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# Re-description of *Betta rubra* Perugia, 1893 (Teleostei: Osphronemidae), an enigmatic fighting fish from Sumatra

Wiederbeschreibung von *Betta rubra* Perugia, 1893 (Teleostei: Osphronemidae), einem rätselhaften Kampffisch von Sumatra

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**Summary:** *Betta rubra*, occurring from Meulaboh to Sibolga in north-western Sumatra, is formally re-described based on freshly collected preserved and live specimens. The species can be differentiated from other members of the genus by the combination of the following characters and character states: an iridescent light blue patch at pectoral fin origin, alternating black bars and red blocks ventrolaterally on the flank, presence of a dark triangular patch below the eye, absence of red twin bars on the opercle when preserved. Based on the differential diagnosis *B. rubra* is herein removed from the *Betta foerschi* species group, in which it was tentatively placed, and transferred into its own group. Uncertainties regarding its distribution are resolved. Biogeography and possible speciation of *B. rubra* are briefly discussed.

Key words: Osphronemidae, Bettini, Betta rubra, Betta foerschi, species group, biogeography.

**Zusammenfassung:** *Betta rubra* wird anhand von lebenden und konservierten Exemplaren wiederbeschrieben. Die Art ist im nordwestlichen Sumatra von Meulaboh bis Sibolga verbreitet. Sie unterscheidet sich von den übrigen Arten der Gattung durch die Kombination folgender Merkmale und Merkmalsausprägungen: ein irisierender hellblauer Fleck am Ansatz der Brustflosse, alternierend schwarze Balken und rote Zonen auf den ventralen Körperseiten, ein dunkler, dreieckiger Fleck unter dem Auge, Fehlen von roten, parallelen Balken auf dem Kiemendeckeln bei konservierten Exemplaren. Basierend auf den Ergebnissen (vergleichende Diagnose) wird die Art von der *Betta foerschi*-Artengruppe (in der sie vorläufig eingeordnet wurde) in eine eigenständige Gruppe überführt. Unsicherheiten in Bezug auf das Verbreitungsgebiet werden geklärt. Die Biogeografie und mögliche Artentstehung von *B. rubra* werden kurz diskutiert.

Schlüsselwörter: Osphronemidae, Bettini, Betta rubra, Betta foerschi, Artengruppe, Biogeographie.

## 1. Introduction

The Southeast Asian osphronemid genus *Betta* (generally called 'fighting fish') includes nearly 70 species (TAN & NG 2005 a, b, 2006, SCHINDLER & SCHMIDT 2006, FROESE & PAULY 2012). *Betta* species are small fishes (up to about 100 mm SL). The majority has been described in the last two decades. One of the oldest species names in the genus is *Betta rubra* Perugia, 1893. Originally described from the west coast of Sumatra, for a long time it was known only from the type specimens. Although a first drawing of one of the types

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was already published by REGAN (1910), *B. rubra* remained an elusive species due to the lack of fresh material. As colouration of live specimens (in particular in males) is an important diagnostic character and often a major characteristic feature to distinguish species (TAN & TAN 1994, 1996, TAN & NG 2005 a, b), it was not possible to classify *B. rubra* with adequate certainty. The species name *rubra* was erroneously used for a specimen from Singapore (HERRE 1940) and different forms of the *Betta splendens* group (DONOSO-BÜCHNER & SCHMIDT 1999) and has even been regarded as a synonym of *B. imbellis* (see SCHMIDT 1996). Tweedie (1952) noted that the specimen identified as B. rubra by HERRE (1940) is probably Betta pugnax. The taxon B. rubra was also confused or even synonymized with Betta picta in the popular literature (VIERKE 1986). WITTE & SCHMIDT (1992) confirmed the taxonomic validity of *B. rubra* and pointed out that the characteristic triangular mark below the eye (WITTE & SCHMIDT 1992: fig. 8h) separates it from the members of the Betta splendens- group. They placed B. rubra in its own species group. The photographs of two type specimens by KOTTELAT (1993, KOT-TELAT in SCHÄFER 1997) indicated that *B. rubra* differs in appearance from all other nominal Betta species. TAN & NG (2005b) provided a first short re-description of *B. rubra* based on some of the types and a few new, but improperly preserved specimens from Aceh Barat, collected in 1982; however, live colours were not recorded. TAN & NG (2005a, b) classified this species as a member of the *Betta foerschi* group. The lack of freshly collected material and colour photographs of live specimens made it impossible to confirm their classification and complete the description of the taxonomically important colour pattern.

