**Bucephalus damriyasai** n. sp. (Digenea: Bucephalidae) from the blacktip trevally *Caranx heberi* (Bennett) (Perciformes: Carangidae) off Bali, Indonesia

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Received: 13 July 2018 / Accepted: 28 October 2018 / Published online: 21 November 2018
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**Abstract** The new species *Bucephalus damriyasai* n. sp. is described from *Caranx heberi* (Bennett) from off Bali, Indonesia. It can be distinguished from other *Bucephalus* spp. recorded from carangid hosts by its narrow elongate body shape and the relatively long distance between the rhynchus and the vitellarium, as well as other features distinguishing it from individual species. The most similar species are differentiated from *B. damriyasai* n. sp. as follows: *B. carangis* Yamaguti, 1970 has a much greater length, the rhynchus is smaller and the cirrus-sac is small, not always reaching to the posterior testis; *B. fragilis* Velasquez, 1959 is a tiny species, the pre-vitelline distance is short and the caecum is saccular; *B. gorgon* (Linton, 1905) is much longer and relatively broader, the uterus reaches distinctly anterior to the vitellarium and the rhyncheal tentacles appear more complex; *B. labracis* Paggi & Orecchia, 1965 is distinctly longer, slightly broader, with a slightly larger rhynchus, and has shorter pre-uterine and pre-mouth distances; *B. paraheterotentaculatus* Velasquez, 1959 is much longer, relatively rather broad, the rhynchus is said to bear 21 tentacles, the post-testicular region and cirrus-sac reach are longer and the caecum is described as saccular; *B. sphyraenae* Yamaguti, 1952 is longer, slightly broader, the uterus reaches anteriorly to the vitellarium and the caecum is claviform and oriented anteriorly; *B. margaritae* Ozaki & Ishibashi, 1934 (syn. *B. varicus* Manter, 1940) is relatively squat, has shorter pre-vitelline and pre-mouth distances and a longer post-testicular distance and cirrus-sac reach; *B. yamagutii* Gupta & Singh, 1985 is broader, with a relatively short pre-vitelline distance, the caecum extends anteriorly to the pharynx, but not posteriorly and the rhynchus is said to carry five tentacles. The distinctive features of *B. damriyasai* n. sp. are compared with those of all other marine *Bucephalus* spp. in a table. The number of bucephalid trematodes known from Indonesian waters is now 13, two of them await further identification. They have been described from the fish families Carangidae, Platycephalidae, Sciaenidae, Serranidae and Sphyraenidae.

This article was registered in the **Official Register of Zoological Nomenclature** (ZooBank) as 82399122-C2FC-4E47-B7D5-1BBBF2279C1. This article was published as an Online First article on the online publication date shown on this page. The article should be cited by using the doi number. This is the Version of Record.

This article is part of the Topical Collection Digenea.

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https://doi.org/10.1007/s11230-018-9828-7
Introduction

The Indonesian fish parasite fauna is species-rich, resulting from the high number of fish species surrounding about 17,000 islands of this maritime nation. However, though being a hot spot of aquatic biodiversity, fish parasites are far less studied. As stated by Bray & Palm (2009) and considering recent studies (Bray et al., 2016; Yong et al., 2016; Bray et al., 2017), over 80 fish-parasitic trematode species have been reported from Indonesian waters.

According to Palm & Bray (2014), many fish parasites that have been reported off the Hawaiian Islands in the Central Pacific have an Indo-Pacific or even worldwide distribution. Although it can be expected that a high number of new trematode taxa will be described from Indonesia, the same importance should be placed on having reliable identifications of already known species from other regions. Without proper identification the use of fish parasites as biological indicators (Palm, 2011), of increasing importance in many regions (Truong et al., 2017), is difficult and in some cases impossible. Palm & Rückert (2009), Palm et al. (2011) and Neubert et al. (2016) have developed a method to use grouper fish parasites as biological indicators for pollution and environmental change in Indonesian coastal waters, but several bucephalids recovered were only tentatively identified (Bray & Palm, 2009).

The genus Bucephalus Baer, 1826 includes many species reported from fresh and marine waters. It is characterised by having a sucker-like rhynchus with a hood bearing tentacles (usually seven). The tentacles may be found withdrawn and difficult to see and in such cases the worms look very similar to members of Rhipidocotyle Diesing, 1858. Recent molecular studies by Nolan et al. (2015) have indicated that the genus is polyphyletic, with at least three separate monophyletic groups embedded within an assortment of species of Rhipidocotyle, Prosurhynchoides Dollfus, 1929 and Paurorhynchus Dickerman, 1954.

