. meghalayensis* (RC0565–0568) in an analysis using both COI and nuclear rhodopsin (RHO) sequences. Their sequences support the morphologically

Table 7. Component loadings from Principal Component Analysis of morphometric data from *Danio dangila* (N=9), *D. assamila* (N=7), *D. catenatus* (N=15), *D. concatenatus* (N=9), *D. sysphigmatus* (N=11), and *D. meghalayensis* (N=5). The four 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	0.234	-0.165	-0.150	0.034	0.035	0.177	0.181
Body depth	0.276	0.253	0.268	-0.089	-0.087	0.272	0.277
Head length	0.193	-0.033	-0.022	0.098	0.098	-0.147	-0.144
Snout length	0.206	0.067	0.079	0.178	0.179	-0.304	-0.300
Head depth	0.193	-0.147	-0.135	-0.053	-0.052	0.017	0.020
Head width	0.219	-0.155	-0.142	0.044	0.045	-0.229	-0.225
Upper jaw length	0.180	-0.116	-0.106	0.123	0.124	-0.288	-0.285
Lower jaw length	0.107	-0.118	-0.108	0.182	0.183	-0.365	-0.362
Orbital diameter	0.163	0.086	0.096	-0.075	-0.074	-0.166	-0.163
Interorbital width	0.216	0.118	0.130	0.061	0.062	-0.108	-0.104
Caudal peduncle length	0.171	-0.681	-0.668	0.023	0.024	0.013	0.016
Caudal peduncle depth	0.262	-0.154	-0.139	-0.191	-0.190	0.330	0.335
Dorsal-fin base length	0.302	0.160	0.177	0.485	0.487	0.025	0.031
Anal-fin base length	0.309	0.376	0.393	0.297	0.298	0.355	0.361
Predorsal length	0.234	-0.123	-0.109	0.019	0.020	0.075	0.080
Preanal length	0.241	-0.151	-0.137	-0.105	-0.104	0.219	0.224
Prepelvic length	0.232	-0.101	-0.087	-0.155	-0.154	0.127	0.131
Pectoral-fin length	0.229	0.286	0.298	-0.268	-0.267	-0.390	-0.385
Pelvic-fin length	0.257	0.158	0.172	-0.648	-0.647	-0.117	-0.112
Eigenvalue	0.625	0.018	N/A	0.005	N/A	0.004	N/A
Cumulative variance (%)	93.0	95.8	N/A	96.6	N/A	97.3	N/A

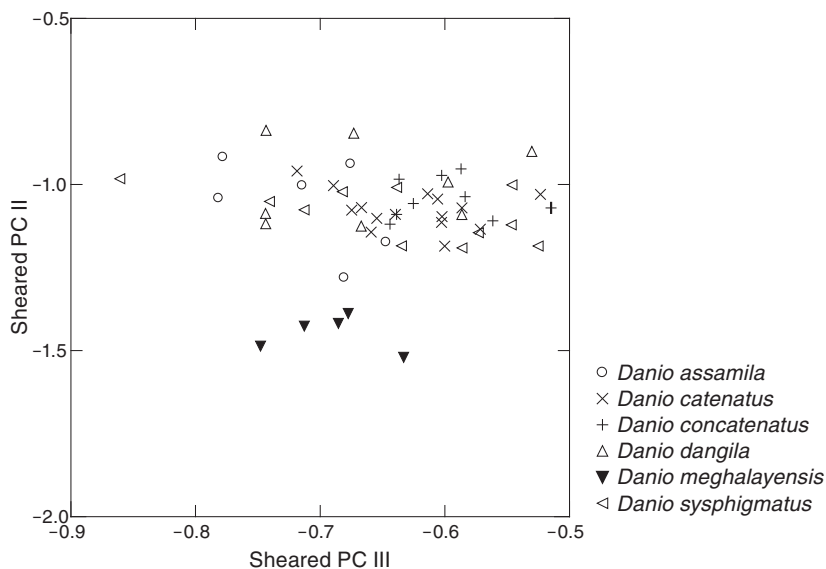


Fig. 5. Principal component analysis of pooled morphometric data from *Danio assamila*, *D. catenatus*, *D. concatenatus*, *D. dangila*, *D. meghalayensis*, and *D. sysphigmatus*. Scores on sheared principal component II plotted against sheared principal component III.

established species diagnoses presented here. Their neighbour joining trees show these taxa as a monophyletic group but with variable internal trees. Tentative identifications of their *D. aff. dangila* and *D. cf. dangila* were made on the basis of photos available in BOLD (2014).

The chain danios (*D. assamila*, *D. catenatus*, *D. concatenatus*, *D. dangila*, *D. sysphigmatus*) share several presumably derived states distinguishing them from other *Danio*, viz. the greater number of branched dorsal-fin rays, the prolonged first ray of the pelvic and pectoral fins, the pattern of dark circles along the side, the very long barbels, and the broad caudal fin of adults. Among danionines, long, filamentous unbranched ray in the pelvic and pectoral fins is shared only with species of *Esomus* Swainson and *Luciosoma* Bleeker. In *Chela* Hamilton, and species of *Laubuka* Bleeker, the unbranched pelvic-fin ray is prolonged, but not the unbranched pectoral-fin ray.