Recently, a local fisherman collected new material of *B. rubra* at the west coast of Sumatra. Besides preserved specimens also live fish were imported. Therefore it is now possible for the first time to describe the live colour pattern and to clarify the taxonomical position of *B. rubra*.

The purpose of this paper is to present a re-description of *Betta rubra* from preserved material and photographs of live specimens and consequently to place it in its own species group based on apomorphic characteristics. We also resolve the confusion regarding its distribution and provide an English translation of Perugia's original Italian description as an appendix.

#### 2. Material & methods

The measurements taken follow WITTE & SCHMIDT (1992) with the modification that all measurements are taken as a straight-line

between two critical points (as described in SCHINDLER & SCHMIDT 2006). The distances are measured with a dial calliper reading to the nearest 0.1 mm. Ratios are expressed as percentages of standard length (SL). Counts were made as described by WITTE & SCHMIDT (1992), except for the number of predorsal scales which are counted continuously (NG & KOTTELAT 1994). Numbers in parentheses indicate the number of specimens examined with that particular count. Terminology of colour patterns follows TAN & NG (2005a) with modifications after Schindler & SCHMIDT (2006). The description follows the general format used by TAN & NG (2005a) and SCHINDLER & SCHMIDT (2006). Besides the data recorded herein data from previous descriptions were included (VIERKE 1979, SCHALLER & KOT-TELAT 1989, TAN & NG 2005a, b. 2006).

The terminology and application of phylogenetics follows HENNIG (1966, see WÄGELE 2004), i.e. that character polarity was estimated independently and prior to a tree construction. It is most parsimonious to treat characters, which appear uniquely in the in group and closely related out groups, *a priori* as apomorphic unless proven otherwise.

The significance of pairwise differences in morphometric data between examined specimens of *Betta rubra* and *Betta foerschi* are tested with the *Student's t-test*. To control the increased type I error in multiple comparisons the step-up false discovery rate procedure (BENJAMINI & HOCHBERG 1995) is used to indicate substantial dissimilarities.

Museum acronyms: BMNH = Natural History Museum, London; MSNG = Museo Civico di Storia Naturale Giacomo Doria, Genova; ZMB = Museum für Naturkunde, Berlin.

Material examined: *Betta rubra*: ZMB 34533, 5, 30.5-41.1 mm SL, Indonesia, Aceh, west coast of northern Sumatra around Meulaboh, licensed import and preserved 2010, don. Colin Dunlop. Collection of the authors, 1 male, 52.7 mm, SL, Meulaboh, Sumatra, Indonesia, preserved 2010. Observations of reproductive behaviour and live colouration are based on five specimens collected from the same locality which have been kept in aquaria; not preserved. *Betta foerschi*: Col-

lection of the authors, 4 ex, 32.7-44.6 mm SL, licenced import from Borneo (no exact locality available), preserved 2010, don. Colin Dunlop.

## 3. Results

## Betta rubra Perugia

**References:** *Betta rubra* Perugia, 1893: 242 (original description; Lago Toba, Siboga); Volz 1904: 493 (referred to Perugia (1893), no newly collected specimens from Lake Toba); Volz 1907:127 (listed); Regan 1910: 781, pl. 77, fig. 1 (taxonomy; description of a syntype); Weber & de Beaufort 1922: 361 (description, re-examination of the BMNH syntype); Tortonese 1963: 340 (MSNG syntypes listed); Witte & Schmidt 1992: 327, fig. 8h (taxonomic status; *B. rubra* species group); Kottelat et al. 1993: 163, pl. 76 (colour photograph of two representative syntypes); Tan & Ng 2005a: 58 (systematic position; *Betta foerschi* species group); TAN & NG (2005b): 119, fig. 1 (photograph of type specimens, taxonomy, *B. foerschi* species group). Type specimens: MSNG 13019 (10 specimens; Sibolga); BMNH 1893.5.29.1 (1 specimen; Lake Toba).