Caranx heberi (Bennett) (syn. C. sem Cuvier) is a common carangid throughout the Indo-Pacific region. The only reports of digeneans we are aware of from this host are the bucephalid Bucephalus margaritae Ozaki & Ishibashi 1934 from off Natal, South Africa (Bray, 1984) and an unidentified sclerodistomid Prosorchis sp. from the Arabian Gulf (El-Naffar et al., 1992; Al Kawari et al., 1996). We herewith present a description of new bucephalid species from this host from the Balinese coast, Indonesia.

Materials and methods

The present study is based on material collected during the First Educational Workshop on Marine Fish Parasites in Bali, July 21st - August 2nd 2013, of Indonesian and international students and researchers investigating a wide range of hosts from Balinese waters. Three specimens (15.7–16.7 cm total length, 66.2–70.6 g) of Caranx heberi were caught by artisanal fishermen and landed at Kedonganan Bay, transported alive into the laboratory of the Veterinary Faculty, Udayana (UNUD) University, Denpasar, Bali, and directly studied for fish parasites. Kedonganan Bay is located at the western side of the southern tip of Bali, directly next to the Ngurah Rai Kuta international airport. The airstrip of the airport reaches into the ocean and acts as the northern border of the bay. Kedonganan is a typical fishing village but is heavily influenced by tourism. There is no harbour; the small ships lay directly in front of the beach which is used to land captures. The fishermen catch fish from the Bali Strait and from nearby areas off South Bali and East Java. They use drift nets, troll lines and hand lines. A cooperation of the local fishermen manages the market (Proctor et al., 2003). Digeneans were collected according to the gut wash methodology described by Cribb & Bray (2010). Unfortunately, although these worms were collected with a view to sequencing, these specimens have not yielded usable rDNA.

Whole-mounts were stained with Mayer’s paracarmine, cleared in beechwood creosote and mounted in Canada balsam. Measurements were made through a drawing tube on an Olympus BH-2 microscope, using a Digicad Plus digitising tablet and Carl Zeiss KS100 software adapted by Imaging Associates, and are quoted in micrometres, as the range and the mean in parentheses. ‘Cirrus-sac reach’ is the distance between the posterior extremity of the worm and the anteriormost extent of the cirrus-sac. The type-material is deposited in the following museum collections: the Natural History Museum, London, UK (NHMUK); the National Biodiversity Collection, Museum Zoologicum Bogoriense, Cibinong, Bogor, Java, Indonesia.
Results

All C. heberi sampled were infected with a new bucephalid (100% prevalence), but levels of intensity were not recorded.

Family Bucephalidae Poche, 1907
Genus Bucephalus Baer, 1827

Bucephalus damriyasai n. sp.

Type-host: Caranx heberi (Bennett) (Perciformes: Carangidae), blacktip trevally.
Type-locality: Off South Bali, Indonesia. Purchased from artisanal fishermen, 23.vii.2013, 26.vii.2013, 31.vii.2013.
Type-specimens: Holotype ZMB E.7629. Paratypes: E.7630–1; MZBTr 246–250; NHMUK 2018.6.7.1–3.
Site in host: Intestine.

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the International Code of Zoological Nomenclature (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for Bucephalus damriyasai n. sp. is urn:lsid:zoobank.org:act:F68217B4-831B-4D2A-84CE-F731F41CFCCFC.

Etymology: This species is named in honour of Professor Dr I Made Damriyasa, Faculty of Veterinary Sciences, Udayana University, for his continuous support of fish parasite research in Balinese waters.

Description (Figs. 1, 2)

[Based on 15 whole-mount preparations.] Body elongate, narrow, gradually widening to maximum at about level of gonads; length 851–1,544 × 76–123 (1,126 × 97); width 7.57–10.4 (8.71)% of body length. Tegument spinous throughout; spines tiny. Rhynchus 67–85 × 55–87 (77 × 71), bearing 7 tentacles, each with side branches and elongate central branch; most often withdrawn and difficult to see; rhynchus length 5.53–8.34 (7.01)% of body length; rhynchus width 77.8–112 (92.7)% of rhynchus length. Mouth at level of ovary, well inside posterior half of body, pre-mouth distance 559–1,011 (737), 63.4–69.1 (65.4)% of body length. Pharynx globular; 48–66 × 47–60 (59 × 55), width 3.82–6.32 (5.00)% of body length. Caecum elongate, 72–450 × 16–44 (351 × 27); length 28.1–44.3 (33.8)% of body length; mostly reaching anterior to pharynx almost to anterior extremity of vitellarium, but with distinct posteriorly directed part overlapping testes, pre-caecal distance 234–706 (452), 27.5–52.6 (38.8)% of body length; caecum to rhynchus distance 164–614 (385).

Pharynx globular; 48–66 × 47–60 (59 × 55), width 3.82–6.32 (5.00)% of body length. Caecum elongate, 72–450 × 16–44 (351 × 27); length 28.1–44.3 (33.8)% of body length; mostly reaching anterior to pharynx almost to anterior extremity of vitellarium, but with distinct posteriorly directed part overlapping testes, pre-caecal distance 234–706 (452), 27.5–52.6 (38.8)% of body length; caecum to rhynchus distance 164–614 (385).

