

THE FIGHTING FISHES (TELEOSTEI: OSPHRONEMIDAE: GENUS *BETTA*) OF SINGAPORE, MALAYSIA AND BRUNEI

Tan Heok Hui

Department of Biological Sciences, National University of Singapore,
Kent Ridge, Singapore 119260, Republic of Singapore
Email: dbsth@nus.edu.sg

Peter K. L. Ng

Department of Biological Sciences, National University of Singapore,
Kent Ridge, Singapore 119260, Republic of Singapore
Email: dbsngkl@nus.edu.sg

ABSTRACT. – The taxonomy of the fighting fishes of the genus *Betta* from Singapore, Malaysia and Brunei are revised, and 23 species are recognised. The taxonomy of some allied species in other parts of Southeast Asia are also considered. Species groups for the entire genus are redefined and two new groups are recognised: the *B. bellica* and *B. albimarginata* groups. *Betta rubra* is tentatively referred to the *B. foerschi* group. The *B. pugnax* and *B. splendens* groups are the most widely distributed; whilst those of the *B. coccina* and *B. waseri* groups are the most restricted, being essentially stenotopic blackwater species. The problematic *B. pugnax* group is revised and two new species, *B. stigmosa* and *B. lehi*, are described from Peninsular Malaysia and Sarawak, respectively. *Betta climacura* is regarded as a junior subjective synonym of *B. akarensis*; and a new species from the group, *B. obscura*, is described from Kalimantan Tengah. *Betta ocellata* is redescribed from fresh material and regarded as distinct from *B. unimaculata*; and from this group, two new species: *B. gladiator*, from the Maliau Basin, Sabah; and *B. pallifina*, from Kalimantan Tengah, are described. *Betta taeniata* (*B. picta* group) is redescribed from fresh material and its range is extended to Kalimantan Barat. The taxonomy of *B. imbellis* (*B. splendens* group) is discussed and the complicated taxonomic status of *B. splendens* and *B. marchei* dealt with. *Betta marchei* is suppressed and *B. stiktos*, new species, from Cambodia is described.

KEY WORDS. – *Betta*, new species, Osphronemidae, taxonomy.

INTRODUCTION

Betta Bleeker, 1850, is the most speciose genus in the family Osphronemidae. Britz (1994, 1995, 2001) and Britz et al. (1995) recently included in the Osphronemidae species previously placed in the families Luciocephalidae and Belontiidae. The large number of species of *Betta* is probably due to several factors. The warm and humid climate of Southeast Asia provides a stable environment with numerous niches and habitats (Whitmore, 1986: 15). The presence of many types of water-bodies, e.g. rivers, ox-bow lakes, forest streams, open country streams, hill streams, freshwater and peat swamps supports a great diversity (see Kottelat & Ng, 1994). Many species are also adapted to survive in extreme environmental conditions, like in blackwaters with high acidity (pH between 3 and 5) in peat swamp forests. *Betta* species also tend to have ranges restricted to one or a few drainage systems, delimited by various obstacles like mountain ranges or large rivers (see Kottelat & Ng, 1994).

The genus as currently defined, contains 48 recognised species (Kottelat et al., 1993; Ng, 1993; Kottelat & Ng, 1994; Tan & Tan, 1994, 1996; Ng & Kottelat, 1994; Kottelat, 1994, 1995; Tan & Ng, 1996, 2004a; Tan, 1998; Tan & Kottelat, 1998a, 1998b; Tan & Lim, 2004; Tan & Ng, 2004). Six additional species are described here making it a total of 54 species known thus far from the genus (Table 1).

Preserved specimens of *Betta* are generally difficult to identify. Colour is helpful in distinguishing live specimens, but this is a character often difficult to use by ichthyologists unfamiliar with the infraspecific variation. Colour may be dependent upon maturity, sex, reproductive condition and geographic variation. Large and old specimens tend to be darker, which may mask body and opercle patterns, making species identifications even more difficult (Roberts, 1989; Kottelat et al., 1993; Kottelat & Ng, 1994). Juveniles are also taxonomically unusable in most instances. Their physiognomy is often quite different from that of the adult

(e.g. relatively larger eyes, proportionately larger heads, undeveloped or indistinct colour patterns, etc.) and most lack sufficient diagnostic characters to be useful (Ng, 1993). Meristic characters are generally conservative, especially within species groups. Species distinction based only on the presence, absence or number of spines in the dorsal and anal fins are often unreliable (Tan & Tan, 1996). Morphometrics are useful to distinguish certain species, but characters of given species groups are difficult to define objectively and may possess some geographic variation (see Tan & Tan, 1996). Morphometric characters are useful for distinguishing between species groups (e.g. *B. coccina* group), but is rather conservative for members within the same group (see Tan & Ng, 1996). Fin and head shapes are generally useful characters, especially when enough fresh material is available to ascertain intraspecific variation. For example, members of the *B. bellica* and *B. unimaculata* groups can be effectively separated by their head shapes (Tan & Ng, 1996; present study).

This present revision deals with the species native to Singapore, Malaysia (Peninsular Malaysia, Sarawak, Sabah) and Brunei; but also includes the description of three new species from Kalimantan Tengah and Cambodia. The feral *B. splendens* populations which are found in Peninsular Malaysia and Singapore are excluded in this study (Tweedie, 1952a, b; Lim & Ng, 1990; Ng et al., 1993). Certain species found just outside the present area of study have also been included (e.g. *B. unimaculata*, *B. patoti*) to clarify their taxonomic status and aid in the general discussions.

MATERIAL AND METHODS

The species concept used is the phylogenetic species concept (Cracraft, 1989; Warren, 1992; see discussion in Kottelat, 1997, and methods in Tan & Kottelat, 1998a). For the literature citation, only primary scientific literature is used. However, in some cases, useful aquarium literature has been cited, for instance the books by Linke (1991) and Kubota et al. (1996). These two books are covered, even though the coverage of the genus *Betta* is incomplete and certain information is inaccurate (e.g. locality data, scientific names) primarily because of their excellent illustrations and synopses (where English versions are available). Other aquarium literature are used only when useful information on breeding and habitats are provided.

Specimens examined are deposited in the Natural History Museum, London (ex British Museum of Natural History, BMNH); Muzium Brunei, Brunei Darussalam (BRM); California Academy of Sciences, San Francisco (CAS); the collection of Maurice Kottelat, Cornol (CMK); Danum Valley Field Centre, Lahad Datu, Sabah (DVFC); Field Museum of Natural History, Chicago (FMNH); Muséum d'Histoire Naturelle, Genève (MHNG); Muséum National D'Histoire Naturelle, Paris (MNHN); Museo Civico di Storia Naturale, Genova (MSNG); Research and Development Centre for Biology (ex Museum Zoologicum Bogoriense), The Indonesian Institute of Sciences (MZB); Nationaal

Natuurhistorisch Museum, Leiden (ex Rijksmuseum van Natuurlijke Historie, RMNH); Sabah Museum, Kota Kinabalu, Sabah (SBM); Sabah Parks Collection, Sabah (SBP); Sarawak Museum, Kuching, Sarawak (SM); Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main (SMF); Universiti Malaysia Sabah, Sabah (UMS); U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Instituut voor Systematiek and Populatiebiologie, Universiteit van Amsterdam (ZMA); Zoologisches Museum der Universität, Zürich (ZMZ); and the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC).

Toponymy: Kampung = village; Batang or Sungai = river; Bukit or Gunung = hill; Tasik = lake; Pulau = island. Abbreviations used: SL = standard length; TL = total length; and HL = head length.

A diagnosis of each species group is provided and this is followed by the treatment of each species covered in the study area. The term 'species group' is used here for an assemblage of species sharing a set of diagnostic characters and which may or may not be a monophyletic lineage. For the two recently revised species groups, *B. coccina* and *B. waseri*, only a diagnosis of each species is provided. Instead, the reader is referred to Witte & Schmidt (1992), Ng & Kottelat (1992, 1994) and Tan (1998) for the detailed reports on the *B. coccina* and *B. waseri* groups.

All measurements were taken point to point on the left side of the specimens with dial calipers allowing readings to the nearest 0.05 mm. Methods for obtaining meristic and morphometric data follow Witte & Schmidt (1992), except that all measurements are taken from point to point and that the predorsal scale counts are counted continuously (following Ng & Kottelat, 1994). Chin-bar is used to refer to the dark thin stripe running from throat area below snout to eye, just under the preorbital stripe (Fig. 1). The pattern of dark, narrow, often slightly curved bars perpendicular to the rays on the interradial membranes of the dorsal, caudal and anal fins are called dorsal, caudal and anal transverse bars (Fig. 2) (Tan & Kottelat, 1998a).

Freshly caught specimens were fixed in 10% formalin solution for one to two weeks, then placed into water for leaching before permanent storage in 70-75% denatured ethanol. Colour descriptions are based on live and acclimatised specimens unless otherwise stated. The keys provided are for use with mature specimens only.

TAXONOMIC KEYS

The keys to the species groups and members of the species group from the study area are based upon morphological features the authors feel are easy to use. The size ranges are based on wild specimens. Captive specimens can generally grow larger.

Table 1. *Betta* species list and localities

<i>Betta bellica</i> group	
<i>Betta bellica</i> Sauvage, 1884: Malaysia (Selangor*, Perak, Pahang, Johor); Sumatra (North Sumatra)	
<i>Betta simorum</i> Tan & Ng, 1996: Sumatra (Jambi*, Riau, South Sumatra)	
<i>Betta pugnax</i> group	
<i>Betta pugnax</i> (Cantor, 1850): Malaysia (Pulau Penang*, Kedah, Terengganu, Pahang, Selangor, Johor); Singapore; Sumatra (Riau, Jambi), Anambas	
<i>Betta fusca</i> Regan, 1910: Sumatra (North Sumatra*)	
<i>Betta schalleri</i> Kottelat & Ng, 1994: Sumatra (Banka*)	
<i>Betta prima</i> Kottelat, 1994: Thailand (East Thailand*); Cambodia (West Cambodia)	
<i>Betta enisae</i> Kottelat, 1995: Kalimantan Barat (Kapas*)	
<i>Betta pulchra</i> Tan & Tan, 1996: Malaysia (Johor*)	
<i>Betta breviobesus</i> Tan & Kottelat, 1998: Kalimantan Barat (Kapas*)	
<i>Betta lehi</i> , new species: Sarawak (south Sarawak*); Kalimantan Barat (Kapas)	
<i>Betta stigmatosus</i> , new species: Malaysia (Terengganu*)	
<i>Betta akarensis</i> group	
<i>Betta akarensis</i> Regan, 1910: Sarawak (north to central* Sarawak); Brunei (Belait, Tutong and Bandar Seri Begawan Districts)	
<i>Betta balunga</i> Herre, 1940: Sabah (Tawau*); Kalimantan Timur (Sebuku, Mahakam)	
<i>Betta chini</i> Ng, 1993: Sabah (Beaufort*)	
<i>Betta pinguis</i> Tan & Kottelat, 1998: Kalimantan Barat (Kapas*)	
<i>Betta aurigans</i> Tan & Lim, 2004: Natuna Besar*	
<i>Betta ibanorum</i> Tan & Ng, 2004: Sarawak (south Sarawak*)	
<i>Betta obscura</i> , new species: Kalimantan Tengah (Barito*)	
<i>Betta unimaculata</i> group	
<i>Betta unimaculata</i> (Popta, 1905): Kalimantan Timur (Kayan*, Howong*)	
<i>Betta macrostoma</i> Regan, 1910: Sarawak (north Sarawak*); Brunei (Belait District)	
<i>Betta patoti</i> Weber & de Beaufort, 1922: Kalimantan Timur (Balikpapan*, Samarinda)	
<i>Betta ocellata</i> de Beaufort, 1933: Sabah (Sandakan*, Kinabatangan, Lahad Datu, Tawau); Kalimantan Timur (Sebuku)	
<i>Betta gladiator</i> , new species: Sabah (Maliau*)	
<i>Betta pallifina</i> , new species: Kalimantan Tengah (upper Barito*)	
<i>Betta picta</i> group	
<i>Betta picta</i> (Valenciennes, in Cuvier & Valenciennes, 1846): Java (Bogor*, Bandung, Yogyakarta)	
<i>Betta taeniata</i> Regan, 1910: Sarawak (south Sarawak*); Kalimantan Barat (Kapas)	
<i>Betta simplex</i> Kottelat, 1994: Thailand (south Thailand - Krabi*)	
<i>Betta falx</i> Tan & Kottelat, 1998: Sumatra (Jambi*, Sumatra Utara)	
<i>Betta splendens</i> group	
<i>Betta splendens</i> Regan, 1910: Thailand (central Thailand*)	
<i>Betta smaragdina</i> Ladiges, 1972: Thailand (east and north* Thailand)	
<i>Betta imbellis</i> Ladiges, 1975: Thailand (south Thailand); Malaysia (Selangor*, Pulau Penang, Perak, Kedah, Terengganu, Johor); Singapore; Sumatra (North Sumatra)	
<i>Betta stiktos</i> , new species: Cambodia*	
<i>Betta coccina</i> group	
<i>Betta coccina</i> Vierke, 1979: Sumatra (Jambi*, Riau); Malaysia (Johor)	
<i>Betta tussya</i> Schaller, 1985: Malaysia (Pahang*)	
<i>Betta persephone</i> Schaller, 1986: Malaysia (Johor*)	
<i>Betta rutilans</i> Witte & Kottelat, in Kottelat, 1991: Kalimantan Barat (Kapas*)	
<i>Betta brownorum</i> Witte & Schimdt, 1992: Sarawak (central* to south Sarawak; Kalimantan Barat)	
<i>Betta livida</i> Ng & Kottelat, 1992: Malaysia (Selangor*)	
<i>Betta miniopinna</i> Tan & Tan, 1994: Sumatra (Riau - Bintan*)	
<i>Betta burdigala</i> Kottelat & Ng, 1994: Sumatra (Banka*)	
<i>Betta waseri</i> group	
<i>Betta waseri</i> Krummenacher, 1986: Malaysia (Pahang*, Terengganu, Kuantan)	
<i>Betta hipposideros</i> Ng & Kottelat, 1994: Malaysia (Selangor*); Sumatra (Riau)	
<i>Betta spilotogena</i> Ng & Kottelat, 1994: Sumatra (Riau - Bintan*, Singkep)	
<i>Betta chloropharynx</i> Kottelat & Ng, 1994: Sumatra (Banka*)	
<i>Betta renata</i> Tan, 1998: Sumatra (Jambi*, South Sumatra)	
<i>Betta pi</i> Tan, 1998: Thailand (south Thailand - Sungai Kolok*); Malaysia (Kelantan)	

Table 1. *Betta* species list and localities (Cont'd)

<i>Betta edithae</i> group	
<i>Betta edithae</i> Vierke, 1984: Kalimantan Selatan*, Tengah and Barat; Sumatra (Riau - Bintan, Banka, Biliton)	
<i>Betta foerschi</i> group	
<i>Betta foerschi</i> Vierke, 1979: Kalimantan Tengah (Mentaya*)	
<i>Betta strohi</i> Schaller & Kottelat, 1989: Kalimantan Tengah (Sukamara*)	
? <i>Betta rubra</i> Perugia, 1893: Sumatra (North Sumatra*, Aceh)	
<i>Betta anabatooides</i> group	
<i>Betta anabatooides</i> Bleeker, 1851: Kalimantan Selatan* and Tengah	
<i>Betta albimarginata</i> group	
<i>Betta albimarginata</i> Kottelat & Ng, 1994: Kalimantan Timur (Sebuku*)	
<i>Betta channoides</i> Kottelat & Ng, 1994: Kalimantan Timur (Mahakam*)	
<i>Betta dimidiata</i> group	
<i>Betta dimidiata</i> Roberts, 1989: Kalimantan Barat (Kapuas*)	

* type locality

Key to the *Betta* species groups occurring in Malaysia, Singapore and Brunei

- 1. Males with dark iridescent opercle scales when alive; with darkly pigmented opercle and throat when preserved 2
- Males without dark iridescent opercle scales when alive; opercle and throat not darkly pigmented when preserved 6
- 2. Body brown; iridescent opercle scales blue or green when alive; chin-bar present or absent (Fig. 1) 3
- Body clay-yellow; iridescent opercle scales gold (present in mature male of all species except *B. tomi*) when alive; throat with black blotches which may join with black lower jaw (Fig. 3); chin-bar absent *Betta waseri* group
- 3. Unpaired fins without broad, coloured margins when alive, thin dark margin may be present when preserved; chin-bar present or absent; adult size small (SL less than 40 mm) or large (SL more than 60 mm) 4
- Unpaired fins with broad iridescent green or blue margin when alive, dark when preserved (*B. taeniata* mature males) (Fig. 4); chin-bar present; adult size medium (SL between 40 and 60 mm) *Betta picta* group
- 4. Caudal fin rounded (Fig. 5a); caudal transverse bars absent or present; chin-bar present or absent; adult size large or small, body depth variable 5
- Caudal fin lanceolate (Fig. 5b-c); caudal transverse bars usually present (mature male) (Fig. 2); chin-bar present; adult size medium to large, body relatively stocky (body depth 24-37% SL) *Betta pugnax* group
- 5. Body depth 18.5-24.7% SL; opercle scales with green iridescence or red patch when alive; caudal transverse bars present or absent, or caudal fin with black margin; pelvic fins with distinct filamentous anterior rays; adult size large (SL more than 60 mm) *Betta unimaculata* group
- Body depth 24.2-32.2% SL; opercle scales with green iridescence when live; caudal transverse bars absent or present, caudal fin with red distal crescent margin when alive, yellowish when preserved (Fig. 5a); pelvic fins with all rays elongate; adult size small (SL less than 40 mm) *Betta splendens* group
- 6. Body brown; iridescent green scales on body, lateral median iridescent scales absent; pelvic fin hyaline, tip white when alive; adult size medium to large (SL more than 40 mm) 7
- Body red or black; no iridescent scales on body, lateral median iridescent green scales present in some species (Fig. 6a); pelvic fin red or black, pelvic fin tip black, white or green when alive; adult size small (SL 25-40 mm) *Betta coccina* group
- 7. Head large; caudal transverse bars distinct in male; lanceolate caudal fin with 2-3 median rays elongated; anal fin with posterior 1-2 rays elongated into filaments in male; anal-fin rays 27-30; dorsal-fin rays 8-11 *Betta akarensis* group
- Head small; caudal transverse bars absent; rounded caudal fin with 4-6 median rays elongated into filaments; anal fin with posterior 3-4 rays elongated into filaments in male; anal-fin rays 30-33; dorsal-fin rays 11-13 *Betta bellica* group

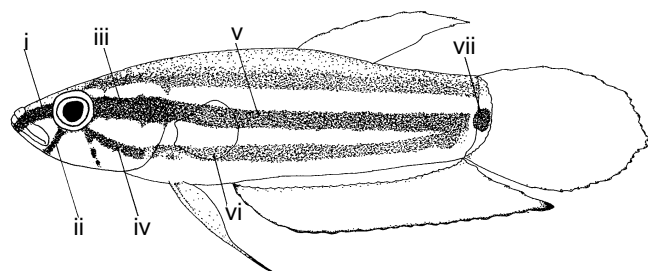


Fig. 1. Schematic diagram of an adult fighting fish showing: i) preorbital stripe, ii) chin-bar, iii) postorbital stripe, iv) second postorbital stripe, v) central stripe, vi) second central stripe, vii) black spot at base of caudal fin.

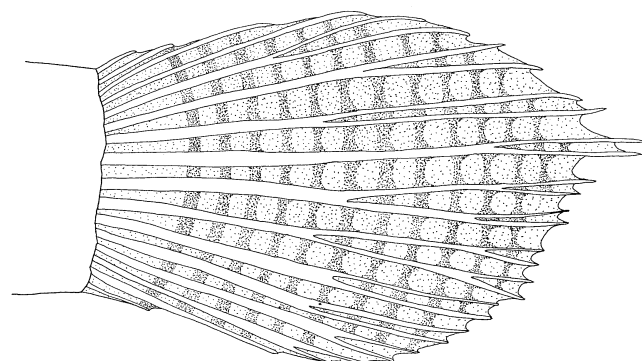


Fig. 2. Transverse bars on caudal fin (similar bars on dorsal and anal fins).

Key to the *Betta* species

The key is for 47 out of 55 species of *Betta* recognised and is only for the species groups covered in the study area. The species covered in the study area are indicated by an asterisk (*). All characters listed here are for mature specimens only. When colour notes are used, they are for live and aquarium-acclimatised specimens.

***Betta bellica* group**

1. Head slanted, dorsal surface distinctly concave just behind eye; pelvic fin filamentous tip extending up to 14th anal ray (pelvic fin length 31.3-48.3% SL); lateral scales 33¹/₂-35 (mode 34); adpressed pelvic fin reaching beyond anal-fin origin (distance between pelvic and anal-fin origins 8.5-13.1% SL, mean 9.9). Central to southern Sumatra, Kalimantan Barat (Kapuas) *Betta simorum*
- Head rounded, dorsal surface not concave just behind eye; pelvic fin filamentous tip extending up to 8th anal ray (pelvic fin length 23.6-38.8% SL); lateral scales 33-34 (mode 33); adpressed pelvic fin not reaching anal-fin origin (distance between pelvic and anal-fin origins 10.5-12.6% SL, mean 11.2). Peninsular Malaysia, northern Sumatra *Betta bellica**

***Betta pugnax* group**

1. Dark anal and caudal fin distal margins when preserved (blueish when alive) 2
- No dark anal and caudal fin distal margins when preserved 5
2. No dorsal, caudal and anal transverse bars in male and female; no interrupted second postorbital stripe on opercle in male and female (Fig. 1); interorbital width 64-84% postorbital length 3
- Dorsal, caudal and anal transverse bars present in male and female (Fig. 2); interrupted second postorbital stripe on

- opercle present in male and female; interorbital width 62-65% postorbital length. Peninsular Malaysia (Terengganu) *Betta stigmosa**
3. No caudal transverse bars; lateral scales 28-30; predorsal length 62.1-67.5% SL 4
- Caudal transverse bars present; lateral scales 26-28; predorsal length 67.3-70.3% SL. Kalimantan Barat (middle Kapuas) *Betta enisae*
4. Two black marks below postorbital stripe on opercle in female and juvenile (Fig. 6b); chin-bar present; orbital diameter 27.2-32.2% HL; interorbital width 70-84% postorbital length. Southern Sarawak, Kalimantan Barat (lower Kapuas) *Betta lehi**
- No black marks below postorbital stripe on opercle; no chin-bar; orbital diameter 24.2-28.5% HL; interorbital width 48-69% postorbital length. Kalimantan Barat (upper Kapuas) *Betta brevibesues*
5. No chin-bar 6
- Chin-bar present (Fig. 1) 7
6. Anal-fin rays 27; dorsal-fin rays 10-11; lateral scales 31; predorsal scales 17-19. Banka *Betta schalleri*
- Anal-fin rays 24-25; dorsal-fin rays 8-9; lateral scales 29; predorsal scales 22-23. Northern Sumatra *Betta fusca*
7. No complete second postorbital stripe on opercle; caudal transverse bars present; predorsal scales 18-21 (mode 20); preanal length 40.6-51.2% SL 8
- Complete second postorbital stripe on opercle (Fig. 1); no caudal transverse bars; predorsal scales 20-22 (mode 22); preanal length 50.6-54.8% SL. Cambodia, eastern Thailand *Betta prima*
8. Caudal fin narrowly lanceolate in male (Fig. 5c); opercle scales iridescent green when alive; body depth 26-37% SL; pelvic-fin length 29.1-53.2% SL; adult size medium (SL up to 55 mm); stenotopic blackwater species. Peninsular Malaysia (Pontian) *Betta pulchra**
- Caudal fin broadly lanceolate in male (Fig. 5b); opercle scales iridescent blue when alive; body depth 24-32% SL; pelvic-fin length 26.6-43.8% SL; adult size large (SL up to 67 mm); clear to brown water species. Peninsular Malaysia, Singapore, Sumatra (Riau), Anambas, Natuna *Betta pugnax**

***Betta akarensis* group**

1. Opercle pigmentation absent to relatively dense, with 3 or fewer dark marks below postorbital stripe (Fig. 7); body slender to relatively stocky (body depth 23.3-32.7% SL); dorsal-fin origin above lateral scales 14-18 2
- Opercle pigmentation dense, with 5-7 dark marks below postorbital stripe (Fig. 7d); body stocky (body depth 30.6-31.6% SL); dorsal-fin origin above lateral scales 18-19. Kalimantan Barat (Upper Kapuas) *Betta pinguis*

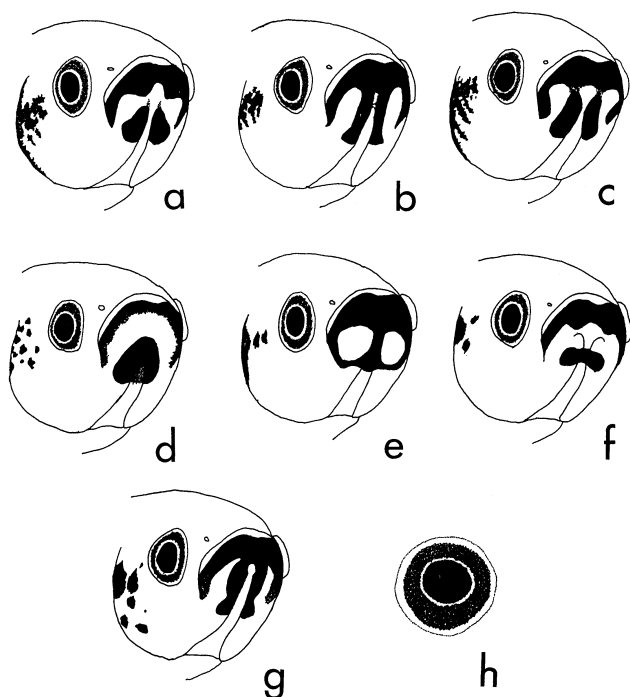


Fig. 3. Schematic diagrams of throat patterns of the *Betta waseri* group and unique eye coloration pattern: a) *B. waseri*, b) *B. hipposideros*, c) *B. tomi*, d) *B. spilotogeta*, e) *B. chloropharynx*, f) *B. renata*, g) *B. pi*, h) unique eye coloration pattern.

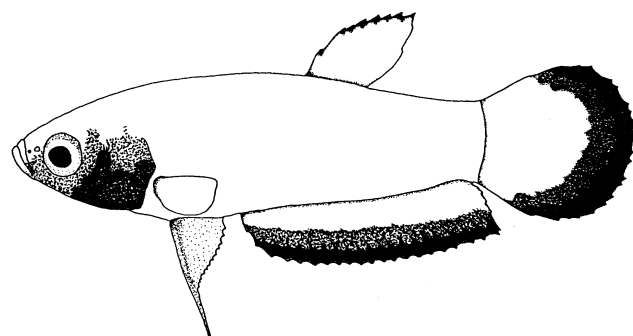


Fig. 4. Schematic diagram of an adult *Betta taeniata* having unpaired fins with broad iridescent darkly pigmented margin.

- 2. Predorsal scales 21-26; dorsal-fin rays modally 9; subdorsal scales modally 5-6; vertebrae 29-32 (modes 30, 31) 3
- Predorsal scales 19-21 (mode 20); dorsal-fin rays modally 10; subdorsal scales modally 6¹/₂; vertebrae 28-30 (mode 28). Kalimantan Tengah (Barito) *Betta obscura*
- 3. Opercle with second postorbital stripe (complete or interrupted) (Fig. 1) 4
- Opercle without second postorbital stripe 6
- 4. Opercle with interrupted second postorbital stripe; lateral scales 29-31 (mode 31); vertebrae 29-31; adult size medium (SL 40-60 mm) 5
- Opercle with complete second postorbital stripe; lateral scales 31-33 (mode 32); vertebrae 31-32; adult size large (SL 60-80 mm). Central to northern Sarawak, Brunei *Betta akarensis**
- 5. Eye yellow when alive; lateral scales 30-31; preanal length 42.6-45.7% SL; anal-fin base length 54.8-58.5% SL. Western Sabah *Betta chini**
- Eye orange to red when alive; lateral scales 29-30; preanal length 48.5-52.6% SL; anal-fin base length 47.8-55.4% SL. Eastern Sabah, Kalimantan Timur (Sebuku) *Betta balunga**
- 6. Iridescent green to blue on posterior half of scales when alive; lateral scales 30-32 (mode 30); predorsal scales 21-23 (mode 22); anal-fin rays 27-29 (mode 28). Southern Sarawak *Betta ibanorum**
- Gold scales on belly and body when alive; lateral scales 33-33¹/₂ (33¹/₂); predorsal scales 24-26; anal-fin rays 29-30 (mode 30). Natuna (Pulau Bunguran) *Betta aurigans*

***Betta unimaculata* group**

- 1. Male with yellowish to brown body; no red blotch on opercle, opercle scales iridescent; no dorsal fin ocellus; dorsal-fin rays 6-9; anal-fin rays 27-33; subdorsal scales 4-6¹/₂ ... 2
- Male with red body; a red blotch on opercle, opercle scales not iridescent; dorsal fin ocellus present (Fig. 8a); dorsal-fin rays 9-11; anal-fin rays 25-28 (mode 27); subdorsal scales 6-8

- (mode 7). Brunei, northern Sarawak *Betta macrostoma**
- 2. Dark opercular scales present when preserved; no dark vertical bars on body; caudal fin rounded or lanceolate; dorsal, caudal and anal transverse bars present; anal-fin rays 27-31 3
- No dark opercular scales absent when preserved; 10-14 dark vertical bars on lower half of body; caudal fin lanceolate; no transverse bars on dorsal, caudal and anal; anal-fin rays 30-33 (mode 31). Kalimantan Timur (Balikpapan) *Betta patoti*
- 3. Sheath scales on anal base; pectoral fin rays 11-14 (mode 12 or 13); lateral scales 31-34 (mode 32 or 33) 4
- No sheath scales on anal base; pectoral fin rays 16-17 (mode 17); lateral scales 34-36 (mode 35). Sabah (Maliau) *Betta gladiator**
- 4. Female with subdistal margin of anal fin uniformly coloured; subdorsal scales modally 5 or 5¹/₂; predorsal length 67.7-73.0% SL; head width 19.6-24.0% SL 5
- Female with subdistal margin of anal fin orange when live, hyaline when preserved; subdorsal scales modally 6; predorsal length 64.6-69.4% SL; head width 17.7-20.8% SL Kalimantan Tengah (Barito) *Betta pallifina*
- 5. Head blunt, slightly truncate (Fig. 8b); anal-fin rays 27-30 (mode 28 or 29); lateral scales 31-33 (mode 32); length of anal-fin base 45.9-53.7% SL; length of dorsal-fin base 7.9-10.4% SL; head width 19.6-21.8% SL. Kalimantan Timur (Kayang, Howong) *Betta unimaculata*
- Head pointed, slightly conical (Fig. 8c); anal-fin rays 30-31 (mode 30); lateral scales 32-34 (mode 33); length of anal-fin base 52.2-54.5% SL; length of dorsal-fin base 10.5-11.3% SL; head width 21.0-24.0% SL. Sabah, Kalimantan Timur (Sebuku) *Betta ocellata**

***Betta picta* group**

- 1. Male with blueish to greenish iridescent opercle scales and chin-bar indistinct; body depth 25.3-32.2% SL; length of anal-fin base 48.3-52.7% SL 2

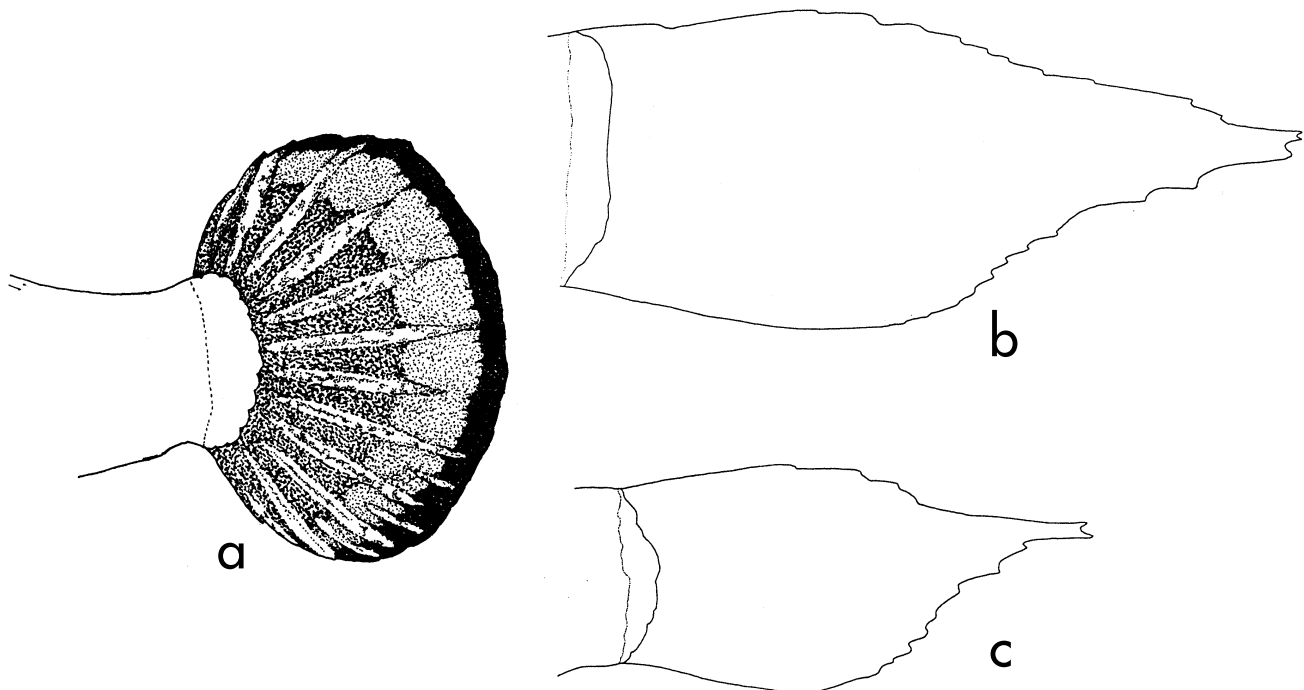


Fig. 5. Schematic diagram of caudal fins: a) rounded caudal fin with darkly pigmented distal margin (*B. imbellis*), b) broadly lanceolate caudal fin (*B. pugnax*), c) narrowly lanceolate caudal fin (*B. pulchra*).

- Male with yellowish gold to greenish-blue iridescent opercle scales, chin-bar distinct and part of second postorbital stripe visible; body depth 21.5-28.0% SL; length of anal-fin base 42.6-50.3% SL 3
- 2. Body and fins yellowish, head blackish, iridescent blue scales present on dorsal half of body in male; anal-fin rays 23-26 (mode 26); transverse scales 9-9½ (mode 9½); predorsal length 62.4-67.7% SL; head length 30.3-34.5% SL; body depth 25.3-30.1% SL. Southern Sarawak, Kalimantan Barat (Kapuas) *Betta taeniata**
- Body and fins pale reddish, head dark reddish, no iridescent blue scales on body in male; anal-fin rays 23-24 (mode 24); transverse scales 9½-11½ (mode 11½); predorsal length 66.7-69.8% SL; head length 34.6-37.2% SL; body depth 29.3-32.2% SL. Southern Thailand (Krabi) *Betta simplex*
- 3. Opercle scales iridescent yellowish gold; blueish anal and caudal fin margins; faint dorsal transverse bars in male; faint caudal transverse bars in female; dorsal-fin origin above 12-14th lateral scale. Java (Bogor, Bandung, Ambarawa) *Betta picta*
- Opercle scales iridescent greenish blue; reddish anal and caudal fin margins; distinct dorsal transverse bars in male; distinct caudal transverse bars female; dorsal-fin origin above 11-12th lateral scale. Sumatra (Sumatra Utara, Jambi) *Betta falx*

Betta splendens group

- 1. Iridescent blue or green scales on opercle, fins iridescent blue or green in male; head and body slender (body depth 24.2-30.1% SL) 2
- No iridescent scales on opercle, with parallel red vertical bars, fins blue, green or red in male; head and body stocky (body depth 27.1-32.2% SL). Central Thailand *Betta splendens*
- 2. No transverse bars on caudal fin; body with more than 8 vertical rows of dark marks on posterior edge of scales; lateral scales 29-32 (mode 30-31); male with chin-bar, postorbital and second postorbital stripes distinct when preserved 3
- Transverse bars on caudal fin in male and female; body with 6-7 vertical rows of dark marks on posterior edge of scales; lateral scales 31-34 (mode 33); male with only second

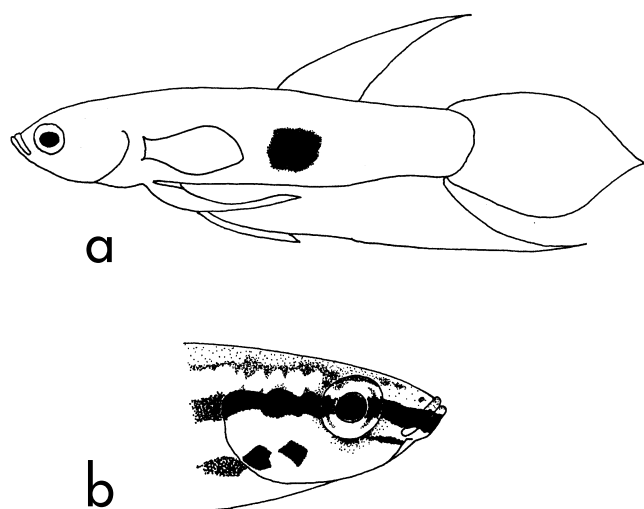


Fig. 6. a) Schematic outline of *Betta livida* showing median lateral blotch, b) head of *B. lehi* showing interrupted second postorbital stripe, usually present as a series of two black blotches.

- postorbital stripes distinct when preserved. Cambodia *Betta stiktos*
- 3. Body dark brown to black, head blackish; opercle with iridescent blue scales; fins iridescent blue; no caudal transverse bars; caudal fin iridescent blue with distal red crescent margin (Fig. 5a); distal half of posterior anal-fin rays red. Southern Thailand, Peninsular Malaysia, northern Sumatra *Betta imbellis**
- Body light brown, head brown; opercle with iridescent green scales; fins reddish with iridescent green rays; caudal transverse bars present; no distal red crescent margin on caudal fin; distal half of posterior anal-fin rays not red. Northern and eastern Thailand, Laos .. *Betta smaragdina*

Betta coccina group

- 1. Body blackish; pelvic fin blackish or red; adult size 25-30 mm SL 2
- Body reddish; pelvic fin red; adult size 30-40 mm SL 3
- 2. Dorsal surface of head behind eye sloping gently; pelvic fin often blackish, sometimes red; predorsal scales 17-18; lateral scales 27-29. Peninsular Malaysia (Ayer Hitam, Muar) ... *Betta persephone**
- Dorsal surface of head behind eye sloping steeply; pelvic fin always red; predorsal scales 20; lateral scales 30-31. Sumatra (Bintan) *Betta miniopinna*
- 3. A mid-lateral iridescent green blotch on body (Fig. 6a) 4
- No mid-lateral iridescent green blotch on body 6
- 4. Male and female with a mid-lateral iridescent green blotch on body; tip of pelvic fin green or white 5

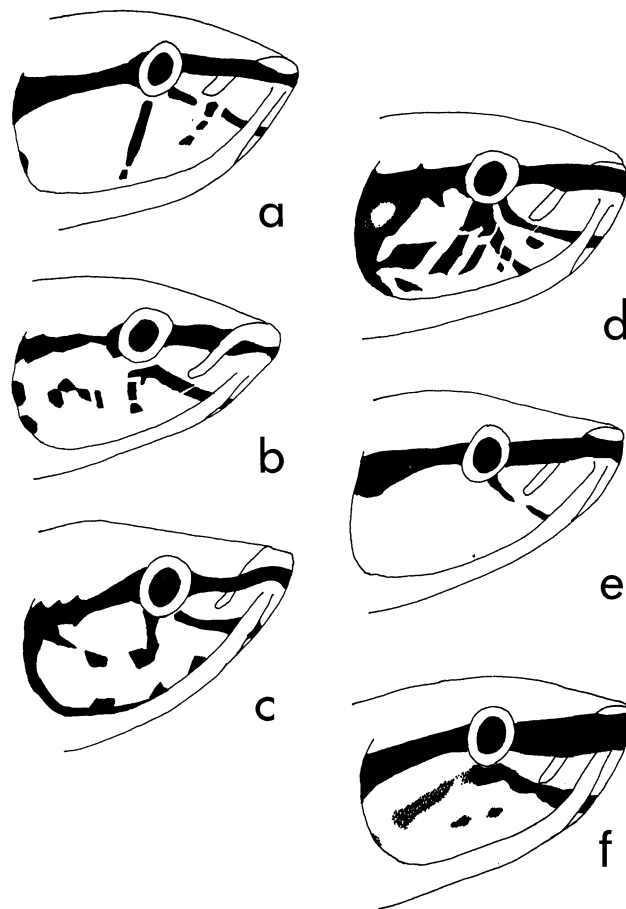


Fig. 7. Schematic diagrams of opercle patterns of the *Betta akarensis* group: a) *B. akarensis*, b) *B. balunga*, c) *B. chini*, d) *B. pinguis*, e) *B. ibanorum* and *B. aurigans*, f) *B. obscura*.

- Only male with a mid-lateral iridescent green blotch on body; tip of pelvic fin black *Betta coccina**
- 5. Discrete iridescent green spots on median fins; parallel vertical iridescent gold bars on opercle; tip of pelvic fin wide, iridescent green; body dark red. Peninsular Malaysia (Selangor) *Betta livida**
- No discrete iridescent green spots on median fins; no parallel vertical iridescent gold bars on opercle; tip of pelvic fin filamentous, white; body magenta red. Southern to central Sarawak *Betta brownorum**
- 6. No discrete iridescent green spots on median fins; subdorsal scales 8-10; dorsal-fin rays 11-12; anal-fin rays 27-28 7
- Discrete iridescent green spots on median fins; subdorsal scales 11-11½; dorsal-fin rays 14-15; anal-fin rays 24-26. Sumatra (Banka) *Betta burdigala*
- 7. Faint parallel vertical iridescent gold bars on opercle; body reddish-orange with darker central and second central stripes; subdorsal scales modally 8. Peninsular Malaysia (Pahang) *Betta tussyaе**
- No faint parallel vertical iridescent gold bars on opercle; body uniform deep red; subdorsal scales modally 9. Kalimantan Barat (Kapuas) *Betta rutilans*

Betta waseri group

1. Dark blotch on throat not joined to black lower lip (Fig. 3) .. 2
- Dark blotch on throat joined to black lower lip (Fig. 3) 5
2. Anal fin never with dark distal margin; throat pattern with non-elongated median dark blotch; subdorsal scales 5½-7 3
- Anal fin usually with broad and distinct dark green distal margin; throat pattern with elongated semi-horseshoe dark blotch (Fig. 3c); subdorsal scales 5-5½ (mode 5). Peninsular Malaysia (Johor) *Betta tomi**
3. Throat pattern with two discrete or semi-fused median dark blotches; no dorsal and caudal transverse bars; subdorsal scales 5½-6½ (5½ or 6); lateral scales 31-32½ (mode 32); anal-fin rays 28-31 (mode 30) 4
- Throat pattern with a single median kidney-shaped dark blotch (Fig. 3f); faint dorsal and caudal transverse bars; subdorsal scales 6-7 (6½); lateral scales 31-32 (mode 31); anal-fin rays 28-31 (mode 29). Central Sumatra *Betta renata*
4. Throat with tear-drop shaped black blotches (Fig. 3a); opercle not spotted, with dark blotch on posterior edge; subdorsal scales 6-6½ (mode 6); postdorsal scales 10½-12 (mode 11); body depth 23.1-27.6% SL. Peninsular Malaysia (Pahang, Terengganu) *Betta waseri**
- Throat with a median pear-shaped black blotch (Fig. 3d); opercle with 7 or more spots; subdorsal scales 5½-6 (mode 5½); postdorsal scales 10-10½ (mode 10); body depth 25.6-28.7% SL. Sumatra (Bintan) *Betta spilotogena*
5. Throat with a pair of elongated black bars; no iridescent greenish-gold opercle scales 6
- Throat with ∞-shaped black pattern (Fig. 3e); iridescent greenish-gold opercle scales. Sumatra (Banka) ... *Betta chloropharynx*
6. Throat with horseshoe shaped black mark (Fig. 3b); dorsal and caudal transverse bars present; anal fin without dark distal margin; lower margin of opercle brown; subdorsal scales 6½-7 (mode 6½); postdorsal scales 9-10 (mode 9½); lateral scales 31-32 (mode 32). Peninsular Malaysia (Selangor), central Sumatra *Betta hipposideros**
- Throat with pi (π)-shaped black mark (Fig. 3g); no dorsal and caudal transverse bars; anal fin with broad and distinct dark blue distal margin; lower margin of opercle black; subdorsal scales 5½-6 (mode 6); postdorsal scales 11-12 (mode 11); lateral scales 32-33 (mode 33). Southern Thailand (Sungai Kolok), Peninsular Malaysia (Kelantan) *Betta pi**

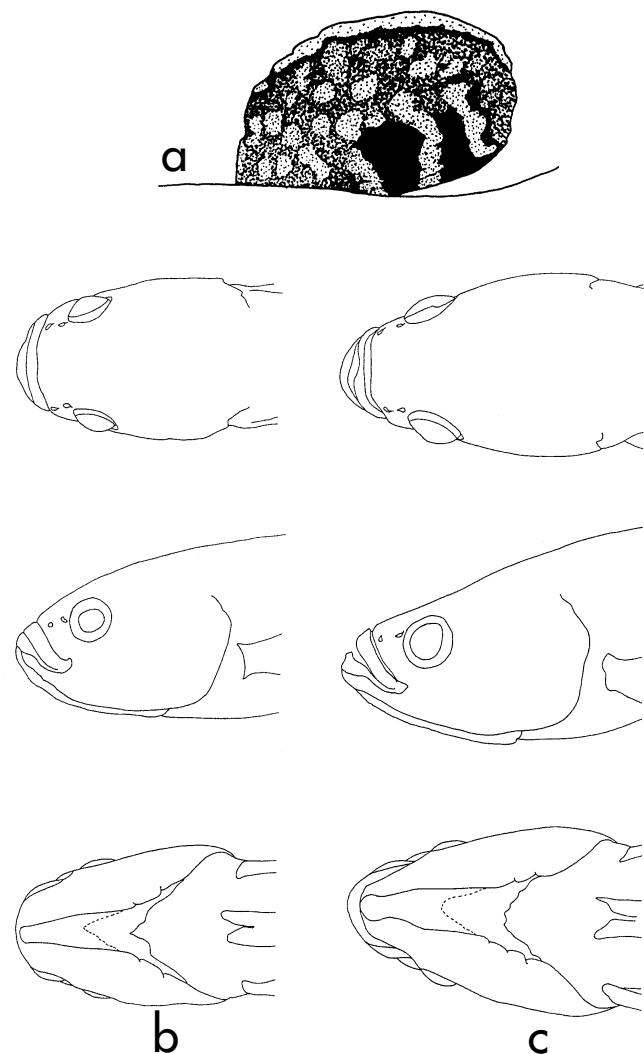


Fig. 8. a) Dorsal fin ocellus of *B. macrostoma*, b) dorsal, lateral and ventral head profiles of *B. unimaculata*, c) dorsal, lateral and ventral head profiles of *B. ocellata*.