**Diagnosis:** *Betta rubra* differs from all other members of the genus by the presence of an iridescent light blue patch at pectoral fin origin in both sexes, an alternating pattern of black bars (with iridescent blue scales in live) and red blocks on flank ventrolaterally, and the presence of a broad chin bar, which appears as a dark triangular mark below eye.

**Description:** For general appearance see figures 1 and 2. Meristic and morphometric data are summarised in table 1. Maximum standard length usually <50 mm. Body slender (body depth at dorsal fin origin <25.5 % of SL); head length comparatively short for a mouth brooding species (head length usually <31 %



Fig. 1: *Betta rubra*, male (39 mm SL), preserved (ZMB 34533). Abb. 1: *Betta rubra*, Männchen (39 mm SL), konserviert (ZMB 34533).



Fig. 2: *Betta rubra*, female (38 mm SL), preserved (ZMB 34533). Abb. 2: *Betta rubra*, Weibchen (38 mm SL), konserviert (ZMB 34533).

of SL); snout slightly pointed. Dorsal and anal fins pointed (more in males); dorsal fin situated comparatively far posteriorly (predorsal length 64-66 % of SL); caudal fin rounded in females; rounded, pointed or lanceolate in males; anal fin base length about half of SL or more (anal fin base 49-55 % of SL); dorsal fin base length 10-13 % of SL; pelvic fins with long filamentous ray (length up to 34 % of SL); pelvic fin spine comparatively short (usually < 5 % of SL); pectoral fins rounded (length 18-20 % of SL). Dorsal fin rays I, 7 (3), I, 8 (2) or II, 8 (1). Anal fin rays III, 22 (1), III, 23 (2), III, 24 (2) or III, 25 (1). Pectoral fin rays 12 or 13. Pelvic fin rays I, 1,4. Lateral scales 29 (3) or 30 (3). Transverse scales at dorsal fin origin 9 (1), 9.5 (3) or 10 (2). Predorsal scales 19-22; postdorsal scales 9-10.

**Preserved colouration:** See figures 1 and 2. Body brown or brownish-olive, dorsum dark brown, ventral parts light brown or whitish. On ventral part of body 5-7 irregular, spaced dark bars (more distinct in males than in females) with reddish blocks in between. Ventral part of head light brown or greyish; lower lip dark. Chin bar broad, reduced to a conspicuous dark triangular mark below eye; pre- and postorbital stripes present, posterior part of the latter on opercle appearing as broad patch (more conspicuous in males than in females); opercle with reddish margin. Dorsal and caudal fins reddish-brown without transverse bars, anal fin grey-brown, distally reddish-brown, pelvic fins reddish-brown to reddish. Pectoral fin hyaline, with a dark patch at origin. Upper stripe on flank absent; central stripe faint in males, more conspicuous in females, running from pectoral fin base to lower caudal fin base, not connected with caudal fin base spot. Caudal fin base spot faint or absent in males, more conspicuous in females. Second central stripe absent or strongly reduced.

**Live colouration:** See figures 3 and 4. Description of male: Body background dark brown dorsally, light brown ventrally. Dorsolaterally some scales highlighted with iridescent blue. Red twin bars on opercle, posterior bar angling down along gill plate. Opercle with faint golden shine. Dark pre- and postorbital stripes distinct.

Suborbital stripe dark, merging with dark chin bar. Dark triangular patch below eye, merging with suborbital stripe and chin bar. Lower lip mostly black. Black spots on dorsum of head. An alternating pattern of 5-7 black bars (with iridescent blue scales) and red blocks on the flanks ventrolaterally. Faint caudal peduncle spot present. Caudal, dorsal and anal fins red, outer margins light-blue or white. Anal fin and central part of caudal fin with whitish-green streaks. Pelvic fins red with faint to dominating whitish-green streaks near origin, filament white. Pectoral fins hyaline. Presence of iridescent light blue patch at pectoral fin origin.

Description of female: Body background dorsally dark brown, ventrally lighter. Some flank scales highlighted with iridescent blue. Opercle with faint golden shine, red twin bars virtually absent or small remnant of posterior bar present. Orbital stripes, chin bar and lower lip colour as described above. Dark triangular patch below eye present. Dorsum of head with black spots. Single horizontal flank stripe on lower half of body just below centre, merging with caudal peduncle spot. Blue iridescence on dorsolateral scales faint or absent. Dark flank bars and red blocks absent. Unpaired fins hyaline to brownish. Pelvic fins faint red, filament white. Presence of whitish-green streaks same as for males, albeit fainter. Pectoral fins hyaline. Pectoral fin origin with iridescent light blue patch, slightly weaker than in males.