Testes 2, oval, tandem or nearly so, in posterior quarter of body; pre-testicular distance 573–1,092 (767), 65.0–71.2 (68.0)% of body length; contiguous or slightly separated, distance 0–19 (8), 0–1.99 (0.78)% of body length; anterior testis 44–78 × 42–69 (58 × 53), length 4.74–5.70 (5.11)% of body length; posterior testis 39–86 × 39–61 (60 × 52), length 4.56–6.47 (5.27)% of body length; post-testicular distance 160–283 (216), 16.9–22.2 (19.3)% of body length. Cirrus-sac elongate, more or less parallel sided, reaching to posterior or anterior testis; 125–254 × 33–58 (172 × 43), length 13.2–16.9 (15.3)% of body length; cirrus-sac reach 208–359 (276), 21.7–28.1 (24.7)% of body length. Seminal vesicle subglobular to oval, in proximal cirrus-sac; 26–52 × 23–41 (37 × 32), length 18.9–25.2 (21.4)% of cirrus-sac length. Pars prostatica long, straight, surrounded by dense layer of gland-cells, lined with filaments; 91–195 (127) long, 20–29 (25) wide. Ejaculatory duct narrow, opens on large, lobed genital lobe, inside genital atrium. Genital atrium large. Genital pore ventral, distinctly separated from posterior extremity by 23–42 (34), 2.46–4.16 (3.07)% of body length.

Ovary oval, 41–75 × 35–62 (55 × 45), length 4.19–6.09 (4.84)% of body length; pre-testicular, contiguous with anterior testis; pre-ovarian distance 543–1,030 (724), 61.4–66.7 (64.2)% of body length; post-ovarian distance 245–457 (332), 26.7–32.0 (29.6)% of body length. Mehlis’ gland overlaps ovary and anterior testis. Uterine seminal receptacle and Laurer’s canal not detected. Uterus not usually reaching anteriorly to vitelline fields, pre-uterine distance 322–853 (514), 33.1–55.2 (45.0)% of body length; uterus to rhynchus distance 254–771 (447), uterus narrow anteriorly to pharynx, wider posteriorly. Eggs numerous, tanned, operculate; 18–25 × 13–19 (22 × 16). Metraterm not detected, obscured by eggs. Vitellarium consists of 2 lateral fields of 14–18 (16) follicles, symmetrical or nearly so, but with one...
Figs. 1–2 *Bucephalus damriyasai* n. sp. 1, Holotype, ventral view; 2, Rhynchus with the seven tentacles labelled for clarity. Scale-bars: 1, 200 μm; 2, 100 μm
slightly longer than other, long field 180–385 (265) long, 20.3–26.5 (23.3)% of body length; shorter field 168–360 (248) long; anterior extremity usually anterior to uterus and caecum; pre-vitelline distance 359–587 (438), 36.9–42.4 (39.0)% of body length; vitellarium to rhynchus distance 287–504 (363); posterior extremity just anterior to or overlapping pharynx; post-vitelline distance 290–600 (415), 33.5–39.7 (36.9)% of body length.

Excretory pore terminal; anterior extent of vesicle visible in some specimens reaching just anterior to vitellarium.

Discussion

We are aware of 48 described nominal species of *Bucephalus* in marine fishes and we have examined the descriptions of all except *B. arabiana* Varma, 1982, the description of which we have been unable to find. We have developed a visual key similar to that to *Prosorhynchus* developed by Bray & Palm (2009) (http://www.nhm.ac.uk/bray2009). Ten characters are used, most of which are listed as a percentage of body length: 1. Length; 2. Width %; 3. Rhynchus length %; 4. Tentacle number; 5. Pre-vitelline distance %; 6. Preuterine distance %; 7. Pre-mouth distance %; 8. Post-testicular distance %; 9. Cirrus-sac reach %; and 10. Egg length.

Eight species have none of the above listed percentage characters more than 10% either more or less than that quoted in the original description or derived from the original illustrations, or are distinctly different in size, tentacle number or egg-size. These are *B. carangis* Yamaguti, 1970; *B. fragilis* Velasquez, 1959; *B. gorgon* (Linton, 1905) (syn. *B. introversus* Manter, 1940); *B. labracis* Paggi & Orecchia, 1965; *B. paraheterotentaculatus* Velasquez, 1959; *B. sphryraenae* Yamaguti, 1952; *B. varicus* Manter, 1940 (usually considered a synonym of *B. margaritae* Ozaki & Ishibashi, 1934); and *B. yamagutii* Gupta & Singh, 1985.