TAXONOMY

Betta Bleeker, 1850

- Betta* Bleeker, 1850: 12 (type species *Betta trifasciata* Bleeker, 1850, by monotypy).
- Micracanthus* Sauvage, 1879: 95 (type species *Micracanthus marcheii* Sauvage, 1879, by monotypy).
- Parophiocephalus* Popta, 1905: 184 (type species *Parophiocephalus unimaculatus* Popta, 1905, by monotypy).
- Oshimia* Jordan, 1919: 342 (unnecessary replacement name for *Micracanthus* Sauvage, 1879).
- Pseudobetta* Richter, 1981: 273 (type species *Macropodus pugnax* Cantor, 1850, by original designation).

Remarks. – The first fighting fish species described was *Pancrux pictum* by Valenciennes (in Cuvier & Valenciennes, 1846) from Java. The genus name *Betta*, however, was only established by Bleeker (1850) for his new species, *B. trifasciata*, also from Java. Cantor (1850) described

Macropodus pugnax from the Malay Peninsula and Bleeker (1851) described *B. anabatooides*, from Borneo. Bleeker (1879), however, decided that all described species of fighting fishes up to that time were conspecific with *B. picta*.

Sauvage (1879) described *Micracanthus marcheii* on the basis of a single specimen with the locality data “bassin de l’Ogououé” in Africa. The erroneous locality data is discussed by Roberts (1981) who argued that *M. marcheii* is a synonym of *B. splendens*. Roberts (1981) also commented that the specimen of *M. marcheii* was most probably from Thailand or Peninsular Malaysia. There are, however, complications as there are several species in that same region which could fit Sauvage’s (1879) description. For example, Roberts (1981) did not take into consideration *B. smaragdina* and *B. imbellis*. In any case, there is no doubt that *Micracanthus*, is a subjective junior synonym of *Betta*. *Oshimia* was proposed by Jordan (1919) to replace *Micracanthus* because he thought that the genus name had been used earlier by Swainson (1839) for *Microcanthus* (family Chaetodontidae). Jordan’s action was unnecessary because the spellings for the names are not identical. The names *Micracanthus* and *M. marcheii* have been proposed for suppression by Tan & Ng (2000) and had been suppressed by the International Commission on Zoological Nomenclature in 2003.

Parophiocephalus was established by Popta (1905) for *P. unimaculatus*. Regan (1910) treated *Parophiocephalus* as a synonym of *Betta* but did not provide reasons. There is no doubt, after our examination of a large series of preserved and fresh *B. unimaculata* that *Parophiocephalus* is a subjective junior synonym of *Betta*. Richter’s (1981) proposal of restricting *Betta* to bubble-nest building species and to recognise a new genus, *Pseudobetta*, for oral-brooding species is nomenclaturally unsound. The type species for *Betta* is *B. picta*, which is an oral brooder; as is *B. pugnax*, the designated type species of *Pseudobetta*. Moreover, oral-brooding and bubble-nest brooding traits are probably not evolutionary stable characters in *Betta*, and may have been selected for repeatedly in different species (Roberts, 1989) and within *Betta* (Rüber et al., 2004). In any case, Richter’s proposal has not been adopted by most authors.

SPECIES GROUPS

The term ‘species group’ is used here for an assemblage of species sharing a set of diagnostic characters and which may or may not be a monophyletic lineage. In some cases, available data may support the monophyly of a given group (e.g. the *B. coccina* group, fide Witte & Schmidt, 1992), while for other groups such data are (still) missing or have to be re-evaluated. Our current inability to demonstrate monophyly does not automatically imply that a given group is not monophyletic.

Several authors have recognised species groups in *Betta* based mainly on superficial similarities, behavioural (breeding and brood care mainly) and morphological characters. These are, however, not necessarily apomorphic character states.

Schaller (1985) and Schaller & Kottelat (1989) separated the genus into two categories: mouthbrooders and bubble-nest brooders. Schaller (1985) further divided the bubble-nest brooders into the *B. splendens* and *B. bellica* groups. These two groups were not described with apomorphies, but with superficial similarities, behavioural and physiological adaptations to different environments, viz. *B. splendens* group (*B. imbellis*, *B. smaragdina*, *B. splendens*, *B. persephone*, *B. strohi*): characterised by a compressed and relatively slender body, presence of two vertical iridescent patches on opercle and members inhabiting stagnant to slow flowing waters; and *B. bellica* group (*B. bellica*, *B. coccina* and *B. tussyaie*): characterised by a cylindrical and slender body, dark stripe running through snout and eye to opercle edge (preorbital and postorbital stripes) with iridescent scales and members inhabiting flowing waters.

Vierke (1991), however, suggested the recognition of three species groups based almost entirely on ethological characters and overall body shape, viz. the *B. splendens* group (*B. persephone*, *B. tussyaie*, *B. coccina*, *B. bellica*, *B. smaragdina*, *B. imbellis*, *B. splendens*, *B. foerschi*), the *B. pugnax* group (*B. taeniata*, *B. picta*, *B. edithae*, *B. climacura*, *B. pugnax*, *B. anabatooides*) and the *B. macrostoma* group (*B. unimaculata*, *B. patoti*, *B. macrostoma*). The first group consists of supposed bubble-nest brooders, except for the oral-brooding *B. foerschi*. The second and third groups consist of oral-brooders only.

Witte & Schmidt (1992) tentatively recognised 15 species groups based on easily recognisable behavioural and morphological characters, and to a large extent on details of the head and body patterns which are usually diagnostic. These are the *B. unimaculata*, *B. patoti*, *B. edithae*, *B. picta*, *B. akarensis*, *B. anabatooides*, *B. pugnax*, *B. species E*, *B. splendens*, *B. coccina*, *B. foerschi*, *B. macrostoma*, *B. dimidiata*, *B. bellica* and *B. rubra* groups. The last four groups consisted of a single taxon each. In particular, Witte & Schmidt (1992: 318-319) highlighted the *B. coccina* group as having a monophyletic origin, using a partly resolved cladogram of 28 characters and with other *Betta* groups as outgroups.

Ng & Kottelat (1994) subsequently separated out the *B. waseri* group from the *B. anabatooides* group of Witte & Schmidt (1992) on the basis of morphological, meristic and colour characters.

In this paper, the species groups are a modification of Witte & Schmidt’s (1992) version as well as Ng & Kottelat’s (1994) additional group, together with some alterations. The 13 recognised species groups are discussed below. The species found in the present study area are indicated with an asterisk (*).

Betta bellica group

We recognise a new species group, the *B. bellica* group, characterised by: long and slender body which has the dorsal and ventral margins of the body almost parallel, body depth

Table 2. Meristic and morphometric data of *Betta bellica*

	<i>Betta bellica</i>	<i>Betta fasciata</i>
	NEOTYPE ZRC 39196	LECTOTYPE BMNH 1889.12.26:30
Vertebrae	2+8+22 (32)	2+8+23 (33)
Standard length (mm)	51.4	69.1
Total length (mm)	68.8	-
Head length (mm)	13.6	16.1
MERISTICS		
Anal-fin rays	I, 29	II, 30
Dorsal-fin rays	I, 12	0, 11
Caudal-fin rays	ii, 5+6, ii	ii, 5+6, ii
Pelvic-fin rays	I, 1, 4	I, 1, 4
Pectoral-fin rays	13	13
Subdorsal scales	9	7
Transverse scales	9	9
Lateral scales	33	35
Predorsal scales	26	27
Postdorsal scales	8	9
MORPHOMETRICS		
In % SL		
Total length	133.9	-
Predorsal length	63.0	65.3
Preanal length	38.9	37.0
Head length	26.5	23.3
Body depth at dorsal-fin origin	23.9	23.9
Pelvic fin length	32.7	19.8
Anal-fin base length	58.9	60.5
Dorsal-fin base length	18.7	16.2
Height of anal fin	14.4	-
Distance between pelvic- and anal-fin origins	10.5	13.2
In % HL		
Orbit diameter	30.1	26.1
Postorbital length	48.5	50.9
Interorbital distance	33.1	32.9

23-28% SL; short blunt head, head length 23-28% SL; anal-fin rays 30-33, dorsal-fin rays 11-13; total vertebrae 32-34; body dark brown with iridescent green patch on every scale. The members of the *B. bellica* group are bubble-nest builders.

Witte & Schmidt (1992: 325) defined *B. bellica* as having a total anal-fin ray count of 30-34; some posterior rays of dorsal and anal fins branched; caudal fin somewhat rhomboid with a few long, filamentous principal rays and TL up to 110 mm. Tan & Ng (1996) described an allied species (*B. simorum*) from Jambi, Sumatra. Subsequently, *B. simorum* had been found in the lower Kapuas basin in Kalimantan Barat (pers. observ.).

Included species: *B. bellica**, *B. simorum*.

***Betta pugnax* group**

Members of the *B. pugnax* group are distinguished by the following set of characters: a relatively large head, 28-40% SL; usually brown with greenish to blueish iridescent spots on body scales when alive; male with strongly coloured (blue, green or greenish blue) iridescent opercle scales, occasionally even covering anterior portion of belly in life; juvenile and female usually with a light brown background displaying a central and a second central stripe, with a caudal peduncle spot; head rhombic when viewed from above, with or without chin-bar; and fins of mature specimens pointed, often

elongated, caudal fin lanceolate, male may exhibit caudal-fin transverse bars. All members are male oralbrooders.

Witte & Schmidt (1992: 325) did not define this group and merely stated the reported localities in which the member species can be found. They also established a "*Betta* sp. E" group which they characterised by having no chin-bar; body depth at dorsal-fin origin 2.8-3.1 times in SL; head length 2.9-3.1 times in SL, head without light spots; body length up to 72-92 mm SL; pelvic fin with very long, bright blueish-white filamentous ray; adult male with bright iridescent opercle and throat and light blue body; and occurring in Sumatra (Jambi), Kalimantan Barat (Kapuas basin) and Sarawak. These characters are too general and we can discern no clear evidence to recognise their *Betta* sp. E group and we consider their *Betta* sp. E group as part of the *B. pugnax* group, along with *B. fusca*. All species share the common feature of having a green or blue iridescent opercle in life, a lanceolate caudal fin, and pointed anal and dorsal fins.

Included species: *B. pugnax**, *B. fusca*, *B. schalleri*, *B. prima*, *B. enisae*, *B. pulchra**, *B. breviobesus*, *B. stigmosa**, *B. lehi**.

***Betta akarensis* group**

Members of the *B. akarensis* group are distinguished by the following character suite (see Tan & Kottelat, 1998a): presence of preorbital and postorbital stripes (postorbital stripe may be

Table 3. Meristic and morphometric data of *Betta stigmatosus* and *B. lehi*.

	<i>Betta stigmatosus</i>	<i>Betta lehi</i>
Standard length (mm)	31.2-41.1	35.9-60.8
n	5	19
MERISTICS (mode)		
Vertebrae	10 + 18-19 (total 28-29, 29)	10 + 18-20 (total 28-30, 29)
Anal fin rays	I-II, 21-23 (total 23-24, 24)	II, 23-27 (total 25-29, 28)
Dorsal fin rays	0-I, 8-9 (total 9-10, 9)	I, 8-10 (total 9-10, 10)
Caudal fin rays	ii, 5 + 6, ii	ii, 5 + 6, ii
Pelvic fin rays	I, 1, 4	I, 1, 4
Pectoral fin rays	12-13 (13)	12
Subdorsal scales	6 ^{1/2}	5-6 ^{1/2} (6)
Transverse scales at dorsal-fin origin	9 ^{1/2} -10 (10)	9 ^{1/2}
Lateral scales	29-30 (29)	28-30 (29)
Lateral scales below dorsal-fin origin	14-15 (14)	-
Lateral scales above anal-fin origin	6-7 (7)	-
Predorsal scales	20-21 (20)	20-23 (22)
Postdorsal scales	10-11 (10)	10-11 (11)
MORPHOMETRICS - % SL		
Total length	141.5-148.0	136.2-152.7
Predorsal length	62.8-67.5	62.6-67.5
Postdorsal length	21.2-23.6	-
Caudal peduncle depth	14.4-17.3	-
Preanal length	47.2-52.8	47.4-52.5
Head length	33.6-36.5	33.4-36.8
Body depth at dorsal-fin origin	25.6-28.2	27.3-32.5
Pelvic fin length	33.2-51.8	34.8-50.6
Anal-fin base length	48.2-51.3	48.1-54.2
Dorsal-fin base length	12.2-13.9	12.3-15.6
Body length	64.4-69.1	-
Head width	19.0-21.5	-
% HL		
Orbit diameter	26.7-28.4	27.2-32.2
Postorbital length	47.6-51.1	42.2-48.5
Interorbital width	29.8-32.1	31.7-37.4
Snout length	22.0-25.2	22.8-27.9
Head width	56.0-58.9	-
% Postorbital length		
Orbit diameter	52-60	59-74
Interorbital width	62-65	70-84
% Predorsal length		
Head length	51.7-55.4	51.2-56.1

interrupted or faint), and a chin-bar; caudal fin lanceolate, median rays distinctly elongated in mature male, with branching of caudal-fin rays starting from ca. 40 mm SL, usually with caudal-fin transverse bars (always distinct in mature male); greenish to blueish iridescent body scales in some species; opercle without iridescent scales (fide Witte & Schmidt, 1992; Ng, 1993). Adult specimens may possess greenish-gold opercle scales which tend to disappear in captivity. Juvenile may possess gold opercle scales, but these disappear with age. The faintly coloured greenish-gold opercle scales of the adults could be due to stress from handling. All members are male oralbrooders.

The *B. akarensis* and *B. pugnax* groups can be readily differentiated by two characters: the presence of faintly coloured greenish-gold opercle scales in members of the *B. akarensis* group (vs. the intense blueish-green opercle scales in members of the *B. pugnax* group) and usually more anal-fin rays (28-30, vs. 25-28).

Included species: *B. akarensis**, *B. balunga**, *B. chini**, *B. pinguis*, *B. ibanorum**, *B. aurigans*, *B. obscura*.

Betta unimaculata group

Members of the *B. unimaculata* group are characterised by the following unique combination of characters: long, relatively slender body (body depth at dorsal-fin origin 18-25% SL); large blunt head (head width 19-24% SL); long maxilla and lower lip (distance from tip of lower jaw to posterior end of maxilla 27-54% HL); caudal fin rounded, occasionally with elongated median rays; short filamentous pelvic fin; relatively pointed dorsal and anal fins.

Members of the *B. unimaculata* group differ from the other groups in breeding behaviour. The breeding display consists of an open gape (unique to this group) and flaring of dorsal, pelvic, anal and caudal fins (vs. expansion of branchiostegal membranes with fins flaring). The female of some members do not participate in the egg gathering or egg transfer to the male (van den Nieuwenhuizen, 1995; Tan, 1997).

Included species: *B. unimaculata*, *B. macrostoma**, *B. patoti*, *B. ocellata**, *B. gladiator**, *B. pallifina*.

Table 4. Meristic and morphometric data of *Betta akarensis*, *B. balung*, *B. chini*, *B. ibanorum* and *B. obscura*.

	<i>Betta akarensis</i>	<i>Betta balung</i>	<i>Betta chini</i>	<i>Betta ibanorum</i>	<i>Betta obscura</i>
Number of specimens	18	2	8	16	14
MERISTICS (mode)					
Anal-fin rays	I-II, 26-28 (total 28-30, 28)	0-III, 27	II, 24-28 (total 26-30, 28)	I-II, 25-27 (total 27-29, 28)	II-III, 24-27 (total 26-29, 28)
Dorsal-fin rays	I, 7-8 (total 7-9, 8)	0-II, 8-9	I, 7-9 (total 8-10, 8)	I, 8-10 (total 9-10, 9)	0-II, 8-9, (total 8-10, 10)
Pectoral-fin rays	12-13 (13)	12	12-13 (12)	13-14 (13)	10-13 (11, 12)
Sub-dorsal scales	5-6 (5)	6	5½-7 (6)	5-6 (5½)	5½-7 (6½)
Lateral scales	31-33 (32)	29-30	30-31 (31)	30-32 (30)	28-30 (29)
Lateral scales below dorsal-fin origin	16-18 (17)	15-16	16-17 (16)	15-17 (16)	14-15 (15)
Lateral scales above anal-fin origin	6-8 (6)	6	5-7 (6)	6-7 (7)	6-7½ (7)
Predorsal scales	22-25 (23)	21-23	22-24 (23)	21-23 (22)	19-21 (20)
Postdorsal scales	10-12 (11)	9-10	9-11 (10)	10-11 (11)	10-11 (11)
MORPHOMETRICS					
In % SL					
Total length	134.4-154.2	132.8-141.3	137.2-144.6	138.2-165.6	135.5-160.2
Head length	29.8-34.9	32.6-35.5	31.4-33.3	31.7-36.4	30.9-35.4
Body depth at dorsal-fin origin	25.1-30.9	28.0-31.5	26.3-29.0	23.3-28.1	28.7-32.7
Predorsal length	64.3-70.0	66.7-71.7	64.5-69.8	64.5-68.5	63.8-68.3
Preal length	43.4-48.5	49.2-52.2	42.6-45.7	45.8-49.4	46.1-50.7
Postdorsal length	19.9-25.1	22.6	19.9-23.3	18.9-24.2	19.8-23.9
Anal-fin base length	49.6-56.8	47.8-55.4	54.8-58.5	50.0-55.8	51.3-56.4
Dorsal-fin base length	9.9-14.1	13.7-14.1	11.0-14.0	10.6-14.8	12.1-15.4
Pelvic-fin length	30.0-50.0	35.0-40.6	30.3-45.8	28.5-50.6	33.1-52.6
Lower jaw length	8.8-10.7	10.2	8.9-11.3	9.3-12.0	9.2-11.3
Height at pectoral-fin origin	15.7-19.6	16.1	16.9-21.5	15.0-21.9	16.5-20.4
In % HL					
Orbit diameter	24.5-32.3	29.5-33.3	26.2-30.8	22.2-30.5	21.1-25.3
Postorbital length	45.7-51.6	46.7-49.2	46.7-52.5	45.7-50.2	45.0-50.0
Interorbital width	29.4-37.4	28.8-35.3	29.3-37.7	29.6-37.7	29.9-37.1
Lower jaw length	25.4-34.4	28.8	25.8-31.5	28.0-36.1	28.9-34.1
Height at pectoral-fin origin	47.3-61.9	45.5	47.6-59.3	44.7-59.9	49.5-61.6

Table 5. Meristic and morphometric data of *Betta macrostoma*, *B. ocellata*, *B. unimaculata*, *B. patoti*, *B. gladiator* and *B. pallifina*.

	<i>Betta macrostoma</i>	<i>Betta ocellata</i>	<i>Betta unimaculata</i>	<i>Betta patoti</i>	<i>Betta gladiator</i>	<i>Betta pallifina</i>
No. of specimens	14	13	13	8	16	25
MERISTICS (mode)						
Dorsal-fin rays	0-I, 9-11 (total 9-11, mode 10)	0-I, 7-8 (total 8, mode 8)	0-I, 6-8 (total 6-8, mode 8)	0-I, 7-9 (total 8-9, mode 8)	0, 7-9 (total 7-9, mode 8)	0-I, 6-9 (total 7-9, mode 8)
Anal-fin rays	0-I, 24-27 (total 25-28, mode 27)	I-II, 28-30 (total 30-31, mode 30)	I-II, 26-30 (total 27-30, mode 28 or 29)	I, 29-32 (total 30-33, mode 31)	I-II, 27-30 (total 28-31, mode 30)	I-II, 26-31 (total 27-32, mode 30)
Pectoral-fin rays	13 or 14	12-13 (13)	12-13 (12)	12-14 (13)	16-17 (17)	11-14 (13)
Subdorsal scales	6-8 (7)	5-5 ^{1/2} (5 ^{1/2})	4-5 (5)	6-6 ^{1/2} (6)	5-6 ^{1/2} (6)	5-6 ^{1/2} (6)
Body depth at dorsal-fin origin	9 ^{1/2} -10 (9 ^{1/2})	9 ^{1/2}	9-9 ^{1/2} (9 ^{1/2})	9 ^{1/2} -10	9 ^{1/2} -10 (9 ^{1/2})	9-10 (9 ^{1/2})
scales						
Lateral scales	32-33 (33)	32-34 (33)	31-33 (32)	33-34 ^{1/2} (34)	34-36 (35)	32-34 (33)
Lateral scales below dorsal-fin origin	15-17 (17)	18-20 (18 or 19)	17-20 (18)	18-19	19-21 (19, 20)	16-19 (18)
Lateral scales above anal-fin origin	7-11 (8)	6-8 (7 or 8)	7-9 (7)	5-8 (7)	6-8 (8)	6-8 (6)
Predorsal scales	21-24 (23)	24	24-26 (24)	24-26 (25)	24-27 (26)	21-26 (23)
Postdorsal scales	10-11 (11)	10-11 (11)	10-11 (11)	11-12	10-12 (11)	10-13 (11)
MORPHOMETRICS						
in % SL						
Total length	131.0-137.0	131.9-135.6	130.5-139.7	132.3-143.0	135.4-139.2	129.7-140.9
Predorsal length	62.3-66.7	68.8-71.9	67.7-73.0	67.5-69.9	68.0-72.8	64.6-69.4
Postdorsal length	18.2-22.0	20.3-22.5	20.2-25.5	19.3-21.8	17.2-22.2	19.1-23.3
Caudal peduncle depth	12.9-17.3	14.8-17.0	13.3-16.4	14.3-16.5	13.5-15.3	13.2-16.2
Preal length	44.7-50.3	44.8-46.8	43.9-51.3	41.1-46.1	43.4-47.2	39.6-50.5
Head length	30.4-33.3	31.4-33.3	29.0-33.3	29.7-31.4	28.5-31.3	26.8-33.4
Body depth at dorsal-fin origin	18.5-21.1	21.6-24.5	18.9-24.7	20.0-22.6	18.4-20.4	20.5-23.0
Pelvic-fin length	21.6-27.6	24.0-32.1	20.4-32.4	25.9-34.7	29.0-35.7	22.5-34.7
Anal-fin base length	43.2-49.2	52.2-54.5	45.9-53.7	51.0-56.3	48.1-52.8	47.4-57.7
Dorsal-fin base length	12.2-15.7	10.5-11.3	7.9-10.4	9.4-11.4	7.3-11.4	9.3-12.5
Height at pectoral-fin origin	10.6-16.0	16.7-18.7	12.4-18.6	12.7-16.6	10.6-16.5	12.1-16.0
Head width	17.7-22.4	21.0-24.0	19.6-21.8	18.0-20.7	19.2-23.4	17.7-20.8
in % HL						
Orbit diameter	19.8-26.4	21.6-24.8	21.4-27.4	20.5-24.8	22.6-28.3	19.0-24.8
Postorbital length	49.3-56.7	51.3-56.0	49.7-56.3	48.6-53.3	46.3-53.5	50.3-55.5
Interorbital width	29.2-35.8	28.7-33.0	30.4-35.4	30.8-40.1	29.5-38.3	30.4-36.9
Lower jaw length	38.0-54.0	27.3-33.1	31.6-37.9	32.9-38.5	28.3-38.3	30.6-39.6
Head width	57.4-70.2	63.3-74.2	61.3-69.6	57.9-67.2	64.5-77.3	56.4-70.2
Height at pectoral-fin origin	34.1-49.6	50.0-57.7	42.7-56.5	40.6-53.7	35.2-57.3	37.6-59.5

Table 6. Meristic and morphometric data of *Betta taeniata*

	<i>Betta taeniata</i> type material	<i>Betta taeniata</i> fresh material
Number of specimens	4	8
MERISTICS (mode)		
Vertebrae	2 + 8 + 18 (total 28) (n=3)	2 + 8 + 17-19 (total 27-29, mode 28) (n=8)
Anal-fin rays	total 23-24	total 23-26 (26)
Dorsal-fin rays	total 9	total 8-10 (10)
Pelvic-fin rays	I,1,4	I,1,4
Pectoral-fin rays	11-12 (12)	12
Caudal-fin rays	ii,5+7,i	ii,5+6-7,i (ii,5+7,i)
Pelvic-fin length to anal-fin ray	5-7 (6)	5-6 (6)
Subdorsal scales	5-6 (6)	5-6 (6)
Body depth at dorsal-fin origin	ca. 9	9-9½
Lateral scales	ca. 25-26 (26)	27-29 (28)
Lateral scales below dorsal-fin origin	ca. 12-14 (12)	13-14 (13)
Lateral scales above anal-fin origin	ca. 6-8 (7)	7
Predorsal scales	19	19-20
Postdorsal scales	9-10 (9)	9-10 (10)
MORPHOMETRICS		
In % SL (mean)		
Total length	133.7-140.3 (137.3)	132.9-139.9 (135.7)
Predorsal length	65.9-70.4 (67.5)	62.4-66.5 (64.6)
Postdorsal length	21.4-23.4 (22.4)	20.3-25.5 (22.5)
Preanal length	49.1-53.3 (51.8)	49.5-54.1 (51.8)
Head length	33.5-37.6 (35.6)	30.3-36.1 (33.0)
Body depth at dorsal-fin origin	24.4-30.4 (27.4)	24.8-28.9 (26.7)
Pelvic-fin length	26.5-32.5 (29.4)	23.5-28.4 (25.9)
Anal-fin base length	43.8-51.8 (48.9)	49.4-53.2 (51.0)
Dorsal-fin base length	11.2-15.4 (14.0)	10.8-15.8 (13.0)
Caudal peduncle depth	15.3-17.1 (16.4)	15.2-16.7 (15.9)
In % HL (mean)		
Orbit diameter	27.2-31.0 (29.1)	23.8-30.4 (27.1)
Postorbital length	45.5-46.5 (46.0)	41.1-48.1 (45.9)
Interorbital distance	24.6-28.6 (26.4)	26.9-36.2 (31.2)

Betta picta group

Members of the *B. picta* group are characterised by: rounded unpaired fins (anal fin occasionally bluntly pointed); anal-fin rays I-III,18-24; dark pigmented distal margin on anal and caudal fins, especially in mature male (Fig. 4); preorbital and postorbital stripes present, throat with chin-bar; opercle with iridescent gold, green or blue scales (after Witte & Schmidt, 1992). All members are male oralbrooders.

Included species: *Betta picta*, *B. taeniata**, *B. simplex*, *B. falx*.

Betta splendens group

Members of this group were defined by Witte & Schmidt (1992: 325-327) as having a small head (22-31% SL); often brightly coloured body; iris of eye with iridescent green or blue patches; bubblest brooders; body elongate or slender; head with parallel opercles when viewed dorsally; red or brown anal and caudal fin rays contrasting with iridescent interradiating membranes (especially in male); unpaired fins without fine iridescent margin; in male, opercle with red or iridescent blue bars; TL up to 70 mm, SL up to 57 mm; iridescent green opercle scales (*B. imbellis*, *B. smaragdina*) or red parallel bars on opercle (*B. splendens*); distinct red distal crescent on the caudal fin (in *B. imbellis*) (Fig. 5a); iridescent green

body scales (other colours for domesticated stocks of *B. splendens*); dorsal-fin rays 0-II, 7-9; anal-fin rays II-V, 21-26.

Included species: *B. splendens*, *B. smaragdina*, *B. imbellis**, *Betta stiktos*.

Betta coccina group

The *B. coccina* group is unique in having a small adult size (less than 40 mm SL), either a uniform red or black body colour, mid-lateral body blotch present in some species (see Key) (Fig. 6a) and nine abdominal vertebrae (vs. 10-12 in all other species groups) (Witte & Schmidt, 1992: 325). All members of the group are stenotopic inhabitants of peat swamp forests. They typically inhabit the shallow pools of submerged leaf litter. All are bubblest brooders.

Included species: *B. coccina**, *B. tussya**, *B. persephone**, *B. rutilans*, *B. brownorum**, *B. livida**, *B. miniopinna*, *B. burdigala*.

Betta waseri group

The *B. waseri* group is diagnosed by: black mark(s) (various species-specific shapes) on throat and black lower lip (Fig. 3); distinctive markings on opercle; large adult size (more than 60 mm SL); clay-yellow body colour; and golden iridescent belly and opercle scales

Table 7. Meristic and morphometric data of the *Betta splendens*, *B. imbellis*, *B. smaragdina* and *B. stiktos*.

	<i>B. splendens</i>	<i>B. imbellis</i>	<i>B. smaragdina</i>	<i>B. stiktos</i>
Number of specimens	7	24	5	5
MERISTICS (mode)				
Anal fin rays	28-30 (30)	25-31 (27)	26-29 (29)	27-29 (29)
Dorsal fin rays	10-14 (11)	9-12 (10)	9-11 (10)	10-11 (10)
Pectoral fin rays	11-12 (11)	11-12 (12)	12	12
Subdorsal scales	7-10 (7, 8)	5 ¹ / ₂ -8 (7)	6-7 (6)	6 ¹ / ₂ -7 (7)
Transverse scales	9-9 ¹ / ₂ (9 ¹ / ₂)	9-9 ¹ / ₂ (9 ¹ / ₂)	9 ¹ / ₂ -10 (9 ¹ / ₂)	9 ¹ / ₂ -10 (9 ¹ / ₂)
Lateral scales	29-31 (29, 31)	30-32 (31)	29-32 (30)	33-34 (33)
Predorsal scales	22-26 (25)	21-24 (23)	22-24 (23, 24)	24-25 (25)
Postdorsal scales	8-11 (9)	9-12 (11)	10-11 (10)	10-11 (10)
Lateral scales below dorsal-fin origin	14-16 (14)	15-17 (16)	15-16 (15)	16
Lateral scales below anal-fin origin	5-7 (6)	6-8 (7)	5-7 (6, 7)	6-7 (6)
MORPHOMETRICS (% SL)				
Total length	128.4-136.6	131.9-141.7	132.3-140.4	136.0-139.7
Predorsal length	60.1-65.6	61.3-66.7	63.9-66.4	63.5-66.4
Postdorsal length	15.3-22.8	17.3-22.1	21.4-23.2	17.5-20.1
Preanal length	40.5-45.3	38.7-45.8	42.3-45.1	40.5-43.5
Head length	28.2-30.9	25.8-30.9	27.8-30.1	27.7-30.3
Body depth	27.1-32.2	24.2-30.1	24.7-28.4	26.2-27.7
Caudal peduncle depth	18.6-20.3	15.9-19.2	18.1-19.3	15.4-17.4
Pelvic fin length	26.1-63.9	31.6-51.0	36.8-51.0	33.2-39.0
Anal fin base length	56.8-58.8	54.2-61.9	54.2-60.0	53.7-60.3
Dorsal fin base length (% HL)	16.7-23.8	12.9-18.9	14.9-16.7	15.2-15.6
Orbit diameter	22.7-26.6	24.7-31.1	25.0-29.0	27.7-29.7
Postorbital length	49.6-52.7	43.6-55.2	48.8-51.2	45.9-50.0
Interorbital width	30.2-34.3	25.6-36.0	31.0-32.5	26.4-31.6
Snout length	21.1-26.9	15.6-28.2	17.5-23.0	16.9-21.6

in some species (Ng & Kottelat, 1994). An additional diagnostic character is the colour zonation of the eye (Fig. 3h). The pupil is surrounded by an iridescent yellow rim, followed with a reddish iris rimmed with another thicker iridescent yellow ring on the circumference of the orbit. This is most obvious in juveniles and sub-adults. Eyes of old or large specimens are darker and the colour zonation may not be so obvious. The throat markings of each of the species of the *B. waseri* group are diagnostic (Fig. 3). They are only displayed when specimens are disturbed, well acclimatised or in breeding condition. Well-acclimatised specimens invariably display a brown body colour, with a black or brown postorbital and central stripe which runs from just behind the eye to the middle of the caudal peduncle. A distinct broken black stripe runs just above the anal fin sheath scales.

All the species in the *B. waseri* group are paternal oral-brooders. They exhibit a 'S' mating embrace. The male curves its body around the female, positioning its genital opening next to the female's in order to fertilize the eggs as they are extruded. The embrace of the male and female resembles a 'S' shape. The female recovers from the embrace first and collects the fertilized eggs from the cup formed by the curved anal fin of the male. The female spits the eggs out one at a time in front of the male. The male then collects the egg quickly, otherwise the female gulps the egg back. This egg gulping ritual is repeated until the male has collected all the eggs in its buccal sac. At this stage, the male will have a grossly enlarged throat. The above mating ritual had been observed for *B. spilotogeta* and there can be as many as 180 fry in the mouth (Tan & Tan, 1994; pers. observ.). An apparently undescribed species of the *B. waseri* group from Pekan Nanas (misidentified as *B. macrophthalmia* by Schmidt, 1988) also possesses this form of behaviour. Unfortunately, we do not have sufficient material to resolve the identity of this species.

Included species: *B. waseri**, *B. chloropharynx*, *B. hipposideros**, *B. tomi**, *B. spilotogeta*, *B. renata*, *B. pi**.

Betta edithae group

The *B. edithae* group is characterised by: branchiostegal membrane and posterior part of opercle translucent or opaque; and size up to 62 mm SL. Witte & Schmidt (1992: 326) commented that they had seen specimens resembling *B. edithae* from Malay Peninsula. Despite extensive collections in Peninsular Malaysia, we have not come across any specimens resembling *B. edithae* yet. Also, there are no preserved museum specimens from this area which can be referred to this species group.

The group currently has a single member, *B. edithae*, known from several widely separated areas: Kalimantan Barat, Kalimantan Tengah, Kalimantan Selatan, Kalimantan Timur (Roberts, 1989; Witte & Schmidt, 1992), Palembang (unpublished data), Banka (unpublished data), Biliton (unpublished data) and Pulau Bintan (Tan & Tan, 1994). Whether all these populations are conspecific has yet to be determined. Witte & Schmidt (1992: 324) listed Jambi, Sumatra as another locality (*B. (edithae)* sp. B), however, these are likely to be *B. falx* (Tan & Kottelat, 1998b) instead.

Betta foerschi group

The *B. foerschi* group was defined by Witte & Schmidt (1992: 325) as having iridescent blue or green unpaired fins, with rays and interradi membranes not contrasting; dorsal fin with thin iridescent white margin; opercle with two distinct reddish-yellow bars; and size up to 51 mm SL.

The position of *B. rubra* requires comment. Witte & Schmidt (1992) defined *B. rubra* as having a triangular mark below the eye; found in the lowlands of northwestern Sumatra; and size up to 38 mm SL. They accommodated this taxon into its own species group based on the above mentioned characters. We tentatively place *B. rubra* in the *B. foerschi* group on the basis of the following features: presence of two vertical lighter coloured bars on opercle; vertical bars on body when preserved (also present, but faint in *B. strohi*); and general body shape. Until fresh material becomes available, the relationships of *B. rubra* can only be speculated. However, considering the known characters, there is little reason to treat *B. rubra* as a distinct species group. The prime character used by Witte & Schmidt (1992: 325) to delineate the '*B. rubra*' group was the triangular patch beneath the eye, which is a weak character as this mark is part of the chin-bar extending to the opercle. In head and body form, *B. rubra* is clearly either a member of the *B. foerschi* or *B. splendens* group. These two species groups are very close morphologically. From the distinctiveness of the two vertical bars on the opercle and stockiness of the head of *B. rubra*, it fits better in the *B. foerschi* group as currently understood.

Included species: *B. foerschi*, *B. strohi*, *B. rubra*.

***Betta anabatooides* group**

The *B. anabatooides* group was defined by Witte & Schmidt (1992) by the following characters: no iridescent opercle scales; filamentous pelvic ray usually not extended; head with two light spots behind eye; adult body colour uniform reddish brown or black. The group is further characterised by: body relatively short and stout (body depth 30-33% SL); no chin bar; terminal portion of caudal rays protruding behind caudal membrane; caudal transverse bars present or absent; convex head dorsal profile and stout body reminiscent of *Anabas*.

The group includes a single species, *B. anabatooides*, which Witte & Schmidt diagnosed as having no markings on lower jaw or no throat pattern; central stripe between lower lip and eye with "variable modifications" [sic, no further elaboration]; size up to 90 mm SL; found in Kalimantan Selatan, Kalimantan Tengah, Kalimantan Barat and possibly in Sarawak. Bleeker (1851: 269) described *B. anabatooides* from Banjarmasin (=Banjarmasin), Borneo, on the basis of two specimens 101 and 115 mm TL. He provided the anal-fin ray count II, 29; dorsal-fin ray count II, 7; and lateral scale count 33. There was no accompanying figure, but the high anal-fin ray count, extended fin ray tips and convex head profile allies *B. anabatooides* to the *B. waseri* and *B. akarensis* groups. It differs, however, mainly in the shape of the head and anterior part of body. Vierke (1979b) commented on *B. anabatooides*, on the basis of fresh specimens collected from the type locality of *B. foerschi* - Mentaya basin, 250 km northwest from Banjarmasin. His figure of *B. anabatooides* and the figure in plate 75 of Kottelat et al. (1993) depict specimens that come closest to Bleeker's description and to its namesake - *Anabas* (Anabantidae). To confirm the status of this species group, the types should be examined, together with fresh topotypic material. The *B. anabatooides* group is tentatively regarded as valid and confined to Borneo.

***Betta albimarginata* group**

The *B. albimarginata* group is characterised by: broad head and body; flat head top; pelvic fin broad and falcate (seldom filamentous); great number of anal-fin spines (IX-XII vs. 0-IV in other species); few articulated anal-fin rays (11-13 vs. 18-32); dorsal-

fin origin almost above anal-fin origin; and small size (all known specimens less than 30 mm SL); and a unique colour pattern (fide Kottelat & Ng, 1994). Paternal oral-brooder (Grams & Dickmann, 1997).

Included species: *B. albimarginata*, *B. channoides*.

***Betta dimidiata* group**

The *B. dimidiata* group includes a single species. Witte & Schmidt (1992: 323) defined it as having: elongate body, body depth 21-25% SL; pale interspace between upper and central stripe thin, about half a scale apart, appearing like a thin stripe; largest known size 35 mm SL; 22-26 articulated anal-fin rays. This species certainly deserves its placement in its own group, which can be further distinguished by the following characters: extreme sexual dimorphism (observed from captive specimens), male with greatly elongated unpaired and pelvic fins, bright blueish-white pelvic fin reaching up to two-thirds of anal fin, anal fin with iridescent light blue distal margin reaching up to lower margin of caudal fin; female with somewhat rounded unpaired fins; throat with chin-bar and opercle with iridescent green scales (in both sexes, more intense in male), mature male with anterior portion of throat purple, up to anterior portion of opercle; several vertical black bars on body just behind opercle edge in both sexes, more prominent in male. Oral-brooder.

SPECIES ACCOUNTS

BETTA BELLICA GROUP

***Betta bellica* Sauvage, 1884**

(Figs. 9a-b, 46a)

Betta bellica Sauvage, 1884: 217, fig.; Regan, 1910: 779; Weber & de Beaufort, 1922: 363; Herre, 1940: 43 (key only); Kottelat, 1989: 19 (list only); Witte & Schmidt, 1992: 326 (part); Ng et al., 1992: 28; 1994: 210; Kottelat et al., 1993: 161 (part), pl. 75; Tan & Ng, 1996: 144, fig. 3a, 4a.

Betta fasciata Regan, 1910: 782, pl. 75, Fig. 4; Weber & de Beaufort, 1922: 362; Herre, 1940: 42 (key only); Witte & Schmidt, 1992: 326; Tan & Ng, 1996: 149, fig. 3b.

Material examined. - Neotype - **Malaysia:** ZRC 39196, 51.4 mm SL male; Malaysia: Selangor, north Selangor peat swamp forest, 43 km towards Sungai Besar (3°39'12.9"N 101°18'00.4"E); D. S. L. Chung et al., Sep.1993.

Others - **Malaysia:** ZRC 39253, 2 ex., 43.2-44.1 mm SL; Aug.1992, - ZRC 39254, 1 ex., 54.4 mm SL; Sep.1992, - ZRC 39255, 3 ex., 43.9-48.3 mm SL; Jul.1993, - ZRC 39256, 1 ex., 49.8 mm SL; Sep.1993, - ZRC 39262, 3 ex., 39.0-40.7 mm SL; Jul.1993, same locality data as neotype. — ZRC 39257, 1 ex., 49.4 mm SL; Jul.1993, - ZRC 39258, 7 ex., 39.1-57.6 mm SL; Sep.1993, - ZRC 39263, 1 ex., 48.6 mm SL; Mar.1993; Malaysia: Selangor, north Selangor peat swamp forest, streams running parallel to road at 46.5 km towards Sungai Besar (3°39'51.4"N 101°19'43.0"E); D. S. L. Chung et al. — ZRC 39259, 1 ex., 49.4 mm SL; Sep.1992, - ZRC 39260, 1 ex., 54.3 mm SL; Jul.1993, - ZRC 39261, 2 ex., 46.0-49.7 mm SL; Sep.1993; Malaysia: Selangor, north Selangor peat swamp forest, stream parallel to road at 47.6 km towards Sungai Besar (3°40'12.7"N 101°20'10.2"E); D. S. L. Chung et al. — ZRC 15059, 1 ex., 56.1 mm SL; Malaysia: Selangor, north Selangor peat swamp forest, stream at 43 km mark on road to Sungai Besar; 1991-92

Honours class, 19 Jun.1991. — ZRC 39577, 2 ex., 39.8-47.7 mm SL; Malaysia: Selangor, north Selangor peat swamp forest, stream at 43 km mark on road to Sungai Besar, coll. P. K. L. Ng et al., Sep.1994. — ZRC 39578, 2 juv.; Malaysia: Selangor, north Selangor peat swamp forest, road from Sungai Besar to Tanjung Malim, 0.65 km from 35 km stone, coll. P. K. L. Ng et al., Sep.1994. — ZRC 38274, 1 juv.; Malaysia: Selangor, north Selangor peat swamp forest, coll. P. K. L. Ng et al., Sep.1994. — ZRC 15053-54, 2 juv.; Peninsular Malaysia, north Selangor peat swamp forest, stream at 34 km mark on road to Tanjung Malim; NUS 1991-92 Honours class, 17 Jun.1991. — ZRC 16700, 1 juv.; - ZRC 15055-58, 4 juv.; Malaysia: Selangor, north Selangor peat swamp forest, stream at 50 km mark to Tanjung Malim (United Plantations Berhad); NUS 1991-92 Honours class, 18 Jun.1991. — ZRC 17374-76, 3 juv.; Malaysia: Selangor, north Selangor peat swamp forest, coll. P. K. L. Ng, Aug.1991. — ZRC 39195, 1 ex., 47.7 mm SL; Malaysia: Selangor, north Selangor peat swamp forest, stream running through edge of United Plantations; D. S. L. Chung et al., Sep.1993. — ZRC 28636-37, 2 ex., 48.2-58.0 mm SL; Malaysia: Johor, Segamat; aquarium collectors, Oct.1992. — ZRC 29126, 1 ex., 39.5 mm SL; - ZRC 29052, 1 juv.; Malaysia: Johor, Pontian, Sri Bunian, Kampung Pt. Tekong, blackwater stream, coll. P. K. L. Ng et al., 8 May.1992. — ZRC 28799-800, 2 juv.; Malaysia: Johor, near Pontian, Tenggoyon (between Pekan Nanas and Kukup), coll. P. K. L. Ng et al., 4 Mar.1992. — ZRC 21949-50, 2 juv.; Malaysia: Johor, 56 km Pontian-Johor Bahru road, blackwater stream, coll. K. K. P. Lim & D. S. L. Chung, 14 May.1992. — ZRC 17377-79, 3 juv.; Malaysia: Johor, about 2 km north of Ayer Hitam, blackwater stream, coll. P. K. L. Ng & K. K. P. Lim, 23 May.1991. — ZRC 17373, 1 juv.; Malaysia: Johor, about 2 km north of Ayer Hitam, in swamp forest, coll. P. K. L. Ng & K. K. P. Lim, 23 May.1991. — ZRC 28676-77, 2 juv.; Malaysia: Pahang, pool along Mersing-Pekan road (73 km to Kuantan, 400 m to Sungai Beto), coll. M. Kottelat & P. K. L. Ng, 9 Mar.1992. — ZRC 25674-76, 3 juv.; Malaysia: Pahang, 69 km, Mersing-Kuantan road, blackwater stream, coll. P. K. L. Ng et al., 10 Mar.1992. — ZRC 29408, 1 ex., 42.8 mm SL; Malaysia: Pahang, Pekan road, 66 km from Mersing to Kuantan road, blackwater stream, coll. P. K. L. Ng et al., 24 Jul.1992. — ZRC 38049, 1 ex., 77.3 mm SL; Malaysia: Selangor, Serbak Bernam, coll. P. K. L. Ng, Jun.1991. **Sumatra:** BMNH 1889.12.26:30, lectotype of *B. fasciata*, 69.1 mm SL; Indonesia: Sumatra, North Sumatra, Deli (Medan); Iversen. — ZRC 42468, 10 ex., 15.3-40.1 mm SL; Indonesia: Sumatra, North Sumatra, ca. 80 km south of Medan, Sei Rampah, Pantai Berdagai, pond at Kampung Nagur (3°31'14.0"N 99°10'32.2"E), coll. H. H. Tan et al., 15 Jun.1996.