Colour intensity mood-dependant. No particular male brood colouration was observed. Female individuals before and during spawning with lighter brown stripe running along dorsum of head to dorsal fin and from dorsal fin to caudal fin.

**Reproductive behaviour:** Observations in captivity showed that *Betta rubra* is a paternal mouth brooder. Spawning always commences on a substrate ranging from floating leaf to the bottom. After spawning the male goes essentially into hiding until releasing the fry.

**Distribution:** Lowlands of north western Sumatra; from Meulaboh in the north to Sibolga in the south (fig. 5).

**Etymology:** PERUGIA (1893) did not explain the species name. It is doubtlessly derived from



**Fig. 3:** Live colouration of *Betta rubra*, adult male (not preserved). **Abb. 3:** Lebendfärbung von *Betta rubra*, adultes Männchen (nicht konserviert).



**Fig. 4:** Live colouration of *Betta rubra*, adult female (not preserved). **Abb. 4:** Lebendfärbung von *Betta rubra*, adultes Weibchen (nicht konserviert).



Fig. 5: Distribution of *Betta rubra*; dots: (1) Meulaboh; (2) Sibolga (type locality). Abb. 5: Verbreitung von *Betta rubra*. Punkte: (1) Meulaboh, (2) Sibolga (Typuslokalität).

the Latin adjective 'ruber', meaning red, which was most likely assigned to the species for its colouration.

**Comparative notes:** TAN & NG (2005a, b) tentatively placed Betta rubra in the Betta foerschi group. It differs from the species of this group (Betta foerschi, Betta strohi and Betta mandor) by the possession of an iridescent light blue patch at pectoral fin origin (versus absent), presence of a dark triangular patch beneath the eye (versus absent), a prominent central stripe on lower half of body just below midline (no upper or second central stripe present), bars on flank comparatively broad (versus usually narrower), presence of red blocks between bars ventrolaterally (versus such pattern absent) and absence of red twin bars on opercle when preserved (versus present). See table 1 for differences in morphometric data between examined specimens.

Besides the diagnostic characters provided above, *B. rubra* can be distinguished from all other species groups as recognized in TAN & NG (2005a, b) as follows: from the *Betta bellica* group by lateral scales 29 or 30 (versus 33), oral brooding (versus bubblenest brooding); from the *Betta pugnax* group by absence of a green or blue iridescent opercle in life (versus present), lack of upper and second central stripes (versus present); from the *Betta akarensis* group by lack of transverse bars in caudal fin (versus usually present and always well-defined in mature males), absence of faintly coloured greenishgold scales on opercle (versus present); from the Betta unimaculata group by having a relatively small head and mouth (versus large blunt head and large mouth), pelvic fins with long filamentous ray up to 34 % of SL (versus short pelvic fin filament); from the Betta picta group by absence of upper and second central stripes (versus present), pointed fins (versus rounded), anal fin and ventral part of caudal fin lacking dark margin (versus broad dark margins present); from the *Betta splendens* group by oral brooding (versus bubblenest brooding), lack of upper central stripe (versus present); from the *Betta coccina* group by having a larger adult size (usually >38 versus <38 mm SL), multi-coloured body (versus a uniform red or black), oral brooding (versus bubblenest brooding); from the *Betta waseri* group by absence of dark throat markings (versus present), lack of distinct dark markings on opercle (versus **Tab. 1:** Morphometric data (in percent of standard length; SL in mm) of *Betta rubra* and *B. foerschi*. Mean = arithmetic mean; min = lowest value; max = highest value; sd = standard deviation; t-test = results (uncorrected p-values) of Student's test; \* = p < 0.05; \*\* = p < 0.01.

Tab. 1: Morphometrische Daten (in Prozent der Standardlänge; SL in mm) von Betta rubra und B. foerschi.
Mean = arithmetischer Mittelwert, min = kleinster Wert, max = höchster Wert, sd = Standardabweichung,
t-test = Ergebnisse (unkorrigierte p-Werte) des Student-Test, $* = p < 0,05$ , $** = p < 0,01$ .