*Bucephalus carangis* Yamaguti, 1970 is reported from the black jack *Caranx lugubris* Poey and the bluefin trevally *C. melampygus* Cuvier off Hawaii (Yamaguti, 1970; Palm & Bray, 2014). It apparently grows to a much greater size than *B. damriyasai* n. sp. (to 3,500 μm), the rhynchus is smaller (3–5% of body length), and the cirrus-sac is small, not always reaching to the posterior testis (cirrus-sac reach about 18% of body length).

*Bucephalus fragilis* Velasquez, 1959 is also reported from carangids, the torpedo scad *Megalaspis cordyla* (L.), the doublespotted queenfish *Scomberoides lyran* (Forskål) and *Caranx* sp. from off the Philippines, the South China Sea and Masirah Bay off Oman in the northern Indian Ocean (Velasquez, 1959; Parukhin, 1966, 1976). In this tiny species (length 660–900 μm), the pre-vitelline distance is short (about 27% of body-length) and the caecum is saccular.

*Bucephalus gorgon* (Linton, 1905) (syn. *Bucephalus introversus* Manter, 1940) is a widely reported species known only from carangids and mainly from members of the genus *Seriola* in the Pacific, Indian and Atlantic Oceans. It was described by Linton (1905) as *Gasterostomum gorgon* in the yellowtail amberjack *Seriola lalandi* Valenciennes from the North-West Atlantic at Beaufort, North Carolina. Eckmann (1932) placed this species in *Bucephalus*. It was redescribed and illustrated (apparently a badly contracted specimen) by Linton (1940) as *Nannoenterum gorgon* from *S. lalandi* at Woods Hole, Massachusetts. Bartoli et al. (2005) redescribed this species from the greater amberjack *Seriola dumerili* (Risso) off Corsica in the western Mediterranean Sea. They considered *Bucephalus introversus* Manter, 1940, from the crevalle jack *Caranx hippos* (L.), *S. dumerili*, *S. lalandi* and *Seriola* sp. from the eastern Pacific off Mexico and Columbia (Manter, 1940a) as a synonym of *B. gorgon*. Further descriptions and descriptive matter have been given by Oshmarin (1965) from *Seriola ‘nigromaculata’* off Vietnam; Corkum (1967) from *S. dumerili*, and the banded rudderfish *Seriola zonata* (Mitchill) off Louisiana; Fischthal et al. (1982) from *S. dumerili* off Israel in the eastern Mediterranean; and Luque & Oliva (1993) from *S. lalandi* (as *S. mazatlania*) off Antofagasta, Chile. Other hosts recorded are the threadfin jack, *Carangoides otrynter* (Jordan & Gilbert), the white trevally *Pseudocaranx dentex* (Bloch & Schneider) and the Almaco jack *Seriola rivoliana* Cuvier and the distribution includes the Gulf of Mexico and off Canary Islands in the Atlantic, the Balearic Sea in the western Mediterranean, the Gulf of Mannar in the Indian Ocean and the South China Sea and off New South Wales and Victoria, eastern Australia in the Pacific Ocean (Bravo-Hollis & Sogandares-Bernal, 1956; Parukhin, 1966; Nahhas &...
from the same host species in the Suez Canal at Ismailia, Egypt (Nisreen Ezz El-Dien et al., 1990). The description is poor, but it does not appear to be conspecific with its senior homonym and may not be in this genus.

**Bucephalus paraheterotentaculatus** Velasquez, 1959 was originally reported in the blackbanded trevally *Seriolina* [as *Seriola*] nigrofasciata (Rüppell) from Malabon, Rizai, Luzon Island, Philippines (Velasquez, 1959). It has subsequently been reported in *S. nigrofasciata*, *S. dumerili* and *Seriola* sp. from the South China Sea and Masirah Bay off Oman in the Northern Indian Ocean (Parukhin, 1966, 1970). This species grows to 4,070 μm long, is relatively rather broad (maximum width about 12–13% of length), the rhynchus bears “21 tentacles grouped in multiples of 3 conforming to the basic number of 7”, the post-testicular region is about 31% of body length and the cirrus-sac reach is about 36% of body length. The caecum is described as saccular.

**Bucephalus sphyraenae** Yamaguti, 1952 was originally reported from *Sphyraena* sp. off Makassar, Sulawasi, Indonesia (Yamaguti, 1952). Subsequently it has been reported from the blackfin barracuda *Sphyraena genie* Klunzinger (as *S. tessera*), the false stonefish *Scorpaenopsis diabolus* (Cuvier), the obtuse barracuda, *Sphyraena obtusata* Cuvier and the yellowstripe barracuda *Sphyraena chrysotaenia* Klunzinger from the Red Sea, off Okinawa, Japan and the Arabian Gulf off Kuwait (Parukhin, 1970; Dyer et al., 1988; Nahhas et al., 2006). This species grows to 2,800 μm, its width is about 12–16% of body length and the uterus reaches anteriorly to the vitellarium. The caecum is claviform and oriented anteriorly.