— ZRC 42478, 4 ex., 18.8-24.3 mm SL; Indonesia: Sumatra, North Sumatra, ca. 250 km south of Medan, Rantau Berapat, tributary of Sungai Semang Alam (2°27'06.4"N 99°43'03.0"E), coll. H. H. Tan et al., 16 Jun.1996.

Diagnosis. — *Betta bellica* differs from *B. simorum* (the only other member of the species group) in the following characters: lower mode of anal-fin rays (31, vs. 32); lower mode of dorsal-fin rays (12, vs. 11); lower mode of lateral scales (33, vs. 34); lower mode of postdorsal scales (8, vs. 9); shorter pelvic fin (length 23.6-38.8% SL, vs. 31.3-48.3; reaching base of 8th anal ray, vs. 14th); shorter pelvic fin flange (ends halfway down pelvic fin filament, vs. two-thirds way); adpressed pelvic-fin not reaching anal-fin origin (vs. overlapping); and a less sloping lateral head profile (vs. more sloping and slightly concave).

Description. — General body shape and appearance as shown in Figs. 9a-b, 46a. Body long, slender, body depth at dorsal-fin origin 23.7-26.2% SL; head length 26.0-28.0% SL; head blunt and small; opercle without iridescent scales; body brown with green iridescence on scales; caudal fin rounded with median rays extended, dorsal and anal fins pointed, pelvic fin filamentous, flange (a narrow membrane) on first simple pelvic fin ray ending abruptly before one-third of ray. Meristics: lateral scales 33-35; transverse scales at dorsal-fin origin 8½-9; predorsal scales 24-27; subdorsal scales 7-10; postdorsal scales 7-9; dorsal-fin rays 0-I, 11-12 (total 12-13, mode 12); caudal fin rays ii, 5+6, ii; anal-fin rays I-II, 29-31 (total 30-32, mode 31); pelvic fin rays I, 1, 4; pectoral fin rays 12-13; vertebrae 2 + 8-9 + 22-23 = 32-33 (mode 33, n=10). Meristic and morphometric data of neotype in Table 2. Maximum known size 77.3 mm SL (ZRC 38049).

Coloration. — For live coloration, see Fig. 46a (see also Linke, 1991: 28; Kubota et al., 1996: 28). Background body colour dark brown dorsally, lighter brown ventrally. Fins with whitish to golden distal margins, brownish with some greenish iridescence in mature specimens when alive. Dorsal fin with transverse bars. Pelvic fin with white tip. Male with more iridescent green scales than female. Eye with bright blue iridescence. Juvenile with distinct central stripe.

Distribution. — Widely distributed in Peninsular Malaysia: Terengganu, Perak, Selangor, Pahang and Johor. Also found near Medan, North Sumatra (Fig. 10).

Field notes. — *Betta bellica* is usually found in peat swamp habitats, although it can also be found in swamp forest habitats (Ng et al., 1992). Other syntopic *Betta* species are: *B. tussyaie*, *B. waseri* (Pahang), *B. hipposideros*, *B. livida* (Selangor), *B. imbellis*, *B. persephone*, *B. pulchra* (Johor). Gut contents of wild caught specimens include a relatively high proportion of odonate nymphs (Chung et al., 1994).

Betta bellica is the largest known bubble-nest brooding *Betta*. Details of its spawning are given in Vierke (1987, 1991) and van den Nieuwenhuizen (1993). Mohsin & Ambak (1983: 249) listed *B. bellica* as rare or extinct, but this is incorrect, as recent collections show. Their statement probably reflects the poor knowledge and lack of sampling in peat swamp



Fig. 9. a) *Betta bellica* – ZRC 39196, neotype, 51.4 mm SL, b) *B. fasciata* – BMNH 1889.12.26:30, lectotype, 69.1 mm SL.

habitats until recent findings have found otherwise (see Ng et al., 1994).

Remarks. – See Tan & Ng (1996) for details of the taxonomic history of *B. bellica*. The record of *B. fasciata* from Jambi by Weber & de Beaufort (1922) is likely to be based on *B. simorum* (fide Tan & Ng, 1996).

Betta fasciata was originally described from Sumatra and from meristic and morphometric counts, it is no different from *B. bellica*. *Betta fasciata* was demonstrated to be a junior synonym of *B. bellica* with the designation of the larger syntype as the lectotype by Tan & Ng (1996) (BMNH 1889.12.26:30, 69.1 mm SL), and a species (*B. simorum*) closely allied to *B. bellica* was described from Sumatra (where both *B. bellica* and *B. simorum* occur). In the same paper, Tan & Ng (1996) chose a neotype for *B. bellica* to stabilise the taxonomy. The neotype is a male specimen, 51.4 mm SL (ZRC 39196) collected from the north Selangor peat swamp forest in the state of Selangor, Peninsular Malaysia. This locality is adjacent to the state of Perak, the original type locality of *B. bellica*.

BETTA PUGNAX GROUP

***Betta pugnax* (Cantor, 1850)**
(Figs. 11a-b, 46b)

Macropodus pugnax Cantor, 1850: 84.

Betta anabatooides (non Bleeker, 1851) - Bleeker, 1860a: 334; 1860b:

101; Weber & de Beaufort, 1922: 357; Herre & Myers, 1937: 72; Fowler, 1938: 121; Herre, 1940: 46.

Betta pugnax - Günther, 1861: 389; Hanitsch, 1901: 4; 1912: 27; Duncker, 1904: 164; Breder, 1934: 128; Tweedie, 1952b: 73; 1953: 50, pl. 9, fig. 5; Alfred, 1958: 161; 1961a: 162; 1961b: 18; 1963: 147, fig. 2; 1966: 49, pl. 8, fig. 1; Moshin & Ambak, 1983: 173; Kottelat, 1984: 275; Zakaria-Ismail, 1987: 409; Kottelat, 1989: 19; Lim & Ng, 1990: 94; Lim et al., 1990a: 317; 1990b: 49; Witte & Schmidt, 1992: 327; Kottelat, 1994: 297; Tan & Tan, 1994: 357; Lim, 1995: 161; Tan & Tan, 1996: 420; Vidhayanon et al., 1997: 54; Sim, 2002: 74; Tan & Lim, 2004: 111.

Betta picta (non Valenciennes, in Cuvier & Valenciennes, 1846) - Bleeker, 1879: 26; Weber & de Beaufort, 1922: 360; Fowler, 1938: 121; Herre, 1940: 44.

Betta trifasciata (non Bleeker, 1851) - Károli, 1881: 172 (part).

Betta macrophthalma Regan, 1910: 781.

Betta bleekeri Regan, 1910: 780 (part).

Betta brederi Myers, 1935: 25.

Betta fusca (non Regan, 1910) - Tweedie, 1936: 22; Fowler, 1938: 259; Herre, 1940: 46.

Betta taeniata (non Regan, 1910) - Tweedie, 1936: 22; Herre & Myers, 1937: 72; Herre, 1940: 45.

Betta rubra (non Perugia, 1893) - Herre, 1940:45.

Material examined. – Lectotype - **Malaysia: Pulau Penang:** BMNH 1860.3.19:930, 60.6 mm SL; Pinang, coll. Cantor.

Paralectotypes – **Malaysia: Pulau Penang:** BMNH 1860.3.19:317-318, 2 ex. 51.8-66.2 mm SL; same data as lectotype.

Others – **Malaysia: Pulau Penang:** ZRC 1610, 8 ex., 40.3-59.4 mm SL; Batu Ferringi Catchment Area; Alfred et al., 1961. — ZRC

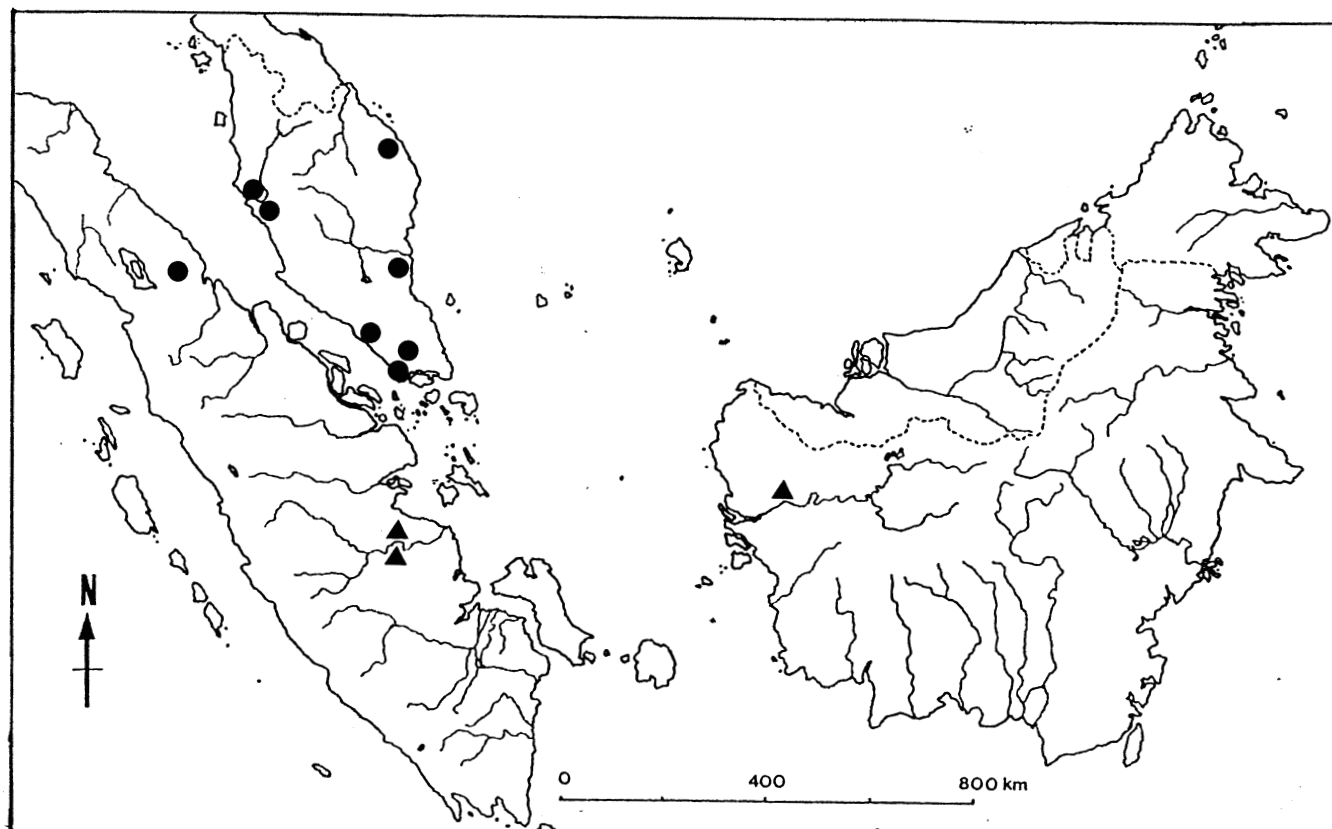


Fig. 10. Distribution map of *B. bellica* (circle) and *B. simorum* (triangle).

1611, 2 ex., 36.4-37.1 mm SL; Sungai Bayan Lepas; Alfred et al., 1961. — ZRC 1612, 6 ex., 42.4-58.2 mm SL; Sungai Telok Bahang, 14½ miles Telok Bahang Road; Alfred et al., 1961. — ZRC 1613, 1 ex., 27.4 mm SL; Pulau Betong, Kampung Trang; Alfred et al., 1961. — ZRC 1614, 1 ex., 36.3 mm SL; Sungai Balik Pulau, 1 mile north-east of Balik Pulau; Alfred et al., 1961. — ZRC 14753, 2 ex., 48.4-48.9 mm SL; Kolam Ayer; Alfred et al., 1964. — ZRC 31990, 4 ex., 44.3-57.0 mm SL; Kampung Tengah, coll. H. H. Tan & S. H. Tan, 8 Jun.1993. — ZRC 32047, 2 ex., 44.4-59.5 mm SL; Pantai Acheh, coll. H. H. Tan & S. H. Tan, 8 Jun.1993. — ZRC 32065, 7 ex., 40.3-50.9 mm SL; Sungai Relau (upper reaches), Kampung Darat, coll. H. H. Tan & S. H. Tan, 9 Jun.1993. — ZRC 32302, 1 ex., 48.1 mm SL; Balik Pulau, Kampung Titi Serong (upstream), coll. H. H. Tan & S. H. Tan, 10 Jun.1993. — ZRC 39264, 1 ex., 60.1 mm SL; Penang, coll. K. K. P. Lim, 1995. **Kedah:** ZRC 11631, 1 ex., 47.3 mm SL; Pulau Langkawi, Dayang Bunting; not known, Mar.1960. — ZRC 29633, 3 ex., 35.9-51.5 mm SL; Pulau Langkawi, Telaga Tujuh waterfalls, coll. K. K. P. Lim, 30 Jan.1990. **Terengganu:** ZRC 21720, 1 ex., 41.2 mm SL; Sekayu waterfalls, coll. P. K. L. Ng et al., 18 Mar.1992. **Pahang:** ZRC 9003, 3 ex., 46.9-52.4 mm SL; Tasik Chini; 205 SQN RAF, Changi, 19-25 Aug.1967. — ZRC 8306-9, 3 ex., 46.7-67.3 mm SL; Rompin, eastern tributaries of Sungai Kinchin; Rompin-Endau Expedition ZRC team, 13 Jun.1989. — ZRC 3476, 5 ex., 45.4-56.0 mm SL; Tasik Bera; C. C. Lindsey, 29-31 Mar.1965. **Perak:** ZRC uncat., 4 ex., 41.3-52.9 mm SL; Taiping, base of Bukit Larut, coll. K. K. P. Lim et al., 21 Dec.1994. — ZRC 39572, 2 ex., Taiping, base of Bukit Larut, coll. H. H. Tan et al., 18 Nov.1995. **Selangor:** ZRC 435, 2 ex., 48.7-49.1 mm SL; West of Ginting Sempak (14³/₄ miles from Kuala Lumpur); A. W. Herre & Tweedie, 1937. — ZRC 19138, 1 ex., 54.5 mm SL; University of Malaya campus, in peaty stream, coll. P. K. L. Ng, 20 Nov.1989. — ZRC uncat., 3 ex., 41.7-48.6 mm SL; University of Malaya campus, in remnant swamp forest, coll. H. H. Tan et al., 22 Dec.1994. — ZRC 39579, 1 ex., north Selangor peatswamp forest, coll. P. K. L. Ng et al., Sep.1994. **Johor:** ZRC 23096, 2 ex., 47.5-48.6 mm SL; Ulu Endau, Sungai Anak Jasin; T. H. T. Tan & J. B. Tay, 4 Apr.1992. — ZRC 28404, 3 ex., 38.9-39.8 mm SL; Kota Tinggi, Sungai Tementang, coll. P. K. L. Ng et al., 15 Oct.1992. — ZRC 38220, 2 ex., 55.2-55.8 mm SL; Kota Tinggi, Sungai Tementang, coll. H. H. Tan et al., 21 Aug.1994. — ZRC 11912, 2 ex., 49.0-54.3 mm SL; Kota Tinggi; C. F. Lim. — ZRC 25765, 1 ex., 47.6 mm SL; Sungai Mupor along Kota Tinggi-Mersing road, coll. P. K. L. Ng et al., 24 Jul.1992. — ZRC 18130, 2 ex., 42.4-45.2 mm SL; 100 m north of road marker 175 km on Johor Bahru-Kuantan road (north of Mersing), coll. P. K. L. Ng et al., 19 Oct.1991. — ZRC 19490, 1 ex., 43.1 mm SL; swamp near

Mersing, coll. P. K. L. Ng, Sep.1991. — ZRC 8442, 2 ex., 53.1-55.0 mm SL; Muar, 14th mile on Yong Peng Road; anon., 7 May.1962. — ZRC 19072, 1 ex., 47.3 mm SL; Mawai district; M. W. F. Tweedie, 1935. — ZRC 8501, 1 ex., 48.3 mm SL; 14th mile on Muar-Yong Peng road; E. R. Alfred, 28 Sep.1967. — ZRC 28720, 1 ex., 42.2 mm SL; near Pontian, coll. P. K. L. Ng et al., 4 Mar.1992. — ZRC 28995, 1 ex., 53.1 mm SL; Gunung Pulai Reservoir, coll. P. K. L. Ng et al., 4 Mar.1992. — ZRC 19135, 1 ex., 50.6 mm SL; stream near Gunung Pulai Reservoir (south), coll. P. K. L. Ng, 14 Mar.1990. — ZRC 1576.1-1576.11, 11 ex., 58.4-67.2 mm SL; Gunung Pulai; L. K. Charles, Apr.1934. — ZRC uncat., 2 ex., 41.7-42.1 mm SL; Gunung Pulai, stream running under access road towards Pekan Nanas, coll. H. H. Tan et al., 20 May.1993. — ZRC 38240, 5 ex., 38.3-46.8 mm SL; Pontian, stream draining from Gunung Pulai Reservoir, coll. P. K. L. Ng et al., 29 Sep.1994. — ZRC 13887, 3 ex., 42.9-52.5 mm SL; Gunung Pantii foothills, coll. P. K. L. Ng, 31 Aug.1990. — ZRC 19492, 2 ex., 59.0-59.6 mm SL; Gunung Pantii, forest, coll. P. K. L. Ng, Oct.1991. — ZRC 32485, 1 ex., 49.9 mm SL; Air Hitam, Parit Botak, blackwater stream, km 8; Yong, 23 I 1993. — USNM 094400, holotype of *B. brederi*, 64.2 mm SL female, Johor; A. Ramsperger, 22 Oct.1934. **Singapore:** ZRC 38297, 9 ex., 44.7-52.6 mm SL; Nee Soon swamp forest, coll. P. K. L. Ng et al., 23 Aug.1993. — ZRC 38298, 9 ex., 41.6-56.3 mm SL; Nee Soon swamp forest, coll. P. K. L. Ng et al., 29 Jul.1993. — ZRC 12196, 2 ex., 42.4-49.2 mm SL; forest stream draining into northern arm of Lower Pierce Reservoir, coll. P. K. L. Ng, 13 Jul.1990. — ZRC 34621, 1 ex., 54.3 mm SL; Rifle Range road; C. Y. Chang et al., 27 May.1993. — ZRC 30376, 2 ex., 40.6-44.2 mm SL; Nee Soon swamp forest, edge of abandoned kampung near Upper Thomson road, coll. P. K. L. Ng, 15 Jan.1993. — BMNH 1868.7.10:28, holotype of *B. macrophthalmia*, 36.3 mm SL juvenile; Singapore.

Diagnosis. — *Betta pugnax* is distinguished from other members of the *B. pugnax* species group by the following combination of characters: chin-bar present; no dark marks below postorbital stripe on opercle; dorsal transverse bars present; caudal transverse bars present only in male; greenish to blueish iridescent scales on opercle and body; anal-fin with red subdistal band and black edge; no dark edge on caudal-fin; anal-fin rays 25-28 (mode 26); lateral scales 28-31 (mode 29); postdorsal scales 11-12 (mode 11); pelvic fin length 26.6-43.8% SL; head length 27.5-35.2% SL; inter-orbital width 32.4-53.0% HL.

Description. — General body shape and appearance as in Figs. 11a-b, 46b. Body slender; dorsal-fin origin above 13th lateral scale; posterior extremity of dorsal fin pointed, reaching about anterior third of caudal fin; anal-fin origin below 7th lateral scale; posterior extremity of anal fin pointed and reaching beyond midlength of caudal fin; caudal fin broadly lanceolate (Fig. 5b); pelvic fin filamentous. Meristics: lateral scales 29-30; predorsal scales 19-22 (mode 21); subdorsal scales 5-8 (mode 6); postdorsal scales 11-12 (mode 11); dorsal-fin rays 0-II, 7-10 (total 8-10, mode 9); anal-fin rays I-II, 24-26 (total 25-28, mode 26); caudal fin rays ii, 4+5, ii; pelvic fin rays I, 1, 4; pectoral fin rays 13; vertebrae 2 + 8 + 18-21 = 28-31. Morphometrics: total length 130.6-148.1% SL; predorsal length 60.9-73.4% SL; preanal length 40.6-51.2% SL; pelvic-fin length 26.6-43.8% SL; head length 27.5-35.2% SL; body depth at dorsal-fin origin 24.8-32.1% SL; length of anal-fin base 44.2-54.0% SL; length of dorsal-fin base 9.9-15.7% SL; orbital diameter 27.9-38.5% HL; postorbital length 45.0-

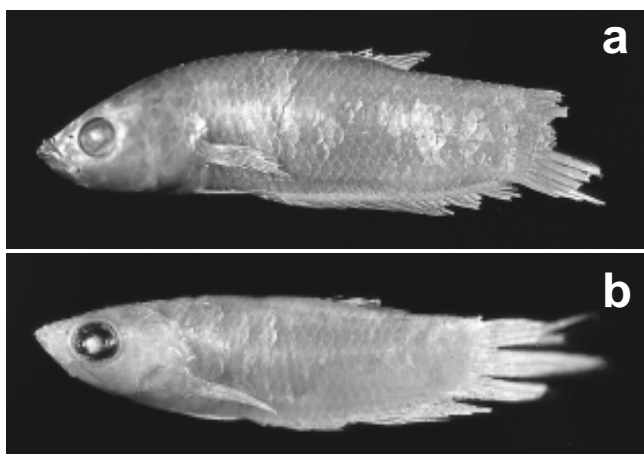


Fig. 11. a) *Betta pugnax* - BMNH 1860.3.19:930, lectotype, 60.6 mm SL, b) *B. macrophthalmia* - BMNH 1868.7.10:28, holotype, 36.3 mm SL.

55.7% HL; interorbital width 32.4-53.0% HL; head length 41.6-54.3 in% predorsal length. Maximum known size 67.3 mm SL (ZRC 8306).

Coloration. – For live coloration, see Fig. 46b (see also Linke, 1991: 43; Kubota et al., 1996: 38). Live topotypes from Penang have blue iridescent opercle with a light brown background. Each scale of body and opercle, a median area with blue to greenish-blue iridescence. Specimens from Taiping, Perak, also exhibit the same character (these two localities are hill streams with clear waters, pH 7 and above). Specimens from more acidic waters (e.g., Singapore), usually with less blue and more green iridescence. Caudal transverse bars in males (alive: strongly barred depending on state of fish; in preserved specimens: faintly barred or not apparent) (Fig. 2). Preserved specimens dark brown dorsally and light brown ventrally, fins slight brownish to hyaline; male with blackened opercle region, female and juvenile with chin-bar, central and second central stripes fairly distinct, with caudal peduncle spot.

Distribution. – *Betta pugnax* is widely distributed in Peninsular Malaysia. It is found in Pulau Penang, Kedah, Terengganu, Pahang, Perak, Selangor, Johor and Singapore (Fig. 12). It is also found in the Anambas islands (Tan & Lim, 2004), Riau Archipelago, Lingga Archipelago, Riau province and Jambi province (Tan & Ng, 2005) (present volume).

Field notes. – Specimens from Pulau Penang were mainly collected in hill streams and foothills. These waters were clear

and ranged from fast flowing to sluggish. The substrate was usually sandy with rocks. There was little or no submerged vegetation. Overhanging bank vegetation, submerged leaf litter and exposed roots of bank vegetation constituted the main habitats for *B. pugnax*. It was mostly found in and at the periphery of stagnant areas. The pH was around 7.4 (range 7.1-7.6). The water depth ranged from 10 to 80 cm. There were no other syntopic osphronemids in these habitats. The only other *Betta* found on Pulau Penang is *B. imbellis*.

Comparative notes. – *Betta pugnax* is distinguished from the other members of the *B. pugnax* species group by the following characters: more anal-fin rays than *B. fusca* (25-28, mode 26, vs. 24-25); more predorsal scales than *B. schalleri* (19-21, mode 20, vs. 17-19, mode 19); fewer predorsal scales than *B. fusca* (19-21, mode 20, vs. 22-23); shorter preanal length than *B. prima* and *B. enisae* (40.6-51.2% SL, vs. 50.1-54.8); relatively shorter head length than *B. fusca*, *B. enisae*, *B. schalleri*, *B. pulchra*, *B. prima* and *B. lehi* (27.5-35.2% SL, vs. 32.7-37.7); larger orbital diameter than *B. fusca* and *B. enisae* (27.9-38.5% HL, vs. 23.8-28.5).

Remarks. – Bleeker (1879) identified 130 specimens from various localities as *B. picta*. In the volume 9 of his Atlas (1877: pl. 395, fig. 3), he figured the species, but he did not indicate the origin of the figured specimen. Neither did he in his 1879 paper. The text due to accompany this plate has never been published (Bleeker died in 1878).

Regan (1910: 780) described *B. bleekeri* based on Bleeker's 1877 figure and 1879 text. He listed *B. picta* (sensu Bleeker)

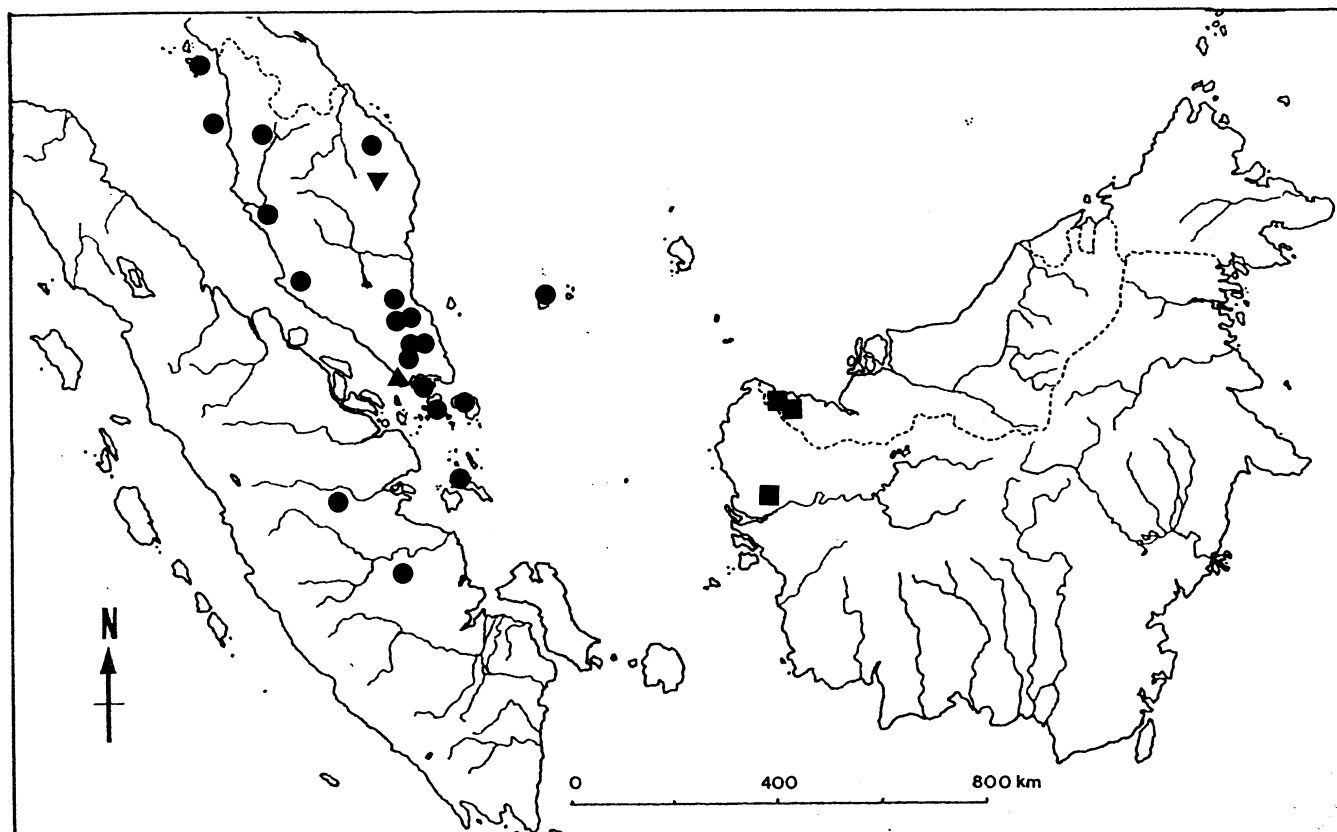


Fig. 12. Distribution map of *Betta pugnax* (circle), *B. pulchra* (triangle), *B. stigmosa* (upside-down triangle) and *B. lehi* (square).

as a synonym of *B. bleekeri*. He also commented that the description of *B. picta* (sensu Bleeker) is based on the figure in Bleeker's Atlas (1877: pl. 395, fig. 3). Regan (1910) clearly considers the figure in Bleeker's Atlas to be a species distinct from *B. picta*. This means that all of the specimens mentioned or used by Bleeker (1877, 1879) for *B. picta* are syntypes of *B. bleekeri* (except the one used by Regan for description of *B. bleekeri*, based on Bleeker's 1877 figure). Since Bleeker (1879) included *B. trifasciata*, *B. pugnax* and *B. anabatooides*, in the synonymy of *B. picta*, all his specimens of *B. trifasciata* and *B. anabatooides* and all his and Cantor's specimens of *B. pugnax*, also are syntypes of *B. bleekeri*. This is problematic when selecting a lectotype or clarifying the identity of *B. bleekeri*.

Witte & Schmidt (1992: 326) synonymised *B. bleekeri* with *B. bellica*. Bleeker's (1877) figure of *B. picta* is very unlikely to be based on a specimen of *B. bellica*. General morphology of the figured specimen, meristics and morphometrics, it seems to belong to the *B. waseri* group, as defined by Ng & Kottelat (1994). Interestingly, Witte & Schmidt (1992: 326) regarded Bleeker's figure as coming close to *B. patoti*, but they still provisionally synonymised *B. bleekeri* under *B. bellica*, arguing the single *B. picta* (RMNH 10741) they had examined from Bleeker's 130 specimens (!), presumably from Sumatra, matched *B. bellica*. They did not state how they identified the locality of the specimen.

In order to definitively fix the nomenclatural status of *B. bleekeri*, we have decided to synonymise *B. bleekeri* with *B. pugnax*. *Betta pugnax* is listed by Bleeker (1879) as a synonym of *B. picta*, and all the material which Bleeker considered as belonging to *B. picta* constitutes the type series of *B. bleekeri*, therefore the type series of *B. pugnax* is part of the type series of *B. bleekeri*. We have chosen as the lectotype of *B. bleekeri* the same specimens (BMNH 1860.3.19.930) which had been designated as lectotype of *B. pugnax* by Alfred (1964). This makes *B. bleekeri* a junior objective synonym of *B. pugnax*. This action will not affect the taxonomy of the other *Betta* species, as the name *B. bleekeri* had been only used thrice (Regan, 1910: 780; Weber & de Beaufort, 1922: 357; Witte & Schmidt, 1992: 326). Other details of the taxonomic history of *B. pugnax* are discussed in Tan & Tan (1996).

***Betta pulchra* Tan & Tan, 1996**
(Figs. 13, 46c)

Betta pulchra Tan & Tan, 1996: 428.

Material examined. – Holotype - **Malaysia:** - ZRC 28860, 49.9 mm SL; Malaysia: Johor, Pontian, Kampung Jasa Sepakat, coll. P. K. L. Ng et al., 8 May.1992.

Paratypes – ZRC 28861-28899, 39 ex., 19.8-46.5 mm SL; same locality data as holotype. — ZRC 17368-17370, 3 ex., 34.4-55.9 mm SL; Malaysia: Johor, Pontian, coll. P. K. L. Ng et al., 1989. — ZRC 29123-29125, 3 ex., 44.8-50.2 mm SL; Malaysia: Johor, Pontian, Sri Bunian, Kampung Pt. Tekong, coll. P. K. L. Ng et al., 8 May.1992. — ZRC. 39252, 5 ex., 39.0-45.3 mm SL; Malaysia:

Johor, Pontian, ca. 4 km towards Pontian Kechil from Sri Bunian (1°27'13.1"N 103°24'52.1"E), coll. P. K. L. Ng et al., 15 Aug.1995. Others - ZRC. 39251, 15 ex., 21.5-36.5 mm SL; Malaysia: Johor, Pontian, Sri Bunian, Kampung Pt. Tekong (1°27'59.2"N 103°26'07.7"E), coll. P. K. L. Ng et al., 15 Aug.1995. — ZRC. 39250, 13 ex., 21.7-43.1 mm SL; Malaysia: Johor, Pontian, Sri Bunian, Kampung Jasa Sapakat (1°31'30.5"N 103°27'47.7"E), 5 km into side road leading into oil-palm estate, coll. P. K. L. Ng et al., 15 Aug.1995.

Diagnosis. – *Betta pulchra* is distinguished from other members of the *B. pugnax* species group by the following combination of characters: chin-bar present; no dark marks below postorbital stripe on opercle; dorsal transverse bars present; caudal transverse bars present only in male; greenish iridescent scales on opercle and body; anal fin with red subdistal border and black edge; caudal fin without distal dark edge; anal-fin rays 24-28 (mode 26); lateral scales 28-30 (mode 29); postdorsal scales 10-11 (mode 10); pelvic fin length 29.1-53.2% SL; head length 32.7-37.6% SL; inter orbital width 34.3-41.8% HL.

Description. – General body shape and appearance as in Figs. 13, 46c. Body short and stocky, body depth at dorsal-fin origin 25.9-36.9% SL; head length 32.7-37.6% SL; head pointed and stout; caudal fin narrowly lanceolate (Fig. 5c); pelvic fin filamentous; dorsal and anal fins pointed, anal fin reaching to half or more of caudal fin. Meristics: lateral scales 28-30 (mode 29); transverse scales at dorsal-fin origin 9¹/₂; subdorsal scales 6-7¹/₂ (mode 7); predorsal scales 18-21 (mode 20); postdorsal scales 10-11 (mode 10); dorsal-fin rays I-II, 8-9 (total 9-10, mode 9); anal-fin rays I-II, 22-26 (total 24-28, mode 26); caudal fin rays ii, 4+5, ii; pectoral fin rays 12; pelvic fin rays I, 1, 4; vertebrae 2 + 8 + 19 = 29. Morphometrics: total length 136.6-156.6% SL; predorsal length 60.8-66.0% SL; preanal length 44.7-50.0% SL; pelvic-fin length 29.1-53.2% SL; head length 32.7-37.6% SL; body depth at dorsal-fin origin 25.9-36.9% SL; length of anal-fin base 49.8-52.9% SL; length of dorsal-fin base 13.9-15.9% SL; orbital diameter 26.0-31.3% HL; postorbital length 44.3-49.7% HL; interorbital width 34.3-41.8% HL; head length 49.8-58.5% predorsal length. Maximum known size 55.9 mm SL (ZRC 17368).

Coloration. – For live coloration, see Fig. 46c (see also Kubota et al., 1996: 39, bottom figure identified as *B. pugnax*). Pattern similar to that of *B. pugnax* sensu stricto, except that more distinctly greenish iridescent scales (cf. blue in *B. pugnax*). Guanophores on body generally more intense than



Fig. 13. *Betta pulchra* – ZRC 28860, holotype, 49.9 mm SL (right side, reversed).

those of *B. pugnax* in life. Opercle with iridescent greenish-blue scales; body brown with iridescent green scales. Head with preorbital and postorbital stripes, continuous with central stripe, second central stripe and caudal peduncle spot in both sexes and juvenile. Distal part of pelvic ray iridescent green; dorsal transverse bars present; caudal fin brownish, caudal transverse bars present in mature male; anal fin with red subdistal margin and black edge.

Field notes. – *Betta pulchra* is found in blackwater habitats; other syntopic osphronemids present are *Belontia hasseltii*, *Betta bellica*, *B. imbellis*, *Sphaerichthys osphromenoides*, *Parosphromenus* sp. and *Trichopsis vittata*. This species is common only in the overgrown bank vegetation of the irrigation canals. Much of the district of Pontian was peat swamp forest in the past, but most of it has been logged and planted with oil-palm, pineapple and rubber trees. The pH of the waters range from 3.9 to 4.2. *Betta pulchra* is an oral brooder (Tan, 1997).

Distribution. – *Betta pulchra* appears to be restricted to the blackwaters in Pontian, southwest Johor, Malaysia (Fig. 12).

Comparative notes. – *Betta pulchra* is distinguished from the other members of the *B. pugnax* species group in having: more subdorsal scales than *B. fusca*, *B. prima* and *B. enisae* (6-7¹/₂, vs. 5-6); more lateral scales than *B. enisae* (28-30, mode 29, vs. 26-28, mode 27); fewer lateral scales than *B. schalleri* (28-30, vs. 31); fewer predorsal scales than *B. fusca* (18-21, vs. 22-23); shorter predorsal length than *B. fusca*, *B. prima* and *B. enisae* (60.8-66.0% SL, vs. 67.3-70.3); shorter preanal length than *B. prima* and *B. enisae* (44.7-50.0% SL, vs. 50.1-54.8); relatively greater head length than *B. pugnax* (32.7-37.6% SL, vs. 27.5-35.2); greater length of dorsal-fin base than *B. fusca* and *B. schalleri* (13.9-15.9% SL, vs. 12.4-13.9); greater orbital diameter than *B. fusca* (26.0-31.3% HL, vs. 23.8-26.7); greater interorbital width than *B. fusca* (34.3-41.8% HL, vs. 33.5-34.2); greater head length than *B. fusca* (49.8-58.5% predorsal length, vs. 47.2-49.4).

***Betta stigmosa*, new species**

(Figs. 14a-b, 46d)

Betta pugnax (non Cantor, 1850) - Tweedie, 1952a: 73 (part); Mohsin & Ambak, 1983: 173; Tan & Tan, 1996: 420 (part).
Betta cf. *pugnax* (non Cantor, 1850) - Kottelat et al., 1992: 11 (list only).

Material examined. – Holotype - ZRC 43392, male, 36.9 mm SL; Malaysia: Terengganu, Sekayu waterfalls (04°57'49.7"N 102°57'14.0"E), near swampy stream, coll. P. K. L. Ng et al., 10 Oct.1997.

Paratypes – ZRC 41710, 5 ex., 22.3-34.0 mm SL; same locality data as holotype. — ZRC 43393, 7 ex., 29.2-37.5 mm SL; Malaysia: Terengganu, Sekayu, swampy stream draining into concrete pond near chalets (04°57.80'N 102°57.21'E), coll. H. H. Tan & K. K. P. Lim, 21 & 28 Oct.1998. — ZRC 21720, 1 male, 41.1 mm SL; Malaysia: Terengganu, Sekayu waterfalls (4°57'49.7"N 102°57'14.0"E), coll. P. K. L. Ng et al., 18 Mar.1992.

Others – ZRC 21800, 1 ex., 20.0 mm SL; Malaysia: Terengganu, Pasir Puteh Air Terjun, 4 km from turnoff, coll. P. K. L. Ng et al., 20 Mar.1992.

Diagnosis. – *Betta stigmosa* is distinguished from the other members of the *B. pugnax* group by the following unique combination of characters: 5-10 regularly spaced black transverse bars on caudal fin of male and female; in life, both male and female with alternating blueish and black transverse bars on dorsal and caudal fins; both male and female with black transverse bars on posterior few anal-fin rays; anal fin with dark distal edge. *Betta stigmosa* shares with *B. prima* the presence of a second postorbital stripe on opercle; small adult size (31-41 mm SL); total anal-fin rays 23-24; lateral scales 29-30 (mode 29); postdorsal scales 10-11 (mode 10); pelvic fin length 33.2-51.8% SL; head length 33.6-36.5% SL; interorbital width 29.8-32.1% HL.

Description. – General appearance as illustrated in Figs. 14a-b, 46d. Meristic and morphometric data in Table 3. Body relatively slender (body depth at dorsal-fin origin 25.6-28.2% SL), head relatively long and blunt (head length 33.6-36.5% SL; head width 19.0-21.5% SL and 56.0-58.9% HL). Dorsal, caudal and anal fins pointed; dorsal fin placed relatively far back (predorsal length 62.8-67.5% SL); caudal fin with distal part of rays extended slightly beyond interradiial membrane, median rays elongated in male; length of anal-fin base about half of standard length (48.2-51.3% SL); pelvic fin rounded with relatively long filamentous ray (33.2-51.8% SL); pectoral fin rounded. Vertebrae 2 + 8 + 18-19 = 28-29 (mode 29, n = 7). Maximum known size 41.1 mm SL (ZRC 21720).

Coloration. – The following is based on freshly preserved specimens. Male: reddish brown body, darker brown head, opercle and throat area greenish-blue iridescence (darkly pigmented when preserved longer). Lower lip black, chin-bar present but may be masked by dark pigmentation. Pre- and postorbital stripes present, second postorbital stripe masked by dark pigmentation. Belly whitish, ventral part of body lighter reddish brown. Dorsal and caudal fins brown. Dorsal fin with distinct or faint 3-5 black transverse on interradiial membrane. Caudal fin with thin black edge on

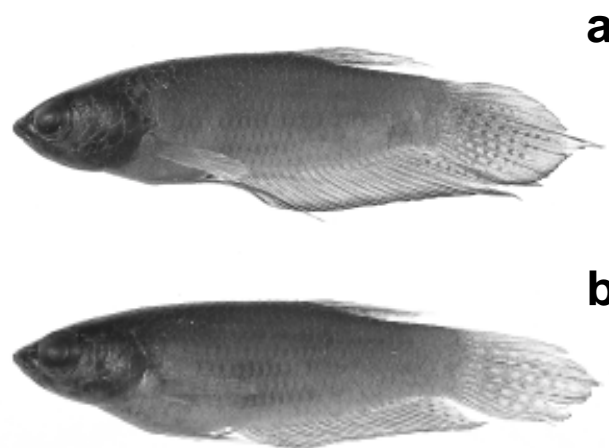


Fig. 14. a) *Betta stigmosa* – ZRC 43392, male holotype, 36.9 mm SL, b) ZRC 41710, female paratype, 32.2 mm SL.

lower half, 5-10 regularly spaced dark brown or black transverse bars on interradial membrane. Anal fin reddish with thin black edge, 2-6 regularly spaced dark brown transverse bars on posterior 3-4 rays. Pelvic fin brown, filament darkly pigmented. Pectoral fin hyaline.

Female: yellowish brown body, darker brown head, opercle and throat area yellowish (not darkly pigmented after long-term preservation). Lower lip black, chin-bar present with anterior portion elongated towards mouth (Fig. 15). Pre- and postorbital stripes present, second postorbital stripe interrupted into 4-5 staggered parts (Fig. 15). Belly whitish, ventral part of body light brown. Dorsal and caudal fins brown. Caudal fin without thin black edge on lower half, 3-8 regularly spaced black transverse bars on interradial membrane. Anal fin reddish brown with thin black edge, 2-5 regularly spaced dark brown transverse bars on posterior 3-4 rays. Pelvic and pectoral fins hyaline, pelvic filament hyaline. Juvenile with faint central and second central stripes, dorsal and caudal fins hyaline, anal fin with 2 longitudinal rows of dark brown spots.

Life coloration. The color pattern is similar to above described (see Fig. 46d). The transverse bar pattern on dorsal and caudal fins consist of alternating slightly iridescent blue and black transverse bars. Pelvic fin bright white.

Distribution. – *Betta stigmosa* is currently known only from the hill streams in Sekayu area, Terengganu, Peninsular Malaysia (Fig. 12).

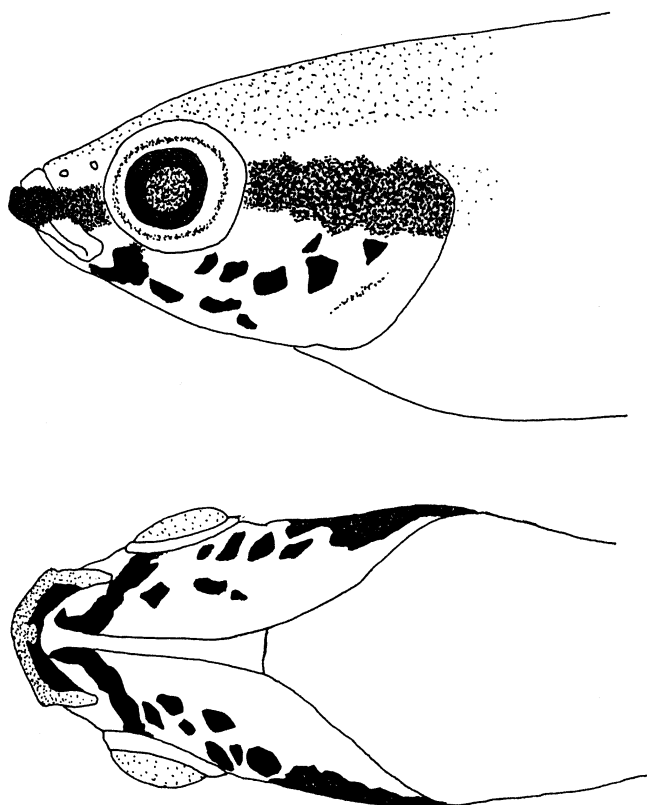


Fig. 15. Schematic drawings of lateral and ventral head views of *B. stigmosa* (ZRC 41710, female, 31.6 mm SL).

Field notes. – The type locality is a swampy stream draining out from a small hill into the Sekayu waterfalls. Syntopic species present: *Poropuntius smedleyi*, *Puntius binotatus*, *Rasbora* cf. *bunguranensis* (Cyprinidae), *Clarias* sp. (Clariidae), *Amblyceps mangois* (Amblycepididae), *Channa gachua*, *C. melasoma* (Channidae) and tilapia (Cichlidae).

Etymology. – From the Latin *stigmōsus*, meaning full of marks, pertaining to the patterned opercle and barred pattern on dorsal, caudal and anal fins of both male and female specimens.