	Betta rubra				Betta foerschi				
	min	max	mean	sd	min	max	mean	sd	t-test
Standard length (mm)	30.5	52.7	38.9	7.9	32.7	44.6	37.2	5.2	0.7092
Total length	128.2	138.1	133.3	3.76	136.2	140.7	138.5	3.14	0.1354
Predorsal length	63.6	66.2	65.5	1.01	63.8	66.6	65.1	1.15	0.2432
Preanal length	44.3	48.1	46.1	1.59	44.9	46.7	45.8	0.94	0.7262
Body depth	23.0	25.5	23.9	1.04	22.9	23.8	23.4	0.38	0.3942
Caudal peduncle depth	13.1	15.9	15.0	1.01	16.5	17.3	16.8	0.34	0.0114
Head length	26.7	30.4	28.8	1.25	31.3	32.9	32.2	0.68	0.0012**
Orbital diameter	7.1	8.4	7.7	0.57	8.1	9.5	9.1	0.66	0.0083*
Postorbital length	12.9	14.8	14.1	0.78	15.6	15.9	15.7	0.20	0.0037*
Interorbital width	7.5	9.7	8.9	0.79	9.2	9.6	9.4	0.18	0.2689
Dorsal fin base length	10.3	13.6	11.7	1.11	12.8	14.8	13.9	0.89	0.0106*
Anal fin base length	49.9	55.6	52.4	2.04	50.4	52.9	51.9	1.04	0.6422
Pelvic fin length	20.9	33.4	26.1	4.12	25.7	31.4	28.5	2.62	0.3435
Pelvic fin spine length	4.0	6.1	4.8	0.80	7.5	8.0	7.7	0.20	0.0001**
Postdorsal length	22.6	24.9	23.5	0.86	20.6	22.2	21.4	0.70	0.0035**

present); from the *Betta edithae* group by fewer anal fin rays (22-25 versus 28-30); from the *Betta anabatoides* group by pelvic fins with long filamentous ray (versus pelvic fin filamentous ray usually not extended), head without two light spots behind eye (versus present), smaller body depth (<25.5 versus 30-33 % of SL); from the *Betta albimarginata* group by having fewer anal fin spines (<IV versus IX-XII), more anal fin rays (22-25 versus 11-13); from the *Betta dimidiata* group by lacking extremely elongated unpaired and pelvic fins (versus present), anterior part of throat up to anterior part of opercle not purple (versus purple in mature males).

#### 4. Discussion

The genus *Betta* has been proven to be monophyletic by using molecular data and osteological features (BRITZ 2001, RÜBER et al. 2006). Although not all species were analysed or included, we here follow the historic and current concept (e.g. Regan 1910, Britz 2001, Tan & Ng 2005a, b, Rüber et al. 2006) of the genus.

The name of the subfamily that includes the genus *Betta* is listed as Macropodusinae (e.g. BRITZ 2001, RÜBER et al. 2006). However, the family group names Trichogastrini and Bettini proposed by BLEEKER (1879) and Parophiocephalidae (POPTA 1905) are available and have priority. Accordingly, we follow the classification suggested by VAN DER LAAN (2010; based on the phylogeny presented by RÜBER et al. 2006: fig. 2) and regard Trichogastrinae Bleeker, 1879 as the valid name. This subfamily can be divided into two tribes. For the tribe including, among others, the genera *Betta* and *Macropodus*, the oldest available and thus valid name would be Bettini Bleeker, 1879.

*Betta rubra* has long been an enigmatic taxon because it was known only from the type specimens and no live colour data were available. After having been re-diagnosed by TAN & NG (2005b), *B. rubra* became of interest to aquarists and importers alike, and appeared in the ornamental fish trade for the first time in 2007 (LINKE 2007). The reddish colour elements of the type specimens lead to the misconception that *B. rubra* is part of the *Betta splendens* group (WITTE 1997: 12) or even regarded as conspecific with Betta imbellis Ladiges, 1972 (SCHMIDT 1996, DONOSO-BÜCHNER & SCHMIDT 1999). The latter species is well known by its bright reddish colour in life (LINKE 2007, DONOSO-BÜCHNER & SCHMIDT 1999). Specimens labelled 'B. rubra' in the popular literature of the early twentieth century were actually a reddish form of Betta splendens (see RACHOW 1937). Betta rubra shares with the species of the *Betta splendens* group the lack, or at least strong reduction, of a second central stripe and a comparatively small head length. However, the additional description of B. rubra presented herein and discussion below make it apparent that it is not a member of the Betta splendens group. Besides the characters given in the diagnosis, *B. rubra* differs in being a mouthbrooder (see reproductive behaviour above), while the species of the B. splendens group are bubblenest builders (SCHMIDT 1996).