**Bucephalus varicus** Manter, 1940 is usually considered one of several synonyms of *B. margaritae* Ozaki & Ishibashi, 1934. A fairly high proportion of records of *Bucephalus* species from carangids are of *B. margaritae* and its synonyms. It was originally described as a furcocercous cercaria from the pearl oyster *Pinetada imbricata* Röding (as *Pinetada imbricata mertensii*) off Japan (Ozaki & Ishibashi, 1934). A series of papers by Sakaguchi (1962, 1964, 1966a, b, 1968) reported on the completion of the life-cycle of this species and concluded that it was conspecific with *B. varicus* Manter, 1940. Manter (1940a) in describing *B. varicus* from “a young specimen of an unidentified species of *Caranx*, or jack” off Bahia Honda, Panama, considered that *B. polymorphus* of Nagaty (1937) from carangids in the Red Sea was a misidentification, as *B. polymorphus*...
is a freshwater species. Overstreet (1969) and Velasquez (1975) considered *B. pseudovaricus* Velasquez, 1959 synonymous with *B. varicus*. Bray (1984) also considered that *B. retractilis* Yamaguti, 1959, *B. carangoides* Yamaguti, 1970 and *B. ulua* Yamaguti, 1970 are synonyms of *B. margaritae*. Nahhas et al. (2006) confirm this synonymy and described the worm from the cleftbelly trevally *Atropus atropos* (Bloch & Schneider), the largemouth queenfish *Scomberoides commersonnianus* Lacepède, the Malabar trevally *Carangoides malabaricus* (Bloch & Schneider), the whipfin silver-biddy *Gerres filamentosus* Cuvier and the pickhandle barracuda *Sphyraena jello* Cuvier in the Arabian Gulf off Kuwait. Chinchilla et al. (2006) accepted these synonymies, and described the worm from the southern sennet *Sphyraena picudilla* Poey off Venezuela. Marchiori et al. (2010) accepted the synonymy and described the life-cycle in the brown or South American rock mussel *Perna perna* (L.), the combtooth blenny *Hypleurochilus fissicornis* (Quoy & Gaimard) and the southern kingcroaker *Menticirrhus americanus* (L.) in the waters off Brazil. Many of the more recent records of *B. margaritae* are of non-carangid hosts. Al-Zubaidy (2011) described *B. margaritae* and *B. varicus* as separate species, from the great barracuda *Sphyraena barracuda* (Edwards) and the orange-spotted trevally *Carangoides bajad* (Forskål), respectively, from Yemeni Red Sea coastal waters off Hodeidah. The illustrations suggest that several species are involved. Nolan et al. (2015) used sequences of worms identified as *B. margaritae* from *Caranx cryos* (Mitchill), from the Gulf of Mexico in their molecular study and showed that, of sequenced species, it is the sister of *B. cynoscion* Hopkins, 1956. *Bucephalus margaritae* differs from *B. damriyasai* n. sp. in its relatively squat shape, short pre-vitelline distance, shorter pre-mouth distance and longer post-testicular distance and cirrus-sac reach. The species has been described many times under the same or different names and clearly needs careful revision. It is likely, if not virtually certain, that a complex of similar species is now known under this name.

*Bucephalus yamagutii* Gupta & Singh, 1985 is reported only from the Malabar trevally *Carangoides malabaricus* (Bloch & Schneider) (as *Caranx malabaricus*) off the Puri coast in the Bay of Bengal (Gupta & Singh, 1985). It is relatively broad (width about 16% of length), with a relatively short pre-vitelline distance (about 28% of body-length) and the caecum extends anteriorly to the pharynx, but not posteriorly. The rhynchus is said to carry five tentacles.

The features that distinguish marine *Bucephalus* spp. from *B. damriyasai* n. sp. are tabulated in Table 1.

### Concluding remarks

It is not clear why we have not been successful in securing useful DNA from this species as it was fixed in the same way as other digeneans recovered from the Bali Workshop that have been successfully sequenced (Cribb et al., 2014; Bray et al., 2016; Yong et al., 2016; Bray et al., 2017). Successful and experienced molecular biologists in the Rostock and the University of Queensland Laboratories have been frustrated in their attempts to extract DNA from these worms. The species described here is morphologically distinct enough to be easily recognised so it was felt worthwhile to describe it and add a further detail to our depauperate knowledge of the marine fish digeneans of Indonesia.