Comparative notes. – *Betta stigmosa* is distinguished from the other members of the *B. pugnax* group in the following characters: presence of caudal transverse bars in male and female (vs. in male only or absent in both sexes); transverse bar pattern on posterior anal-fin rays (vs. absent); fewer anal-fin rays than other members (23-24, vs. 25-29); more subdorsal scales than *B. fusca*, *B. prima* and *B. enisae* ($6\frac{1}{2}$, vs. 5-6); more lateral scales than *B. enisae* (29-30, vs. 26-28); fewer lateral scales than *B. schalleri* (29-30, vs. 31-33); more predorsal scales than *B. schalleri* (20-21, vs. 17-19); fewer predorsal scales than *B. fusca* (20-21, vs. 22-24); smaller predorsal length than *B. fusca*, *B. prima* and *B. enisae* (62.8-67.5% SL, vs. 67.3-70.3); smaller postdorsal length than *B. prima* (21.2-23.6% SL, vs. 24.1-26.3); greater head length than *B. fusca* (51.7-55.4% predorsal length, vs. 47.2-49.4); smaller body depth at dorsal-fin origin than *B. fusca*, *B. prima* and *B. breviobesus* (25.6-28.2% SL, vs. 28.1-33.5); greater length of dorsal-fin base than *B. enisae* (12.2-13.9% SL, vs. 8.7-12.1); smaller length of anal-fin base than *B. breviobesus* (48.2-51.3% SL, vs. 51.1-55.7); greater orbit diameter than *B. fusca* (26.7-28.4% HL, vs. 23.8-26.7); smaller head width than *B. fusca* (56.0-58.9% HL, vs. 59.7-69.8); smaller orbit diameter than *B. schalleri* (52-60% postorbital length, vs. 61-76); smaller interorbital width than *B. fusca*, *B. schalleri*, *B. prima*, *B. enisae*, and *B. lehi* (62-65, vs. 65-84) (data for *B. prima*; *B. schalleri*; *B. enisae*; *B. pugnax* and *B. pulchra*; and *B. breviobesus* from Kottelat, 1994, 1995; Kottelat & Ng, 1994; Tan & Tan, 1996; and Tan & Kottelat, 1998, respectively).

Remarks. – Tan & Tan (1996) revised the taxonomy of *B. pugnax* from Peninsular Malaysia. They overlooked the distinctiveness of *B. stigmosa* for which they had only two specimens (ZRC 21720, ZRC 21800) at the time. The larger series now available shows the unique character of the black transverse bars on the caudal fin of both male and female. This is the second species of the *B. pugnax* group in which this character is observed, the other being *B. enisae*.

Betta lehi, new species

(Figs. 16, 46e)

Betta pugnax (non Cantor, 1850) - ?Károli, 1881: 172.

Betta (sp. E) sp. E Witte & Schmidt, 1992: 324 (key), 327 (part).

Betta spec. Brown & Brown, 1987: 166.

Betta sp. Kottelat & Lim, 1995: 248.

Material examined. – Holotype - ZRC 39267, 50.7 mm SL male,

Borneo: Sarawak, Sungai Stuum Muda (1°28'51.3"N 109°58'18.1"E), ca. 58 km to Sematan on road from Bau to Lundu, 21.1 km before Lundu ferry over Batang Kayan, coll. H. H. Tan & D. C. J. Yeo, 7 Sep.1995.

Paratypes – ZRC 41582, 15 ex., 18.5-47.8 mm SL, same locality data as holotype. — ZRC 41583, 11 ex., 14.0-49.1 mm SL; CMK 13021, 5 ex., 21.1-48.7 mm SL; ZMA 121.674, 5 ex., 22.5-47.9 mm SL; SM uncat., 5 ex., 25.5-41.6 mm SL; same locality data as holotype, coll. H. H. Tan et al., 6 Sep.1995.

Others – ZRC 37875, 4 ex., 23.1-60.8 mm SL; Borneo: Sarawak, Lundu-Bau road, 27 km before Bau, coll. M. Kottelat et al., 8 May.1994. — ZRC 26055-57, 3 ex., 22.7-47.3 mm SL; - CMK 8414, 3 ex., 16.1-45.9 mm SL; Borneo: Sarawak, 42 km before Lundu from Kuching, after Sungai Stinggang, coll. M. Kottelat, P. K. L. Ng & K. K. P. Lim, 3 Jul.1992. — ZRC 40925, 38 ex., 17.4-41.6 mm SL; USNM 344462, 10 ex., 26.0-36.3 mm SL; MZB uncat., 5 ex., 26.8-33.1 mm SL; Borneo: Sarawak, Sungai Sebiris (1°41'32.0"N 109°47'00.8"E), 13.8 km after Kampung Pueh turnoff, towards Lundu on Lundu-Sematan road, coll. P. K. L. Ng et al., 1 Sep.1996. — ZRC 40926, 2 ex., 37.3-38.0 mm SL; Borneo: Sarawak, Sungai Stunggang (1°37'28.5"N 109°53'10.9"E), 4.8 km before Lundu ferry over Batang Kayan, coll. P. K. L. Ng et al., 2 Sep.1996. — ZRC 40927, 39 ex., 14.9-49.6 mm SL; Borneo: Sarawak, Sungai Stuum Muda (1°28'51.3"N 109°58'18.1"E), 21.1 km before Lundu ferry point over Batang Kayan, coll. P. K. L. Ng et al., 2 Sep.1996. — ZRC 46268, 9 ex., 43.8-54.0 mm SL; Kalimantan Barat, Pontianak, aquarium trade; donor F. Yuwono, Oct.1999.

Diagnosis. – *Betta lehi* is distinguished from the other members of the *B. pugnax* species group by the following combination of characters: no chin-bar; dorsal fin transverse bars present; no caudal fin transverse bars; green iridescent scales on opercle and body; anal fin with iridescent light blue distal border; and two black marks below postorbital stripe on opercle of female and juvenile (Fig. 11); anal-fin rays 25-29 (mode 28); lateral scales 28-30 (mode 29); postdorsal scales 10-11 (mode 11); pelvic fin length 34.8-50.6% SL; head length 33.4-36.8% SL; interorbital width 31.7-37.4% HL.

Description. – General body shape and appearance as in Figs. 16, 46e. Meristic and morphometric data in Table 3. Body stocky, relatively long and pointed head; caudal fin lanceolate, dorsal and anal fins pointed, anal fin reaching end of caudal fin, pelvic fin filamentous. Maximum known size 60.8 mm SL (ZRC 37875).

Coloration. – For live coloration, see Fig. 46e (see also Kubota et al., 1996: 42, figures identified as *B. sp. aff.*



Fig. 16. *Betta lehi* – ZRC 39267, male holotype, 50.7 mm SL.

pugnax). Mature male with an iridescent light blue margin on anal fin and faintly on caudal fin when live, not visible when preserved. Body iridescence faint when alive, absent when preserved. Opercle iridescent green when alive, dark brown when preserved. Dorsal fin pointed, may reach midlength of caudal fin; penultimate anal ray sometimes extending beyond tip of caudal fin; tip of pelvic fin white; caudal fin interradiial membrane faint blue when alive, brown when preserved. Females with less colour and shorter fins. Throat with chin-bar, female and juvenile with two black marks on opercle below postorbital stripe (Fig. 6b). Pattern on male opercle obscured by iridescent scales, darkly pigmented when preserved. Upper half of eye shiny yellow when alive. Preserved specimens dark brown dorsally and lighter brown ventrally. Fins light brown, anal and caudal fins with faint darkly pigmented margin.

Distribution. – *Betta lehi* is apparently restricted to the area southwest of Kuching, between the towns of Bau and Lundu in south Sarawak; and in the lower Kapuas basin in Kalimantan Barat (Fig. 12).

Field notes. – *Betta lehi* inhabits peat swamp forests and acid water swamp forests within the area mentioned, and appears to replace *B. ibanorum* in these habitats. At the type locality, Sungai Stuum Muda is a stream about 3 m wide and at some parts up to 1.5 m deep (water level can rise much more after heavy rains; pers. observ.). The water was fast flowing and clear with a pH ca. 6.8. All specimens of *B. lehi* were collected from quiet parts of the stream among the overgrown submerged bank vegetation. The aquatic plant *Barclaya motleyi* (Nymphaeaceae) was found upstream of the bridge, indicating the presence of freshwater swamp forest nearby. Fish species syntopic with *B. lehi* include: *Rasbora sarawakensis*, *R. sumatrana*, *Puntius banksi*, *P. kuchingensis*, *Hampala macrolepidota* (Cyprinidae), *Homaloptera tweediei*, *Nemacheilus saravacensis* (Balitoridae), *Acanthopsoides robertsi*, *Pangio semicineta*, *P. shelfordii* (Cobitidae), *Pseudomystus fuscus* (Bagridae), *Glyptothorax cf. major* (Sisoridae), *Hemirhamphodon kuekenthali* (Hemiramphidae), *Doryichthys martensii* (Syngnathidae), *Pseudogobiopsis siamensis* (Gobiidae), *Nandus nebulosus* (Nandidae), *Luciocephalus pulcher* (Osphronemidae), *Channa lucius* (Channidae), *Phenacostethus* sp. (Phallostethidae) and *Carinotetraodon salivator* (Tetraodontidae).

Etymology. – Named after Charles M. U. Leh, curator of Zoology at the Sarawak Museum, in recognition of his kind help.

Comparative notes. – *Betta lehi* is distinguished from the other members of the *B. pugnax* species group in having: more anal-fin rays than *B. fusca* (25-29, mode 28, vs. 24-25); more lateral scales than *B. enisae* (28-30, mode 29, vs. 26-28, mode 27); fewer lateral scales than *B. schalleri* (28-30, vs. 31); more predorsal scales than *B. schalleri* (20-23, mode 22, vs. 17-19, mode 19); shorter predorsal length than *B. fusca*, *B. enisae* and *B. prima* (62.6-67.5% SL, vs. 67.3-70.3); greater head length than *B. fusca* (33.4-36.8% SL, vs. 33.2-33.8); greater body depth at dorsal-fin origin than *B.*

schalleri (27.3-32.5% SL, vs. 26.7-27.6); greater length of dorsal-fin base than *B. enisae* (12.3-15.6% SL, vs. 8.7-12.1); greater orbital diameter than *B. breviobesus* (27.2-36.8% HL, vs. 24.2-28.5); shorter postorbital length than *B. fusca* (42.2-48.5% HL, vs. 48.3-50.5); greater interorbital width than *B. breviobesus* (70-84% postorbital length, vs. 64-74); greater head length than *B. fusca* (51.2-56.1% predorsal length, vs. 47.2-49.4).

Remarks. – Károli (1881) listed *B. pugnax* from Matang and Palandok in Borneo. Specimens obtained from recent collections from Matang area in Sarawak consist only of *B. ibanorum* (see later). Thus, Károli may have misidentified the specimens from Matang, Sarawak. The locality Palandok cannot be found in current maps and cannot match any site in Sarawak (assuming it is in Sarawak). Witte & Schmidt (1992: 327) treated material from Sumatra and Sarawak as a *Betta* (sp. E) sp. E. Based on their locality data, their Sarawak specimens are most probably *B. lehi*. Kottelat & Lim (1995) had only collected very few specimens of *B. lehi* up to 1995 and had listed it tentatively as only *Betta* sp.

BETTA AKARENSIS GROUP

Betta akarensis Regan, 1910

(Figs. 17 a-b, 46f)

Betta akarensis Regan, 1910: 779, pl. 77, Fig. 3; Weber & de Beaufort, 1922: 357; Roberts, 1989: 172 (table only); Witte & Schmidt, 1992: 326; Kottelat et al., 1993: 161, pl. 75 (part); Ng, 1993: 289 (part); Kottelat & Ng, 1994: 74 (part); Kottelat & Lim, 1995: 248 (part); Tan & Ng, 2004a: 278, figs. 3, 7.

Betta climacura Vierke, 1988: 336; Witte & Schmidt, 1992: 326; Kottelat et al., 1993: 161 (part); Ng, 1993: 290 (part); Kottelat & Ng, 1994: 74 (part).

Betta anabatooides (non Bleeker, 1851) - Regan, 1910: 780, pl. 78, fig. 4 (part); Vinciguerra, 1926: 592; Kottelat & Lim, 1995: 248.

Betta unimaculata (non Popta, 1905) - Zakaria-Ismail, 1984:73; Kottelat & Lim, 1995: 248.

Betta spec. affin. *taeniata* (non Regan, 1910) - Brown & Brown, 1987:160, pl. 12.

Material examined. – Holotype - **Sarawak:** BMNH 1895.7.2:44, 31.6 mm SL juvenile; Sungai Akar, coll. C. Hose.

Others - BMNH 1868.6.9:18-20, 2 ex., 46.4-56.1 mm SL; Sarawak, coll. M. Doria. — BMNH 1889.7.31:4-5, 2 ex., 58.5-62.5 mm SL; Baram, coll. C. Hose. — BMNH 1891.1.27:26-27, 2 male ex., 78.8-79.7 mm SL; Baram, coll. C. Hose. — BMNH 1893.3.6:139, 1 female ex., 52.0 mm SL; Poeh, coll. A. Everett. — BMNH 1893.3.6:141-144, 4 ex., 49.5-67.5 mm SL; north Borneo, coll. A. Everett. — BMNH 1894.8.3:28-30, 3 ex., 52.1-54.4 mm SL; Baram River, coll. C. Hose. — BMNH 1895.7.2:43, 1 male ex., 61.1 mm SL; Baram district, coll. C. Hose. — ZRC 37993, 1 ex., 37.9 mm SL; Marudi Airport-Lubok Nibong road, at 12.1 km, coll. M. Kottelat & T. H. T. Tan, 19 Jun.1994. — ZRC 37967, 1 ex., 52.5 mm SL; Sungai Tebu at 8 km, Daro-Matu road, coll. M. Kottelat & T. H. T. Tan, 14 Jun.1994. — ZRC 37972, 1 ex., 52.2 mm SL; Parit Nyadok, 200 m after 10 km stone, Daro-Matu road, coll. M. Kottelat & T. H. T. Tan, 14 Jun.1994. — ZRC 37858, 3 ex., 19.3-56.1 mm SL; Sungai Nibong, ca. 1 km north of Durin ferry on Sri Aman-Sibu road, coll. M. Kottelat et al., 15 May.1994. — ZRC 37929, 2 ex., 39.5-50.9 mm SL; outskirts of Sibu, Sungai Teku, 5.2 km north

of airport runway end on Jalan Teku, coll. M. Kottelat et al., 15 May.1994. — ZRC 37845, 8 juv.; outskirts of Sibu, 4.2 km north of airport runway end on Jalan Teku, coll. M. Kottelat et al., 15 May.1994. — ZRC 37925, 6 ex., 19.7-60.2 mm SL; ditch 34 km from Mukah, on Mukah-Sibu road, coll. M. Kottelat et al., 14 May.1994. — ZRC 37914, 1 juv.; Sungai Mantala, about 28 km from Mukah on Mukah-Sibu road, coll. M. Kottelat et al., 14 May.1994. — ZRC 37940, 2 juv.; Sungai Gayao, about 40 km from Mukah on Mukah-Sibu road, coll. M. Kottelat et al., 14 May.1994. — ZRC 37902, 1 juv.; Sungai Ngeli, about km 6 Simunjan-Balai road, coll. M. Kottelat et al., 11 May.1994. — ZRC37952, 5 ex., 17.5-50.8 mm SL; Sibu-Sarikei road, 2-3 km south of Durin ferry, coll. M. Kottelat et al., 15 May.1994. — ZRC 40928, 7 ex., 10.8-51.1 mm SL; Miri, stream below cascades flowing out of Lambir Hill park (3°45'20.1"N 113°45'25.5"E), coll. H. H. Tan & Y. Y. Goh, 26 Sep.1996. — ZRC 40929, 20 ex., 12.6-32.7 mm SL; Miri, lower Tukao, remnant swampforest ca. 200m from sea (4°18'53.7"N 113°58'07.5"E), coll. H. H. Tan & Y. Y. Goh, 26 Sep.1996. — MNHN 1891-515 to 518, 4 ex., 68.4-75.6 mm SL; Borneo, coll. Chaper. — MNHN 1891-521 to 528, 8 ex., 49.7-71.3 mm SL; Borneo, coll. Chaper. **Brunei:** ZRC 31812-17, 6 ex., 9.4-56.6 mm SL; Belait District, near Seria, coll. K. K. P. Lim, 11 May.1993. — ZRC 35437-441, 5 ex., 34.1-71.6 mm SL; Belait District, Sungai Liang area, coll. Helen & S. C. Choy, 4 Oct.1992. — ZRC 31863-64, 2 juv.; Tutong District, Lamunin, coll. K. K. P. Lim & S. C. Choy, 14 May.1993. — ZRC 40930, 25 ex., 15.3-71.1 mm SL; Belait District, Sungai Bang Balat, Sungai Kebun, Sungai Mengiris, Sungai Temusu - all draining into Sungai Melilas, tributary of Sungai Belait (jetty point 4°15'24.3"N 114°39'40.2"E), coll. H. H. Tan et al., 8 and 12 May.1996. — ZRC 40931, 3 ex., 39.3-75.1 mm SL; Belait District, Sungai Ingei (4°9'42.6"N 114°42'59.5"E), coll. H. H. Tan et al., 9-11 May.1996. — ZRC 40932, 3 ex., 22.7-61.4 mm SL; Belait District, Sungai Jaung, stream below hot spring, coll. H. H. Tan et al., 10 May.1996. — ZRC 40933, 40 ex., 16.8-72.7 mm SL; Belait District, Sungai Sepan, tributary of Sungai Ingei running through Kerengas forest, coll. H. H. Tan et al., 11 May.1996. — ZRC 40986, 42 ex., 20.7-59.1 mm SL; Belait District, peat swamp forest next to Sungai Sepan, coll. H. H. Tan et al., 11 May.1996. — ZRC 40934, 47 ex., 12.8-72.5 mm SL; BRM uncat., 10 ex., 24.8-51.1 mm SL; CMK 13121, 10 ex., 23.6-62.8 mm SL; ZMA 121.676, 5 ex., 34.4-60.4 mm SL; CAS 91716, 5 ex., 33.7-57.4 mm SL; Belait District, Sungai Pelok, tributary of Sungai Ingei, coll. H. H. Tan et al., 11 May.1996. — ZRC 40935, 50 ex., 21.1-60.5 mm SL; BRM uncat., 10 ex., 29.0-50.0 mm SL; CMK 13122, 10 ex., 27.4-58.1 mm SL; BMNH 1997.4.3.1-5, 5 ex., 28.9-52.0 mm SL; RMNH

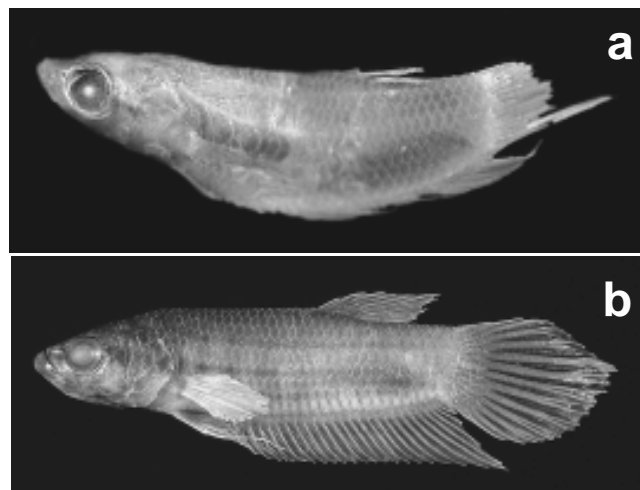


Fig. 17. a) *Betta akarensis* - BMNH 1895.7.2:44, holotype, 31.6 mm SL, b) ZRC 40928, 51.8 mm SL.

33085, 5 ex., 28.4-50.4 mm SL; Belait District, two streams near old padi fields ca. 200m downstream of Kampung Melilas, coll. H. H. Tan et al., 12 May.1996. — ZRC 40936, 2 ex., 23.6-53.7 mm SL; Bandar Seri Begawan, Mentiri waterfalls, Sungai Mengkubau downstream and tributaries (4°57'54.8"N 115°1'7.8"E), coll. H.H. Tan et al., 14 May.1996. — ZRC 40937, 39 ex., 18.9-73.8 mm SL; Tutong District, Sungai Ratuhan Uluh, ca. 200m behind basecamp (Pankalang Kabo) at Tasik Merimbun (4°34'52.9"N 114°41'24.4"E), coll. H. H. Tan et al., 15 and 18 May.1996. — ZRC 40938, 13 ex., 24.8-63.9 mm SL; Tutong District, Sungai Siong Mitom, tributary to Tasik Merimbun (4°35'16.3"N 114°40'42.5"E), coll. H. H. Tan et al., 16 May.1996. — ZRC 40939, 1 ex., 37.4 mm SL; Tutong District, Sungai Merimbun, outflow from Tasik Merimbun (4°36'5.7"N 114°40'41.1"E), leads to Sungai Tutong, coll. H. H. Tan et al., 16-17 May.1996. — ZRC 40940, 1 ex., 32.3 mm SL; Tutong District, Logon Uluh Boyoh, Bawang Ulop (4°36'33.7"N 114°26'55.2"E), coll. H. H. Tan et al., 17 May.1996. — ZRC 40941, 41 ex., 19.1-69.0 mm SL; BRM uncat., 10 ex., 28.1-51.4 mm SL; FMNH 105717, 10 ex., 26.5-54.9 mm SL; Belait District, Sungai Mau tributary, draining out of peatswamp forest (4°33'41.5"N 114°29'41.7"E), coll. H. H. Tan et al., 19 May.1996.

Diagnosis. — *Betta akarensis* is distinguished from the other members of the *B. akarensis* species group by the following combination of characters: opercle with uninterrupted second postorbital stripe; yellow eye when alive; anal-fin rays 28-30 (mode 28); subdorsal scales 5-6 (mode 5); lateral scales 31-33 (mode 32); predorsal scales 22-25 (mode 23); postdorsal scales 10-12 (mode 11); preanal length 43.4-48.5% SL; head length 29.8-34.9% SL; length of anal-fin base 49.6-56.8% SL.

Description. — General appearance is shown in Figs. 17a-b, 46f. Body relatively stout; caudal fin lanceolate; dorsal and anal fins pointed; pelvic fin filamentous. Mature males from Brunei (ZRC 35437, 35439) with concave head profile, but only for large males. Large males from Sarawak without concave head profile. Vertebrae 2 + 8-9 + 20-21 = 31-32 (mode 31, n = 11). Meristic and morphometric data in Table 4. Maximum known size 79.7 mm SL (BMNH 1891.1.27: 26-27).

Coloration. — For live coloration, see Fig. 46f (see Kubota et al., 1996, identified as *B. climacura*). Fig. 7 shows schematic head drawings with opercle patterns. Mature male with iridescent blue or green posterior half of body scales; pelvic fin with a white tip; caudal-fin transverse bars distinctly present in males; black distal margin on anal fin. Female with less iridescence on body and without caudal-fin transverse bars. During mating, female with central and second central stripes on body converging into one stripe ending on caudal peduncle.

Distribution. — *Betta akarensis* occurs in Brunei (Bandar Seri Bagawan, Belait and Tutong Districts) and Sarawak (Miri, Marudi, Sungai Akar, Sungai Tebu, Parit Nyadok, Sungai Nibong, Sungai Teku, Mukah) (Fig. 18).

Comparative notes. — *Betta akarensis* is distinguished from the other members in the species group in having: opercle with uninterrupted second postorbital stripe (Fig. 7a); yellow

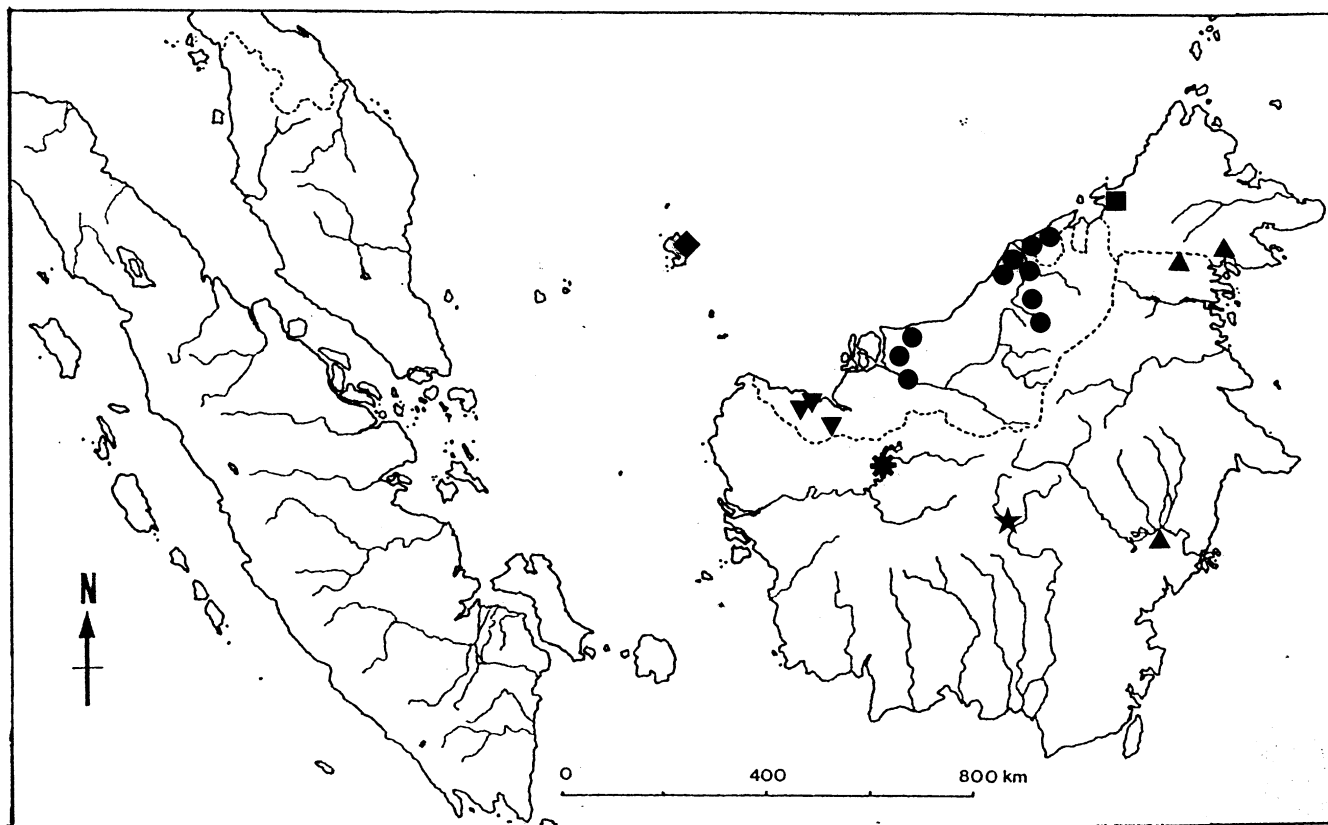


Fig. 18. Distribution map of *B. akarensis* (circle), *B. balunga* (triangle), *B. chini* (square), *B. pinguis* (asterix), *B. aurigans* (diamond), *B. ibanorum* (upside-down triangle), *B. obscura* (star).

eye when alive (vs. orange in *B. balunga*); slightly more vertebrae than *B. chini* (total 31-32, mode 31, vs. total 29-31, mode 30); more lateral scales than *B. balunga* (31-33, mode 32, vs. 29-30); dorsal-fin origin above 16-18th lateral scale (vs. 18-19th in *B. pinguis*); greater postdorsal length than *B. pinguis* (19.9-25.1% SL, vs. 18.0-20.9); smaller preanal length than *B. balunga* (43.4-48.5% SL, vs. 49.2-52.2); smaller body depth at dorsal-fin origin than *B. pinguis* (25.1-30.9% SL, vs. 30.6-31.6); greater orbital diameter than *B. pinguis* (24.5-32.3% HL, vs. 22.9-25.0); relatively smaller lower jaw length than *B. ibanorum* (8.8-10.7% SL vs. 9.3-12.0; 25.4-34.4% HL vs. 28.0-36.1).

Remarks. – Please refer to Tan & Ng (2004a) for more details.

Betta balunga Herre, 1940

(Figs. 19, 46g)

Betta balunga Herre, 1940: 44; Inger & Chin, 1962: 157; Witte & Schmidt, 1992: 324 (key only); Kottelat et al., 1993: 161 (comments only); Ng, 1993: 292 (discussion).

Material examined. – Holotype - **Sabah:** - CAS/SU 33203, 49.3 mm SL; Borneo: Sabah, Tawau, Sungai Balung, coll. A. W. C. T. Herre, 23 Jan.1937.

Others - CAS 17361, 2 ex., 33.3-46.7 mm SL; Borneo: Sabah, Tawau, Sungai Balung, coll. A. W. C. T. Herre, 1937. **Kalimantan Timur:** ZRC 35497, 1 ex., 37.2 mm SL, CMK 9451, 8 ex., 17.2-33.4 mm SL; Borneo: Kalimantan Timur, Sebuku basin, near Pembeliangan, creek along road from base camp to Semunad, draining into Sungai Tikung (4°0'48"N 117°2'54"E), coll. M. Kottelat & P. McKee, 10 Feb.1993.

Betta cf. balunga - ZRC 46332, 3 ex., 31.9-42.3 mm SL; Kalimantan Timur: Mahakam basin; black water stream along road km 124 from Kota Bangun to Samarinda (km 9.5 to Kota Bangun) (00°14.60'S 116°38.48'E), coll. H. H. Tan & D. Wowor, 10 Nov.1999. — ZRC 46333, 50 ex., 9.2-43.4 mm SL; Kalimantan Timur: Mahakam basin; clear water stream 10 km before Muara Badak (00°19.62'S 117°20.93'E), coll. H. H. Tan & D. Wowor, 11 Nov.1999.

Diagnosis. – *Betta balunga* is distinguished from the other members of the *B. akarensis* group by the following combination of characters: opercle with interrupted second postorbital stripe; eye colour orange when alive; anal-fin rays 27-30; subdorsal scales 6-7; lateral scales 29-30; predorsal

scales 21-24; postdorsal scales 10-12; preanal length 48.5-52.6% SL; head length 32.6-37.5% SL; length of anal-fin base 47.8-55.4% SL.

Description. – General appearance is shown in Figs. 19, 46g. Body relatively stout; caudal fin lanceolate, dorsal and anal fins pointed, pelvic fin filamentous. Vertebrae 2 + 8-9 + 19-21 = 30-31 (n=2). Meristic and morphometric data in Table 4. Maximum known size 49.3 mm SL (CAS/SU 33203).

Coloration. – See Fig. 46g for the live coloration of the Kalimantan specimen (see also Kubota et al., 1996: 45). Males have both dorsal and caudal transverse bars. For comparison of opercle patterns of members of the *B. akarensis* group, see Fig. 7. The specimens from Kalimantan retain a slight yellow body coloration when preserved (ZRC 35497); and in life, had iridescent blue on body scales.

Distribution. – *Betta balunga* is found in Tawau, Sabah and the Sebuku and Mahakam basins, Kalimantan Timur (Inger & Chin, 1962; Ng, 1993; unpublished data) (Fig. 18).

Field notes. – The Sebuku specimens were caught from forest streams with moderate current, in very shallow water (5-10 cm deep) amongst plant roots and submerged leaf litter along the banks. *Betta albimarginata* was also caught from the same stream (M. Kottelat, pers. comm.). *Betta balunga* is an oral brooder (Rehwinkel, 1995). The Mahakam specimens were obtained from slow flowing black water streams, from amongst submerged stream bank vegetation and submerged leaf litter.

Comparative notes. – *Betta balunga* is distinguished from the other members of the species group in having: reddish-orange iris of eye (vs. light yellow or green when alive); more subdorsal scales than *B. pinguis* (6-7, vs. 5-5¹/₂, mode 5¹/₂); fewer lateral scales than *B. akarensis* and *B. pinguis* (29-30, vs. 31-33); dorsal-fin origin above 15-16th lateral scale (vs. 18-19th in *B. pinguis*); anal-fin origin below 6-6¹/₂th lateral scale (vs. 7th in *B. pinguis*); smaller total length than *B. pinguis* (132.8-141.3% SL, vs. 145.5-153.5); greater preanal length than *B. akarensis*, *B. balunga*, *B. chini* and *B. ibanorum* (48.5-52.6% SL, vs. 42.6-49.4); greater head length than *B. pinguis* (32.6-37.5% SL, vs. 31.3-31.7); smaller length of anal-fin base than *B. chini* and *B. pinguis* (47.8-55.4% SL, vs. 54.5-58.5); greater lower jaw length than *B. pinguis* (10.2-10.4% SL, vs. 9.3-9.9); greater orbital diameter than *B. pinguis* (25.4-33.3% HL, vs. 22.9-25.0).

Remarks. – Herre (1940) described *B. balunga* on the basis of one specimen (CAS/SU 33203) of 49.3 mm SL. The use of the presence of spines in anal or dorsal fin and small differences in the number of spines in fin ray counts to distinguish between species as used by Herre (1940) is now regarded as untenable (see Tan & Tan, 1996). The material of *B. balunga* is scarce and more material is required before the species status can be ascertained (Kottelat et al., 1993: 161). The specimens from the Mahakam drainage differ from the holotype in the following aspects: fewer anal-fin rays (27 vs. 30); fewer predorsal scales (21 vs. 23); smaller predorsal length (66.7% SL, vs. 71.7); and smaller length of anal-fin

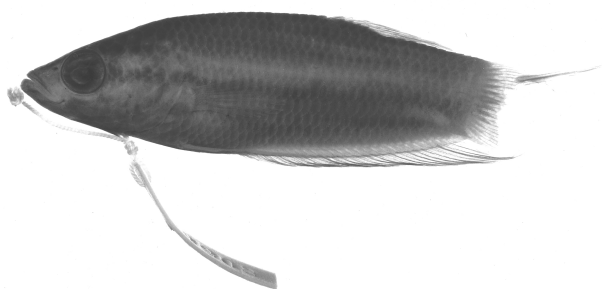


Fig. 19. *Betta balunga* – CAS/SU 33203, holotype, 49.3 mm SL (taken by Susan Middleton).

base (47.8% SL, vs. 55.4). The significance of these differences, however, cannot be ascertained due to the low number of specimens from the type locality and its immediate vicinity. For the time being, these specimens are regarded as conspecific (see Ng, 1993: 292).

***Betta chini* Ng, 1993**

(Figs. 20, 46h)

Betta chini Ng, 1993: 290, figs. 1-3; Kottelat & Ng, 1994: 74.

Material examined. – Holotype - **Sabah**: - ZRC 35086, 51.0 mm SL male; Borneo: Sabah, Beaufort area, peat swamps, along logging trail, ca. 12 km from Beaufort, on road from Kota Kinabalu to Beaufort (5°33'06"N 115°50'23"E), coll. P. K. L. Ng & R. B. Stuebing, 29 Dec.1992.

Paratypes - ZRC 35087-093, 7 ex., 17.4-54.2 mm SL; - SBM uncat., 2 ex., 31.0-33.3 mm SL; same locality data as holotype. — ZRC 35096-35102, 7 ex., 22.8-45.5 mm SL; Borneo: Sabah, Beaufort area, Sungai Mawao, peat swamps, coll. R. B. Stuebing, 11 Jan.1993. — ZRC 35094-95, 2 ex., 25.4-47.3 mm SL; Borneo: Sabah, Beaufort area, Kampung Lumat, coll. R. B. Stuebing, 7 Jan.1993.

Diagnosis. – *Betta chini* is distinguished from the other members of the *B. akarensis* group by the following combination of characters: opercle with interrupted second postorbital stripe; eye colour yellow when alive; anal-fin rays 26-30 (mode 28); subdorsal scales 5½-7 (mode 6); lateral scales 30-31 (mode 31); predorsal scales 22-24 (mode 23); postdorsal scales 9-11 (mode 10); preanal length 42.6-45.7% SL; head length 31.4-33.3% SL; length of anal-fin base 54.8-58.5% SL.

Description. – General appearance is shown in Figs. 20, 46h. Body relatively stout, caudal fin lanceolate; dorsal and anal fins pointed; pelvic fin filamentous. Vertebrae 2 + 8 + 19-21 = 29-31 (mode 30, n = 8). Meristic and morphometric data in Table 4. Maximum known size 54.2 mm SL (ZRC 35087).

Coloration. – See Fig. 46h for live coloration and Ng (1993) for more details (see also Kubota et al., 1996: 46).

Distribution. – *Betta chini* is apparently restricted to the peat swamps of Beaufort in Sabah (Ng, 1993) (Fig. 18).

Field notes. – *Betta chini* was collected from badly disturbed and logged peat swamps. Specimens were collected from

shallow water (less than 50 cm depth). This species is an oral brooder (Dickman, 1995).

Comparative notes. – *Betta chini* differs from the other members of the species group in having: yellow eye when alive (vs. orange of *B. balunga*); more subdorsal scales than *B. akarensis* (5½-7, mode 6, vs. 5-6, mode 5); dorsal-fin origin above 16-17th lateral scale (vs. 18-19th in *B. pinguis*); fewer vertebrae than *B. akarensis* (total 29-31, mode 30, vs. total 31-32, mode 31); smaller total length than *B. pinguis* (137.2-144.6% SL, vs. 145.5-153.5); greater postdorsal length than *B. pinguis* (19.9-23.3% SL, vs. 18.0-20.9); smaller preanal length than *B. balunga* and *B. ibanorum* (42.6-45.7% SL, vs. 45.8-52.2); smaller body depth at dorsal-fin origin than *B. pinguis* (26.3-29.0% SL, vs. 30.6-31.6); greater length of anal-fin base than *B. balunga* and *B. ibanorum* (54.8-58.5% SL, vs. 47.8-55.8); greater orbital diameter than *B. pinguis* (26.2-30.8% HL, vs. 22.9-25.0); smaller snout length than *B. pinguis* (20.0-24.4% HL, vs. 25.0-27.8); smaller height at pectoral-fin origin than *B. pinguis* (47.6-59.3% HL, vs. 58.1-62.0). Fig. 7 shows schematic head drawings with the opercle patterns of *B. akarensis*, *B. balunga*, *B. chini*, *B. ibanorum* and *B. obscura*.

Remarks. – *Betta chini* is one of the smallest species of the *B. akarensis* group. Ng (1993) has provided a detailed comparison with the other members of the *B. akarensis* group.

***Betta ibanorum* Tan & Ng, 2004**

(Figs. 21, 47a)

Betta ibanorum Tan & Ng, 2004: 273, figs. 3, 7; Grinang & Lim, 2004: 292.

Betta anabatooides - Regan, 1910: 780, pl. 78, fig. 4 (part).

Betta akarensis (non Regan, 1910) - Witte & Schmidt, 1992: 326 (part); Kottelat et al., 1993: 161, pl. 75 (part); Ng, 1993: 290 (part); Kottelat & Ng, 1994: 74 (part); Kottelat & Lim, 1995: 248 [part].

Betta climacura (non Vierke, 1988) - Kottelat et al., 1993: 161 (part); Ng, 1993: 289 (part); Kottelat & Ng, 1994: 74 (part).

Betta spec. affin. taeniata (non Regan, 1910) - Brown & Brown, 1987: 169, pl. 13.

Material examined. – Holotype - **Sarawak**: - ZRC 41584, 65.0 mm SL male; Borneo: Sarawak, Kuching, Bako National Park, Bukit Gondol, coll. N. Sivasothi et al., 28 Jun.1994.

Paratypes - ZRC 37750, 2 males, 53.9-65.1 mm SL, 1 female, 43.8 mm SL, same locality data as holotype. — ZRC 37757, 22 ex., 9.4-



Fig. 20. *Betta chini* – ZRC 35086, male holotype, 51.0 mm SL.



Fig. 21. *Betta ibanorum* – ZRC 41584, male holotype, 65.0 mm SL (right side, reversed).

76.1 mm SL; Borneo: Sarawak, Kuching, Bako National Park, Tajor waterfalls, coll. T. H. T. Tan & A. T. C. Wong, 29 Jun.1994.

Others - ZRC 37764, 7 ex., 17.1-51.7 mm SL; Borneo: Sarawak, Kuching, Bako National Park, Sungai Serait at goldmine, coll. N. Sivasothi et al., 30 Jun.1994. — ZRC 37755, 3 juv., 16.2-18.3 mm SL; Borneo: Sarawak, Kuching, Bako National Park, Sungai Nipah, coll. D. S. L. Chung et al., 29 Jun.1994. — ZRC 39273, 2 males, 75.3-77.4 mm SL, 1 female, 66.1 mm SL; Borneo: Sarawak, Bako National Park, coll. NUS Honours class 1994-95 (kept in aquaria), Jun.1994. — ZRC 35435-36, 2 males, 71.5-80.8 mm SL; Borneo: Sarawak, blackwater stream at km-stone 7 from Kuching to Batu Kawa (1°31'N 110°18'E), coll. P. K. L. Ng et al., 3 Jul.1992. — ZRC 27830-35, 6 ex., 12.4-75.3 mm SL; Borneo: Sarawak, 7 km Kuching to Batu Kawa road, coll. P. K. L. Ng et al., 3 Jul.1992. — ZRC 37838, 4 juv., Borneo: Sarawak, Matang Wildlife Centre, small forest creek 100 m beyond Sungai Rayu, coll. M. Kottelat et al., 5 May.1994. — ZRC 39584, 13 ex., 22.9-50.2 mm SL; Borneo: Sarawak, Batu Kawa-Matang area, Taman Koperkasa (1°34'42.0"N 110°16'24.7"E), ca. 2 km after bridge over blackwater river, ca. 10 km after Kuching town, coll. P. K. L. Ng et al., 14 Jan.1996. — ZRC 39585, 2 ex., 24.5-32.9 mm SL; Borneo: Sarawak, Batu Kawa-Matang area (1°34'27.1"N 110°17'34.9"E), ca. 50 m before blackwater river in flooded peat swamp forest, access via first right track after bridge over blackwater river, coll. P. K. L. Ng et al., 14 Jan.1996. — ZRC 39586, 1 ex., 27.2 mm SL; Borneo: Sarawak, ca. 50 m into peat swamp forest and ditch on left side of road (1°10'50.0"N 110°39'22.1"E), ca. 8 km towards Gedong after turnoff from Serian-Sri Aman road, coll. H. H. Tan & S. H. Tan, 16 Jan.1996. — ZRC 40942, 33 ex., 13.6-70.5 mm SL; SM uncat., 5 ex., 31.1-54.7 mm SL; CMK 13123, 5 ex., 30.0-63.9 mm SL; Borneo: Sarawak, peat swamp forest, 11.4 km towards Gedong from turnoff on Serian-Sri Aman road (1°12'07.8"N 110°39'51.2"E), coll. P. K. L. Ng et al., 31 Aug.1996. — ZRC 40943, 20 ex., 25.2-50.4 mm SL; Borneo: Sarawak, peat swamp forest, 38.1 km towards Simunjan, from Kuching-Sri Aman road (1°18'55.3"N 110°51'43.6"E), coll. H. H. Tan & S. H. Tan, 4 Sep.1996. — ZRC 40944, 27 ex., 12.0-64.8 mm SL; SM uncat., 5 ex., 29.0-50.8 mm SL; CMK 13124, 5 ex., 22.7-53.2 mm SL; Borneo: Sarawak, water cascade from Gunung Santubong, ca. 1 km before Damai Beach Resort (1°44'10.1"N 110°19'8.6"E), coll. H. H. Tan & S. H. Tan, 5 Sep.1996.

Diagnosis. – *Betta ibanorum* is distinguished from the other members of the *B. akarensis* group by the following combination of characters: opercle without second postorbital stripe; eye colour yellow when alive; anal-fin rays 27-29 (mode 28); subdorsal scales 5-6 (mode 5^{1/2}); lateral scales 30-32 (mode 30); predorsal scales 21-23 (mode 22); postdorsal scales 10-11 (mode 11); preanal length 45.8-49.4% SL; head length 31.7-36.4% SL; length of anal-fin base 50.0-55.8% SL.

Description. – General appearance is shown in Figs. 21, 47a. Body relatively slender, caudal fin broadly lanceolate; dorsal and anal fins pointed; pelvic fin filamentous. Large male with a concave head profile. Rays of unpaired fins of males elongated, and may appear filamentous. Vertebrae 2 + 9 + 19-21 = 30-32 (mode 31, n = 9). Meristic and morphometric data in Table 4. Maximum known size 80.8 mm SL (ZRC 35435).

Coloration. – For live coloration, refer to Fig. 47a and Kottelat et al. (1993: pl. 75, identified as *B. akarensis*) (see Linke,

1991: 29, identified as *B. climacura*). Body dark brown dorsally, lighter ventrally. Mature male with iridescent green to blue posterior half on body scales, dorsal and caudal transverse bars. Female with possess less iridescence and without caudal transverse bars. Juvenile with a distinct black central stripe on body and a black caudal peduncle spot. A narrow distinct chin-bar in all specimens. Opercle with little or no pattern (Fig. 7).

Distribution. – *Betta ibanorum* is found in Bako National Park, in the adjacent areas around Kuching and appears to be restricted to southern Sarawak (Fig. 18). It is confined east towards Bau area (e.g. Matang, Serian, Gedong, Simunjan, Sri Aman) and is replaced by *B. lehi* in the area west of Bau (e.g. Lundu).

Comparative notes. – *Betta ibanorum* differs from the other members of the species group in having: opercle without second postorbital stripe (Fig. 7); yellow eye when alive (vs. orange of *B. balunga*); largest adult size (80.8 mm SL); dorsal-fin origin above 15-17th lateral scale (vs. 18-19th in *B. pinguis*); fewer predorsal scales than *B. pinguis* (21-23, mode 22, vs. 23-24, mode 24); greater preanal length than *B. chini* (45.8-49.4% SL, vs. 42.6-45.7); smaller preanal length than *B. balunga* (45.8-49.4% SL, vs. 49.2-52.2); greater head length than *B. pinguis* (31.7-36.4% SL, vs. 31.3-31.7); smaller body depth at dorsal-fin origin than *B. balunga* and *B. pinguis* (23.3-28.1% SL, vs. 28.0-31.6); smaller length of anal-fin base than *B. chini* and *B. pinguis* (50.0-55.8% SL, vs. 54.5-58.5); smaller orbital diameter than *B. balunga* (22.2-30.5% HL, vs. 29.5-33.3); greater snout length than *B. balunga* (22.9-29.5% HL, vs. 20.0-21.2). *Betta ibanorum* can be differentiated from *B. aurigans* by the following characters: blueish iridescence on scales (vs. gold scales); fewer anal-fin rays (27-29, mode 28, vs. 29-30, mode 30); fewer lateral scales (30-32, mode 30, vs. 33-33^{1/2}, mode 33^{1/2}); fewer predorsal scales (21-23, vs. 24-26); fewer postdorsal scales (10-11, mode 11, vs. 11-13, mode 13); and smaller length of anal-fin base (50.0-55.8, vs. 55.4-58.1% SL). Fig. 7 shows schematic head drawings with the opercle patterns of *B. akarensis*, *B. balunga*, *B. chini* and *B. ibanorum*.