The genus Betta is divided into several species groups (TAN & NG 2005a, b). The groups are not necessarily based on synapomorphies but rather on superficial similarity of their members (Tan & Kottelat 1998). Tan & Ng (2005a, b) placed *B. rubra* in their *Betta foerschi* species group. Besides *B. rubra*, the *Betta foerschi* group currently consists of the following species (TAN & NG 2005a, 2006): B. foerschi Vierke 1978, B. strohi Schaller & Kottelat 1989 and B. mandor Tan & Ng 2006. Eidonomic features used in TAN & NG (2005a, b) to include *B. rubra* in the *foerschi* group are: presence of two vertical lighter coloured bars on opercle, vertical bars on body when preserved, general body shape. These, however, are trivial (vertical bars on opercle and body are present in many other species and likely plesiomorphic) or imprecise (no proportions of body shape are provided that separate these species from other species groups). Taxonomically these features are impractical for diagnosing a *Betta foerschi* group that includes *B*. rubra. Instead, the latter can be differentiated

from the species of the *Betta foerschi* group by the apomorphic characters or character states given in the diagnosis and comparative notes (see above). WITTE & SCHMIDT (1992) placed B. *rubra* in a group of its own. They based their conclusion mainly on the unusual broad chin bar, which appears as a triangular mark below the eye in preserved specimens. Beside this character (considered here as apomorphic) we find the bright iridescent light blue patch at pectoral fin origin in both sexes, the alternating black bars (with iridescent blue scales in life) and red blocks on flank ventrolaterally and (as compared with other species) the more ventrally situated central stripe (in correlation with the lack of the upper central and second central stripe) to be unique in the genus. These characters (or character states) are treated as apomorphic. The rising number of autapomorphies increases the necessity to recognize a taxonomically separate unit (STUESSY 1997). Since B. rubra is excluded from all the other proposed species groups as distinguished by TAN & NG (2005a) by key characters (see comparative notes), we argue that the patristic distance (counting apomorphies separating taxa), and thus the pheno-cladistic distinctness of *B. rubra* to the other species groups is sufficient to place it (in accordance with WITTE & SCHMIDT 1992) in a separate group.

The only other known species in the genus possessing a comparable patch at the pectoral fin origin is *Betta compuncta* from the upper Mahakam basin in Kalimantan Timur, Borneo; a member of the *Betta unimaculata* species group (TAN & NG 2006). In *B. rubra*, the patch is iridescent light blue in life and black when preserved; in *B. compuncta*, it is black in both live and preserved colouration. Hence, it seems more likely that both species have evolved this patch independently.

Caudal fin shape in *B. rubra* appears to be variable (see figs 1 and 3 and description above). Male specimens with rounded and lanceolate caudal fins have been collected from the same localities. Thus, the caudal fin shape in *B. rubra* is consequently not diagnostic, only informative. Male caudal fin shape has been repeatedly used as a diagnostic character to distinguish species

(e.g. *B. pallida* versus *B. prima* and *B. pulchra* versus *B. pugnax*) or species groups (TAN & TAN 1996, TAN & NG 2005a, KOTTELAT & NG 1994, SCHINDLER & SCHMIDT 2006). As variation in caudal fin shape is described also for *B. schalleri* (see KOTTELAT & NG 1994), the taxonomical value of the feature deserves to be critically reviewed per case.

A lectotype for the taxon *B. rubra* is listed in TAN & NG (2005a, b). However, none of these works contain a valid designation of a lectotype. Likewise, neither TAN & NG (2005a, b) nor ESCHMEYER & FRICKE (2012) provide any reference to a work, in which a lectotype is validly designated, and we were unable to locate one as well. From a taxonomical point of view it is not necessary to select a lectotype because there is no indication that the type series of *B. rubra* includes more than one species.