We are aware of eleven named species of bucephalids in Indonesian waters. These are:

- **Bucephalus damriyasai** n. sp. ex blacktip trevally *Caranx heberi* (Carangidae), off Bali.
- **Bucephalus margaritae** Ozaki & Ishibashi, 1934 (as *B. retractilis* Yamaguti, 1952) ex *Caranx* sp. (Carangidae), off Sulawesi (Yamaguti, 1952).
- **Bucephalus sphyraenae** Yamaguti, 1952 ex *Sphyraena* sp. (Sphyraenidae), off Sulawesi (Yamaguti, 1952).
- **Prosorhynchoides tenuis** (Yamaguti, 1952) ex Indian flathead *Platycephalus indicus* (L.) (Platycephalidae), off Sulawesi (Yamaguti, 1952).
- **Prosorhynchus chorinemi** Yamaguti, 1952 ex doublespotted queenfish *Scomberoides lysis* (Forskål) (Carangidae), off Sulawesi (Yamaguti, 1952).
- **Prosorhynchus longicollis** Yamaguti, 1953 ex *Sphyraena* sp. (Sphyraenidae), off Sulawesi (Yamaguti, 1953).
### Table 1 Comparative table of marine Bucephalus spp. Bold indicates major distinctions, italics indicates minor distinctions. Column 3: Width %; 4: Rhynchus length %; 6: Pre-vitelline distance %; 7: Pre-uterine distance %; 8: Pre-mouth distance %; 9: Post-testicular distance %; 10: Cirrus-sac reach %

| Species                  | Length  | 3       | 4       | Tentacle number | 6       | 7       | 8       | 9       | 10       | Eggs           | Source                          |
|--------------------------|---------|---------|---------|-----------------|---------|---------|---------|---------|---------|----------------|---------------------------------|
| **B. damriyasai** n. sp. | 851–1,544 | 8–10   | 6–8    | 7               | 37–42  | 33–55  | 63–69  | 17–22  | 22–28  | 18–25 × 13–19 | Present study                   |
| **B. anguillae** Špakulová, Macko, Berrilli & Dezfuli, 2002 | 1,118–1,658 | **27–29** | 17–18 | 7               | 21–37  | **16–17** | 54–60  | 22–28  | 34–42  | 28–30 × 18 | Špakulová et al. (2002)         |
|                          | 1,160–2,320 | **26–34** | 15–16 | 5               | 28     | **18**  | 57     | 15     | 26     | 20–34 × 10–18 | Gargouri-Ben Abdullah & Maamouri (2002) |
| **B. arabiansis** Dwivedi, 2007 | 1,020–1,530 | 17–35 | 10–16 | 5               | 12     | 13     | 68     | 23     | 44     | 20–30 × 10–30 | Dwivedi (2007)                  |
| **B. baeri** Maillard & Saad-Fares, 1981 | 1,320–2,640 | 15–17 | 10–13 | 7               | 32     | 17     | 45     | 22     | 28     | 24–27 × 14–16 | Maillard & Saad-Fares (1981)    |
| **B. barina** Srivastava, 1938 | 1,520–2,800 | **24–33** | 7–9    | 5               | 24     | 14     | 55     | 36     | 39     | 15–19 × 9–11 | Srivastava (1938)               |
| **B. binidentacularis** Wang, 1977 | 1,600 | **35**  | 11     | [? 6]           | 15     | 13     | 53     | 38     | 46     | 21–25 × 14–16 | Wang (1977)                     |
| **B. brevittentaculatus** Corkum, 1967 | 660–1,330 | **28–40** | 9–11   | 7               | 15     | 19     | 54     | 37     | **50** | 20 × 13 | Corkum (1967)     |
| **B. carangamys** Yamaguti, 1970 | 1,150–3,500 | 10–14  | 3–5    | 7               | 34     | 38     | 59     | 22     | 18     | 17–23 × 11–14 | Yamaguti (1970)                 |
| **B. carangoides** Yamaguti, 1970 | 1,000–1,650 | **35–44** | 14–17  | 7               | 21     | 12     | 56     | 39     | **43** | 16–21 × 10–14 | Yamaguti (1970)                 |
| **B. confusus** Velasquez, 1959 | **2,800** | 12.5   | 4      | **20**          | ?      | ?      | ?      | ?      | ?      | 24 × 13–18 | Linton (1940)                  |
| **B. cynoscion** Hopkins, 1956 | 600–1,400 | 17–34  | 8–16   | 5 (or 7)        | **13** | 8      | 57     | 30     | 32     | 20–25 × 13–15 | Hopkins (1956)                 |
| **B. elacatus** Yadav, 1977 | **4,160–5,120** | 13–15  | 2–3    | 4               | 36     | 25     | 53     | 18     | 23     | 24–25 × 9–11 | Yadav (1977)                   |
| **B. fischthali** Gupta & Tiwari, 1985 | **2,520–4,000** | 18–27  | 6–8    | 6               | 23     | 25     | 63–64 | 21–23 | 33     | 32–35 × 32–35 | Gupta & Tiwari (1985)           |
| **B. fragilis** Velasquez, 1959 | 660–900 | 15–26  | 6      | 7               | 27     | 33     | 59     | 27     | 30     | 17–18 × 9–13 | Velasquez (1959)               |
| **B. gorgon** (Linton, 1905) | 1,562–2,750 | 7–15   | 8–12   | 7               | 31–45  | 17–24  | 59–65  | 18–22  | 26–28  | 21–24 × 13–15 | Bartoli et al. (2005)           |
|                          | 1,650 | **22**  | 11     | **about 18**    | 29     | 45     | ?      | 16     | 34     | 22 × 14 | Linton (1905)     |
|                          | **2,380–3,130** | 11–14  | 7–10   | **about 20**    | 28     | 8–30  | ?      | ?      | ?      | 18–21 × 10–12 | Linton (1940)                  |
|                          | **2,238** | 12     | 9      | **22**         | 33     | 17     | 59     | 25     | 28     | ?      | Corkum (1967)     |
| **B. hainanensis** Shen, 1990 | 1,337–2,278 | **27–28** | 6–7    | 7               | 19     | 17     | 54     | 30     | 34     | 15–18 × 9–12 | Shen (1990)                    |
| **B. harpodontis** Wang, 1980 | 1,200–1,600 | 11     | 7      | 8               | 22     | 34     | **44** | 26     | 28     | 24–26 × 16–18 | Wang (1980)                    |
| **B. heterotentaculatus** Bravo-Hollis & Sogandares-Bernal, 1956 | **2,080–3,420** | 12–13  | 8–11   | 7               | 36     | 18     | 56–78  | 24     | 29     | 22–28 × 13–17 | Bravo-Hollis & Sogandares-Bernal (1956) |
| **B. hexalobatus** Bilqees, Khatoon & Haseeb, 2006a | **3,790–3,850** | **21–22** | ?      | ?               | ?      | ?      | ?      | ?      | ?      | 20–24 × 17–19 | Bilqees et al. (2006)           |
| **B. introverus** Manter, 1940 | 1,202–1,707 | 17–19  | 14–20  | 7               | 46     | 30     | 61     | 14     | 35     | 22–26 × 12–15 | Manter (1940a)                 |
Table 1 continued