Remarks. – For more details, please refer to Tan & Ng (2004).

BETTA UNIMACULATA GROUP

Betta macrostoma Regan, 1910

(Figs. 22a-b, 47b-c)

Betta macrostoma Regan, 1910: 778, pl. 78, Fig. 3; Weber & de Beaufort, 1922: 355; Herre, 1940 (key only); Witte & Schmidt, 1992 (key only); Kottelat et al., 1993: 162, pl. 76; Kottelat & Lim, 1995: 248.

Material examined. – Holotype - North Sarawak: BMNH 1898.11.2:2, male, 60.0 mm SL; Borneo, coll. Hose, 1898.

Others – Brunei: ZRC 31793-94, 1 male - 69.8 mm SL, 1 female - 59.0 mm SL; Borneo: Brunei, Belait District, Sungai Rampayoh, coll. S. C. Choy, Apr.1992. ZRC 40945, 8 ex., 9.0-59.7 mm SL;

Borneo: Brunei, Belait District, Implasi Batu, small hill stream ca. 750 m after the hot spring, coll. H. H. Tan et al., 10 May.1996. — ZRC 40987, 1 juv., 14.6 mm SL; Belait District, Sungai Jaung, stream below hot spring, coll. H. H. Tan et al., 10 May.1996. — ZRC 40946, 8 ex., 14.7-67.0 mm SL; BRM uncat., 2 ex., 55.8-56.5 mm SL; Borneo: Brunei, Belait District, Labi, Rampayoh, Sungai Mendaram (entrance to falls: 4°20'30.7"N 114°26'55.2"E; cascade: 4°20'20.0"N 114°27'7.7"E), coll. H. H. Tan et al., 19 May.1996.

Diagnosis. – *Betta macrostoma* is distinguished from the other members of the *B. unimaculata* group group by the following combination of characters: dorsal fin ocellus (Fig. 8a); red body colour; transverse black and red bands on caudal fin; opercle with large red blotch in mature male; vertebrae 31-32 (mode 32); dorsal-fin rays 9-11 (mode 10), anal-fin rays 25-28 (mode 27); pectoral-fin rays 13-14; lateral scales 32-33 (mode 33); subdorsal scales 6-8 (mode 7); predorsal scales 21-24 (mode 23); predorsal length 62.3-66.7% SL; head length 30.4-33.3% SL; length of anal-fin base 43.2-49.2% SL; length of dorsal-fin base 12.2-15.7% SL; lower jaw length 38.0-54.0% HL.

Description. – General appearance is shown in Figs. 22a-b, 47b-c. Body slender; head large; caudal, dorsal and anal fins rounded; pelvic fin falcate with short filamentous soft ray. Vertebrae 2-3 + 8 + 21-22 = 31-32 (mode 32, n=11). Meristic and morphometric data in Table 5. Maximum known size 67.0 mm SL (ZRC 40946).

Coloration. – For live coloration, refer to Figs. 47b-c (see also Linke, 1991: 38; Kubota et al., 1996). Mature male with bright red body, red opercle blotch surrounded by black, ocellus on dorsal fin (Fig. 8a) and transverse black and red bars on caudal fin, anal fin red with black distal margin, pelvic fin with white tip. Females and juveniles with black central and second central stripes on body and a black caudal peduncle spot (Fig. 1). Preserved male specimens still with some red on body, mostly faded to yellow and light brown. Black stripe pattern on a light brown body distinct in preserved female and juvenile.

Field notes. – *Betta macrostoma* was obtained in clear waters



Fig. 22. a) *Betta macrostoma* - BMNH 1898.11.2:2, male holotype, 60.0 mm SL, b) ZRC 40945, 59.8 mm SL.

in Belait district, Brunei. They were found in shallow (ca. 30 cm deep) near stagnant pools along a clayey stream bed. There were only an adult pair or an adult with several juveniles in each pool sampled. There were no other fish in this locality. The pH was 5.7.

Betta macrostoma was also collected at the Mendaram waterfalls, Rampayoh in Labi area, Belait district. The terrain was rocky, with fast flowing clear water, pH 4.4. *Dipteris* fern (Polypodiaceae) was growing along the banks of the streams. *Betta macrostoma* was in small pools in tributaries and in the quiet pools along the main confluence of the river. Only one adult or several juveniles could be located in each of these microhabitats. The only other fish was *Rasbora tubbi* (Cyprinidae). *Betta macrostoma* is an oral brooder (Etrich, 1992; Kubota et al., 1996: 54).

Distribution. – *Betta macrostoma* is presently known from Belait District, Brunei Darussalam; and has been reported from the area around Marudi, North Sarawak (pers. observ.) (Fig. 23).

Comparative notes. – *Betta macrostoma* is distinguished from the other members of the species group by the following characters: dorsal fin ocellus (vs. absence) (Fig. 8a); transverse black and red bands on caudal fin (vs. absence); opercle with large red blotch in mature males (vs. absence); more dorsal-fin rays (9-11 vs. 6-9), fewer anal-fin rays (25-28 vs. 27-31); more subdorsal scales (6-8 vs. 4-6^{1/2}); dorsal-fin origin above 15-17th lateral scale (vs. 17-21st); smaller predorsal length (62.3-66.7% SL vs. 67.7-73.0); smaller length of anal-fin base (43.2-49.2% SL vs. 45.9-54.5); greater length of dorsal-fin base (12.2-15.7% SL vs. 7.3-11.4); greater lower jaw length (38.0-54.0% HL vs. 27.3-38.3).

Remarks. – *Betta macrostoma* is a very distinctly coloured species with long jaws that extend beyond orbital towards the opercle in mature male. There are a few populations in which the dorsal fin ocellus is present (Regan, 1910; Yamazaki, 1995) and some others apparently absent (Linke, 1991; Kottelat et al., 1993). The intensity of coloration, however, differs among populations. Tentatively, all populations are regarded as conspecific.

Betta ocellata de Beaufort, 1933

(Figs. 24a-b, 47d-e)

Betta ocellata de Beaufort, 1933: 35; Herre, 1940: 43; Inger & Chin, 1962: 159; Witte & Schmidt, 1992: 327; Martin-Smith & Tan, 1998: 593.

Betta unimaculata: (non Popta, 1905) - Inger, 1955: 70; Inger & Chin, 1962: 159; Lim & Wong, 1994: 62; Chin & Samat, 1995: 29.

Material examined. – Holotype - **Sabah**: - BMNH 1959.7.7:1, 70.0 mm SL; Borneo: Sabah, Sandakan, Bettotan.

Others - BMNH 1893.5.30:52, 1 ex., 50.1 mm SL; Borneo: Sabah, Bongon, coll. A. Everett. — ZRC 37642, 26 ex., 23.4-60.0 mm SL; Borneo: Sabah, Kampung Batu Puteh (Kinabatangan basin), shaded

forest stream in SAFODA, coll. K. K. P. Lim et al., 7-13 Apr.1994. — ZRC uncat., 3 ex., 62.1-68.9 mm SL; Borneo: Sabah, Kampung Batu Puteh (Kinabatangan basin), shaded forest stream in SAFODA, coll. K. K. P. Lim et al., 7-13 Apr.1994 (kept in aquaria for one year). — FMNH 44901, 5 ex., 15.6-46.5 mm SL; Borneo: Sabah, Sandakan, Sandala Estate, North road, coll. Fisheries Department, 8 Oct.1948. — FMNH 44902, 4 ex., 28.0-50.8 mm SL; Borneo: Sabah, Sandakan, mile 6 on North road, coll. J. A. Tubb, 25 Jul.1950. — FMNH 44903, 1 ex., 42.2 mm SL; Borneo: Sabah, Sandakan, mile 7 on North road, coll. Fisheries Department, 31 Jul.1950. — FMNH 44904, 2 ex., 43.1-46.7 mm SL; Borneo: Sabah, Sandakan, Tenosa, coll. J. A. Tubb, 9 Dec.1947. — FMNH 51634, 10 of 16 ex., 33.9-55.0 mm SL; Borneo: Sabah, Kinabatangan, clear water tributary of Sungai Kretam Kechil below falls, coll. R. F. Inger, 11 May.1950. — FMNH 51635, 5 of 9 ex., 43.6-53.8 mm SL; Borneo: Sabah, Kinabatangan, southeast end of Dewhurst Bay, west fork of Gaja River above rapids, coll. R. F. Inger, 30 May.1950. — FMNH 51638, 5 of 11 ex., 38.8-58.5 mm SL; Borneo: Sabah, Kinabatangan, southeast end of Dewhurst Bay, west fork of Gaja River, 0.25 miles upstream from station 11, coll. R. F. Inger, 3 Jun.1950. — FMNH 51639, 5 ex., 26.8-61.7 mm SL; Borneo: Sabah, Sandakan, tributary of Sapagaya River, coll. R. F. Inger, 16 Jul.1950. — FMNH 51641, 9 ex., 12.1-67.8 mm SL; Borneo: Sabah, Kinabatangan, southeast end of Dewhurst Bay, tributary of Sungai Kretam Kechil, coll. R. F. Inger, 15 Jun.1950. — FMNH 68430, 5 of 10 ex., 54.1-79.8 mm SL; Borneo: Sabah, Sandakan, Sepilok Forest Reserve, coll. R. F. Inger, 9 Apr.1956. — FMNH 68435, 5 of 13 ex., 48.6-67.4 mm SL; Borneo: Sabah, Kinabatangan, Deramakot camp, hill stream below falls, coll. R. F. Inger & P. K. Chin, 2 May.1956. — FMNH 68436, 10 ex., 43.7-71.0 mm SL; Borneo: Sabah, Kinabatangan, Deramakot camp, below waterfall, coll. R. F. Inger, 3 May.1956. — FMNH 68439, 5 ex., 29.3-60.4 mm SL; Borneo: Sabah, Tawau, Pulau Sebatik, coll. R. F. Inger, 28 May.1956. — FMNH 68440, 1 ex.,

32.8 mm SL; Borneo: Sabah, Tawau, Kalabakan, Sungai Tibas camp, Sungai Tawan, coll. R. F. Inger, 6 Jun.1956. — FMNH 68441, 1 ex., 24.5 mm SL; Borneo: Sabah, Tawau, Kalabakan, Sungai Tibas camp, ca. 1 km upstream of Sungai Tawan, coll. R. F. Inger, 8 Jun.1956. — FMNH 68442, 2 ex., 18.1-30.4 mm SL; Borneo: Sabah, Tawau, Brantian River estate, semi-isolated pool, coll. R. F. Inger, 8 Jul.1956. — ZRC 40947, 6 ex., 35.1-56.8 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, Kallang Sebaru stream, tributary of Sepat Kalisun stream, km 64.5 from main road to Danum Valley Field Centre (4°58'04.8"N 117°48'56.5"E), coll. H. H. Tan et al., 1 Oct.1996. — ZRC 40948, 3 ex., 21.4-44.9 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, Sepat Kalisun stream, coll. H. H. Tan et al., 1 Oct.1996. — ZRC 40949, 1 ex., 42.7 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, Sungai Paulm Tambun, tributary of Sungai Segama, upstream of Danum Valley Field Centre, coll. H. H. Tan et al., 1 Oct.1996. — ZRC 40950, 1 ex., 59.1 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, small tributary of Sungai Bole, ca. 500 m into coupe 93 (4°58'17.8"N 117°51'48.0"E), coll. H. H. Tan et al., 2 Oct.1996. — ZRC 40951, 7 ex., 23.3-40.5 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, cabin stream right, km 50 on road to Danum Valley Field Centre, drains from Bukit Rafflesia (4°59'08.5"N 117°54'05.1"E), coll. H. H. Tan et al., 2 Oct.1996. — ZRC 40952, 3 ex., 33.7-50.4 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, West six, forest stream 600 m into conservation area, tributary of Sungai Segama, coll. H. H. Tan et al., 4 Oct.1996. — ZRC 40953, 4 ex., 34.4-60.3 mm SL; Borneo: Sabah, Lahad Datu, Danum Valley, West eight, forest stream 800 m into conservation area, tributary of Sungai Segama, coll. H. H. Tan et al., 4 Oct.1996. — ZRC 40954, 6 ex., 14.1-35.7 mm SL; Borneo: Sabah, Tawau, stream by Air Panas, near base of Tawau Hills park (4°18'03.0"N 117°54'20.7"E), coll. H. H. Tan et al., 5 Oct.1996. — ZRC 40955, 3 ex., 19.6-52.4 mm SL; Borneo: Sabah, Tawau, Jalan Sin On Jaya, swampy area (4°16'07.6"N

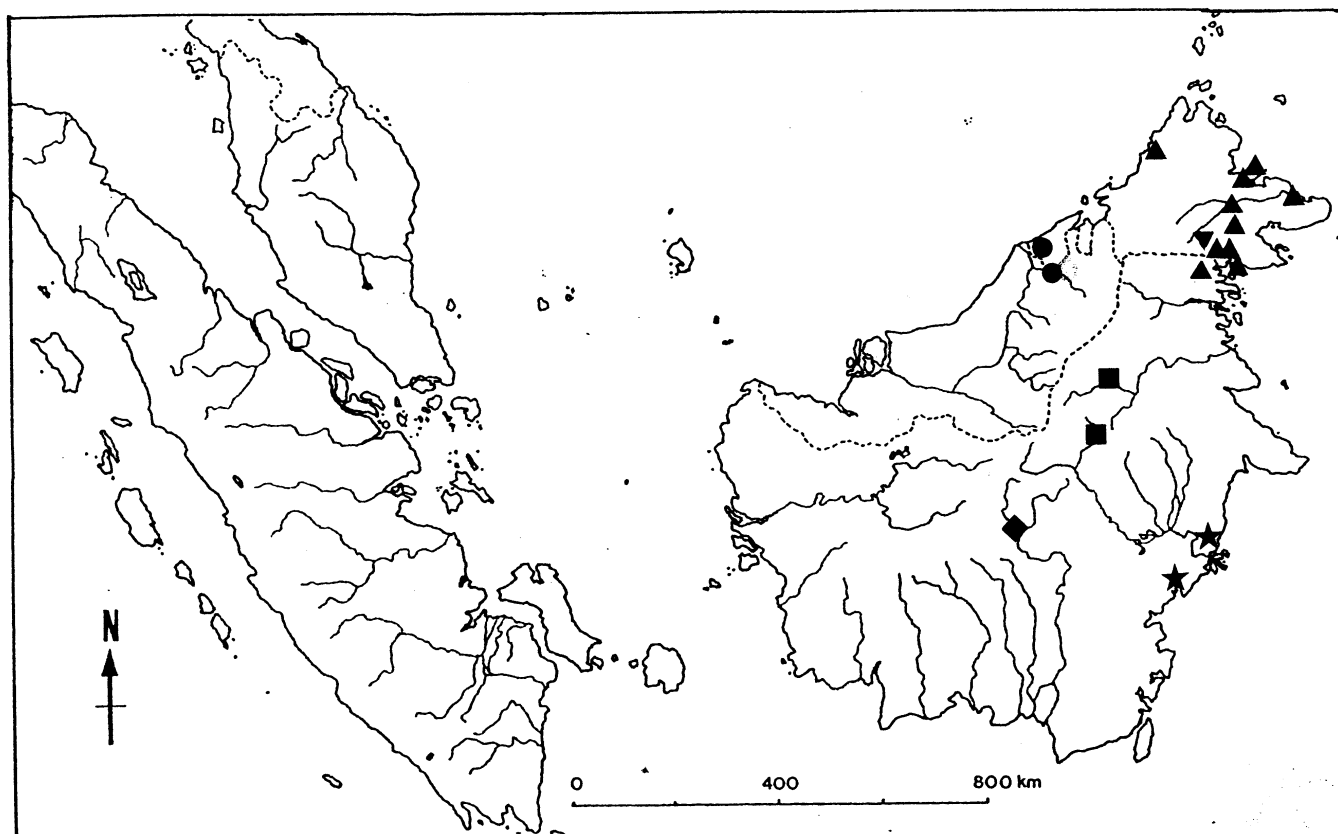


Fig. 23. Distribution map of *B. macrostoma* (circle), *B. ocellata* (triangle), *B. gladiator* (upside-down triangle), *B. unimaculata* (square), *B. patoti* (star), *B. pallifina* (diamond).

117°54'25.6"E), coll. H. H. Tan et al., 5 Oct.1996. — ZRC 40956, 70 ex., 9.7-59.4 mm SL; SBM uncat., 10 ex., 20.9-42.7 mm SL; ZMA 121.677, 10 ex., 24.7-46.9 mm SL; BMNH 1997.4.3.6-15, 10 ex., 26.3-45.8 mm SL; RMNH 33086, 10 ex., 26.8-45.4 mm SL; FMNH 105718, 10 ex., 27.5-41.9 mm SL; Borneo: Sabah, Tawau, stream at km 76 to Semporna, km 32 to Tawau (4°20'17.4"N 118°05'32.3"E), coll. H. H. Tan et al., 5 Oct.1996. — ZRC 40957, 52 ex., 11.7-63.7 mm SL, CMK 13016, 5 ex., 40.0-48.2 mm SL; Borneo: Sabah, Tawau, stream at km 77 to Semporna, km 31 to Tawau (4°19'37.8"N 118°05'36.8"E), coll. H. H. Tan et al., 5 Oct.1996. — ZRC 40958, 1 ex., 44.9 mm SL; Borneo: Sabah, Tawau, Sungai Nasib Katib, ca. km 66.5 to Semporna, km 41.5 to Tawau (4°22'41.2"N 118°07'55.6"E), coll. H. H. Tan et al., 6 Oct.1996. — ZRC 40959, 25 ex., 25.0-65.5 mm SL; Borneo: Sabah, Tawau, Jalan Madai, Gua Madai (limestone outcrop), Sungai Matarid runs through caves (4°43'08.7"N 118°09'14.7"E), coll. H. H. Tan et al., 6 Oct.1996. **Kalimantan Timur:** CMK 9540, 1 ex., 24.2 mm SL; Borneo: Kalimantan Timur, Sungai Sebuk basin, Sungai Sanul, tributary of Sungai Tikung, ca. km 7 on RMK logging road from Semunad to Apas (4°2'25"N 116°58'46"E), coll. M. Kottelat & P. McKee, 14 Feb.1993.

Diagnosis. – *Betta ocellata* is distinguished from the other members of the *B. unimaculata* species group by the following combination of characters: distinct black spot near caudal peduncle; body brownish; opercle blue; uniform caudal fin coloration; vertebrae 33-34 (mode 33); anal-fin rays 30-31 (mode 30); dorsal-fin rays 8; pectoral fin rays 12-13 (mode 13); subdorsal scales 5-5½ (mode 5½); lateral scales 32-34 (mode 33); predorsal scales 24; predorsal length 68.8-71.9% SL; head length 31.4-33.3% SL; length of anal-fin base 52.2-54.5% SL; length of dorsal-fin base 10.5-11.3% SL; lower jaw length 27.3-33.1% HL.

Description. – General body shape and appearance as in Figs. 24a-b, 47d-e. Body relatively stocky, broad but relatively pointed head; caudal fin rounded, dorsal and anal fins relatively pointed, pelvic fin filamentous. Mature males with a steep rise behind eye. Vertebrae 2 + 9 + 22-23 = 33-34 (mode 33, n=13). Meristic and morphometric data in Table 5. Maximum known size 79.8 mm SL (FMNH 68430).

Coloration. – For live coloration, see Figs. 47d-e (see also Linke, 1991: 73; Kubota et al., 1996: 50, both identified as



Fig. 24. a) *Betta ocellata* - BMNH 1959.7.7:1, holotype, 70.0 mm SL, b) ZRC 37642, 56.6 mm SL.

B. unimaculata). Mature male with iridescent blue opercle scales when alive, blackish when preserved, with a single iridescent scale on upper region of head. Faintly iridescent scales on body; specimens from Kinabatangan basin with very little iridescence; male from Tawau with full body iridescence; specimens from Danum valley and Tawau with irregular black marks along flank. Body light to dark brown when alive, light brown when preserved. Caudal peduncle spot below lateral scale series near end of hypural plate, present in both sexes and juveniles (Fig. 1). Female with very few or no iridescent opercle scales. When alive, faint or distinct dorsal, caudal and anal fin transverse bars; faint when preserved.

Distribution. – *Betta ocellata* is restricted to northeastern Borneo, found only in Sabah (Bettotan, Sandakan, Kinabatangan, Lahad Datu, Tawau and Bongon) and the northern part of East Kalimantan (Sebuku basin) (de Beaufort, 1933; Inger & Chin, 1962; pers. observ.; M. Kottelat, pers. comm.) (Fig. 23).

Field notes. – Specimens collected from Sabah were mainly from headwater habitats. The fishes were usually obtained from ravines and isolated elevated pools. A single adult and several juveniles are usually obtained from the submerged leaf litter. Adults may take cover under floating leaves. They are excellent jumpers, which may explain their presence in isolated elevated pools. Their diet consist mainly of terrestrial insects and occasional aquatic invertebrates (Inger, 1955; Inger & Chin, 1965).

Specimens collected within the Kinabatangan basin were from lowland forest streams and ox-bow lakes. The water in these habitats was murky. This species inhabits the shallow parts of ox-bow lakes among the flooded grass banks and among the submerged leaf litter and tree roots in the forest streams. Other species collected from the forest streams included: *Rasbora sumatrana*, *Puntius sealei*, *P. banksi* (Cyprinidae), *Pangio mariarum*, *Lepidocephalichthys sandakanensis* (Cobitidae), *Nemacheilus olivaceus* (Balitoridae), *Ompok sabanus* (Siluridae), *Clarias teijsmanni* (Clariidae) and *Trichogaster trichopterus* (Osphronemidae).

Specimens from Lahad Datu (Danum valley) were in stagnant or slow moving clearwater pools along headwater streams. Syntopic species include *Garra borneensis* (Cyprinidae), *Homaloptera stephensoni*, *Gastromyzon danumensis*, *G. lepidogaster*, *G. cf. punctulatus*, *Protomyzon griseoldi*, *P. whiteheadi*, *Nemacheilus olivaceus* (Balitoridae) (Martin-Smith & Tan, 1998). Specimens from Tawau were from quiet murky pools along the coast in oil palm plantations. Numerous specimens of *B. ocellata* inhabit these quiet pools and it is the numerically dominant species.

The figure in Kottelat et al. (1993: pl. 77) shows an adult male with full body iridescence. Through selective breeding, a blue form has been developed (Linke, 1991: 74). Breeding report shows that, as in *B. ocellata*, the female does not help in the transfer of eggs to the male for oral-brooding, the male picks up the fertilised eggs and oral-brood without any

participation of the female (van den Nieuwenhuizen, 1995; Tan, 1997). This behaviour, along with the open mouth display, are uniquely found in the *B. unimaculata* group.

Comparative notes. – *Betta ocellata* is distinguished from the other members of the species group in the following characters: greater body depth at dorsal-fin origin than *B. macrostoma* and *B. gladiator* (21.6-24.5% SL, vs. 18.4-21.1); greater length of anal-fin base than *B. macrostoma* and *B. gladiator* (52.2-54.5% SL, vs. 43.2-52.8); greater height at pectoral-fin origin than *B. macrostoma* and *B. gladiator* (16.7-18.7% SL, vs. 10.6-16.5). *Betta ocellata* is further distinguished from *B. unimaculata* in the following characters: more pointed lateral head profile and more cone-like dorsal head profile (vs. blunter and more bulbous head profile, Fig. 23b); caudal-fin transverse bars faint or absent (vs. distinct); posterior extremity of maxilla at vertical through front margin of orbit (vs. behind front margin, Figs. 23c-d); more subdorsal scales ($5\frac{1}{2}$, vs. 5); more lateral scales (33, vs. 32); more anal-fin rays (30-31, mode 30, vs. 27-30, mode 28 or 29); greater length of dorsal-fin base (10.5-11.3% SL, vs. 7.9-10.4); greater head width (21.0-24.0% SL, vs. 19.6-21.8).

Remarks. – *Betta ocellata* was described by de Beaufort (1933) on the basis of a single specimen 99 mm TL from Bettotan, near Sandakan. He described the fish as having "... a black blotch ... and bordered anteriorly by a white area, forming an indistinct ocellus, below the median line at base of caudal ..." (de Beaufort, 1933: 36). He also noted that this specimen has no anal spines. Fresh specimens that we examined have one or two anal-fin spines and the white area around the black spot at caudal peduncle is indistinct. Inger (1955) commented that *B. unimaculata* was the only species found in the headwaters of Sungai Pinang, which drains into Sungai Kretam Kechil. But all these specimens actually are *B. ocellata*, whose type locality is not very far northwest of the area actually sampled by Inger.

Inger & Chin (1962: 159) synonymised *B. ocellata* and *B. unimaculata* on the argument that the placement of the eye above the maxilla, the segmentation of the first anal-fin ray and the colour at the base of the caudal fin fell within the normal variation and coloration of populations examined by them. They had not examined the type material of *B. unimaculata* and a comparison of the type material of both species shows that there are clear differences between the two species (see above).

Betta gladiator, new species

(Figs. 25a-b, 47f)

Material examined. – Holotype - SBM uncat., 45.5 mm SL; Borneo: Sabah, Maliau Basin, northeast of basecamp 1996 (ca. 5°14'N 116°53'E), stream at right trail ca. 2 km into Jalan Babi towards Maliau falls, coll. S. H. Tan, T. H. T. Tan et al., 22 May.1996.

Paratypes - ZRC 40960, 9 ex., 13.3-55.5 mm SL; RMNH 33088, 2 ex., 42.0-48.5 mm SL; CMK 13125, 2 ex., 37.7-49.2 mm SL; SBM uncat., 13 ex., 26.0-42.9 mm SL; same locality data as

holotype. — ZRC 40961, 6 ex., 21.8-51.8 mm SL; same locality data as holotype, 23 May.1996.

Others - UMS uncat., 14 ex., 21.6-41.1 mm SL; SBP uncat., 14 ex., 23.0-38.3 mm SL; same locality data as holotype. — SBM uncat., 6 ex., 24.7-52.2 mm SL; UMS uncat., 6 ex., 24.3-40.7 mm SL; SBP uncat., 6 ex., 23.0-41.6 mm SL; same locality data as holotype, 23 May.1996. — ZRC 40962, 6 ex., 12.5-50.8 mm SL, SBM uncat., 6 ex., 14.1-24.5 mm SL, UMS uncat., 6 ex., 17.0-25.1 mm SL, SBP uncat., 6 ex., 17.7-22.9 mm SL; Borneo: Sabah, Maliau Basin, small stream near camp 1988 (ca. 5°14'N 116°53'E), ca. 7 km northeast of basecamp 1996 (ca. 5°14'N 116°53'E), coll. S. H. Tan, T. H. T. Tan et al., 15-17 May.1996. — SBM uncat., 3 ex., 15.7-23.4 mm SL, UMS uncat., 2 ex., 15.8-16.1 mm SL, SBP uncat., 2 ex., 14.3-14.9 mm SL; Borneo: Sabah, Maliau Basin, small streams at right trail ca. 3 to 4 km into Jalan Babi towards Maliau falls, coll. S. H. Tan, T. H. T. Tan et al., May.1996.

Diagnosis. – *Betta gladiator* is distinguished from the other members of the *B. unimaculata* group in: no anal-fin base sheath scales; no dorsal-fin spine; body yellowish brown, opercle blueish; caudal fin plain brown; vertebrae 33-34; anal-fin rays 28-31 (mode 30); dorsal-fin rays 7-9 (mode 8); pectoral-fin rays 16-17 (mode 17); subdorsal scales 5-6 $\frac{1}{2}$ (mode 6); lateral scales 34-36 (mode 35); predorsal scales 24-27 (mode 26); predorsal length 68.0-72.8% SL; head length 28.5-31.3% SL; length of anal-fin base 48.1-52.8% SL; length of dorsal-fin base 7.3-11.4% SL; lower jaw length 28.3-38.3% HL.

Description. – General body shape and appearance as in Figs. 25a-b, 47f. Body slender, head broad and blunt; caudal fin rounded with distal part of rays protruding, dorsal and anal fins bluntly pointed, pelvic fin filamentous. Vertebrae 2-3 + 8 + 22-23 = 33-34 (mode 33 or 34, n = 10). Meristic and morphometric data in Table 5. Maximum known size 55.5 mm SL (ZRC 40960).

Coloration. – For live coloration, see Fig. 47f. When alive, dorsal half of body dark brown, ventral half lighter brown or slight yellowish. Male with dark blue iridescent opercle, with a little yellowish-green iridescence on body; when preserved, opercle appearing black. Female without dark pigmented



Fig. 25. a) *Betta gladiator* – ZRC 40960, paratype, 56.0 mm SL, b) ZRC 40960, paratype, 39.2 mm SL, without dorsal fin.

opercle when alive or preserved. Pelvic fin filamentous, tip white, rest iridescent whitish. Anal fin with blueish subdistal band, edge iridescent green. Dorsal, caudal and anal-fin transverse bars present. Caudal peduncle black blotch present in both sexes and juveniles. Preserved specimens uniformly dark brown dorsally and lighter brownish yellow ventrally.

Distribution. – *Betta gladiator* is currently known only from the Maliau basin, a near circular plateau enclosed by high elevations in the Sabah inland, part of the Kinabatangan basin (Fig. 23) (S. H. Tan & Ng, 1997, and Martin-Smith et al., 1998; as *B. unimaculata*).

Field notes. – Specimens were collected from heath forest, in acidic water of pH 4.2-4.8. The only syntopic fishes are *Puntius sealei* (Cyprinidae) and *Hemibagrus* aff. *baramensis* (Bagridae). *Betta gladiator* is an aggressive and territorial species. Single adults were found about one metre apart, usually together with a small number of juveniles. Specimens kept in captivity fought continuously and had to be kept separately, otherwise they would have killed each other (pers. observ.).

Etymology. – From the Latin *gladiator* for warrior or fighter, alluding to the aggressive behaviour of the species. Used as a noun in apposition.

Comparative notes. – *Betta gladiator* is distinguished from the other members of the species group in the following characters: more pectoral fin rays (16-17, vs. 11-14); more lateral scales (34-36, vs. 31-34½); flat lateral head profile and a bulbous dorsal head profile (head width 64.5-77.3% HL, vs. 56.4-74.2); more vertebrae than *B. macrostoma* and *B. unimaculata* (33-34, vs. 30-32); more subdorsal scales than *B. ocellata* and *B. unimaculata* (5-6½, vs. 4-5½); fewer subdorsal scales than *B. macrostoma* (5-6½, vs. 6-8); dorsal-fin origin above 19-21st lateral scale (vs. 15-19th in *B. patoti* and *B. macrostoma*); more predorsal scales than *B. ocellata* and *B. macrostoma* (24-27, vs. 21-24); more lateral scales than *B. unimaculata* and *B. macrostoma* (34-36, vs. 31-33); greater total length than *B. ocellata* (135.4-139.2% SL, vs. 131.9-135.6); greater predorsal length than *B. macrostoma* (68.0-72.8% SL, vs. 62.3-66.7); smaller head length than *B. ocellata* (28.5-31.3% SL, vs. 31.4-33.3); smaller body depth at dorsal-fin origin than *B. ocellata* (18.4-20.4% SL, vs. 20.5-24.5); greater pelvic-fin length (29.0-35.7% SL, vs. 21.6-27.6) and smaller length of anal-fin base than *B. macrostoma* (48.1-52.8% SL, vs. 43.2-49.2); smaller length of anal-fin base than *B. ocellata* (48.1-52.8% SL, vs. 52.2-54.5); smaller length of dorsal-fin base than *B. macrostoma* (7.3-11.4% SL, vs. 12.2-15.7); smaller height at pectoral-fin origin than *B. ocellata* (10.6-16.5% SL, vs. 16.7-18.7).

Remarks. – *Betta gladiator* seems to be most closely allied to *B. ocellata*, a common species in the lowlands of Sabah. The isolated geography of the Maliau Basin has probably facilitated the evolution of this species. Specimens without dorsal fins (three out of 150 specimens) could be due to inbreeding or other unknown factors (Fig. 25b).

BETTA PICTA GROUP

***Betta taeniata* Regan, 1910**

(Figs. 26a-b, 47g-h)

Betta taeniata Regan, 1910: 781, pl. 78, fig. 1; Weber & de Beaufort, 1922: 362 (part); Herre, 1940: 45 (part); Vierke, 1984: 58, 1988: 335; Witte & Schmidt, 1992: 3245 (key only); Kottelat et al., 1993: 163, pl. 77; Kottelat & Lim, 1995: 248.

Betta spec. affin. *edithae* & affin. *foerschi*: Brown & Brown, 1987: 168, pl. 14.

Material examined. – Lectotype - **Sarawak**: - BMNH 1893.3.6:147, 42.1 mm SL male; Borneo: Sarawak, Sungai Senah, coll. A. Everett.

Paralectotypes - BMNH 1893.3.6:148-150, 3 ex., 33.8-37.2 mm SL, same locality data as lectotype.

Others - ZRC 39266, 4 ex., 31.4-42.2 mm SL, CMK 13020, 2 ex., 36.4-38.1 mm SL, SM uncat., 2 ex., 26.6-34.4 mm SL; Borneo: Sarawak, Sungai Kuhas (1°09'10.0"N 110°29'22.7"E), 5.8 km into right side-road at 6.9 km into Tebelu Tebakang turnoff after Serian town, coll. P. K. L. Ng et al., 5 Sep.1995. — ZRC 39581, 6 ex., 15.2-39.6 mm SL; CMK 13017, 2 ex., 25.5-35.2 mm SL; SM uncat., 2 ex., 25.4-31.6 mm SL; Borneo: Sarawak, tributary of Sungai Kuhas (1°9'23.1"N 110°29'29.9"E), 0.5 km into Kampung Lanchang, 5.8 km into right track of side-road at 6.9 km into Tebelu Tebakang turnoff after Serian town, coll. P. K. L. Ng et al., 14 Jan.1996. — ZRC 40963, 7 ex., 26.9-40.5 mm SL; Borneo: Sarawak, tributary of Sungai Kuhas (1°9'23.1"N 110°29'29.9"E), 0.5km into Kampung Lanchang, 5.8 km into right side-road at 6.9 km into Tebelu Tebakang turnoff after Serian town, coll. P. K. L. Ng et al., 31

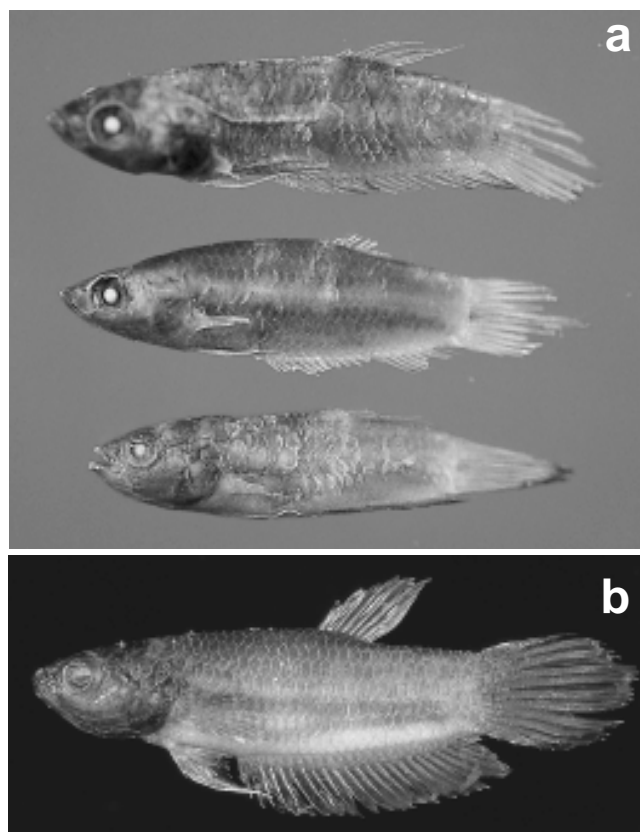


Fig. 26. a) *Betta taeniata* - BMNH 1893.3.6:147, male lectotype (uppermost), 42.1 mm SL, BMNH 1893.3.6:148-150, 3 paralectotypes (2 depicted), 33.8-37.2 mm SL, b) ZRC 39581, 36.6 mm SL.

Aug.1996. — ZRC 40964, 2 ex., 21.7-27.6 mm SL; Borneo: Sarawak, Sungai Kuhas (1°09'10.0"N 110°29'22.7"E), 5.8 km into right side-road at 6.9 km into Tebelu Tebakang turnoff after Serian town, coll. P. K. L. Ng et al., 31 Aug.1996. — ZRC 40988, 3 ex., 14.8-38.2 mm SL; Borneo: Sarawak, Sungai Semabang, 21.7 km towards Simunjan from Kuching-Sri Aman road (1°12'46.4"N 110°55'40.4"E), coll. H. H. Tan & S. H. Tan, 4 Sep.1996. **Kalimantan Barat:** CMK 11758, 7 ex., 13.9-54.9 mm SL; ZRC 39271, 5 ex., 23.3-45.2 mm SL; ZRC 39272, 2 males, 38.8-41.2 mm SL; Borneo, Indonesia: Kalimantan Barat, Kapuas basin, Sungai Palat at Pala Hulu (Kec. Siberuang, Kampung Renyai Hulu), km 101 on road from Sintang to Putussibau, coll. M. Kottelat, 16 Jun.1995. — CMK 10546, 4 ex., 12.2-52.2 mm SL; Borneo, Indonesia: Kalimantan Barat, Kapuas basin, Sungai Palat at Pala Hulu (Kec. Siberuang, Kampung Renyai Hulu), km 99 on road from Sintang to Putussibau, coll. M. Kottelat, 16 Sep.1993.

Diagnosis. — *Betta taeniata* is characterised by a relatively weakly contrasted sexual dimorphism. Mature males have more intense coloration, but when disturbed they are similar to the females. In both sexes, the opercle has blue to green iridescent scales depending on angle of reflected light. The anal and caudal fins (and sometimes the dorsal fin) are bordered distally by a dark blue edge, followed by an iridescent blue or green border when live (Fig. 4); only a blackish distal border is visible when preserved. *Betta taeniata* is distinguished from the other members of the *B. picta* species group by the following combination of characters: anal-fin rays 23-26 (mode 26); subdorsal scales 5-6 (mode 6); lateral scales $27\frac{1}{2}$ -30 (mode 29); caudal peduncle depth 14.8-19.7% SL; head length 30.3-34.5% SL; body depth at dorsal-fin origin 25.3-30.1% SL; length of anal-fin base 47.9-52.7% SL; interorbital width 29.2-36.2% HL.

Description. — General body shape and appearance as in Figs. 26a-b, 47g-h. Meristic and morphometric data of type and fresh material in Table 6. Body stout and short, head relatively pointed. Unpaired fins rounded, anal fin maybe bluntly pointed, pelvic fin with first simple ray filamentous but short, extending to sixth anal ray (including spines). Vertebrae (type material) 2 + 8 + 18 = 28 (mode 28, n = 3), (fresh material) 2 + 8 + 17-19 = 27-29 (mode 28, n = 8). Maximum known size 54.9 mm SL (CMK 11758).

Coloration. — For live coloration, see Figs. 47g-h (see also Linke, 1991: 68; Kubota et al., 1996: 36). Mature male with iridescent blue to green opercle scales when alive, blackish when preserved. Iridescent scales on body faint, concentrated on dorsal half of body when alive, not visible when preserved. In mature male, unpaired fins brownish-red, distal margin of anal and caudal fins dark blue with iridescent light blue border anteriorly and a thin iridescent blue edge. Dorsal fin with distal iridescent green edge. Iridescent blue edges on anal and caudal fins most obvious when male in antagonistic behaviour or freshly preserved. Pelvic fin with distal half of filamentous ray white, rest brownish-red. Preserved male retaining distinct dark fin edges, faint in female both alive and preserved. Female with more distinct black markings or spots on unpaired fins when alive, faint or absent when preserved. Juvenile with central and second central black stripes on body. A black caudal peduncle spot also present. Preserved specimens dark brown dorsally and light brown ventrally, fins brownish to hyaline, with distinct dark edges.

Distribution. — *Betta taeniata* is apparently restricted to hill

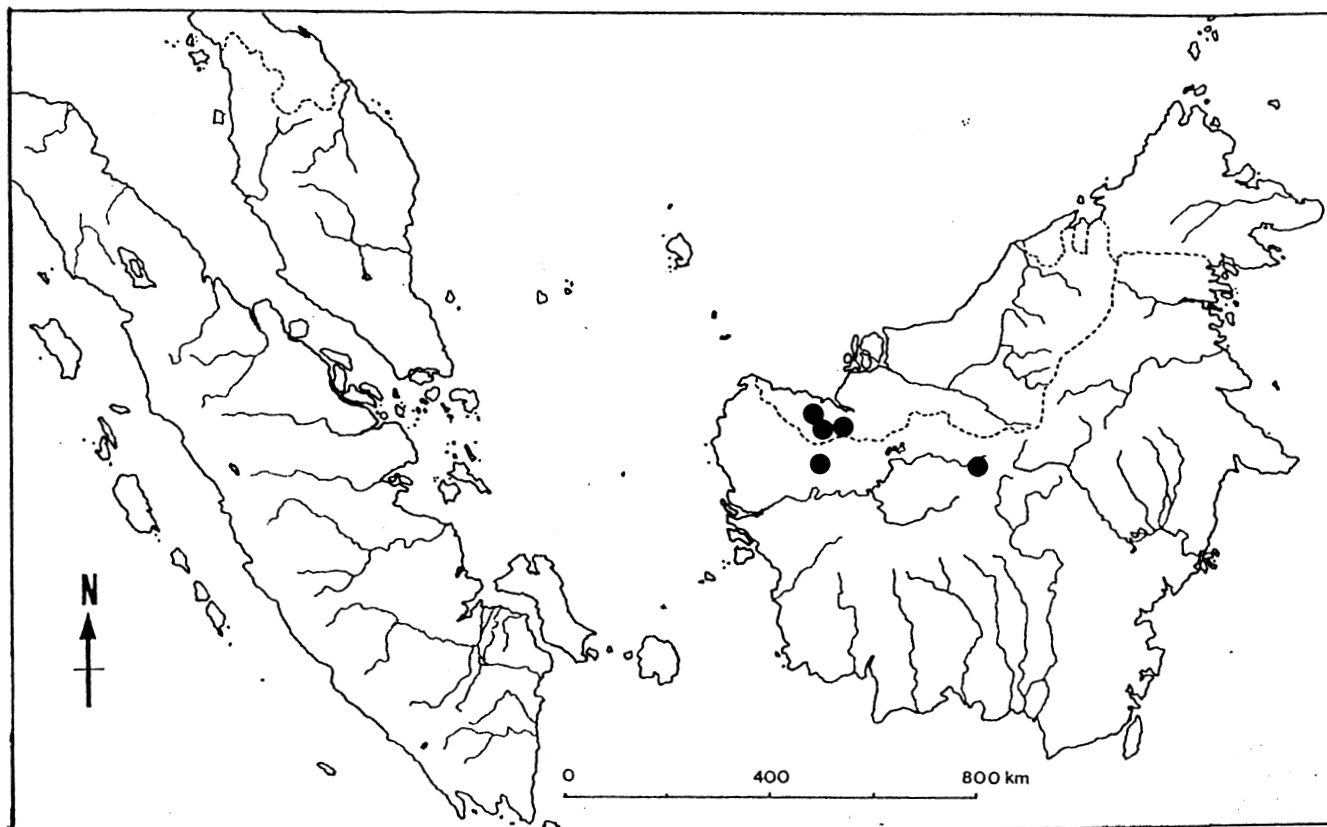


Fig. 27. Distribution map of *B. taeniata* (circle).

streams of southern Sarawak and northern part of Kalimantan Barat (Fig. 27).

Field notes. – Most of the fresh samples of *B. taeniata* were collected from a fast flowing clear water hill stream near Serian, south Sarawak (pH 7.0). The substratum was quartz gravel littered with rocks of variable size. The width of the stream was about 10 m at its widest and water depth was from 5 cm to 80 cm. No aquatic vegetation was present. *Betta taeniata* was collected from the more stagnant stretches of the stream, among the submerged leaf litter, tree roots and overhanging bank vegetation. Syntopic species include: *Barbodes collingwoodi*, *Paracrossochilus vittatus*, *Puntius kuchingensis*, *P. banksi*, *P. orphoides*, *P. sealei*, *Rasbora sarawakensis*, *R. caudimaculata* (Cyprinidae), *Gastromyzon* cf. *fasciata*, *G.* cf. *punctulatus*, *Homaloptera tweediei*, *Nemacheilus saravacensis* (Balitoridae), *Glyptothorax* cf. *major* (Sisoridae), *Clarias teijsmanni* (Clariidae), *Hemiramphodon kuekenthali* (Hemiramphidae), *Channa lucius* (Channidae) and *Macrogathus maculatus* (Mastacembelidae). The Iban name for this species is ikan t'pachi. This species is an oral brooder (pers. observ.).

Comparative notes. – *Betta taeniata* is distinguished from the other members of the species group by the following of characters: greater mode of anal-fin rays than *B. picta* and *B. simplex* (26, vs. 22-24); greater mode of subdorsal scales than *B. picta* and *B. simplex* (6, vs. 5-5¹/₂); lower mode of transverse scales than *B. simplex* (9¹/₂, vs. 11¹/₂); greater mode of lateral scales than *B. picta* and *B. simplex* (29, vs. 28); dorsal-fin origin above modal 14th lateral scale (vs. 15th in *B. simplex*); relatively smaller predorsal length than *B. simplex* (62.4-67.7% SL, vs. 66.7-69.8); smaller head length than *B. simplex* (30.3-34.5% SL, vs. 34.6-37.2); greater body depth at dorsal-fin origin than *B. picta* (25.3-30.1% SL, vs. 21.5-25.5); smaller body depth at dorsal-fin origin than *B. simplex* (25.3-30.1% SL, vs. 29.3-32.2); greater length of anal-fin base than *B. picta* (47.9-52.7% SL, vs. 42.6-48.4) (data of *B. simplex* from Kottelat, 1994).