The type locality given by PERUGIA (1893) is Lago Toba, Siboga. 'Siboga' is obviously alternative spelling for Sibolga (cf. KOTTELAT et al. 1993), a seaport at the west coast of the province Sumatera Utera. REGAN (1910) and WEBER & DE BEAUFORT (1922) listed 'Lago Toba, Sumatra' as type locality. This enforced the incorrect impression that *B. rubra* inhabits the volcanic lake Toba at an altitude of over 900 m a.s.l. (e.g. VIERKE 1978). TORTONESE (1962) restricted the locality to 'Siboga [= Sibolga], Sumatra occidentale [= western Sumatra]'. As pointed out by TAN (2008), Lake Toba is not the type of habitat where fighting fish species are expected to occur. In fact, Betta species can usually be found in the lowlands or at the foothills of low mountain ranges. Betta rubra has not been identified in subsequent collections from the Lake (Volz 1904), and WITTE (1997) argued that *B. rubra* does not occur in Lake Toba.

Besides its taxonomical distinctness, *B. rubra* is also remarkable from a zoographical point of view. It is distributed in the lowlands of northwestern Sumatra where all major drainages empty into the Indian Ocean (see distribution provided above; WITTE & SCHMIDT 1992, TAN & NG 2005b). This region is hydrographically isolated from the eastern parts of the island by the Barisan Mountains which run parallel to the

coast line from the north to the south. Northwestern Sumatra harbours a rich endemic fish fauna and is treated as a separate ichthyofaunal province (LUMBANTOBING 2010). The examined specimens of *B. rubra* were collected in the vicinity of Meulaboh (north-western Sumatra, Aceh). In consideration of the information given by TAN & NG (2005a, b) and in accordance with WITTE & SCHMIDT (1992) and WITTE (1997), we conclude that *B. rubra* is restricted to the lowlands of north-western Sumatra (fig. 5). Hence, *B. rubra* is another example of an endemic species for this ichthyofaunal province.

The ichthyogeographic isolation from the species of the Betta foerschi group supports the view of the evolutionary uniqueness of *B. rubra*. The ichthyofaunal province (northwestern Sumatra; LUMBANTOBING 2010) corresponds to a presumed tropical forest refugium during the Last Glacial Maximum (MEIJAARD 2003). Forest refugia are believed to have a major impact on the allopatric speciation in Amazonia (HAFFER 2008). It is suspected that such refugia have played a major role in the evolution of species groups and subgenera within the tropical aplocheiloid killifish families (HUBER 1998). Since killifish occupy similar ecological niches in tropical forest areas of South America and West Africa as do members of the genus *Betta* in Southeast Asia (HUBER 1998, pers. obs.), it is not unlikely that such macro-ecological processes force allopatric speciation and the development of independent evolutionary assemblages within the genus *Betta* as well. The biogeography, and in particular the fluctuating sea levels over geological time, palaeo-climates, landform developments and the distribution of rainforest refugia and swamp areas (see VORIS 2000, MEIJAARD 2003) are not yet included in taxonomic studies on Southeast Asian fighting fishes. It is well known that such processes influenced the evolution of species and species groups in Southeast Asia (e.g. MEIJAARD & GROVES 2004, ALFARO et al. 2004). Hence, the incorporation of such data may support the hypotheses about the taxonomy and speciation within Betta.

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## Appendix

We provide a translation of the original description by Perugia 1893, originally published in Italian.

## Betta rubra, n. sp.

D. 8. A. 22. Ll. 30.

Lake Toba. Siboga.

The body height is a quarter of the total length, the head length is one third of the total length. The mouth is shaped obliquely, jaws of the same length and with very small teeth. The eye diameter is relatively large; it is about a quarter of the head length and equal to the interorbital width. The scales on the head have the same size as the scales on the body; on the pre-operculum are three series, all haired.

The dorsal fin, with eight soft rays, has the penultimate ray elongate and when folded back reaching to the middle of the caudal fin. The anal fin also has the last rays elongated. The pectorals are as long as the head. The ventral fins have the outer ray elongate and reach the 6th or 7th ray of the anal fin.

Lateral line absent.

The general colouration of the body and the fins is red with five to six large dark blotches on the flanks.