Danio has a wide distribution with eighteen species within an area including rivers of Myanmar, the Malay Peninsula, Thailand, Laos, and Cambodia, and Sumatra (Kullander, 2001), but only five species – *D. rerio*, *D. dangila*, *D. assamila*, *D. meghalayensis* and *D. jaintianensis* – in northern India, Nepal, Bangladesh and Pakistan. Among those four, *D. rerio* is ubiquitous, present even in southern states of India and in Pakistan (Engeszer

et al., 2007; Mirza, 1975). *Danio jaintianensis* is known only from Meghalaya (Sen & Dey, 1985). A vicariance pattern is established for two species pairs among *Danio*. *Danio choprae* (around Myitkyina) and *D. flagrans* (near Putao) are allopatric in the upper Ayeyarwaddy drainage (Kullander, 2012). *Danio erythromicron* (Inle Lake) and *D. margaritatus* (swamps north of Inle) are allopatric in a small area on the Shan Plateau (Roberts, 2007; pers. obs.). Relationships and distribution patterns for other species are still incompletely studied, although most species have limited, discrete distribution. The series of species from the Ganga and Brahmaputra basins to Tenasserim, formed by the chain danios, represents a unique pattern of distribution in the genus and in its particular geographical extension it is unparalleled among fishes in the region. Abundant collections are available from the middle and upper Ayeyarwaddy and Salween Rivers, and chain *Danio* are absent from those collections, making it highly likely that chain danios in Myanmar are restricted to the southern part of the country. The coastal region of Myanmar is less well explored, and additional localities and potentially species of chain danios may be expected. The Indian and Bangladeshi distribution is very sketchily known, but based on the present literature and collecting record, chain *Danio* are known only from scattered

localities in the Brahmaputra and Ganga basins, and possibly the Bakkhali and Godavari Rivers, and there is a potential for additional species within this vast area. The putative sister taxon of the chain danios, *D. meghalayensis* is restricted to the Meghalaya which has a high degree of endemism of fishes and other organisms (Allen et al., 2008; Britz & Kullander, 2014; Yazdani, 1985). One more species of *Danio* is known from that region, viz. *D. jaintianensis*, of uncertain relationships.

Whereas extensive stream capture may be invoked as an explanation for the distribution of the chain danios, it is noticeable that they are associated with distinct highland areas, including the Rakhine Yoma, Patkai and Naga Hills Indo-Myanmar Ranges), Meghalaya (Shillong Plateau), Hazaribagh Plateau, Himalayan forelands, Bago Yoma/Shan Plateau, and the Tenasserim Ranges (southern Sino-Myanmar Ranges), and available habitat data suggest that they typically inhabit small hill streams. This in turn suggests that the present patchy distribution is a fragmentation of a wider distribution range of one or a few ancestral species adapted to hill or mountain streams. In a longer geological perspective, stream piracy along the margins of the seismically active Indo-Myanmar Ranges and is a scenario that fits with speciation over a longer period of time, and would explain the Indian and Western Myanmar occurrences. With the reservation for incomplete sampling, it does, however, not provide an alternative explanation for the presence of a hillstream member of the group in the Bago and Tenasserim hills, as they have been isolated from the southern part of the Indo-Burman Ranges for all of their existence, first by a marine bay and later by expansive lowlands, with only the younger Bago Yoma as an intermediate highland (Bender, 1983). A possible explanation for the distribution pattern of the chain danios may be provided by the sea level regression during glacial periods. During the last glacial maximum (21 000 years before present) world ocean levels were 120–135 m below present levels (Clark & Mix, 2002). Thus, an Andaman and Martaban coastline up to 120 m or more lower than at present for 1000 years, coinciding with a cooler climate and reduced water from the Himalayan rivers (Yasuda et al, 1990; Voris, 2000) would have provided for a different river landscape and a larger extent of pericoastal lowlands with lower temperatures favouring dispersal of chain danios. The present Holocene transgression would have forced the species to

higher elevations with speciation in separate river systems that once were headwaters of rivers reaching further out in the Andaman Sea and Bay of Bengal. Alternatively, Late Miocene sea level oscillations of the same magnitude as in the Pleistocene would have provided for this scenario (cf. Woodruff, 2013). Sea level transgressions have been relatively modest during the Pleistocene, but could reach about 100 m in the Late Miocene and Pliocene (Woodruff, 2013). For inland taxa sea level oscillations may have had little effect, but for coastal mountain stream taxa, regressions and transgressions would have provided for cycles of expansion and isolation. In the case of Rakhine species, marine regression may have provided very little extra coastland, as the coast is relatively steep, and the 100 m isobath close to the current coastline. Further taxonomic work on the mountain stream fauna of India and Myanmar will be instructive concerning the generality of the pattern of distribution observed in the chain danios and the possible role of sea level oscillations.

Comparative material. In addition to *Danio* material already listed in Fang (1998), Kullander & Fang (2009 a–b), Kullander et al. (2009), and Kullander (2012): *Chela cachius*, NRM 40494; *Devario fraseri*, BMNH 1938.2.22:25–3; *Esomus caudiocellatus*, NRM 36347; *Luciosoma setigerum*, NRM 27311; *Esomus danrica*, NRM 52679; *Laubuka khujairokensis*, NRM 59265; *Laubuka laubuca*, NRM 57234; *Laubuka siamensis*, NRM 31221.

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Cover photograph

Pseudorasbora pugnax (photograph by Toshihiko Morimune)
Seigo Kawase and Kazumi Hosoya
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