| Species                        | Length       | Tentacle number | Eggs | Source                      |
|-------------------------------|--------------|-----------------|------|-----------------------------|
| **B. introversus** Manter, 1940 | 1,720–2,940  | 16 3–4          | 23 × 17 | Luque & Oliva (1993)       |
| **B. jagannathai** Verma, 1936  | 1,100–1,700  | **32–38** 11–15 | 19–20 × 12–13 | Verma (1936)               |
| **B. kaku** Yamaguti, 1970     | 1,500–4,700  | 11–13 6–7      | 21–25 × 12–16 | Yamaguti (1970)            |
| **B. kanagurtai** Gupta & Tiwari, 1985 | **3,200–3,570** | 26–27 7–8 | **40–70 × 40–70** (?) | Gupta & Tiwari (1985) |
| **B. kathetostomae** (Manter, 1934) | 688–1,434   | 20–49 12–21 5 | 18–20 × 10–11 | Manter (1934)              |
| **B. labracis** Paggi & Orecchia, 1965 | 1,980–3,310 | 11–14 10–11 | 20–21 × 18–19 | Paggi & Orecchia (1965)   |
| **B. leognathi** Velasquez, 1959 | 680          | 44 13 6 | 17–18 × 11–13 | Velasquez (1959)           |
| **B. margaritae** Ozaki & Ishibashi, 1934 | ?            | 19 8 7 | ?? | Sakaguchi (1968)            |
| **B. marinus** Vlasenko, 1931  | 2,000        | 10 12 ? | 19–20 × 8–11 | Al-Zubaidy (2011)          |
| **B. minimus** (Stossich, 1887) | 900          | 72 13 0? | not given          | Stossich (1887)            |
| **B. priacanthi** Manter, 1940  | 1,020–1,215  | 21 12 7 | 17–19 × 10–12 | Manter (1940b)             |
| **B. pseudovaricus** Velasquez, 1959 | 980–1,000   | 24–30 8 weak | 18–22 × 13–14 | Velasquez (1959)           |
| **B. retractilis** Yamaguti, 1952 | 1,400–1,950 | 21–23 7 | 15–16 × 10–12 | Yamaguti (1952)            |