Remarks. – Regan (1910:78) described *B. taeniata* on the basis of four syntypes. The condition of the syntypes is rather poor, but they fortunately still allow to recognize enough diagnostic characters. The best preserved specimen (BMNH 1893.3.3:147, 42.1 mm SL) is here designated as the lectotype. It is a male, as shown by the dark anal distal margin.

Weber & de Beaufort's (1922: 362) described *B. taeniata* as having the anal penultimate rays in old mature specimens strongly produced and reaching the extremity of the caudal fin and prolonged median rays in the caudal fin and II, 20-25 anal-fin rays. These characters do not fit with those of the *B. picta* group (see earlier). The distribution cited by Weber & de Beaufort (1922) includes Sumatra, where *B. falx* and *B. pugnax* do occur (pers. observ.) and it seems that Weber & de Beaufort's material might be a mixture of several species.

Herre (1940: 45) stated having obtained *B. taeniata* in Singapore, Johore, Pahang, Perak (Malay Peninsula) and Kuching (Sarawak). His identification of specimens from

Singapore and Peninsular Malaysia is erroneous. Examination of specimens collected and identified by Herre and deposited in ZRC reveals that they are all *B. pugnax*. The specimen from Sarawak listed by Brown & Brown (1987: 168, pl. 14) as "*Betta* spec. affin. *edithae* & affin. *foerschi*" is almost certainly *B. taeniata*.

Roberts (1989: 173) listed *B. taeniata* from the Kapuas basin. His specimens had anal ray counts of II, 26-29, which he commented as being agreeable to the description of *B. edithae*. Examination of Roberts' material deposited in MZB (MZB 3867, MZB 3870) confirms that it actually is *B. edithae*.

BETTA SPLENDENS GROUP

Betta imbellis Ladiges, 1975

(Figs. 28, 48a-b)

Betta imbellis Ladiges, 1975: 263; Kottelat, 1989: 19 (list only); Schaller & Kottelat, 1989: 36; Ng et al., 1992: 28, Fig. 100; Witte & Schmidt, 1992: 26 (key); Kottelat et al., 1993: 162, pl. 76; Vidthayanon et al., 1997: 54; Vidthayanon, 2002: 105.

Betta splendens Regan, 1910: 782 (part) (see Schaller & Kottelat, 1989, for details).

Betta splendens (non Regan, 1910) - Herre, 1940: 46; Tweedie, 1952: 75; Alfred, 1963: 147; 1966: 50 (part).

Material examined. – **Malaysia:** ZRC 32130-54, 25 ex., 12.5-36.5 mm SL; Malaysia: Penang, Bayan Lepas, Kampung S. Tiram, ditch off airport, coll. H. H. Tan & S. H. Tan, 9 Jun.1993. — ZRC 32235-262, 28 ex., 13.0-32.6 mm SL; Malaysia: Penang, Kampung Terang, coll. H. H. Tan & S. H. Tan, 10 Jun.1993. — ZRC 437, 11 ex., Malaysia: Kedah, Sungai Patani; E. D. B. Wolf, 1951. — ZRC 442, 9 ex., Malaysia: Kedah, Alor Star; E. L. B. Wolfe, 1951. — ZRC 38418, 1 ex., Malaysia: Perak, Krian, stream flowing from Bukit Merah Reservoir, coll. H. H. Tan et al., 21 Dec.1994. — ZRC 39540, 1 ex., Malaysia: Perak, ca. 11 km before Gerik, tributary of Sungai Kulim, coll. H. H. Tan et al., 19 Nov.1995. — ZRC 18842-47, 6 ex., 19.0-28.9 mm SL males, Malaysia: Selangor, 32 km Rawang-Kuala Selangor road, coll. P. K. L. Ng, 24 Aug.1991. — ZRC 14464-67, 4 ex., Malaysia: Selangor, north Selangor peat swamp forest, stream near padi field on west edge of swamp forest, coll. P. K. L. Ng, 15 May.1991. — ZRC 24656-57, 2 ex., 25.3-26.4 mm SL males, Malaysia: Terengganu, Rantau Abang, swamp at 56 km Kuantan-Kuala Terengganu road; T. H. T. Tan & D. S. L. Chung, 3-5 Aug.1992. — ZRC 17295-99, 5 ex., 22.3-25.1 mm SL; Malaysia: Terengganu, Rantau Abang, stream at 1 km west off East Coast Highway about 53 km south of Kuala Terengganu, coll. K. K. P. Lim, 10-11 Sep.1991. — ZRC 40965, 4 ex., 14.0-23.3 mm SL; Malaysia: Terengganu, Rantau Abang, 56 km to Kuala Terengganu, coll. P. K. L. Ng et al., 16 May.1995. — ZRC 14776-832, 57 ex., 12.8-31.3 mm SL; Malaysia: Johor, Ayer Hitam, in ditch at Kampung Botak Parit, coll. P. K. L. Ng et al., 23 May.1991. —



Fig. 28. *Betta imbellis* – ZRC 32235, 28.1 mm SL male.

ZRC 22148-172, 25 ex., 16.9-32.2 mm SL; Malaysia: Johor, Pontian, Parit Sikom, coll. K. K. P. Lim & D. S. L. Chung, 14 May.1992. — ZRC 14839-144, 6 ex., 18.9-28.8 mm SL; Malaysia: Johor, Ayer Hitam, coll. P. K. L. Ng & K. K. P. Lim, 23 May.1991. **Singapore:** ZRC 37595, 3 ex., 20.5-32.6 mm SL; Singapore: stream at Lorong Banir, coll. K. K. P. Lim et al., 24 May.1994. **Sumatra:** ZRC 40966, 17 ex., 12.1-27.0 mm SL, CMK 13126, 5 ex., 20.3-24.8 mm SL; Indonesia: Sumatra, North Sumatra, ca. 80 km south of Medan, Sei Rampah, Pantai Berdagai, pond at Kampung Nagur (3°31'14.0"N 99°10'32.2"E), coll. H. H. Tan et al., 15 Jun.1996. **Sabah:** ZRC 40967, 12 ex., 8.5-24.4 mm SL; Borneo: Sabah, Tawau, Jalan Sin On Jaya, swampy area (4°16'07.6"N 117°54'25.6"E), coll. H. H. Tan et al., 5 Oct.1996 (most probably introduced).

Diagnosis. – *Betta imbellis* is distinguished from other members of the *B. splendens* group by the following combination of characters: a bright red crescent on distal edge of caudal fin (vs. faint crescent or absence in *B. splendens* and *B. smaragdina*); no caudal transverse bars (vs. presence in *B. smaragdina* and *B. stiktos*); dorsal transverse bars on distal two-thirds of dorsal fin (vs. whole dorsal fin in *B. smaragdina*); iridescent blue opercle scales (vs. parallel red vertical opercle bars in *B. splendens* and green iridescent opercle scales in *B. smaragdina*); dark brown to black body (vs. light brown body in *B. smaragdina* and *B. stiktos*); less lateral scales than *B. stiktos* (30-32, vs. 33-34); more slender body than *B. splendens* (body depth 24.2-30.1% SL, vs. 27.1-32.2); more backwards position of dorsal fin than in *B. splendens* (dorsal-fin origin above lateral scales 15-17, mode 16, vs. 14-16, mode 14); relatively smaller length of dorsal-fin base than *B. splendens* (12.9-18.9% SL, vs. 16.7-23.8); smaller height at pectoral-fin origin than *B. splendens* (14.8-18.9% SL, vs. 18.5-20.7).

Description. – General body shape and appearance as in Figs. 28, 48a-b. Body slender (body depth at dorsal-fin origin 24.2-30.1% SL); head small (HL 25.8-30.9% SL); caudal fin rounded with distal red crescent margin when live, yellowish when preserved (Fig. 5a); pelvic fin falcate; dorsal fin rounded, anal fin pointed, anal fin reaching to half or more of caudal fin. Meristic and morphometric data in Table 7. Maximum known size 36.5 mm SL (ZRC 32130).

Coloration. – For live coloration, see Figs. 48a-b (see Linke, 1991: 34; Kubota et al., 1996: 16). Male with head dark brown, opercle with iridescent blue scales, eye with reflective green top. Body light brown with posterior half of body scales iridescent blue. Dorsal fin iridescent blue, with transverse bars distinct; caudal fin with red distal margin in a crescent, rays iridescent blue; anal fin iridescent blue, posterior ray tips red; pelvic fin falcate, red with white tip; pectoral fin hyaline. Female less colourful, lacking iridescence and red caudal fin crescent. Throat with chin-bar, opercle pale gold. Body with distinct central and second central stripes, with caudal peduncle spot. Fins yellowish to hyaline, dorsal fin with transverse bars.

Distribution. – *Betta imbellis* is widely distributed in Peninsular Malaysia (Fig. 29). This species is probably native to the northern part of Sumatra in Medan (pers. observ.; Schaller & Kottelat, 1989). Its presence in Sabah is most probably due to introduction. *Betta imbellis* is apparently feral in Singapore (Ng et al., 1993).

Field notes. – *Betta imbellis* is often found in stagnant pools and ditches, in clear to brown water.

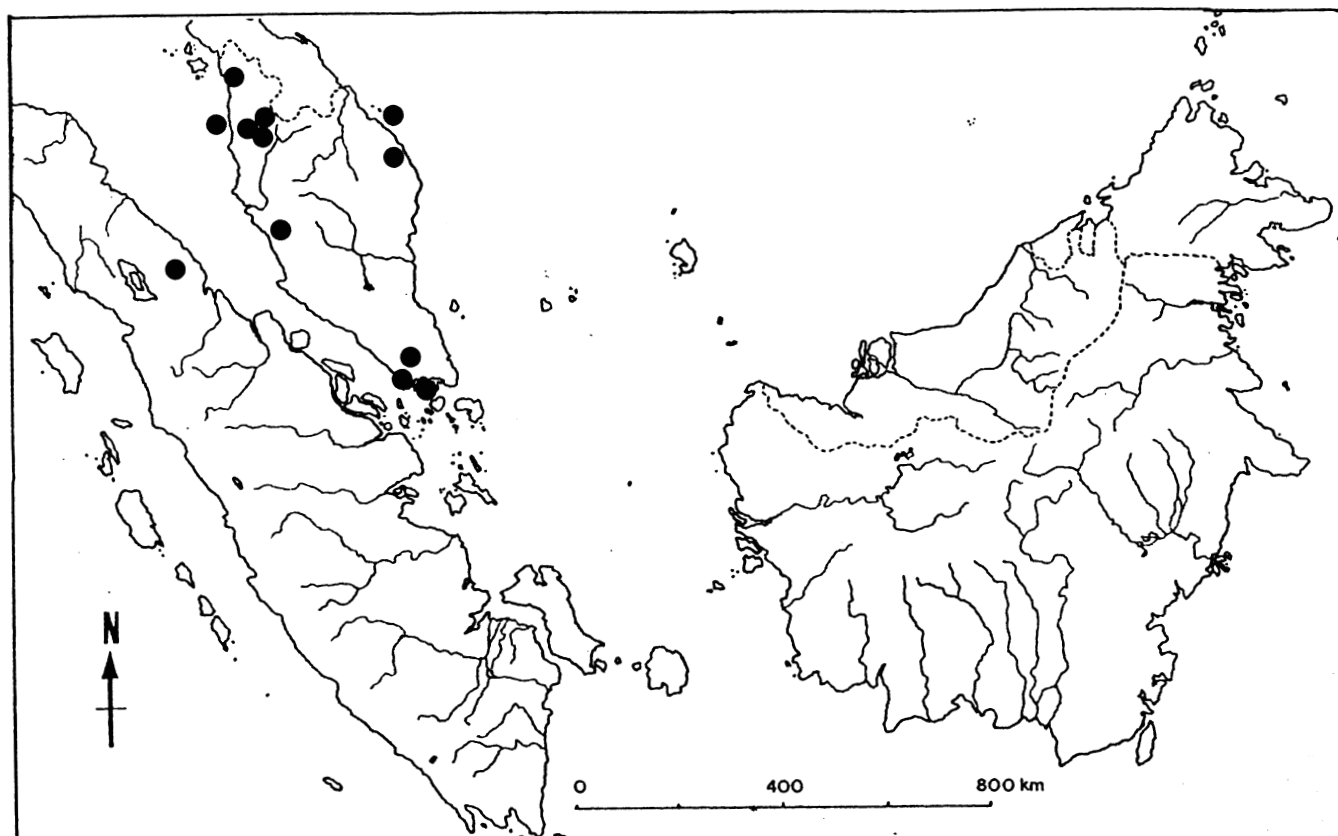


Fig. 29. Distribution map of *B. imbellis* (circle).

Remarks. – There is only one indigenous species in the study area: *B. imbellis*. This species has had a long and confused taxonomic history. Cantor (1850) listed “*B. pugnax* var.” as a domesticated form of *B. pugnax* from Siam (Bangkok, Thailand). This is the species known today as *B. splendens*. Regan (1910: 782) described *B. splendens* on the basis of two lots of specimens (total nine specimens) from Bangkok and Pinang (Pulau Penang). Schaller & Kottelat (1989) examined eight of the syntypes and identified the Bangkok specimens as *B. splendens* and the Penang specimens as *B. imbellis*. They also designated a lectotype from among the Bangkok syntypes (BMNH 1898.11.8:95, 38.6 mm SL). *Betta splendens* has one junior subjective synonym, *B. abbreviata* Pellegrin, 1925. Schaller & Kottelat (1989) commented that the author of *B. abbreviata* was Blanc (1963), but this is incorrect. The term variety was used in the past to name specimens which were not clearly defined. The variety described by Pellegrin (1925) was a captive stock of domesticated origin from Indochina. According to the Code (Article 45.6.4, ICZN, 1999), Blanc’s use of name makes it valid, as it is used in a way equivalent to a subspecies. The correct citation of the author of *B. abbreviata* is thus Pellegrin (1925).

Ladiges (1975) described *B. imbellis* from Kuala Lumpur, Selangor. In literature before 1975, *B. imbellis* had been identified as *B. splendens*, viz. Herre (1940), Tweedie (1952) and Alfred (1963, 1966). Herre (1940) comments on *B. splendens* from Mandai (Singapore) probably refer to *B. imbellis*; although there are feral *B. splendens* in Singapore (Lim & Ng, 1990; Ng et al., 1993; pers. observ.). Tweedie (1952) and Alfred (1963, 1966) listed *B. splendens* from Kedah, Terengganu, Penang and Singapore. Their specimens in ZRC are all *B. imbellis*.

BETTA COCCINA GROUP

Betta coccina Vierke, 1979

(Figs. 30, 48c-d)

Betta coccina Vierke, 1979a: 288; Schaller, 1985: 348, 1986: 299; Kottelat, 1989: 19 (list only); Witte & Kottelat, in Kottelat, 1991: 279; Witte & Schmidt, 1992: 313, 326 (key); Ng & Kottelat, 1992: 178; Kottelat et al., 1993: 161, pl. 75; Tan & Tan, 1994: 44.

Material examined. – **Malaysia:** ZRC 28616-635, 20 ex., 18.8-28.7 mm SL; **Malaysia:** Johor, Segamat-Muar area, purchased from the aquarium trade, coll. P. K. L. Ng, Oct.1992. **Sumatra:** CMK 7290,



Fig. 30. *Betta coccina* – ZRC 28616, 27.3 mm SL.

10 ex., ZRC 21051-21052, 2 ex., 22.4-28.4 mm SL; **Sumatra:** Riau Province, Pulau Padang, Sungai Ponder, 12 km east of Karau, on road to Meribur, coll. M. Kottelat, 12 Feb.1991. — ZRC 38257, 2 ex., 26.1-27.9 mm SL; **Sumatra:** Jambi Province, coll. M. Kottelat, May.1994. — ZRC 38611, 4 ex., 17.0-24.5 mm SL; **Sumatra:** Jambi Province, Danau Rasau, M. Kottelat & H. H. Tan, 1-2 Jun.1994.

Diagnosis. – *Betta coccina* is distinguished from the other members of the *B. coccina* group by the following unique combination of characters: small iridescent green lateral blotch in male, missing in female; dark red body colour; no parallel vertical iridescent gold opercle bars; pelvic fin falcate with black filamentous tip, rest red; median fins with discrete iridescent green spots; dorsal-fin rays 9-12; anal-fin rays 27-29; subdorsal scales 7-8; lateral scales 31-32; predorsal scales 18-21 (adapted from Vierke, 1979; Witte & Schmidt, 1992; Ng & Kottelat, 1992).

Remarks. – See Ng & Kottelat (1992) for a comparative diagnosis. Vierke (1979) described *B. coccina* on the basis of aquarium specimens from Jambi, Sumatra. Recent collections yielded specimens mainly from peat swamps in Jambi (pers. observ.). Specimens from Peninsular Malaysia are from the aquarium trade. These specimens were reportedly collected from the Segamat-Muar area in Johor (Fig. 31), an information which seems reliable. For live coloration, see Figs. 48c-d, Linke (1991: 30) and Kubota et al. (1996: 20).

Betta livida Ng & Kottelat, 1992

(Figs. 32, 48e)

Betta coccina (non Vierke, 1979) - Witte & Schmidt, 1992: 307.

Betta livida Ng & Kottelat, 1992: 177; Tan & Tan, 1994: 44.

Betta, new species - Ng et al., 1992: 28; Fig. 13.

Material examined. – **Holotype - Malaysia:** - ZRC 15287, 29.0 mm SL (38.8 mm TL) male, blackwater stream, north Selangor peat swamp forest, 800 m from 45 km mark, on road from Tanjung Malim to Sungai Besar, coll. 1991 Honours Year class, 18 Jun.1991.

Paratypes - All localities in blackwater streams or pools, north Selangor peat swamp forest, Peninsular Malaysia. — ZRC 15288-15289, 1 male, 30.2 mm SL; 1 female, 31.2 mm SL; 800 m from 45 km mark, on road from Tanjung Malim to Sungai Besar, coll. 1991 Honours Year class, 18 Jun.1991. — CMK 8032, 25 ex., 23.3-29.9 mm SL; **Peninsular Malaysia:** Selangor, north Selangor peat swamp forest, blackwater stream at 47 km milestone on road from Sungei Besar to Tanjung Malim, coll. 1991 Honours Year class, 19 Jun.1991. — ZRC 22764-22767, 2 males, 32.3-35.6 mm SL; 2 females, 28.9-36.3 mm SL; on road from Tanjung Malim to Sungai Besar, coll. P. K. L. Ng, Jun.1991. — ZRC 14439, 1 male, 29.8 mm SL; northwestern boundary of north Selangor peat swamp forest, coll. P. K. L. Ng et al., 15 May.1991. — ZRC 18836-18840, 5 ex., 19.6-29.0 mm SL; 43 km milestone, on road from Tanjung Malim to Sungai Besar, coll. P. K. L. Ng, 14 Sep.1991. — ZRC 15254-15273, 20 ex., 14.8-29.5 mm SL; 50 km milestone, on road from Sungai Besar to Tanjung Malim, coll. 1991 Honours Year class, 18 Jun.1991. — ZRC 15209-15228, 20 ex., 16.9-27.5 mm SL; 200 m from 45 km milestone, on road from Tanjung Malim to Sungai Besar, coll. 1991 Honours Year class, 17 Jun.1991. — ZRC 22768, 1 male, 33.1 mm SL; ZRC 22829, 1 female, 27.3 mm SL; between 32-33 km milestone, in pool surrounded by *Pandanus*, Rawang-Kuala Lumpur road, coll. P. K. L. Ng, Nov.1991. — ZRC 18851-18853,

3 ex., 13.4-22.9 mm SL; Rawang-Kuala Lumpur road, 32 km milestone, coll. P. K. L. Ng et al., 24 Aug.1991.

Others - All localities in blackwater streams or pools, north Selangor peat swamp forest, Peninsular Malaysia. — ZRC 14440-14451, 12 ex., northwestern boundary of north Selangor peat swamp forest, coll. P. K. L. Ng et al., 15 May.1991. — ZRC 15290-15302, 13 ex., 15.6-30.1 mm SL; 800 m from 45 km mark, on road from Tanjung Malim to Sungai Besar, coll. 1991 Honours Year class, 18 Jun.1991. — ZRC 22769-22789, 21 ex., 17.7-34.0 mm SL; road from Tanjung Malim and Sungai Besar, coll. P. K. L. Ng et al., Jun.1991. — ZRC 17962, 1 ex., 29.0 mm SL; 200 m from 37 km milestone, on road from Sungai Besar to Tanjung Malim, coll. P. K. L. Ng et al., 25 Aug.1991. — ZRC 17842, 1 ex., 21.6 mm SL; 39 km milestone, on road from Sungai Besar to Tanjung Malim, coll. P. K. L. Ng et al., 24 Aug.1991. — ZRC 15274-15286, 13 ex., 34 km milestone, Sungai Besar to Tanjung Malim road, coll. 1991 Honours Year class, 17 Jun.1991. — ZRC 18037, 1 ex., 650 m from 35 km milestone, on road from Sungai Besar to Tanjung Malim, coll. P. K. L. Ng, 25 Aug.1991. — ZRC 15204-15208, 5 ex., 15.5-26.4 mm SL; 700 m from 41 km milestone, on road from Sungai Besar to Tanjung Malim, coll. 1991 Honours Year class, 19 Jun.1991. — ZRC 16696-16699, 4 ex., on road from Sungai Besar to Tanjung Malim, coll. 1991 Honours Year class, 17-19 Jun.1991. — ZRC 15202-15203, 2 ex., stream adjacent to Sungai Tengi, coll. 1991 Honours Year class, 20 Jun.1991.

Diagnosis. – *Betta livida* is distinguished from the other members of the *B. coccina* group by the following unique combination of characters: small iridescent green lateral blotch in both male and female, disappearing with age; red body colour; parallel vertical iridescent gold bars on opercle; pelvic fin falcate, with wide, iridescent green tip, rest red;

median fins with discrete iridescent green spots; dorsal-fin rays 9-13; anal-fin rays 25-31; subdorsal scales 7; lateral scales 30-31; predorsal scales 18-21 (from Ng & Kottelat, 1992).

Remarks. – See Ng & Kottelat (1992) for more details. The *B. cf. coccina* from Rawang, Selangor of Witte & Schimdt (1992) is *B. livida*. *Betta livida* is known only from the peat swamp forest in Selangor (Fig. 31). For live coloration, see Fig. 48e and Kubota et al. (1996: 22). This species is a bubble nest brooder (Smith, 1996).

***Betta persephone* Schaller, 1986**
(Figs. 33, 48f)

Betta persephone Schaller, 1986: 298; Kottelat, 1989: 19 (list only); Schaller & Kottelat, 1989: 36; Witte & Kottelat, in Kottelat, 1991: 279; Witte & Schmidt, 1992: 308, 325 (key); Ng & Kottelat, 1992: 179; Tan & Tan, 1994: 42.

Material examined. – **Malaysia:** ZRC 28596-615, 20 ex., 17.5-25.9 mm SL, ZRC uncat., 57 ex., 16.8-25.5 mm SL; Malaysia: Johor, Segamat-Muar area, purchased from aquarium trade, coll. P. K. L. Ng, Oct.1992. — ZRC 24443-452, 10 ex., 14.7-24.4 mm SL; - ZRC 24691-96, 6 ex., 20.8-25.0 mm SL; Malaysia: Johor, ca. 3 km north of Ayer Hitam, north bank of Sungai Sambrong, in swamp forest, coll. K. K. P. Lim & D. G. B. Chia, 6 Aug.1992. — ZRC 38255, 2 ex., 19.9-21.4 mm SL; Malaysia: Johor, Ayer Hitam, in swamp forest, coll. H. H. Tan & D. M. Armitage, Apr.1994.

Diagnosis. – *Betta persephone* is distinguished from the other

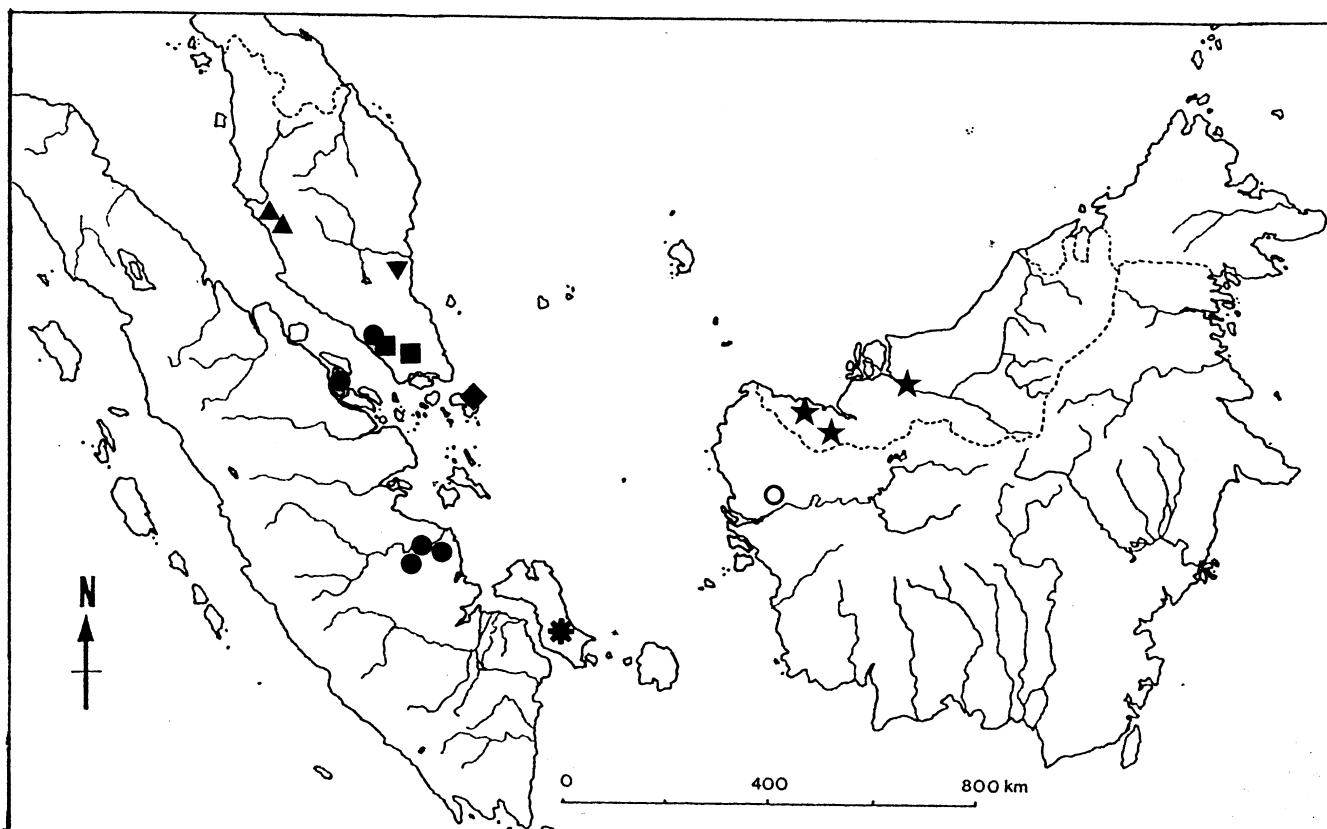


Fig. 31. Distribution map of *B. coccina* (circle), *B. livida* (triangle), *B. persephone* (square), *B. tussyae* (upside-down triangle), *B. brownorum* (star), *B. miniopinna* (diamond), *B. burdigala* (asterix), *B. rutilans* (hollow circle).

members of the *B. coccina* group by the following unique combination of characters: no lateral blotch; blackish body colour; no parallel vertical iridescent gold bars on opercle; pelvic fin falcate with white filamentous tip, rest black to reddish; median fins covered diffusely with light green iridescence; dorsal-fin rays 9; anal-fin rays 24-27; subdorsal scales 6-7; lateral scales 27-29; predorsal scales 17-18 (adapted from Schaller, 1986; Witte & Schmidt, 1992; Tan & Tan, 1994).

Remarks. – See Ng & Kottelat (1992) and Tan & Tan (1994) for comparative diagnosis. Schaller & Kottelat (1989) completed the listings of the type material. This species is restricted to the peat swamps in southwestern Johor (Fig. 31). It is typically found in shallow pools among submerged leaf litter. Syntopic osphronemids include *B. bellica*, *B. imbellis* and *Trichopsis vittata*. The closest allied species is *B. miniopinna* which occupies a similar habitat in Pulau Bintan, Riau Archipelago (Tan & Tan, 1994). *Betta persephone* exhibits kinship care (Witte & Schmidt, 1992; pers. observ.). For live coloration, see Fig. 48f, Linke (1991: 40) and Kubota et al. (1996: 26).

***Betta tussyae* Schaller, 1985**
(Figs. 34, 48g)

Betta tussyae Schaller, 1985: 350; 1986: 300; Kottelat, 1989: 20 (list only); Schaller & Kottelat, 1989: 35; Witte & Kottelat, in Kottelat, 1991: 279; Witte & Schmidt, 1992: 307, 326 (key); Ng & Kottelat, 1992: 179; Tan & Tan, 1994: 44.

Material examined. – Holotype - ZRC 38451/CMK 5947, 36.5 mm SL; Malaysia: Pahang, 17 km south of Pekan, or about 77 km south of Kuantan on road along east coast, ca. 1 km from sea, coll. P. Nagy, 1984.

Others - Peninsular Malaysia: Pahang. — ZRC 18493-18495, 2 males, 24.1-26.4 mm SL, 4 females, 22.7-27.9 mm SL; in pool, about 500 m before 10 km milestone, Kuantan to Gambang (near

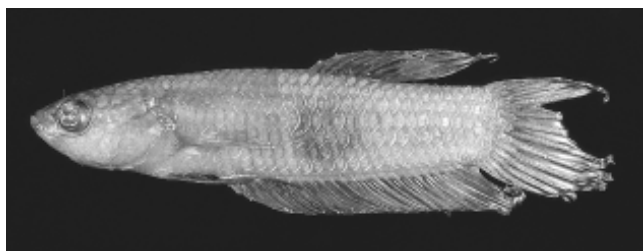


Fig. 32. *Betta livida* – ZRC 15287, holotype, 29.0 mm SL.



Fig. 33. *Betta persephone* – ZRC 24443, 24.0 mm SL.

Kampung Mahkota) road, coll. P. K. L. Ng, J. B. Tay & D. Chia, 20 Oct.1991. — ZRC 22795-22797, 3 ex., CMK 8036, 3 ex., pool along road from Mersing to Pekan, about 80 km before Kuantan, 3°10'31.8"N 103°26'41.8"E, coll. P. K. L. Ng & M. Kottelat, 9 Mar.1992. — ZRC 22790-22794, 5 ex., CMK 8040, 6 ex., pool along road from Mersing to Pekan, 73 km before Kuantan, 3°18'13.0"N 103°25'25.2"E, coll. P. K. L. Ng & M. Kottelat, 9 Mar.1992. — ZRC 22798-22802, 5 ex., CMK 8055, 6 ex., stream across road from Mersing to Pekan, 69 km before Kuantan, coll. P. K. L. Ng & M. Kottelat, 9-10 Mar.1992. — ZRC 22803-22805, 3 ex., CMK 8073, 2 ex., 16 km milestone, on road from Kuantan to Mersing, 3°42'47.3" 103°16'28.5"E, coll. P. K. L. Ng & M. Kottelat, 9 Mar.1992. — ZRC 22806-22812, 7 ex., CMK 8108, 7 ex., stream, road from Pekan to Mersing, 1 km north of 3°22'04.1"N 103°25'13.8"E, coll. P. K. L. Ng & M. Kottelat, 10 Mar.1992. — ZRC 22813-22828, 16 ex., CMK 8115, 17 ex., road from Pekan to Mersing, 3°22'04.1"N 103°25'13.8"E, coll. P. K. L. Ng & M. Kottelat, 10 Mar.1992.

Diagnosis. – *Betta tussyae* is distinguished from the other members of the *B. coccina* group by the following unique combination of characters: no lateral blotch; brick-red body colour; faint parallel vertical iridescent gold bars on opercle; pelvic fin falcate, with narrow white tip, rest red; median fins without iridescent green spots; dorsal-fin rays 11-12; anal-fin rays 27-28; subdorsal scales 8; lateral scales 30-31 (adapted from Schaller, 1985; Witte & Schmidt, 1992; Ng & Kottelat, 1992).

Remarks. – See Ng & Kottelat (1992) for comparative diagnosis. Schaller & Kottelat (1989) clarified the status of the type material. This taxon is restricted to eastern Pahang, where it the coastal peat swamps (Fig. 31). It occurs syntopically with *B. waseri*. For live coloration, see Fig. 48g, Linke (1991: 71) and Kubota et al. (1996: 23). *Betta tussyae* is a bubble nest brooder (Smith, 1994).

***Betta brownorum* Witte & Schmidt, 1992**
(Figs. 35, 48h)

Betta brownorum Witte & Schmidt, 1992: 312, 326 (key); Ng & Kottelat, 1992: 178; Kottelat et al., 1993: 161, pl. 75; Tan & Tan, 1994: 44; Kottelat & Lim, 1995: 248.

Betta spec. affin. *coccina* (non Vierke, 1979) - Brown & Brown, 1987: 169, pl. 11.

Material examined. – ZRC 39582, 60 ex., 8.4-25.9 mm SL, CMK 13018, 10 ex., 10.5-22.3 mm SL, SM uncat., 10 ex., 10.0-23.3 mm SL; Borneo: Sarawak, ca. 200 m into peat swamp forest on left side of road (1°12'08.7"N 110°39'52.2"E), ca. 11 km towards Gedong after turnoff from Serian-Sri Aman road (after 78 km to Kuching from Gedong mark), coll. H. H. Tan & S. H. Tan, 16 Jan.1996. —



Fig. 34. *Betta tussyae* – ZRC 25066, 30.2 mm SL.

ZRC 39583, 3 ex., 18.6-19.4 mm SL; Borneo: Sarawak, ca. 50 m into peat swamp forest and ditch on left side of road (1°10'50.0"N 110°39'22.1"E), ca. 8 km towards Gedong after turnoff from Serian-Sri Aman road, coll. H. H. Tan & S. H. Tan, 16 Jan.1996. — ZRC 40968, 1 ex., 21.8 mm SL; Borneo: Sarawak, peat swamp forest at Balai Ringin, ca. 0.5 km after Sungai Kerang towards Sri Aman (1°03'01.3"N 110°45'38.1"E), coll. H. H. Tan & S. H. Tan, 5 Sep.1996.

Diagnosis. – *Betta brownorum* is distinguished from the other members of the *B. coccina* group by the following unique combination of characters: large iridescent green lateral blotch in both male and female; reddish-magenta body colour; no parallel vertical iridescent bars on opercle; pelvic fin falcate, with white filamentous tip, rest red; median fins without iridescent green spots; dorsal-fin rays 10-11; anal-fin rays 26-28; subdorsal scales 6-7; lateral scales 29¹/₂-31; predorsal scales 18-20 (adapted from Witte & Schmidt, 1992; Ng & Kottelat, 1992).

Remarks. – See Witte & Schmidt (1992) for more details. *Betta brownorum* was collected from the same habitat type as *B. persephone*. The head profile is also similar to that of *B. persephone*. *Betta brownorum* is a bubble nest brooder which exhibits kinship care; the older siblings from the previous batch take care of the younger ones (Witte & Schmidt, 1992). The lateral green spot of *B. brownorum* is consistently larger than that of *B. livida*. Syntopic species collected from Gedong area include *Rasbora kalochroma*, *Boraras maculatus* (Cyprinidae), *Clarias teijsmanni*, *C. cf. nieuhofii* and *Encheloclarias baculum* (Clariidae). *Betta brownorum* is found from Sibuluan to Matang and Kuching (Fig. 31). For live coloration, see Fig. 48h and Linke (1991: 50, identified as *B. spec. affin. coccina*).

BETTA WASERI GROUP

Betta waseri Krummenacher, 1986

(Figs. 36, 49a)

Betta waseri Krummenacher, 1986: 177; Kottelat et al., 1992: 11 (list only); Witte & Schmidt, 1992: 324 (key only); Ng & Kottelat, 1994: 595.

Material examined. – Holotype - ZMZ 129201, male, 90.8 mm SL; Malaysia: Pahang, Kuantan, 22.5 km from Kuantan, coll. W. Schar, Aug.1985 (radiographs and photographs examined only).

Others - ZRC 35402, 80.7 mm SL male; Malaysia: Pahang, 16 km stone, Johor Bahru to Kuantan road, shallow blackwater stream,



Fig. 35. *Betta brownorum* – ZRC 39582, 22.4 mm SL.

pH 4.0, coll. P. K. L. Ng et al., 9 Mar.1992. — ZRC 35403-08, 6 ex., 39.6-80.3 mm SL; Malaysia: Pahang, about 100 m south of 68 km stone, on road from Johor Bahru to Kuantan, near Pekan, well shaded peat swamp forest stream, blackwaters, pH 3.4, coll. P. K. L. Ng et al., 19 Oct.1992. — CMK 8057, 4 ex., 20.6-44.0 mm SL; same locality as previous, coll. M. Kottelat et al., 9 Mar.1992. — ZRC 18617-20, 4 ex., 20.5-33.2 mm SL; Malaysia: Pahang, about 200 m north of 16 km stone, on road from Johor Bahru to Kuantan, coll. P. K. L. Ng et al., 20 Oct.1991. — ZRC 25907, 1 ex., 56.6 mm SL, CMK 8074, 2 ex., ZRC 25210-11, 2 ex., 21.9, 32.0 mm SL; Malaysia: Pahang, stream at 16 km stone, on road from Mersing to Kuantan, coll. P. K. L. Ng et al., 9 Mar.1992. — CMK 3189, 1 ex., 31.1 mm SL; Malaysia: Kuantan, Sungai Soi; P. Nagy, May.1981. — ZRC 24370, 1 ex., 19.7 mm SL; Malaysia: Terengganu, near Rantau Abang, 56 km stone, on road from Kuantan to Kuala Terengganu, coll. P. K. L. Ng et al., 18 Mar.1992.

Diagnosis. – *Betta waseri* is distinguished from the other members of the *B. waseri* group by the unique suite of characters: black tear-drop shape marking on throat (Fig. 3a); opercle usually with gold scales, without iridescent green scales; lower margin of opercle black; no dorsal and caudal transverse bars; hyaline anal-fin edge; predorsal scales 23¹/₂-24 (mode 24); subdorsal scales 6-6¹/₂ (mode 6); postdorsal scales 10¹/₂-12 (mode 11); lateral scales 31¹/₂-32¹/₂ (mode 32); dorsal-fin rays 9-10 (mode 9); anal-fin rays 28-31 (mode 30); head length 28.6-33.3% SL; body depth 23.1-27.6% SL (from Ng & Kottelat, 1994).

Remarks. – There has been some confusion about the status of *B. waseri*. Schmidt (1988) had synonymised *B. waseri* with *B. macrophthalmalma* (type locality Singapore), the type of which is actually a juvenile specimen of *B. pugnax*. Witte & Schmidt (1992) regarded *B. macrophthalmalma* as a junior synonym of *B. pugnax* without providing reasons. This synonymy, however, was confirmed and elaborated on by Tan & Tan (1996). Witte & Schmidt (1992) also placed *B. waseri* into the *B. anabatooides* group. Ng & Kottelat (1994) redescribed *B. waseri* from fresh material. See Fig. 37 for the distribution map. For live coloration, see Fig. 49a, Linke (1991: 37, identified as *B. macrophthalmalma*) and Kubota et al. (1996: 48).



Fig. 36. a) *Betta waseri* – ZMZ 129.201, holotype, 90.0 mm SL (taken by Maurice Kottelat), b) ZRC 35403, 78.5 mm SL.

***Betta hipposideros* Ng & Kottelat, 1994**

(Figs. 38, 49b)

Betta aff. *waseri* (non Krummenacher, 1986) - Ng et al., 1992: 28, Fig. 14, 15, 98.

Betta hipposideros Ng & Kottelat, 1994: 597.

Material examined. - Holotype - **Malaysia:** - ZRC 18688, 69.0 mm SL male; Malaysia: Selangor, north Selangor peat swamp forest, 39 km stone, on road from Sungai Besar to Tanjung Malim, coll. P. K. L. Ng et al., 24 Aug.1991.

Paratypes - **Malaysia:** Selangor - ZRC 18689-18705, 17 ex., 33.4-71.1 mm SL; north Selangor peat swamp forest, 39 km stone, on road from Sungai Besar to Tanjung Malim, coll. P. K. L. Ng et al., 24 Aug.1991. — ZRC 15351, 1 ex., 32.0 mm SL; north Selangor peat swamp forest, stream at 34 km stone, on road to Tanjung Malim; Zoology Honours Class, 17 Jun.1991. — ZRC 15352, 1 ex., 25.9 mm SL; north Selangor peat swamp forest, stream at 50 km stone, on road to Tanjung Malim (United Plantations Estate); Zoology Honours Class, 18 Jun.1991. — ZRC 15353, 1 ex., 43.1 mm SL; north Selangor peat swamp forest, stream at 43 km stone, on road to Sungai Besar; Zoology Honours Class, 18 Jun.1991. — ZRC 15354, 15355, 2 ex., 27.5, 37.0 mm SL; north Selangor peat swamp forest, stream 700 m from 41 km stone, on road to Tanjung Malim; Zoology Honours Class, 19 Jun.1991. — ZRC 15356, 15357, 2 ex., 35.3, 38.7 mm SL; north Selangor peat swamp forest, 47 km stone, on road from Sungai Besar to Tanjung Malim; Zoology Honours Class, 19 Jun.1991. — ZRC 15358-15361, 4 ex., 25.8-39.6 mm SL; north Selangor peat swamp forest, 800 m from 45 km stone, on road to Sungai Besar; Zoology Honours Class, 18 Jun.1991. — ZRC 17097, 1 ex., 54.6 mm SL; north Selangor peat swamp forest, stream at 50 km stone, on road to Tanjung Malim (United Plantations

Estate), coll. K. K. P. Lim, 14 Sep.1991. — ZRC 18029-18034, 6 ex., 29.5-47.3 mm SL; north Selangor peat swamp forest, 500 m from 36 km stone, on road to Tanjung Malim, coll. P. K. L. Ng et al., 25 Aug.1991. — ZRC 27761, 1 ex., 64.0 mm SL; north Selangor peat swamp forest, 650 m from 35 km stone, on road from Sungai Besar to Tanjung Malim, coll. P. K. L. Ng et al., 18 Sep.1992. — ZRC 28550, 1 ex., 25.2 mm SL; north Selangor peat swamp forest, 200 m from 45 km stone, road to Sungai Besar, coll. P. K. L. Ng et al., 18 Sep.1992. — CMK 10037, 16 ex., 37.8-77.8 mm SL; north Selangor peat swamp forest, stream at 43 km stone on road from Tanjung Malim to Sungai Besar, coll. P. K. L. Ng et al., 19 Jun.1991. — CMK 10038, 10 ex., 27.9-59.6 mm SL; north Selangor peat swamp forest, stream at 0.2 km from 45 km stone on road from Tanjung Malim to Sungai Besar, coll. P. K. L. Ng et al., 17 Jun.1991. — ZRC 28515-28517, 69.1-77.9 mm SL; peat swamp forest, north shore of Sungai Bernam; P.K.L. Ng et al., 19 Sep.1992. **Sumatra:** ZRC 39630, 2 male ex., 62.1-67.1 mm SL; Indonesia, Sumatra: Riau, peat swamp draining into Sungai Bengkwan, tributary of Indragiri River; H. H. Ng, S. H. Tan et al., Jun.1995.

Diagnosis. - *Betta hipposideros* is distinguished from the other members of the *B. waseri* group by the unique suite of characters: black horse-shoe shaped marking on throat (Fig. 3b); opercle usually with gold scales, without iridescent green scales; lower margin of opercle brown; dorsal and caudal-fin transverse bars; hyaline anal fin edge; predorsal scales 21-24 (mode 23); subdorsal scales 6¹/₂-7 (mode 6¹/₂); postdorsal scales 9-10 (mode 9¹/₂); lateral scales 31-32 (mode 32); dorsal-fin rays 9-10 (mode 10); anal-fin rays 28-31 (mode 30); head length 28.3-34.1% SL; body depth 23.8-33.1% SL (from Ng & Kottelat, 1994).