**Note:** Eggs: 23 × 17, 19–20 × 12–13, 21–25 × 12–16, 20–21 × 18–19, 18–20 × 10–11, 22–24 × 13–15, 20–38 × 12–23, 19–24 × 9–10, 17–18 × 11–13, 20–22,5 × 10, 14–28 × 4(?)–19, 19–20 × 8–11, 24–25 × 11–18, 18–24 × 10–15, 20–25 × 17–22, 15–26 × 11–18, 17–19 × 10–12, 18–22 × 13–14, 15–16 × 10–12.
| Species                      | Length          | Tentacle number | Eggs               | Source                        |
|------------------------------|-----------------|-----------------|--------------------|-------------------------------|
| B. scorpaenae Manter, 1940   | 2,065–2,792     | 12–15           | 23                 | 19–22 × 13–15                 | Manter (1940b)                |
| B. sebastichthydis Yamaguti, 1959 | 3,450          | 13              | 31                 | 19–22 × 13–16                 | Yamaguti (1959)               |
| B. sexentaculatus Yamaguti, 1970 | 1,800–3,600    | 8–9             | 38                 | 16–21 × 11–16                 | Yamaguti (1970)               |
| B. solitarius Kohn, 1966     | 1,550           | 15              | 33                 | 19–22 × 11–13                 | Kohn (1966)                   |
| B. sphyraenae Yamaguti, 1952 | 2,500–2,800     | 12–16           | 37                 | 18–24 × 12–16                 | Yamaguti (1952)               |
| B. thapari Gupta & Tiwani, 1983 | 3,470–3,850    | 25–26           | 29                 | 16–18 × 16–18                 | Gupta & Tiwani (1985)         |
| B. trifurcatus Wang, 1980    | 2,400–2,480     | 10              | 23                 | 19–21 × 14–15                 | Wang (1980)                   |
| B. uluva Yamaguti, 1970      | 650–1,300       | 28–43           | 21                 | 14–21 × 9–14                  | Yamaguti (1970)               |
| B. uranoscopi Yamaguti, 1934 | 4,860           | 9               | 40                 | 18 × 22                       | Yamaguti (1934)               |
| B. urophyci Szidat, 1961     | 760             | 13              | 28                 | 19 × 10                       | Szidat (1961)                 |
| B. varicus Manter, 1940      | 705–1,458       | 9–28            | 20–25              | 17–20 × 9–16                  | Manter (1940a)                |
| B. xiamenensis Liu, 1994     | 1,620–2,180     | 10              | 21                 | 15–20 × 9–18                  | Al-Zubaidy (2011)             |
| B. yamagutii Gupta & Singh, 1985 | 1,460–1,570    | 16              | 14                 | 18–22 × 12–16                 | Liu (1994)                    |

*This species is unrecognisable; the illustrations are poorly reproduced microphotographs.*
Prosorhynchus luzonicus Velasquez, 1959 ex orange-spotted grouper Epinephelus coioides (Hamilton, 1822) (Serranidae), and brown-marbled grouper E. fuscoguttatus (Forsskål), off Sumatra and Java (Palm & Rückert, 2009; Rückert et al., 2009; Rückert et al., 2010; Kleinertz & Palm, 2015).

Prosorhynchus platycephali (Yamaguti, 1934) ex fringelip flathead Sunagocia otaitensis (Cuvier) (Platycephalidae), off Java (Bray & Palm, 2009).

Rhipidocotyle danai Bray & Palm, 2009 ex black snoek Thysritoides marleyi Fowler (Gempylidae), off Java (Bray & Palm, 2009).

Rhipidocotyle jayai Bray & Palm, 2009 ex largefin croaker Johnius macropterus (Bleeker) (Sciaenidae), off Java (Bray & Palm, 2009).

Rhipidocotyle khalili Nagaty, 1937 ex Sphyraena sp. (Sphyraenidae), off Sulawesi (Yamaguti, 1953).

Two further, as yet unnamed, species are found in Indonesian groupers:

Prosorhynchus sp. 1 of Bray & Palm (2009) (syn. Prosorhynchus australis of Rückert et al. (2009) and Palm & Rückert (2009)) from Epinephelus coioides, off Sumatra, E. fuscoguttatus, off Java and the areolate grouper E. areolatus (Forsskål), off Java (Palm & Rückert, 2009; Rückert et al., 2009; Rückert et al., 2010; Palm et al., 2011; Kleinertz et al., 2014; Kleinertz & Palm, 2015).

Prosorhynchus sp. 2 of Bray & Palm (2009) (Syn. Prosorhynchus cf. crucibulum (Rudolphi, 1819) of Palm & Rückert (2009)) ex Epinephelus fuscoguttatus, off Java and E. areolatus, off Bali (Rückert et al., 2009; Palm et al., 2011; Kleinertz et al., 2014).

Acknowledgements The new species was collected on the 1st Educational Workshop on Marine Fish Parasites in Bali, July 21st–August 2nd, 2013. This study falls under the MOU between the Faculty of Veterinary Sciences, UDAYANA University, Denpasar Bali, and the Professorship of Aquaculture and Sea-ranching, University Rostock, Germany (publication No. 12), to promote fish parasite research in Indonesia.

Funding This study was supported by the German Federal Ministry for Education and Science (BMBF Grant No. 03F0641D) within the framework of the joint Indonesian-German research programme SPICE III-MABICO (Science for the Protection of Indonesian Coastal Marine Ecosystems).
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