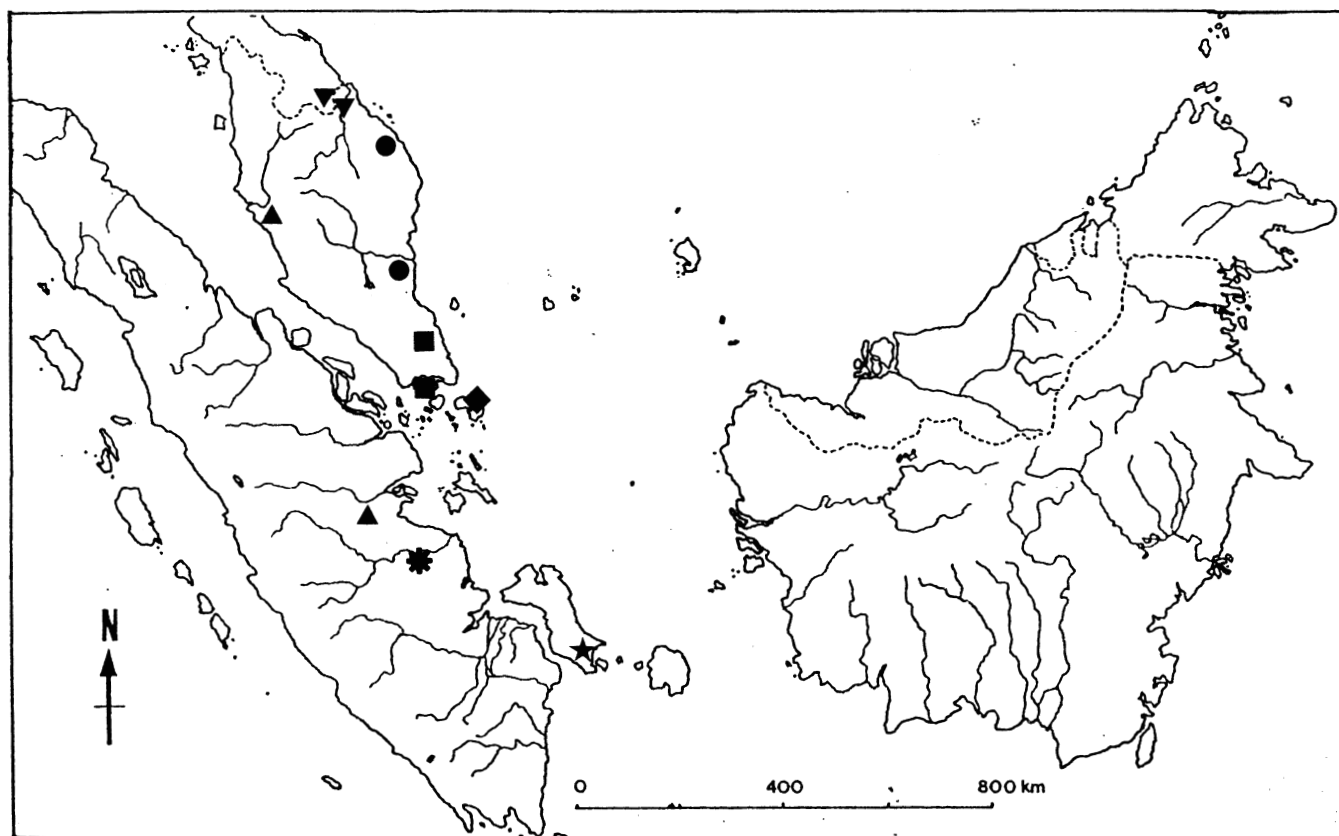


Fig. 37. Distribution map of *B. waseri* (circle), *B. hipposideros* (triangle), *B. tomi* (square), *B. pi* (upside-down triangle), *B. spilotogena* (diamond), *B. renata* (asterisk).

Remarks. – See Ng & Kottelat (1994) for details. The specimens from Sumatra were only observed in blackwater habitats (Fig. 37). They can be found in the slow-flowing to stagnant shallow parts of the peat swamp forest amongst the thick leaf litter and overhanging vegetation. Syntopic osphronemids present are: *Belontia hasseltii*, *Betta coccina*, *B. aff. fusca*, *B. simorum*, *Parosphromenus sumatranus*, *Sphaerichthys osphromenoides* and *Trichogaster leerii*. This new record and extends the range of *B. hipposideros* to Sumatra. For live coloration, see Fig. 49b and Kubota et al. (1996: 47).

***Betta tomi* Ng & Kottelat, 1994**
(Figs. 39, 49c)

Betta tomi Ng & Kottelat, 1994: 603.

Material examined. – Holotype - **Malaysia:** - ZRC 35409, 70.4 mm SL male; Malaysia: Johor, tributary of Sungai Mupor, about 15 km on road from Kota Tinggi to Mersing, about 1°52'N 103°56'E, freshwater swamp forest, coll. P. K. L. Ng, Aug.1992.

Paratypes - ZRC 35410, 1 ex., 37.6 mm SL; same data as holotype. — CMK 9753, 6 ex., 16.8-60.4 mm SL; same locality as holotype, coll. M. Kottelat, P. K. L. Ng & K. K. P. Lim, 22 Jan.1991. — ZRC 35411-35416, 6 ex., 24.8-64.9 mm SL; Malaysia: Johor, tributaries of Sungai Mupor, freshwater swamp forest, coll. P. K. L. Ng et al., 13 Jan.1993.

Others - ZRC 18059-18073, 15 ex., 11.8-20.9 mm SL; Malaysia: Johor, north of Mersing, 177 km milestone, on road from Johor Bahru to Kuantan, coll. P. K. L. Ng et al., 19 Oct.1991. — ZRC 19079-19131, 53 ex.; Malaysia: Johor, Mawai district; M. W. F. Tweedie, 1935. **Singapore:** ZRC 1097, 6 ex.; Singapore: Mandai road; M. W. F. Tweedie, 1937.

Diagnosis. – *Betta tomi* is distinguished from the other



Fig. 38. *Betta hipposideros* – ZRC 18689, male holotype, 69.0 mm SL.



Fig. 39. *Betta tomi* – ZRC 35409, male holotype, 70.4 mm SL.

members of the *B. waseri* group by the unique suite of characters: black semi horse-shoe shaped marking on throat (Fig. 3c); iridescent blueish opercle scales; lower margin of opercle black; no dorsal and caudal-fin transverse bars; broad and distinct dark green anal-fin margin; predorsal scales 21-23 (mode 23); subdorsal scales 5-5¹/₂ (mode 5); postdorsal scales 10-10¹/₂ (mode 10); lateral scales 31-32 (mode 31); dorsal-fin rays 9-10 (mode 9); anal-fin rays 28-31 (mode 30); head length 29.3-37.1% SL; body depth 24.1-29.8% SL (from Ng & Kottelat, 1994).

Remarks. – See Ng & Kottelat (1994) for details. See Fig. 37 for the distribution map. For live coloration, see Fig. 49c and Kubota et al. (1996: 47).

***Betta pi* Tan, 1998**
(Figs. 40, 49d)

Betta pi Tan, 1998: 285, figs. 3-4; Vidthayanon, 2002: 106.

Material examined. – Holotype - ZRC 40289, 54.9 mm SL male; Thailand: Narathiwat Province, Mae Nam Tod Deng, about 6 km north of Sungai Kolok, open area in swamps ca. 100-200 m south before bridge, coll. M. Kottelat et al., 1-3 Nov.1995.

Paratypes - ZRC 40290, 48.5 mm SL male, 43.2 mm SL female, CMK 12030, 3 ex., 20.0 - 41.1 mm SL; same locality data as holotype. — ZRC 40291, 6 ex., 35.9-60.2 mm SL, CMK 13025, 3 ex., 35.9-53.0 mm SL; Thailand: Narathiwat Province, peatswamps in Mae Nam Tod Deng, near Sungai Kolok, coll. K. Kubota et al., Mar.1996. — ZRC 40292, 18 ex., 19.6-43.4 mm SL; Thailand: Narathiwat Province, peatswamps in Mae Nam Tod Deng, near Sungai Kolok, coll. K. Kubota et al., Dec.1995.

Diagnosis. – *Betta pi* is distinguished from the other members of the *B. waseri* group by the unique suite of characters: black pi (p) shaped marking on throat (Fig. 3g); opercle usually with gold scales, without green scales; lower margin of opercle black, black spots on opercle; no dorsal and caudal-fin transverse bars; broad and distinct dark blue anal margin; predorsal scales 24-25; subdorsal scales 5¹/₂-6 (mode 6); postdorsal scales 10-12 (mode 11); lateral scales 32-33 (mode 33); dorsal-fin rays 8-10 (mode 9); anal-fin rays 30-32 (mode 31); head length 32.3-34.4% SL; body depth 26.4-29.7% SL (from Tan, 1998).

Remarks. – The type locality of this species is in the drainage of Sungai Kolok in Thailand. Sungai Kolok makes the border between Thailand and Malaysia and the species is expected to also occur in the peatswamp forests of Kelantan (Fig. 37).



Fig. 40. *Betta pi* – ZRC 40289, male holotype, 54.9 mm SL.

See Tan (1998) for more details. For live coloration, see Fig. 49d.

COMPARATIVE MATERIAL EXAMINED

Betta splendens group. *Betta splendens* - Thailand: ZRC Group no. 57, Cat. no. 443, 40 ex., 27.9-39.8 mm SL males; Thailand: Bangkok; Milton, 12 Oct.1962. — ZRC 39580, 1 ex., 42.4 mm SL male; Thailand: Bangkok, purchased from Chatukchak market, coll. P. K. L. Ng, 21 Sep.1995. — Holotype - *Betta splendens abbreviata* - MNHN 1925-82, 1 ex., 36.3 mm SL; Indochine; D. Coyon. ***Betta smaragdina* - Thailand** - ZRC 37597, 2 male ex., 32.4-34.5 mm SL, 1 female, 27.1 mm SL; Thailand: Nakhon Ratchasima; K. Kubota, 1993. — ZRC 39301, 7 ex.; Thailand: Nakhon Ratchasima; K. Kubota, Dec.1995. — ZRC, 11 ex.; Thailand: Nakhon Ratchasima; K. Kubota et al., 1996.

***Betta edithae* group. *Betta edithae* - Kalimantan Selatan:** Holotype - SMF 18712, 55.3 mm SL, male; Borneo, Kalimantan Selatan: Banjarmasin, Barito delta; J. Vierke, Aug.1983. Paratype - SMF 18713, 56.2 mm SL, female; same locality data as holotype. Others - ZRC 40969, 11 ex., 20.5-31.6 mm SL; Borneo, Kalimantan Selatan: Banjarmasin, stream at 55 km to Martapura on Rantau-Martapura road; H. H. Ng & O. K. S. Chia, 6 Jun.1996. **Kalimantan Barat:** MZB 3867, 10 ex., 21.7-37.4 mm SL; Borneo, Kalimantan Barat: 24 km NE of Pontianak, small forest stream flowing into Sungai Sepatah, a tributary of Sungai Mandor (0°07.5'N 109°30'E), coll. T. R. Roberts, 10 Jul.1976. — MZB 3870, 1 ex., 34.1 mm SL; Borneo, Kalimantan Barat: Sungai Sekilap, tributary to Sungai Mempawah, ca. 64 km N of Pontianak and 38 km by road NE of Andjongan (0°33.5'N 109°22.5'E), coll. T. R. Roberts, 14 Jul.1976. **Banka:** ZRC 31031-31044, 14 ex., 10.6-34.9 mm SL; Indonesia, Sumatra: Banka, ca. 25 km north of Koba, stream between Desa Kurau and Desa Balilik, outlet of an abandoned mine, coll. M. Kottelat et al., 3 Mar.1993. — ZRC 30865-30899, 17 ex., 10.7-28.0 mm SL; Indonesia, Sumatra: Banka, Kwsn. Sungai Liat, Kampung Jelit, 3 km from main road (Sungai Liat) to Tanjung Persema beach, coll. M. Kottelat et al., 2 Mar.1993. — ZRC 35159-35161, 3 ex., 19.4-32.1 mm SL; Indonesia, Sumatra: Banka, 4 km north of Bikang village on road from Koba to Toboali, coll. M. Kottelat et al., 3 Mar.1993. **Bintan:** ZRC 37551, 4 ex., 24.3-42.5 mm SL; Indonesia, Sumatra: Bintan, stream at km 47 Tanjung Uban-Tanjung Pinang road, coll. H. H. Tan et al., 27 Apr.1994. — ZRC 40970, 6 ex., 18.6-39.6 mm SL; Indonesia, Sumatra: Bintan, northern part of island, coll. P. K. L. Ng et al., May.1993. — ZRC 34721-742, 22 ex., 10.4-35.7 mm SL; Indonesia, Sumatra: Bintan, northern part of island; N. Sivasothi et al., 11 May.1993. — ZRC 34877-883, 7 ex., 17.3-33.6 mm SL; Indonesia, Sumatra: Bintan, ditch from reservoir near Gunung Bintan Besar; T. H. T. Tan et al., 14 May.1993.

***Betta picta* group. *Betta picta* - Java:** ZMA 102.149, 10 ex., 22.3-31.6 mm SL, ZRC 40973, 2 ex., 29.9-32.0 mm SL; Indonesia: Java, ponds near Trogon (ca. 6°21'S 106°34'E, ca. 30 km northwest of Bogor); M. Weber, 1888. — ZMA 121.691, 52 ex., 13.3-32.8 mm SL; Indonesia: Java, Buitenzorg (Bogor); M. Weber, 1888. — MZB 1325, 37 ex., 13.8-32.2 mm SL, ZRC 42495, 5 ex., 28.0-32.1 mm SL; Indonesia: Java, Bogor, Tjidjeruk, Sawahbera; Sukardi, 24 Aug.1970. — RMNH 10447, 3 ex., 29.3-32.4 mm SL; Indonesia: Java, Buitenzorg (Bogor); M. Weber. — RMNH 15794, 1 ex., 36.4 mm SL; Indonesia: Java, Buitenzorg (Bogor), Tjiblagoeng; A. Bushkiel, 1935. — ZMA 121.675, 30.9 mm SL, male; ZMA 121.589, 13 ex., 19.5-34.3 mm SL, ZRC 40972, 2 ex., 29.9-31.6 mm SL; Indonesia: Java, Tjipanas (Cipanas: ca. 6°43'S 107°2'E, ca. 30 km southeast of Bogor) near Sindanglaja; M. Weber, 1888. — ZMA

121.694, 38 ex., 14.9-31.2 mm SL; Indonesia: Java, Tjinjirean, after Poentjak Gedeh, ca. 1600m (Gunung Gede: ca. 25 km southeast of Bogor); Kerkhoven, 1921. — MHNG 2090-92, 3 ex., 23.6-30.0 mm SL; Indonesia: Java, Sukabumi (ca. 40 km southeast of Bogor); Walsh, July 1930. — ZMA 121.693, 2 ex., 28.8 mm SL; Indonesia: Java, Bandoeng (Bandung); Huysmans. — ZMA 121.689, 1 ex., 24.5 mm SL; Indonesia: Java, Bandoeng (Bandung), ca. 700m; I. Jacobson, 1934. — RMNH 26940, 4 ex., 31.8-35.3 mm SL; Indonesia: Java, Bezoeki (Besoki) (ca. 7°16'S 109°E, ca. 1050 km southeast of Bogor); J. Semmelink, 1864-65. — RMNH 13698-13699, 2 ex., 32.6-35.2 mm SL; Indonesia: Java, Ambarawa (ca. 7°8'S 110°20'E); J. Sybrandi, 1933. — RMNH 10740, 4 ex., 24.9-34.2 mm SL; Indonesian Archipelago; from P. Bleeker's collections. ***Betta falx* - Sumatra:** MZB 9308, holotype, 32.7 mm SL, male; Indonesia: Sumatra, Jambi, Sungai Alai, km 19.5 on Muara Bungo - Muara Tebo road (bridge at Sungai Alai: 1°28'42.6"S 102°18'31.7"E); H. H. Ng & S. H. Tan, 22 Jun.1995. — ZRC 40974, paratypes, 20 ex., 17.2-33.0 mm SL, ZMA 121.673, paratypes, 6 ex., 21.8-31.0 mm SL, MZB 9307, paratypes, 4 ex., 17.5-26.3 mm SL, RMNH 33087, paratypes, 5 ex., 19.7-26.7 mm SL; same data as holotype. — ZRC 38571, paratypes, 44 ex., 13.8-32.4 mm SL, CMK 11119, paratypes, 44 ex.; Indonesia: Sumatra, Jambi, Sungai Alai at km 28 on Muara Bungo - Muara Tebo road, between half hour downriver of bridge to ca. 1 hour upriver, including small tributaries and Danau Gresik, coll. M. Kottelat & H. H. Tan, 30-31 May.1994. — ZRC 38254, paratypes, 3 ex., 31.7-36.1 mm SL; Indonesia: Sumatra, Jambi, Sungai Alai, coll. M. Kottelat & H. H. Tan, May.1994. — ZRC 42496, paratypes, 10 ex., 17.0-34.9 mm SL, MHNG 2593.95, paratypes, 5 ex., 29.7-30.1 mm SL; Indonesia: Sumatra, Jambi, Sungai Alai, km 19.5 km on Muara Bungo - Muara Tebo road (bridge at Sungai Alai: 1°28'42.6"S 102°18'31.7"E), coll. H. H. Tan & H. H. Ng, 22 Jul.1997.

***Betta foerschi* group. *Betta strohi* - Kalimantan Tengah:** Paratypes - ZRC 32126-32129, 4 ex., 33.0-42.4 mm SL; Borneo: Kalimantan Tengah, Nataik Sedawak (2°41'S 111°13'E), about 30 km south of Sukamara; H. Stroh, Oct.1987. ***Betta rubra* - Sumatra:** MSNG 13019a, lectotype, 28.6 mm SL, MSNG 13019, 4 paralectotypes, 26.9-31.4 mm SL; Sumatra Barat: Siboga; E. Modigliani, 1886. — BMNH 1893.5.29:1, 1 paralectotype, 33.3 mm SL; Indonesia: Sumatra, Lake Toba; Modigliani. — MZB 4784, 3 ex., 23.4-35.0 mm SL, ZRC 42497, 2 ex., 33.4-35.4 mm SL; Sumatra: Aceh, Aceh Barat, Alur Sungai Iamueselatan; H. B. Munaf & M. Toha, 13 Dec.1982.

***Betta anabatooides* group. *Betta anabatooides* - Kalimantan Selatan:** ZRC 40971, 2 ex., 47.2-55.3 mm SL; Borneo: Kalimantan Selatan, Banjarmasin, stream at 55 km to Martapura on Rantau-Martapura road; H. H. Ng & O. K. S. Chia, 6 Jun.1996. **Kalimantan Tengah:** ZRC 22842-43, 2 ex., 46.7-55.9 mm SL, CAS 96958, 4 ex., 35.7-59.4 mm SL; Borneo: Kalimantan Tengah, Mentaya basin, Sungai Ramban, 22 km west of Sampit on road to Pemuanghulu, coll. T. R. Roberts, 11 Jun.1992. — MZB 5326, 1 ex., 60.2 mm SL; Borneo: Kalimantan Tengah, Kotim, Kec. Pulan Malan, Sungai Banjar; A. Saim, 13 Mar.1984. **Kalimantan Barat:** MZB 3846, 1 ex., 58.0 mm SL; Borneo, Kalimantan Barat: 24 km NE of Pontianak, small forest stream flowing into Sungai Sepatah, a tributary of Sungai Mandor (0°07.5'N 109°30'E), coll. T. R. Roberts, 10 Jul.1976.

***Betta albimarginata* group. *Betta albimarginata* - Kalimantan Timur:** Holotype - ZRC 38485, 27.9 mm SL male; Borneo, Indonesia: Kalimantan Timur, Sungai Sebuku basin, Sungai Sanul, a tributary of Sungai Tikung, at about km 7 on logging road from Semunad (4°04.08'N 117°00.4'E) to Apas (3°59.96'N 116°59.32'E), coll. M. Kottelat & P. McKee, 14 Feb.1993. Paratypes - ZRC 35121-22, 2 ex., 21.8-23.8 mm SL, same locality data as holotype. ***Betta channoides* - Kalimantan Timur:** Paratype - ZRC

35165, 1 ex., 17.2 mm SL; Borneo, Indonesia: Kalimantan Timur, Mahakam River basin, unnamed blackwater stream entering Mahakam River on left side near Mujub (0°01'S 115°43'E), coll. M. Kottelat, 3 Aug.1991.

Betta dimidiata group. *Betta dimidiata*: Kalimantan Barat: MZB 3849, holotype, 30.6 mm SL; Borneo: Kalimantan Barat, Kapuas basin, Sungai Seriang Hutan Kecil; T. R. Roberts, 12 Aug.1976. — ZRC 35498-99, 2 ex., 28.8-37.2 mm SL; Borneo: Kalimantan Barat, Kapuas basin, coll. M. Kottelat, Sep.1993. — ZRC 37707, 3 ex., 33.6-40.0 mm SL; Borneo: Kalimantan Barat, Kapuas basin, coll. M. Kottelat, Sep.1993. — ZRC 38782, 10 ex., 16.7-32.5 mm SL; Borneo: Kalimantan Barat, Kapuas basin, Sungai Letang near Kampung Kandung Suli, coll. M. Kottelat, 8 Jun.1995.

ACKNOWLEDGEMENTS

We are grateful to the following who have helped us in many ways small and large: Maurice Kottelat, for his encouragements, loan of material (CMK) and patiently reviewing the manuscript several times; Ralf Britz, for his helpful discussions and reviewing the manuscript; Kelvin K. P. Lim, for his advice and use of his maps; Darrell Siebert (BMNH), David Catania and Susan Middleton (CAS), Barry Chernoff and Mary Ann Rogers (FMNH), Sonia Muller and Claude Weber (MHNG), Guy Duhamel and Patrice Pruvost (MNHN), Giuliano Doria (MSNG), Agus Tjakrawidjaja, Ike Rachmatika, Renny Hardiaty and Daisy Wowor (MZB), Lipke B. Holthuis and Martin van Oijen (RMNH), Lynne Parenti and Susan Jewett (USNM), Hans Nijssen and Isaäc Isbrücker (ZMA), and C. M. Yang (ZRC), for the loan of material; Tyson R. Roberts, for the discussions and suggestions; Marina Wong and staff (BRM), for help with the Brunei trip; Charles M. U. Leh (SM), for help with the Sarawak collections, especially for arranging for permits for Bako; Leo Chai, previously head of Sarawak Forestry Department, for permission to conduct surveys in Bako; P. K. Chin, Alvin Wong of Sabah Fisheries, Anna Wong (SBM), for help with the Sabah trip; Keith M. Martin-Smith and John Salleh bin Otong (DVFC), for help with the Danum trip; Katsuma Kubota, for providing material from Thailand; Gunawan 'Thomas' Kasim, for providing material from Sumatra; Koji Yamazaki and Günther Ettrich, for kindly providing colour slides of various *Betta* species; David M. Armitage, for donation of phototanks; S. H. Tan for his many kind and unselfish radiographing sessions; Research Associate of RMBR – Maurice Kottelat, Systematics and Ecology Laboratory staff, postgraduates, satellites and associated lab denizens (Oliver K. S. Chia, Daphne S. L. Chung, W. K. Goh, Y. Y. Goh, Robert Kerle, O. Y. Kok, Adrian H. B. Loo, H. H. Ng, N. Sivasothi, Diana G. B. Tan, Cheryl G. S. Tan, Tommy H. T. Tan, Alvin T. C. Wong, Darren C. J. Yeo) for their help in the field and criticisms. Last but not least, THH would like to dedicate this work to his late father, thank his parents and sister who have tolerated and nurtured his interests throughout the years. This field work conducted had been partly funded by Research Grants RP 950326, RP 960314 and RP3982327 to P. K. L. Ng by the National University of Singapore.

LITERATURE CITED

- Alfred, E. R., 1958. The food and habitat of the fighting-fish *Betta pugnax*. *Malayan Nature Journal*, **12**: 161-163.
- Alfred, E. R., 1961a. Singapore fresh-water fishes. *Malayan Nature Journal*, **15**: 1-19, pl. 1-4.
- Alfred, E. R., 1961b. The Cantor collection of Malayan fresh-water fishes. *Bulletin of the Raffles Museum*, Singapore, **26**: 183-186.
- Alfred, E. R., 1963. Notes on a collection of freshwater fishes from Penang. *Bulletin of the Singapore National Museum*, **32**: 143-153, 2 pl.
- Alfred, E. R., 1966. The fresh-water fishes of Singapore. *Zoologische Verhandelingen*, **78**: 68pp., 8 pl.
- de Beaufort, L. F., 1933. On some new or rare species of Ostariophysii from the Malay Peninsula and a new *Betta* from Borneo. *Bulletin of the Raffles Museum*, Singapore, **8**: 31-36.
- Blanc, M., 1963. Catalogue des types d'Anabantidae et d'Ophiocephalidae (Poissons téléostéens perciformes) en collection au Muséum national d'Histoire naturelle. *Bulletin du Muséum National d'Histoire naturelle Paris*, **35**: 70-77.
- Bleeker, P., 1850. Bijdrage tot de kennis der visschen met doolhofvormige kieuwen van den Soenda-Molukschen Archipel. *Verhandelingen Batavia Genootschap*, **23**: 1-15.
- Bleeker, P., 1851. Nieuwe bijdrage tot de kennis der ichthyologische fauna van Borneo. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **1**: 259-275.
- Bleeker, P., 1860a. Zoetwartervisschen van Singapoera. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **21**: 334.
- Bleeker, P., 1860b. Vischsoorten nieuw voor de kennis der fauna van Singapoera. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, **22**: 101-102.
- Bleeker, P., 1879. Mémoire sur les poissons à pharyngiens labyrinthiformes de l'Inde archipélagique. *Natuurkundig Verhandelingen Koninkl. Akademie*, **9**, 1-56.
- Breder, C. M., 1934. The reproductive habits of the painted *Betta*, a relative of the Siamese fighting fish, new to the aquaria. *Bulletin of the New York Zoological Society*, **37**: 126-133, 6 figs.
- Britz, R., 1994. Ontogenic features of *Luciocephalus* (perciformes, Anabantoidei) with a revised hypothesis of anabantoid intrarelationships. *Zoological Journal of the Linnean Society*, **112**: 491-508.
- Britz, R., 1995. *Zur phylogenetischen Systematik der Anabantoidei (Teleostei, Percomorpha) unter besonderer Berücksichtigung der Stellung des Genus Luciocephalus. Morphologische und ethologische Untersuchungen*. PhD dissertation, Eberhard-Karls-Universität Tübingen, Germany 125 pp.
- Britz, R., 2001. The genus *Betta* – monophyly and intrarelationships, with remarks on the subfamilies Macropodinae and Luciocephalinae (Teleostei: Osphronemidae). *Ichthyological Exploration of Freshwaters*, **12**: 305-318.
- Britz, R., M. Kokoscha & R. Riehl, 1995. The anabantoid genera *Ctenops*, *Luciocephalus*, *Parasphaerichthys*, and *Sphaerichthys* (Teleostei: Perciformes) as a monophyletic group: evidence from egg surface structure and reproductive behaviour. *Japan Journal of Ichthyology*, **42**: 71-79.
- Brown, B. & A. Brown, 1987. A survey of freshwater fishes of the family Belontiidae in Sarawak. *Sarawak Museum Journal*, **37**: 155-170, 3 pls.
- Cantor, T. E., 1850. Catalogue of Malayan fishes. *Journal of the Royal Asiatic Society, Bengal*, **18**: i-xii + 981-1143, pls. 1-14.

- Chin, P. K. & A. Samat, 1995. Freshwater fishes of Danum Valley, Sabah. *Sabah Society Journal*, **12**: 17-46.
- Chung, D. S. L., P. K. L. Ng & D. H. Murphy, 1994. Preliminary studies of the feeding ecology of blackwater Belontiidae of North Selangor, Peninsular Malaysia. In: *Proceedings of the Fourth Indo-West Pacific Fish Conference: systematics and evolution of Indo-Pacific fishes*, Faculty of Fisheries, Kasetsart University, Bangkok, pp. 76-86.
- Cracraft, J., 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: Otte, D. & J. A. Endler (eds.), *Speciation and its consequences*. Sinauer Associates, Sunderland, MA. Pp. 28-59.
- Cuvier, G. & A. Valenciennes, 1846. *Histoire naturelle des poissons*. Levrault, Paris, **18**: xix + 505pp., pls. 520-553.
- Dickman, P., 1995. Breeding success with another of the threatened *Betta akarensis* group (reproduced from Der Makropode). Anabantoid Association of Great Britain. *Labyrinth*, **79**: 1-5.
- Duncker, G., 1904. Die Fische der malayischen Halbinsel. *Mitteilungen aus dem Naturhistorischen Museum, Hamburg*, **21**: 133-207, pl. 1,2.
- Ettrich, G., 1992. Eine aquaristische herausforderung Bunte Kampffische *Betta macrostoma*. *Die Aquarien- und Terrarien-Zeitschrift*, **45**: 352-354.
- Fowler, H. W., 1938. A list of the fishes known from Malaya. *Fisheries Bulletin of Singapore* **1**: 1-268, i-vi.
- Grams, F. & P. Dickmann, 1997. Kleine rote Maulbrüter - eine Labyrinthfischgruppe stellt sich vor. *Die Aquarien- und Terrarien-Zeitschrift*, **50**: 562-566.
- Grinang, J. & K. K. P. Lim, 2004. Fishes. In: Yong, H. S., F. S. P. Ng & E. E. L. Yen (eds.), Sarawak Bau Limestone Biodiversity. *Sarawak Museum Journal*, Vol. LIX, No. 80 (New Series); Special Issue No. **8**: 285-298.
- Günther, A., 1861. *Catalogue of the acanthopterygian fishes in the collection of the British Museum*, **3**: 586pp., i-xxv.
- Hanitsch, R., 1901. Fishes. *Report of the Raffles Library Museum*, 1900: 3-4.
- Hanitsch, R., 1912. Mosquito larvae and freshwater fish. *Journal of the Straits British Royal Asiatic Society*, **62**: 26-30.
- Herre, A. W. C. T., 1940. Additions to the fish fauna of Malaya and notes on rare or little known Malayan and Bornean fishes. *Bulletin of the Raffles Museum*, Singapore, **16**: 27-61.
- Herre, A. W. C. T. & G. S. Myers, 1937. A contribution to the ichthyology of the Malay Peninsula. Part II. Fresh-water fishes. *Bulletin of the Raffles Museum*, Singapore, **13**: 53-74, pl. 5-7.
- Inger, R. F., 1955. Ecological notes on the fish fauna of a coastal drainage of north Borneo. *Fieldiana, Zoology*, **37**: 47-90.
- Inger, R. F. & P. K. Chin, 1962. The fresh-water fishes of north Borneo. *Fieldiana, Zoology*, **45**: 1-268.
- International Commission on Zoological Nomenclature (ICZN), 1999. *International Code of Zoological Nomenclature*. Fourth edition. The International Trust for Zoological Nomenclature, London, 306 pp.
- International Commission on Zoological Nomenclature, 2003. Opinion 2043 (Case 3113). *Betta* Bleeker, 1850 (Osteichthyes, Perciformes): specific names conserved by the suppression of the generic and specific names *Micracanthus marcheii* Sauvage, 1879. *Bulletin of Zoological Nomenclature*, **60**: 171-172.
- Jordan, D. S., 1919. New genera of fishes. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **70**: 341-344.
- Károli, J., 1881. Prodomus Piscium Asiae Orientalis - a domine Joanne Xanthus annis 1868-70 collectorum. *Természetráji Füzetek*, **5**: 147-187.
- Kottelat, M., 1984. Fresh-water fishes of Kampuchea - a preliminary annotated checklist. *Hydrobiologia*, **121**: 249-279, 1985.
- Kottelat, M., 1989. Zoogeography of the fishes from Indochinese inland waters with an annotated check-list. *Bulletin Zoölogisch Museum*, **12**: 1-56.
- Kottelat, M., 1991. Notes on the taxonomy and distribution of some Western Indonesian freshwater fishes, with diagnoses of a new genus and six new species (Pisces: Cyprinidae, Belontiidae and Chaudhuriidae). *Ichthyological Exploration of Freshwaters*, **2**: 273-287.
- Kottelat, M., 1994. Diagnoses of the two new species of fighting fishes from Thailand and Cambodia (Teleostei: Belontiidae). *Ichthyological Exploration of Freshwaters*, **5**: 297-304.
- Kottelat, M., 1995. Four new species of fishes from the middle Kapuas Basin, Indonesian Borneo (Osteichthyes: Cyprinidae and Belontiidae). *The Raffles Bulletin of Zoology*, Singapore, **43**: 51-64.
- Kottelat, M., 1997. European freshwater fishes - An heuristic checklist of the freshwater fishes of Europe (exclusive of former USSR), with an introduction for non-systematists and comments on nomenclature and conservation. *Biologia Bratislavia, Serie Zoologie*, **52** (Suppl. 1): 1-272.
- Kottelat, M. & K. K. P. Lim, 1995. Freshwater fishes of Sarawak and Brunei Darussalam: a preliminary annotated check-list. *Sarawak Museum Journal*, **48** (69): 227-256.
- Kottelat, M. & P. K. L. Ng, 1994. Diagnoses of five new species of fighting fishes from Banka and Borneo (Teleostei: Belontiidae). *Ichthyological Exploration of Freshwaters*, **5**: 65-78.
- Kottelat, M., P. K. L. Ng & K. K. P. Lim, 1992. Recent collections of freshwater fish from Terengganu, Peninsular Malaysia. *Malayan Naturalist*, **46** (2): 7-12.
- Kottelat, M., A. J. Whitten, S. N. Kartikasari & S. Wirjoatmodjo, 1993. *Freshwater fishes of Western Indonesia and Sulawesi*. Periplus Editions, Hong Kong, 259 pp., 84 pls.
- Krummenacher, R., 1986. *Betta waseri* spec. nov. *Die Aquarien- und Terrarien-Zeitschrift*, **33**: 177-181.
- Kubota, K., M. Majima, K. Miki & K. Yamazaki, 1996. *Anabantoids*. Tropical fish collection **5** (in Japanese). Pisces, Tokyo, 144 pp.
- Ladiges, W., 1975. *Betta imbellis* nov. spec. *Die Aquarien- und Terrarien-Zeitschrift*, **28**: 262-264.
- Lim, K. K. P., 1995. Fishes. In: Chin, S. C., R. T. Corlett, Y. C. Wee & S. Y. Geh (eds.), Rain Forest in the City: Bukit Timah Nature Reserve Singapore. *The Gardens' Bulletin Singapore*, Supplement no. **3**: 159-163.
- Lim, K. K. P. & P. K. L. Ng, 1990. *A guide to the freshwater fishes of Singapore*. Singapore Science Centre, Singapore, 160 pp.
- Lim, K. K. P., M. Kottelat & P. K. L. Ng, 1990a. Freshwater fish of Ulu Kinchin, Pahang, Malaysia. *Malayan Nature Journal*, **43**: 314-320.
- Lim, K. K. P., P. K. L. Ng & M. Kottelat, 1990b. On a collection of freshwater fishes from Endau-Rompin, Pahang-Johore, Peninsular Malaysia. *The Raffles Bulletin of Zoology*, Singapore, **38**: 31-54.
- Lim, K. K. P. & A. Wong, 1994. Fishes of the Kinabatangan basin, Sandakan district, Sabah, East Malaysia. *Sabah Museum Journal*, **1**: 39-71.

- Linke, H., 1991. *Labyrinth fish. The bubble-nest-builders. Their identification, care and breeding*. Tetra-Press (English edition), Melle, 174 pp.
- Martin-Smith, K. M., A. Samat, S. H. Tan & H. T. Tan, 1998. The fish and crustacean fauna of the Maliau Basin, Sabah; p. 119-131. In: Maryati, M., W. Sinun, A. Anton, M. N. Dalimin & A.-H. Ahmad (eds.), *Maliau Basin Scientific Expedition*, 12 - 26 th May 1996. Universiti Malaysia Sabah, Kota Kinabalu.
- Martin-Smith, K. M. & H. H. Tan, 1998. Diversity of freshwater fishes from eastern Sabah: annotated checklist for Danum Valley and a consideration of inter- and intra-catchment variability. *The Raffles Bulletin of Zoology*, Singapore, **46** (2): 573-604.
- Mohsin, A. K. M. & M. A. Ambak, 1983. *Freshwater fishes of Peninsular Malaysia*. Penerbit Universiti Pertanian Malaysia, 284 pp.
- Myers, G. S., 1935. A new anabantid fish of the genus *Betta* from Johore. *Proceedings of the Biological Society of Washington*, **48**: 25-26.
- Ng, P. K. L., 1993. On a new species of *Betta* (Teleostei: Belontiidae) from peat swamps in Sabah, East Malaysia, Borneo. *Ichthyological Exploration of Freshwaters*, **4**: 289-294.
- Ng, P. K. L., L. M. Chou, T. J. Lam, 1993. The status of introduced freshwater animals in Singapore. *Biological Conservation*, **64**: 19-24.
- Ng, P. K. L. & M. Kottelat, 1992. *Betta livida*, a new fighting fish (Teleostei: Belontiidae) from blackwater swamps in Peninsular Malaysia. *Ichthyological Exploration of Freshwaters*, **3**: 177-182.
- Ng, P. K. L. & M. Kottelat, 1994. Revision of the *Betta waseri* group (Teleostei: Belontiidae). *The Raffles Bulletin of Zoology*, Singapore, **42**: 593-611.
- Ng, P. K. L., J. B. Tay, K. K. P. Lim & C. M. Yang, 1992. *The conservation of the fish and other aquatic fauna of the North Selangor peat swamp forest and adjacent areas*. Asian Wetland Bureau, Institute of Advanced Studies University of Malaya, WWF and National University of Singapore, December, 90 pp.
- Ng, P. K. L., J. B. Tay & K. K. P. Lim, 1994. Diversity and conservation of blackwater fishes in Peninsular Malaysia, particularly in the North Selangor peat swamp forest. *Hydrobiologia*, **285**: 203-218.
- van den Nieuwenhuizen, A., 1993. *Betta bellica*. *Die Aquarien- und Terrarien-Zeitschrift*, **46**: 365-369.
- van den Nieuwenhuizen, A., 1995. The Compleat *Betta unimaculata*. *Tropical Fish Hobbyist*, **43**(12): 92-105.
- Pellegrin, J., 1925. Une nouvelle variété de combattant. *Revue d'Histoire Naturelle Appliquée*, Première partie **6**: 177-182.
- Perugia, A., 1893. Di alcuni pesci raccolti in Sumatra dal Dott. Elio Modigliani. *Annali del Museo Civico di Storia Naturale Giacoma Doria, Genova*, **13**: 241-247.
- Popta, C. M. L., 1905. Suite des descriptions préliminaires des nouvelles espèces de poissons recueillies au Bornéo central par M. le Dr. A. W. Nieuwenhuis en 1898 et en 1900. *Notes from Leyden Museum*, **25**: 171-186.
- Popta, C. M. L., 1906. Résultats ichthyologiques des voyages scientifiques de M. le Dr. A. W. Nieuwenhuis le Centre de Bornéo (1898 et 1900). *Notes from Leyden Museum*, **27**: 10-18.
- Regan, C. T., 1910. The Asiatic fishes of the family Anabantidae. *Proceedings of the Zoological Society of London*, 1909[1910]:767-787, pls. 77-79.
- Rehwinkel, J., 1995. Care and breeding of *Betta balunga* Herre 1940 (reproduced from Der Makropode). Anabantoid Association of Great Britain. *Labyrinth*, **80**: 1-2.
- Richter, H. J., 1981. Einführung eines neuen Gattungsnamens für die maulbrütenden Kampffische. *Die Aquarien- und Terrarien-Zeitschrift*, **28**: 272-275.
- Roberts, T. R., 1981. Identification of the presumed African freshwater fishes *Micrakanthus marcheii* (Belontiidae) and *Chonerhinos africanus* (Tetraodontidae). *Cybiurn*, **5**: 91-92.
- Roberts, T. R., 1989. *The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia)*. California Academy of Sciences, San Francisco, 210 pp.
- Rüber, L., R. Britz, H. H. Tan, P. K. L. Ng & R. Zardoya, 2004. Evolution of mouthbrooding and life-history correlates in the fighting fish genus *Betta*. *Evolution*, **58** (4): 799-813.
- Sauvage, H.-E., 1879. Notice sur la faune ichthyologique de l'Ogooué. *Bulletin de la Société Philomathique de Paris*, series 7, **3**: 90-103.
- Sauvage, H.-E., 1884. Note sur une collection de poissons recueillie à Pérak, presqu'île de Malacca. *Bulletin de la Société Zoologie de France*, **9**: 216-220.
- Schaller, D., 1985. *Betta tussyae* spec. nov., ein neuer Kampffisch aus Malaysia (vorläufige Mitteilung). *Die Aquarien- und Terrarien-Zeitschrift*, **38**: 348-350.
- Schaller, D., 1986. Laubschlupf. Eine Überlebensstrategie in einem besonderen Biotop und die Beschreibung einer neuen Kampffischart. *Die Aquarien- und Terrarien-Zeitschrift*, **39**: 297-300.
- Schaller, D. & M. Kottelat, 1989. *Betta strohi* sp. n., ein neuer Kampffisch aus Südborneo (Osteichthyes: Belontiidae). *Die Aquarien- und Terrarien-Zeitschrift*, **43**: 31-37.
- Schmidt, J., 1988. Wasers grosser maulbrütender Kampffisch *Betta macrophthalmia* Regan, 1910. *Die Aquarien- und Terrarien-Zeitschrift*, **41**: 341-344.
- Sim, C. H., 2002. *A field guide to the fish of Tasek Bera Ramsar site, Pahang, Malaysia*. Wetlands International-Malaysia Programme, Malaysia, 99 p.
- Smith, A., 1994. Spawning and brood care in *Betta tussyae*. Anabantoid Association of Great Britain. *Labyrinth*, **78**: 1-4.
- Smith, A., 1996. Care and breeding of the jealous *Betta*. Anabantoid Association of Great Britain. *Labyrinth*, **87**: 5-8.
- Swainson, W., 1839. The natural history and classification of fishes, amphibians, & reptiles, or monocardian animals. Spottiswoode & Co., London. *Natural History & Classifications*. **2**: i-vi + 1-448.
- Tan, H. H., 1997. Notes on the breeding of *Betta pulchra* Tan & Tan, 1996; *B. ocellata* de Beaufort, 1933; and *B. spilotozona* Ng & Kottelat, 1994. Anabantoid Association of Great Britain. *Labyrinth*, **93**: 6-8.
- Tan, H. H., 1998. Two new species of the *Betta waseri* group (Teleostei: Osphronemidae) from central Sumatra and southern Thailand. *Ichthyological Exploration of Freshwaters*, **8**: 281-287.
- Tan, H. H. & M. Kottelat, 1998a. Two new species of *Betta* (Teleostei: Osphronemidae) from the Kapuas basin, Kalimantan Barat, Borneo. *The Raffles Bulletin of Zoology*, Singapore, **46**: 41-51.
- Tan, H. H. & M. Kottelat, 1998b. Redescription of *Betta picta* (Teleostei: Osphronemidae) and description of *B. falx* n. sp. from central Sumatra. *Revue Suisse de Zoologie*, **105**: 557-568, September.

- Tan, H. H. & K. K. P. Lim, 2004. Inland fishes from the Anambas and Natuna Islands, South China Sea, with description of a new species of *Betta* (Teleostei: Osphronemidae). *The Raffles Bulletin of Zoology*, Singapore, Supplement no. **11**: 107-115.
- Tan, H. H. & P. K. L. Ng, 1996. Redescription of *Betta bellica* Sauvage, 1884 (Teleostei: Belontiidae), with description of a new allied species from Sumatra. *The Raffles Bulletin of Zoology*, Singapore, **44**: 143-155.
- Tan, H. H. & P. K. L. Ng, 2000. *Betta* Bleeker, 1850 (Osteichthyes, Perciformes): proposed conservation of the specific names by the suppression of *Micracanthus marcheii* Sauvage, 1879. *Bulletin of Zoological Nomenclature*, **57**: 29-31.
- Tan, H. H. & P. K. L. Ng, 2004. Two new species of freshwater fish (Teleostei: Balitoridae, Osphronemidae) from southern Sarawak. In: Yong, H. S., F. S. P. Ng & E. E. L. Yen (eds.), Sarawak Bau Limestone Biodiversity. *Sarawak Museum Journal*, Vol. LIX, No. 80 (New Series); Special Issue No. **8**: 267-284.
- Tan, H. H. & P. K. L. Ng, 2005. The labyrinth fishes (Teleostei: Anabantoidei, Channoidei) of Sumatra, Indonesia. In: Kottelat, M. & D. C. J. Yeo (eds.), Southeast Asian Freshwater Fish Diversity. *The Raffles Bulletin of Zoology*, Singapore, Supplement no. **13**: 115-138.
- Tan, H. H. & S. H. Tan, 1994. *Betta miniopinna*, a new species of fighting fish from Pulau Bintan, Riau Archipelago, Indonesia (Teleostei: Belontiidae). *Ichthyological Exploration of Freshwaters*, **5**: 41-44.
- Tan, H. H. & S. H. Tan, 1996. The identity of *Betta pugnax* (Teleostei: Belontiidae), with the description of a new species of *Betta* from the Malay Peninsula. *The Raffles Bulletin of Zoology*, Singapore, **44**: 419-434.
- Tan, S. H. & H. H. Tan, 1994. The Freshwater Fishes of Pulau Bintan, Riau Archipelago, Sumatera, Indonesia. *Tropical Biodiversity*, **2**: 351-367.
- Tan, S. H. & P. K. L. Ng, 1997. Decapods of the Maliau Basin, Sabah, Malaysia, with description of a new species of *Thelphusula* (Brachyura: Gecarcinucidae). *Journal of Crustacean Biology*, **17**: 555-561.
- Tweedie, M. W. F., 1936. A list of the fishes in the collection of the Raffles Museum. *Bulletin of the Raffles Museum*, Singapore, **12**: 16-28.
- Tweedie, M. W. F., 1952a. Notes on Malayan fresh-water fishes. 3. The anabantoid fishes. *Bulletin of the Raffles Museum*, Singapore, **21**: 63-76.
- Tweedie, M. W. F., 1952b. Notes on Malayan fresh-water fishes. *Bulletin of the Raffles Museum*, Singapore, **24**: 63-75.
- Tweedie, M. W. F., 1953. Malayan aquarium fishes. *Malayan Nature Journal*, **8**: 47-51, pls. 9-10.
- Vidthayanon, C., 2002. *Peat swamp fishes of Thailand*. Office of Environmental Policy and Planning, Bangkok, Thailand, 136 pp.
- Vidthayanon, C., J. Karnasuta & J. Nabhitabhata, 1997. *Diversity of Freshwater Fishes in Thailand*. Office of Environmental Policy and Planning, Bangkok, Thailand, 102 p.
- Vierke, J., 1979a. *Betta coccina* nov. spec., ein neuer Kampffisch von Sumatra. *Das Aquarium*, **13**: 288-289.
- Vierke, J., 1979b. *Betta anabatooides* und *Betta foerschii* spec. nov., zwei Kampffische aus Borneo. *Das Aquarium*, **13**: 386-388.
- Vierke, J., 1984. *Betta taeniata* Regan, 1910 und *Betta edithae* spec. nov., zwei Kampffische von Süd-Borneo. *Das Aquarium*, **18**: 58-63.
- Vierke, J., 1987. Breeding *Betta bellica*. *Tropical Fish Hobbyist*, 10-15.
- Vierke, J., 1988. *Betta climacura* n. sp. und Anmerkungen zu *Betta taeniata* Regan, 1910. *Das Aquarium*, **22**: 335-340.
- Vierke, J., 1991. Brutpflegestrategien bei Belontiiden (Pisces, Anabantoidei). *Bonner Zoologische Beiträge*, **42**: 299-324.
- Vinciguerra, D., 1926. Catalogo dei pesci raccolti a Borneo dai sigg. Marchese G. Doria e dott. O. Beccari negli anni 1865-67. *Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova*, (3) **10**: 532-628, pl. 1.
- Warren, M. L., 1992. Variation of the spotted sunfish, *Lepomis punctatus* complex (Centrarchidae): meristics, morphometrics, pigmentation and species limits. *Bulletin of the Alabama Museum of Natural History*, **12**: 1-47.
- Weber, M & L. F. de Beaufort, 1922. *The fishes of the Indo-Australian archipelago*. **4**. Brill, Leiden, xiii + 410 pp.
- Whitmore, T. C., 1986. *Tropical Rain Forests of the Far East*. English Language Book Society/ Oxford University Press, 2nd. ed., i-xvi, 352 pp.
- Witte, K.-E. & J. Schmidt, 1992. *Betta brownorum*, a new species of anabantoids (Teleostei: Belontiidae) from northwestern Borneo, with a key to the genus. *Ichthyological Exploration of Freshwaters*, **2**: 305-330.
- Yamazaki, K., 1995. Exploration for small fish in Sarawak, Borneo - on *Betta macrostoma* (Japanese). *Aqualife Magazine*, Tokyo, 194-215.
- Zakaria-Ismail, M., 1984. Aquatic survey including limnological characteristics and fish species composition. Pp. 70-75. In: *An ecological survey of Lambir Hill National Park*. Dept. Botany & Zoology, Universiti Malaya, Kuala Lumpur.
- Zakaria-Ismail, M., 1987. The fish fauna of the Ulu Endau river system, Johore, Malaysia. *Malayan Nature Journal*, **40**: 314-320.

APPENDIX

BETTA AKARENSIS GROUP

Betta obscura, new species

(Fig. 41)

Material examined. – Holotype - MZB 9331, 60.2 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Desa Kerendan, Sungai Lahei and tributaries, coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 23-28 Sep.1992 (DS-3-1995).

Paratypes - BMNH 1996.3.22:253-260, 9 ex., 28.9-69.1 mm SL, - ZRC 41578, 5 ex., 33.0-62.6 mm SL, - MZB 9332, 1 ex., 65.5 mm SL; same data as holotype. — BMNH 1996.3.22:43-44, 2 ex., 55.7-63.1 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Bunes, a small tributary of Sungai Kerendan (a tributary of Sungai Lahei) above (ca. 1 km) Desa Kerendan, coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 24 Sep.1995 (DS-2-1995). — BMNH 1991.9.18:26-28, 3 ex., 26.1-51.1 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Murung near Project Barito basecamp, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 11-13 Feb.1991 (DS-17-1991). — BMNH 1991.9.18:32-37, 6 ex., 20.8-54.5 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Barito at Muara Laung and market at Puruk Cahu, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 20-21 Feb.1991 (DS-20-1991). — MZB 6941, 3 ex., 23.3-57.6 mm SL; Borneo, Kalimantan Tengah: Sungai Mongkumuh and Sungai

Bahadeng, tributary of Sungai Barito, 1.5 km from Muara Laung, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, Feb.1991.

Others - BMNH 1996.3.22: 260-261, 2 ex., 26.5-38.4 mm SL; same data as holotype. — BMNH 1996.3.22:45-47, 3 ex., 17.4-32.3 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Bunes, a small tributary of Sungai Kerendan (a tributary of Sungai Lahei) above (ca. 1 km) Desa Kerendan, coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 24 Sep.1995 (DS-2-1995). — BMNH 1996.3.22:39-40, 2 ex., 20.7-28.8 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Barito at Muara Laung (0°35'34"S 114°44'12"E), coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 8 Jul.1992 (DS-7-1992). — MZB 6793, 1 ex., 30.7 mm SL; Borneo, Kalimantan Tengah: Barito Hulu, Sungai Sapen, tributary of Sungai Joloi, upstream of Sungai Busang, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 7 Feb.1991.

Diagnosis. – *Betta obscura* is distinguished from the other members of the *B. akarensis* group by the following combination of characters: opercle with second postorbital stripe; anal-fin rays 26-29 (mode 28); subdorsal scales 5^{1/2}-7 (mode 6^{1/2}); lateral scales 28-30 (mode 29); predorsal scales 19-21 (mode 20); postdorsal scales 10-11 (mode 11); preanal length 46.1-50.7% SL; head length 30.9-35.4% SL; length of anal-fin base 51.3-56.4% SL.

Description. – General appearance is illustrated in Fig. 41. Meristic and morphometric data in Table 4. Relatively short and stout body (body depth 28.7-32.7% SL), relatively long and pointed head (HL 30.9-35.4% SL). Unpaired fins pointed, dorsal and anal fins pointed with posterior rays elongated, caudal fin lanceolate with median rays elongated. Pelvic fin falcate with long filamentous first ray (33.1-52.6% SL). Maximum known size 69.1 mm SL (BMNH 1996.3.22:253-260).

Coloration. – Live coloration was not recorded, only preserved specimens examined: Body uniformly brown with darker dorsum. Preorbital stripe complete from snout through eye to operculum edge, lower preorbital stripe present. Opercle markings relatively dense, chin-bar incomplete below first preorbital stripe, a few (1-2) black marks below postorbital stripe (Fig. 7f). Thin black distal margin on anal fin. Dorsal and caudal-fin interradiation membranes brownish red, with vertical hyaline bar pattern in male, faint on anal fin; only on dorsal fin membrane in female and juvenile. Pelvic fin filament darkly pigmented, rest brownish-red.

Distribution. – *Betta obscura* is presently known only from the upper Barito basin in Kalimantan Tengah (Fig. 18).



Fig. 41. *Betta obscura* – ZRC 41578, paratype, 62.6 mm SL.

Etymology. – From the Latin adjective *obscurus* meaning indistinct and inconspicuous, referring to the fish in general.

Comparative notes. – *Betta obscura* is distinguished from the other members of the species group by the following characters: opercle pattern less dense (Fig. 7f) than in most other members, except *B. ibanorum* and *B. aurigans*; fewer vertebrae than in *B. akarensis* and *B. pinguis* (28-30, vs. 31-32); greater mode of subdorsal scales (6^{1/2}, vs. 5-6); fewer lateral scales than *B. akarensis*, *B. aurigans* and *B. pinguis* (28-30, vs. 31-33^{1/2}); fewer lateral scales modally than *B. akarensis*, *B. chini*, *B. pinguis* and *B. ibanorum* (29, vs. 30-32); dorsal-fin origin above 14-15th lateral scales (vs. 16-19th of *B. akarensis*, *B. chini* and *B. pinguis*); fewer predorsal scales than *B. akarensis*, *B. chini* and *B. pinguis* (19-21, vs. 22-25); fewer predorsal scales modally (20, vs. 21-24); greater preanal length than *B. chini* and *B. pinguis* (46.1-50.7% SL, vs. 42.6-46.3); greater body depth than *B. ibanorum* (28.7-32.7% SL, vs. 23.3-28.1); relatively greater body depth than *B. chini* (28.7-32.7% SL, vs. 26.3-29.0); smaller orbital diameter than *B. balunga* and *B. chini* (21.1-25.3% HL, vs. 26.2-33.3).

BETTA UNIMACULATA GROUP

Betta unimaculata (Popta, 1905)

(Figs. 42a-b, 49e)

Parophiocephalus unimaculatus Popta, 1905: 184; 1906: 10, pl. 1, Figs. 1a, 1b.

Betta unimaculata - Regan, 1910: 779; Weber & de Beaufort, 1922: 355; Herre, 1940 (key only); Witte & Schmidt, 1992: 327; Kottelat et al., 1993: 163, pl. 77.

Material examined. – Lectotype - RMNH 7660-A, 50.9 mm SL male, Borneo, Kalimantan Timur: Kajan (Kayan basin), coll. M. le Dr. A. W. Nieuwenhuis, Sep-Oct.1900.

Paralectotypes - RMNH 7659, 11 ex., 27.8-51.6 mm SL; Borneo, Kalimantan Timur: Howong (upper Mahakam), coll. M. le Dr. A. W. Nieuwenhuis, 1898. — RMNH 7660, 15 ex., 28.9-53.5 mm SL, same locality data as lectotype.

Others - MNHN 58-180, 1 ex., 66.8 mm SL; Borneo, Kalimantan Timur: Kajan; Pfeffer. — ZRC 46324, 50 ex., 15.0-55.2 mm SL; Kalimantan Timur: Kayan basin; Usat Aran, small rocky hill stream feeding ladang next to Sungai Pingai (02°00.67'N 115°08.97'E, 500 m asl), coll. H. H. Tan et al., 20 Nov.1999 [THH9991]. — ZRC 46325, 110 ex., 18.6-52.5 mm SL; CMK, 10 ex., 33.7-51.0 mm SL; MZB 9347, 10 ex., 23.5-42.4 mm SL; Kalimantan Timur: Kayan basin; Sungai Nap, feeder stream to Sungai Seba Ai (Sungai Seba Ai, tributary to Kayan river - 01°59.86'N 115°06.77'E, 550 m asl), coll. H. H. Tan et al., 22 Nov.1999 [THH9995]. — ZRC 46326, 2 ex., 21.5-24.7 mm SL; Kalimantan Timur: Kayan basin; Sungai Bako, tributary to Kayan river (01°59.02'N 115°06.91'E, 500 m asl), coll. H. H. Tan et al., 23 Nov.1999 [THH9996]. — ZRC 46327, 32 ex., 18.9-54.5 mm SL; Kalimantan Timur: Kayan basin; Sungai Busang Matu, tributary to Kayan river ca. 500 m upstream of Data Dian (01°59.89'N 115°07.81'E, 500 m asl), coll. H. H. Tan et al., 24 Nov.1999 [THH9997]. — ZRC 46328, 3 ex., 15.0-47.7 mm SL; Kalimantan Timur: Kayan basin, Iwan; Sungai Panan, tributary to Iwan river, ca. 60 mins. upstream from Data Dian (02°00.74'N 115°03.56'E, 530 m asl), coll. H. H. Tan et al., 26 Nov.1999

[THH9999]. — ZRC 46329, 10 ex., 22.2-47.6 mm SL; Kalimantan Timur: Kayan basin; Sungai Belanyan Tekan, tributary to Kayan river (01°59.67'N 115°07.59'E, 500 m asl), coll. H. H. Tan et al., 26 Nov.1999 [THH99103]. — ZRC 46330, 35 ex., 18.9-54.2 mm SL; Kalimantan Timur: Kayan basin; Sungai Nah, tributary to Kayan river, ca. 20 mins upstream of fork to Iwan river (01°57.72'N 115°06.59'E, 550 m asl), coll. H. H. Tan et al., 27 Nov.1999 [THH99104].

Diagnosis. – *Betta unimaculata* is distinguished from the other members of the *B. unimaculata* group group by the following combination of characters: distinct black spot near caudal peduncle; body brownish; uniform caudal fin colour; vertebrae 30-32 (mode 31); anal-fin rays 27-30 (mode 28-29); dorsal-fin rays 6-8 (mode 8); pectoral fin rays 12-13 (mode 12); subdorsal scales 4-5 (mode 5); lateral scales 31-33 (mode 32); predorsal scales 24-26 (mode 24); predorsal length 67.7-73.0% SL; head length 29.0-33.3% SL; length of anal-fin base 45.9-53.7% SL; length of dorsal-fin base 7.9-10.4% SL; lower jaw length 31.6-37.9% HL.

Description. – General body shape and appearance as in Figs. 42a-b, 49e. Body slender, broad and blunt head; caudal fin rounded with median rays slightly elongated, tips of rays free of interradial membrane, dorsal and anal fins relatively pointed, pelvic fin filamentous. Vertebrae 2 + 8-9 + 20-21 (total 30-32, mode 31) (n = 13). Meristic and morphometric data in Table 5. Maximum known size 66.8 mm SL (MNHN 58-180).

Coloration. – For live coloration, see Fig. 49e. Mature male with iridescent blue opercle scales when alive, blackish when preserved, with a single iridescent scale on dark upper region of head, which is speckled with black dots. Area below eye with 2 rows of iridescent blue scales, except region behind eye and directly below that. Eye with a thin iridescent light blue lower iris. Chin bar present. Body brown when alive with irregular faint black bars on lower half, dark brown when preserved. Dorsal fin with iridescent white margin, with 5-6 transverse bars. Caudal fin with up to 8 transverse bars. Large black rounded spot at lower half of caudal base, in both sexes and juvenile (Fig. 1). Anal fin with black dots,

distal margin iridescent blue or white. Dorsal, caudal and anal fins sometimes flushed with faint blue iridescence. Pelvic fin filamentous, with first ray iridescent white, rest hyaline. Pectoral fin base black, rest hyaline. Female with very little or no iridescent opercle scales. All transverse bars on fins distinct and iridescence absent in preserved material.

Distribution. – *Betta unimaculata* is known only from the upper Kayan (=Kajan) and Howong (Mahakam) drainages in east Borneo (Popta, 1905:185, 1906: 10-11) (Fig. 23).

Comparative notes. – *Betta unimaculata* is distinguished from the other members of the species group in the following characters: fewer anal-fin rays than *B. ocellata*, *B. patoti* and *B. gladiator* (27-30, vs. 30-33); fewer dorsal-fin rays than *B. macrostoma* (6-8, vs. 9-11); fewer pectoral-fin rays than *B. gladiator* (12-13, vs. 16-17); fewer subdorsal scales than *B. macrostoma* and *B. patoti* (4-5, vs. 6-8); fewer lateral scales than *B. gladiator* (31-33, vs. 34-36); fewer vertebrae than *B. ocellata*, *B. patoti* and *B. gladiator* (30-32, vs. 33-34); smaller predorsal length than *B. macrostoma* (67.7-73.0% SL, vs. 62.3-66.7); smaller length of anal-fin base than *B. ocellata* (45.9-53.7% SL, vs. 52.2-54.5); smaller length of dorsal-fin base than *B. macrostoma* and *B. ocellata* (7.9-10.4% SL, vs. 10.5-15.7); smaller head width than *B. ocellata* (19.6-21.8% SL, vs. 21.0-24.0); smaller lower jaw length than *B. macrostoma* (31.6-37.9% HL, vs. 38.0-54.0). *Betta unimaculata* is further distinguished from *B. ocellata* in the following characters: blunter lateral head profile and more bulbous dorsal head profile (vs. pointed and more conical head profile, Fig. 24c); distinct caudal-fin transverse bars (vs. faint or absence); maxilla ends beyond anterior margin of orbit (vs. in front of anterior margin of orbit); fewer subdorsal scales (5, vs. 5½); fewer lateral scales (32 vs. 33); fewer anal-fin rays (27-30, mode 28 & 29, vs. 30-31, mode 30); smaller length of dorsal-fin base (7.9-10.4% SL, vs. 10.5-11.3).

Remarks. – Popta (1905) described *B. unimaculata* on the basis of 52 syntypes from two locations (Howong and Kajan). We have examined most of this material. A specimen from the Kajan series, RMNH 7660-A (50.9 mm SL, male), is designated as lectotype.

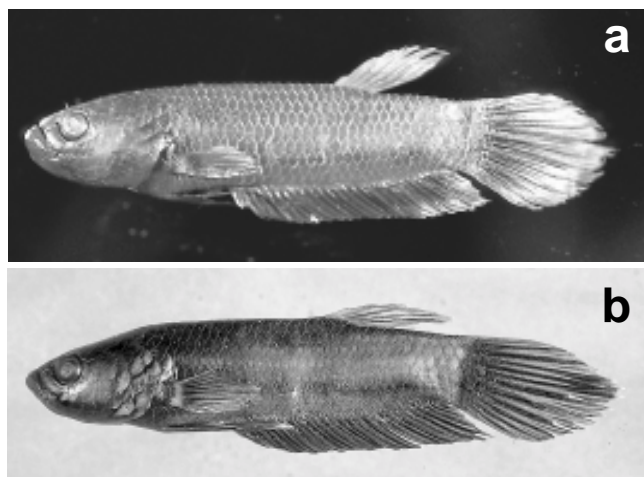


Fig. 42. a) *Betta unimaculata* – RMNH 7660A, lectotype, 50.9 mm SL, b) ZRC 46327, 48.7 mm SL.

***Betta patoti* Weber & de Beaufort, 1922**

(Figs. 43a-b, 49f-g)

Betta patoti Weber & de Beaufort, 1922: 359; Herre, 1940: 41 (key only); Witte & Schmidt, 1992: 323 (key only); Kottelat et al., 1993: 162, pl. 76.

Material examined. – Lectotype - ZMA 112.513, 63.0 mm SL, lectotype; Borneo, Kalimantan Timur: Balikpapan, rivulet 25 km east of Bay of Balikpapan, coll. W. J. Tisot van Patot, 1911.

Parlectotypes - ZMA 121.679, 2 ex., 58.1-75.6 mm SL, paralectotypes; same data as lectotype. — ZMA 112.510, 1 ex., 59.7 mm SL, paralectotype; Borneo, Kalimantan Timur: Balikpapan, freshwater; W. J. Tisot van Patot, 1911. — ZMA 112.511, 1 ex., 57.6 mm SL, paralectotype; Borneo, Kalimantan Timur: Balikpapan, Sungai Manggar; W. J. Tisot van Patot, 1911. ZMA 112.512, 2 ex., 42.4-45.5 mm SL, paralectotypes; Borneo, Kalimantan Timur: Balikpapan, Sungai Manggar; W. J. Tisot van Patot, 1911.

Others - ZMA 121.588, 2 ex., 55.9-71.3 mm SL; Borneo: Balikpapan; L. Rutten, 1911. — RMNH 10440, 2 ex., 46.0-48.8 mm SL; southeast Borneo, before 1921. — MZB 1769, 1 ex., 48.3 mm SL; Borneo, Kalimantan Timur: Samarinda, Sungai Mahakam, coll. D. Darnaedi, Sep.1974. — ZRC 46322, 60 ex., 9.5-48.0 mm SL; CMK, 10 ex., 15.8-41.9 mm SL; MZB 9346, 10 ex., 17.4-37.6 mm SL; Kalimantan Timur: Mahakam basin; Taman Wisata Air Terjun - Tanah Merah, Desa Lempabe, ca. 30 km north of Samarinda (00°26.00'S 117°13.99'E), coll. H. H. Tan & D. Wowor, 11 Nov.1999 [THH9976]. — ZRC 46323, 6 ex., 14.8-60.5 mm SL; Kalimantan Timur: Mahakam basin; downstream of Taman Wisata Air Terjun - Tanah Merah, Desa Lempabe, ca. 30 km north of Samarinda (00°26.00'S 117°13.99'E), coll. H. H. Tan & D. Wowor, 2 Dec.1999 [THH99105].

Diagnosis. – *Betta patoti* is distinguished from the other members of the *B. unimaculata* group by the following combination of characters: 10-14 vertical dark bars on lower half of body; body yellowish brown; lanceolated caudal fin in adults; uniform light brown caudal fin; vertebrae 33-34 (mode 33); anal-fin rays 30-33 (mode 31); dorsal-fin rays 8-9 (mode 8); pectoral-fin rays 12-14 (mode 13); subdorsal scales 6-6½ (mode 6); lateral scales 33-34½ (mode 34); predorsal scales 24-26 (mode 25); predorsal length 67.5-69.9% SL; head length 29.7-31.4% SL; length of anal-fin base 51.0-56.3% SL; length of dorsal-fin base 9.4-11.4% SL; lower jaw length 32.9-38.5% HL.

Description. – General appearance in Figs. 43a-b, 49f-g. Meristic and morphometric data in Table 5. Body long and slender (body depth 20.0-22.6% SL); head blunt and broad (HL 29.7-31.4% SL, head width 18.0-20.7% SL, 57.9-67.2% HL). Dorsal pointed, anal bluntly pointed, caudal strongly lanceolate with median rays elongated. Pelvic with filamentous first ray. Maximum known size 75.6 mm SL (ZMA 121.679).

Coloration. – For live coloration, see Figs. 49f-g. Body with 13-14 black bars on lower two-thirds, dorsum dark brown, lateral light brown, ventrum light yellowish gold. Lower part of iris golden. Postorbital stripe distinct but interrupted. Preorbital stripe distinct. Chin bar present, portion just below

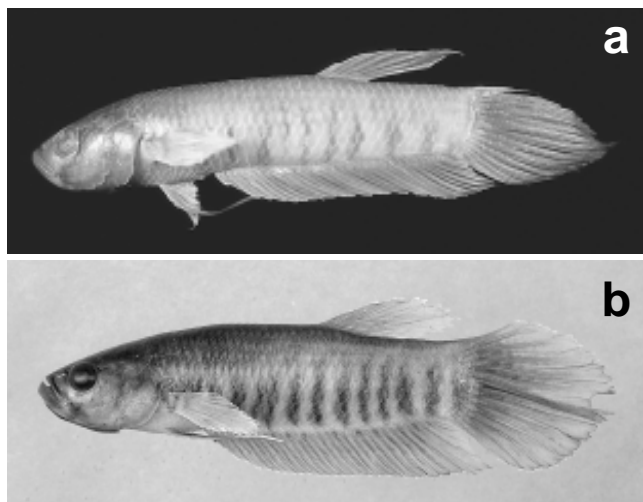


Fig. 43. a) *Betta patoti* – ZMA 112.513, lectotype, 63.5 mm SL, b) ZRC 46323, 60.1 mm SL (right side, reversed).

eye slightly reddish. Region between preorbital stripe and chin bar light iridescent green. Upper and lower lips black. Opercle faintly iridescent green. Dorsal fin with 5-7 faint transverse bars. Caudal fin with 7-8 faint transverse bars on dorsal half, median rays elongated, projecting beyond interradiial membrane. Anal fin darker on anterior region. Pelvic fin filamentous with first ray white, rest hyaline. Pectoral fin base dark brown, rest hyaline. Preserved specimens with light brown body, dorsum darker, 13-14 black bars on body. Transverse bars on fins present but faint.

Distribution. – *Betta patoti* is known only from the the southern part of Kalimantan Timur, around Balikpapan and Samarinda (Fig. 23).

Comparative notes. – *Betta patoti* is distinguished from the other members of the species group by the following characters: caudal fin lanceolate in adults, which is shared to some extent with *B. pallifina* (vs. rounded); 10-14 dark vertical bars on lower half of body (vs. absence); indistinct pattern on opercle (vs. distinct dark and light opercle pattern of *B. macrostoma* and *B. pallifina*); more vertebrae than *B. unimaculata*, *B. macrostoma* (33-34, vs. 30-32); more anal-fin rays than *B. macrostoma* (30-33, vs. 25-28); fewer dorsal-fin rays than *B. macrostoma* (8-9, vs. 9-11); fewer pectoral-fin rays than *B. gladiator* (12-14, vs. 16-17); more subdorsal scales than *B. unimaculata* and *B. ocellata* (6-6½, vs. 4-5½); dorsal-fin origin above 18-19th lateral scales (vs. 15-17th in *B. macrostoma*); greater predorsal length than *B. macrostoma* (67.5-69.9% SL, vs. 62.3-66.7); smaller head length than *B. ocellata* (29.7-31.4% SL, vs. 31.4-33.3); greater length of anal-fin base than *B. macrostoma* (51.0-56.3% SL, vs. 43.2-49.2); smaller length of dorsal-fin base than *B. macrostoma* (9.4-11.4% SL, vs. 12.2-15.7); smaller body height at pectoral fin than *B. ocellata* (12.7-16.6% SL, vs. 16.7-18.7); smaller head width than *B. ocellata* (18.0-20.7% SL, vs. 21.0-24.0); smaller lower jaw length than *B. macrostoma* (32.9-38.5% HL, vs. 38.0-54.0); lower range of predorsal length than all members (except *B. macrostoma*) (64.6-69.4% SL, vs. 67.5-73.0).

Betta patoti is distinguished from *B. pallifina* by having a more distinctly lanceolate caudal fin in adults (vs. less pronounced); vertical dark bars on lower half of body (vs. absence); no dark opercle pattern (vs. presence); no hyaline or whitish subdistal borders on anal and caudal fins in female (vs. presence); no vertical barring pattern on interradiial membranes of caudal and anal fins (vs. presence); slightly more vertebrae (33-34, mode 33, vs. 31-33, mode 32); slightly more anal-fin rays (30-33, mode 31, vs. 27-32, mode 30).

Betta pallifina, new species

(Figs. 44a-b, 49h)

Material examined. – Holotype - MZB 9328, 60.5 mm SL, male; Borneo, Kalimantan Tengah: Muara Teweh, Kec. Laung Tuhup, Desa Maruai, Rawa/Sungai Laung, tributary of Sungai Barito, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 15-18 Jul.1992.

Paratypes - MZB 6978, 60 ex., 20.4-66.3 mm SL; same locality data as holotype. — BMNH 1996.3.22:106-138, 33 ex., 29.8-64.8

mm SL, - ZRC 41576, 15 ex., 17.3-59.5 mm SL, - MZB 9329, 15 ex., 29.5-54.4 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Laung at Desa Maruwei (0°21'59"S 114°44'6"E), coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 15-18 Jul.1992 (DS-12-1992). — BMNH 1996.3.22:171-230, 60 ex., 23.2-62.3 mm SL, - ZRC 41577, 20 ex., 29.0-49.2 mm SL, - MZB 9330, 20 ex., 29.2-49.2 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Desa Kerendan, Sungai Lahei and tributaries, coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 23-28 Sep.1992 (DS-3-1995). — BMNH 1996.3.22:48-57, 10 ex., 41.2-66.3 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Idow above waterfall (20 m high) ca. 7 km upstream from Sungai Kerendan (tributary of Sungai Lahei), coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 26 Sep.1992 (DS-5-1995). — BMNH 1996.3.22:1-38, 38 ex., 15.3-61.0 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Barito at Muara Laung (0°35'34"S 114°44'12"E), coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 8 Jul.1992 (DS-7-1992).

Others - BMNH 1991.9.18:21-25, 5 ex., 22.5-52.1 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Murung near Project Barito basecamp, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 11-13 Feb.1991 (DS-17-1991). — BMNH 1991.9.18:29-31, 3 ex., 28.4-47.7 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Barito at Muara Laung and market at Puruk Cahu, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 20-21 Feb.1991 (DS-20-1991). — BMNH 1996.3.22:41-42, 2 ex., 41.9-42.4 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Bunes, a small tributary of Sungai Kerendan (a tributary of Sungai Lahei) above (ca. 1 km) Desa Kerendan, coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 24 Sep.1995 (DS-2-1995). — BMNH 1996.3.22:76-105, 30 ex., 21.2-50.3 mm SL; same data as holotype. — BMNH 1996.3.22: 231-253, 23 ex., 20.0-43.4 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Desa Kerendan, Sungai Lahei and tributaries, coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 23-28 Sep.1992 (DS-3-1995). — BMNH 1996.3.22: 58-75, 18 ex., 9.0-44.1 mm SL; Borneo, Kalimantan Tengah: Sungai Barito basin, Sungai Idow above waterfall (20 m high) ca. 7 km upstream from Sungai Kerendan (tributary of Sungai Lahei), coll. D. J. Siebert, A. Tjakrawidjaja & A. Mun'im, 26 Sep.1992 (DS-5-1995). — MZB 7019, 11 ex., 19.8-55.9 mm SL; Borneo, Kalimantan Tengah: Laung Tuhup, Sungai Lubi, tributary of Sungai Barito, 1 km from Muara Laung, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 15 Jul.1992. — MZB 8237, 42 ex., 19.3-47.1 mm SL; Borneo, Kalimantan Tengah: Laung Tuhup, Sungai Barito at Muara Laung, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 8

Jul.1992. — MZB 7152, 8 ex., 23.4-45.9 mm SL; Borneo, Kalimantan Tengah: Sungai Murung basecamp, Project Barito Ulu, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 11-13 Feb.1991. — MZB 7075, 2 ex., 16.5-32.8 mm SL; Borneo, Kalimantan Tengah: Laung Tuhup, Sungai Batu landai, tributary of Sungai Barito, 2 km from Muara Laung, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 8 Jul.1992. — MZB 7048, 4 ex., 28.5-35.3 mm SL; Borneo, Kalimantan Tengah: Muara Teweh, Laung Tuhup, Desa Maruei, Sungai Laung, tributary of Sungai Barito, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 15-18 Jul.1992. — MZB 6917, 1 ex., 47.8 mm SL; Borneo, Kalimantan Tengah: Laung Tuhup, DAS Barito, Sungai Maruai, tributary of Sungai Laung, coll. D. J. Siebert, A. Tjakrawidjaja & O. Crimmen, 15 Jul.1992.

Diagnosis. – *Betta pallifina* is distinguished from the other members of the *B. unimaculata* group by the following combination of characters: hyaline subdistal band on anal and caudal fins of female; lanceolate caudal fin in adults; body brownish; lower half of caudal fin with dark distal edge; vertebrae 31-33 (mode 32); anal-fin rays 27-32 (mode 30); dorsal-fin rays 7-9 (mode 8); pectoral fin rays 11-14 (mode 13); subdorsal scales 5-6½ (mode 6); lateral scales 32-34 (mode 33); predorsal scales 21-26 (mode 23); predorsal length 64.6-69.4% SL; head length 26.8-33.4% SL; length of anal-fin base 47.4-57.7% SL; length of dorsal-fin base 9.3-12.5% SL; lower jaw length 30.6-39.6% HL

Description. – General appearance in Figs. 44a-b, 49h. Meristic and morphometric data in Table 5. Body slender and long (body depth 20.5-23.0% SL); head broad and blunt (HL 26.8-33.4% SL, head width 17.7-20.8% SL, 56.4-70.2% HL). Dorsal fin pointed, anal fin bluntly pointed, caudal fin lanceolate with median rays elongated. Pelvic fin with filamentous tip. Maximum known size 66.3 mm SL (BMNH 1996.3.22:48-57).

Coloration. – For live colour, see Fig. 49h. Both male and female specimens with patches of iridescent blue scales on body and opercle. In preserved specimens, dorsum darker brown than ventrum; vertical bar pattern on interradiation membranes of anal and caudal fins, absent on dorsal fin. Thin black distal margin present on anal fin in male. A dark blotch present just after hypural plate below lateral series on anterior portion of caudal fin in both sexes and juvenile. Male with distinct 'pale cheek' pattern on opercle, faint in female. Some specimens with 4-6 irregular vertical bars across body. Female sometime with distinct longitudinal reticulated pattern on lower half of body, others more frequently with hyaline or whitish (orangish iridescence when live) subdistal border with dark anal edge on anal fin and lower half of caudal fin. Pelvic fin with filamentous tip black and rest darkly pigmented.

Distribution. – *Betta pallifina* is currently known only from the upper Barito in Kalimantan Tengah (Fig. 23).

Field notes. – *Betta pallifina* is known only from headwater habitats and is probably a paternal oral-brooder, similar to the other members of *B. unimaculata* group. Syntopic *Betta* present - *B. obscura*.

Etymology. – The name comes from the Latin *pallidus*



Fig. 44. a) *Betta pallifina* – ZRC 41577, male, 56.9 mm SL, b) ZRC 41577, female, 47.3 mm SL.

meaning pale and *finis* meaning boundary, referring to the unique coloration of the bordered anal and caudal fins of the females. Used as a noun in apposition.

Comparative notes. – *Betta pallifina* is distinguished from the other species in the species group by the following characters: caudal fin lanceolate in adults (vs. rounded), a character shared only with *B. patoti*; female with hyaline to whitish subdistal margin (orange iridescence when live) before dark edge (vs. absence); lower mode of vertebrae than *B. ocellata*, *B. patoti* and *B. gladiator* (32, vs. 33-34); more anal-fin rays than *B. macrostoma* (27-32, vs. 25-28); fewer dorsal-fin rays than *B. macrostoma* (7-9, vs. 9-11); fewer pectoral-fin rays than *B. gladiator* (11-14, vs. 16-17); greater mode of subdorsal scales than *B. unimaculata* and *B. ocellata* (6, vs. 5-5½); lower mode of subdorsal scales than *B. macrostoma* (6, vs. 7); lower mode of lateral scales than *B. patoti* and *B. gladiator* (33, vs. 34-35); dorsal-fin origin modally above 18th lateral scale (vs. 19-20th in *B. gladiator*); anal-fin origin modally below 6th lateral scale (vs. 7-8th); and lower mode of predorsal scales than *B. unimaculata*, *B. ocellata*, *B. patoti* and *B. gladiator* (23, vs. 24-26). In preserved specimens, *B. pallifina* has an opercle pattern similar to that of *B. macrostoma* in which a pale central region of the opercle is surrounded by darkly pigmented area in both male (distinct) and female (faint).

BETTA SPLENDENS GROUP

Betta stiktos, new species

(Fig. 45)

Material examined. – Holotype - CAS 204326, 27.3 mm SL male.; Cambodia: Mekong basin, small swampy stream from Stung Treng to Ban Lung (ca. 3/4 to bridge over Tonle Srepok) (ca. 13°30'N 106°30'E), coll. T. R. Roberts, 16 Feb. 1994.

Paratypes - CAS 94155, 19 ex., ZRC 43391 (ex CAS 94155), 3 ex., 16.7-28.2 mm SL; same locality as holotype.

Diagnosis. – *Betta stiktos* is distinguished from other members of the *B. splendens* group by the following combination of characters: up to 5 rows of black rounded marks on interradial membranes of dorsal fin; up to 9 rows of transverse black bars on caudal fin; up to 7 vertical rows of dark marks on posterior edge of scale on body; lateral scales 33-34 (mode 33), predorsal scales 24-25 (mode 25); postdorsal length 17.5-20.1% SL; body depth 26.2-27.7% SL; caudal peduncle depth 15.4-17.4% SL; length of dorsal-fin base 15.2-15.6% SL; orbit diameter 27.7-29.7% HL; postorbital length 45.9-50.0% HL; interorbital width 26.4-31.6% HL.

Description. – General body shape and appearance in Fig. 45. Body slender (body depth at dorsal-fin origin 26.2-27.7% SL); head small (HL 27.7-30.3% SL); caudal fin rounded;

pelvic fin falcate; dorsal fin rounded, anal fin pointed, anal fin reaching to half or more of caudal fin. Meristic and morphometric data in Table 7. Maximum known size 28.2 mm SL (CAS 94155).

Coloration. – Male with dark brown head; opercle black, postorbital stripe present, chin-bar absent. Body light brown. Dorsal fin with up to 5 rows of rounded black marks on interradial membrane; caudal fin with up to 9 rows of transverse bars; anal fin with thin black margin; pelvic fin with extreme tip white, rest hyaline; pectoral hyaline. Body with up to 7 vertical rows of dark marks on posterior edge of scales. Female without black opercle, chin-bar and postorbital stripe present. Body with distinct central and second central stripes, with caudal peduncle spot. Fins yellowish to hyaline, dorsal and caudal fins with transverse bars.

Distribution. – *Betta stiktos* is known from the Mekong drainage in Cambodia.

Etymology. – The name comes from the Greek *stiktos* meaning dappled, spotted, referring to the rows of diagnostic round spots on the dorsal fin. Used as a noun in apposition.

Comparative notes. – *Betta stiktos* is distinguished from the other members of the species group by having: rounded black spots on interradial membranes of dorsal fin (vs. thin vertical bars); up to 9 rows of dark transverse bars on caudal fin (vs. absence); up to 7 vertical rows of dark marks on posterior edge of scales on body (vs. 8 or more); more lateral scales (33-34, vs. 29-31); more predorsal scales than *B. imbellis* (24-25, mode 25, vs. 21-24, mode 23); smaller postdorsal length than *B. smaragdina* (17.5-20.1% SL, vs. 21.4-23.2); smaller body depth than *B. splendens* (26.2-27.7% SL, vs. 27.1-32.2); smaller caudal peduncle depth than *B. splendens* and *B. smaragdina* (15.4-17.4% SL, vs. 18.1-20.3); smaller length of dorsal-fin base than *B. splendens* (15.2-15.6% SL, vs. 16.7-23.8); greater orbit diameter than *B. splendens* (27.7-29.7% HL, vs. 22.7-26.6); smaller postorbital length than *B. splendens* (45.9-50.5% HL, vs. 49.6-52.7); smaller interorbital width than *B. splendens* and *B. smaragdina* (26.4-31.6% HL, vs. 30.2-34.3).



Fig. 45. *Betta stiktos* – CAS 204326, holotype, 27.3 mm SL (right side, reversed).

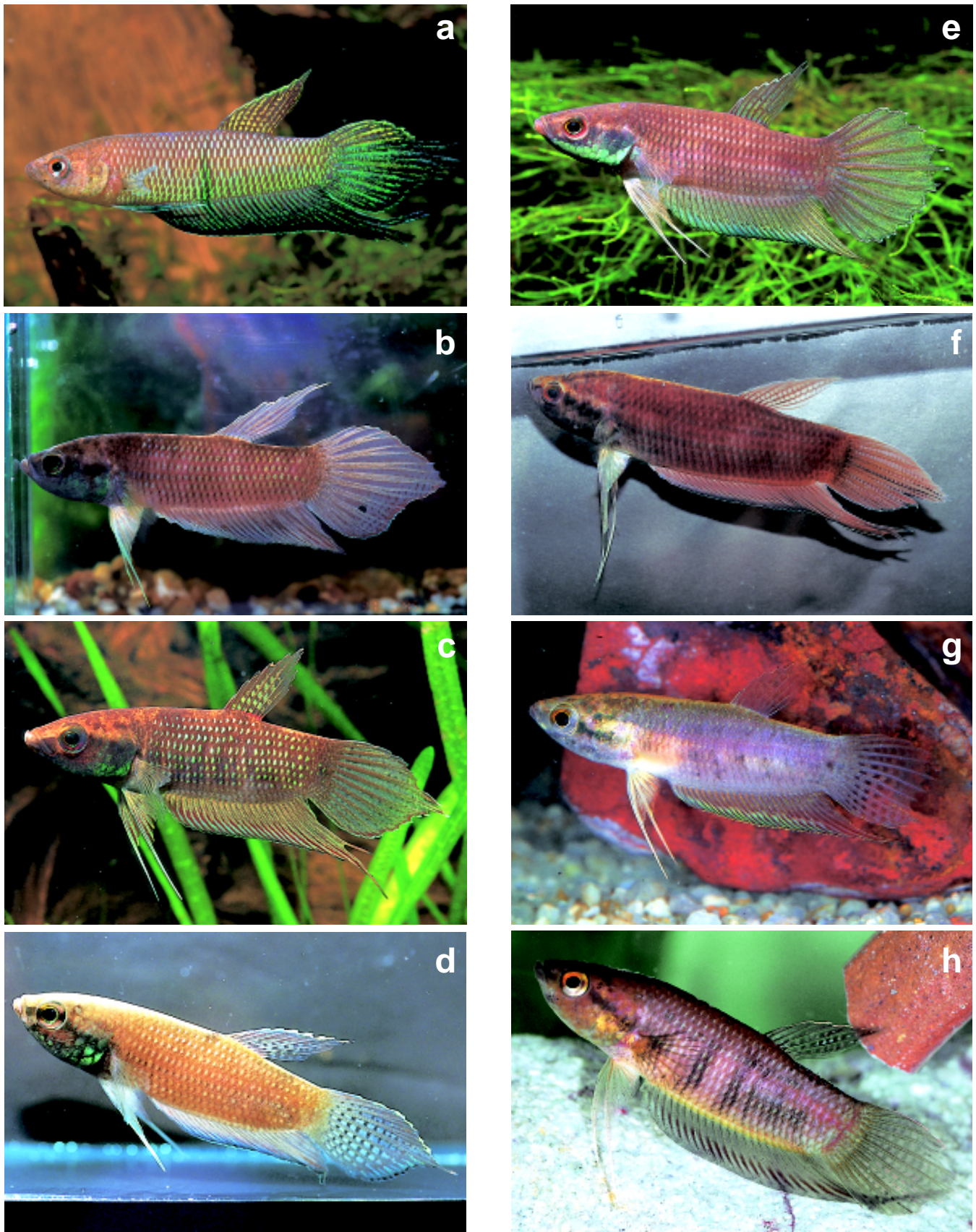


Fig. 46. a) *B. bellica* – not preserved, ca. 50 mm SL (taken by Koji Yamazaki), b) *B. pugnax* – ZRC 39264, 59.6 mm SL, c) *B. pulchra* – not preserved, ca. 40 mm SL (taken by Koji Yamazaki), d) *B. stigmosa* – ZRC 43393, 37.5 mm SL, e) *B. lehi* – not preserved (taken by Koji Yamazaki), f) *B. akarensis* – not preserved, ca. 60 mm SL, g) *B. balunga* – ZRC 35497, 39.2 mm SL, h) *B. chini* – ZRC 35086, holotype, 51.0 mm SL.



Fig. 47. a) *B. ibanorum* – not preserved, ca. 60 mm SL, b) *B. macrostoma* – not preserved (taken by Günther Ettrich), c) *B. macrostoma* – not preserved (taken by Koji Yamazaki), d) *B. ocellata* – ZRC 40956, ca. 40 mm SL, e) *B. ocellata* – not preserved, ca. 35 mm SL (taken by Koji Yamazaki), f) *B. gladiator* – not preserved, ca. 50 mm SL, g) *B. taeniata* – not preserved, ca. 35 mm SL, h) *B. taeniata* – not preserved, ca. 40 mm SL.



Fig. 48. a) *B. imbellis* – not preserved, ca. 30 mm SL (taken by Koji Yamazaki), b) *B. imbellis* – not preserved, ca. 30 mm SL (taken by Koji Yamazaki), c) *B. coccina* – not preserved, ca. 30 mm SL, d) *B. coccina* – not preserved, ca. 30 mm SL, e) *B. livida* – not preserved, ca. 30 mm SL, f) *B. persephone* – not preserved, ca. 25 mm SL, g) *B. tussya* – not preserved, ca. 30 mm SL, h) *B. brownorum* – not preserved, ca. 25 mm SL.

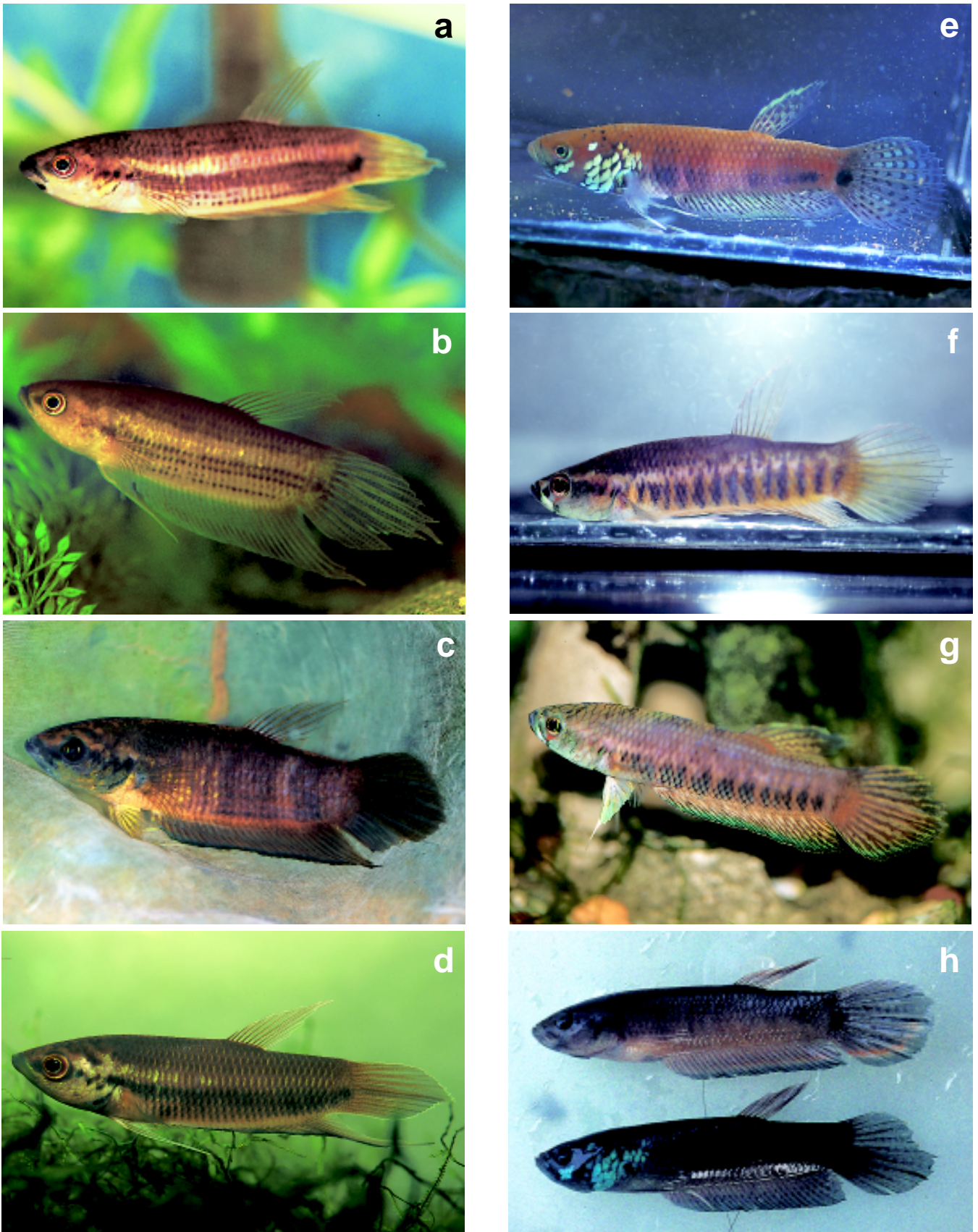


Fig. 49. a) *B. waseri* – ZRC 35402, 80.7 mm SL, b) *B. hipposideros* – ZRC 18689, paratype, 71.1 mm SL, c) *B. tomi* – ZRC 35411, paratype, 64.9 mm SL, d) *B. pi* – not preserved, ca. 40 mm SL, e) *B. unimaculata* – ZRC 46324, ca. 45 mm SL, f) *B. patoti* – ZRC 46322, 48.2 mm SL, g) *B. patoti* – not preserved, ca. 60 mm SL, h) *B. pallifina* – BMNH (taken by Darrell Siebert) (female above, male below).