Diversity of trypanorhynch metacestodes in teleost fishes from coral reefs off eastern Australia and New Caledonia

Ian Beveridge1*, Rodney A. Bray2, Thomas H. Cribb3, and Jean-Lou Justine4

1 Veterinary Clinical Centre, University of Melbourne, Werribee, Victoria 3030, Australia
2 Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom
3 School of Biological Sciences, University of Queensland, Brisbane, Queensland 4072, Australia
4 ISYEB, Institut de Systématique, Évolution, Biodiversité (UMR7205 CNRS, EPHE, MNHN, UPMC), Muséum National d’Histoire Naturelle, CP 51, 55 rue Buffon, 75231 Paris Cedex 05, France

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Abstract – Trypanorhynch metacestodes were examined from teleosts from coral reefs in eastern Australia and from New Caledonia. From over 12,000 fishes examined, 33 named species of trypanorhyncs were recovered as well as three species of tentacularioids which are described but not named. Host-parasite and parasite-host lists are provided, including more than 100 new host records. Lacistorhynchoid and tentacularioid taxa predominated with fewer otobothrioid and gymnorhynchoids. Five species, Callitetrarhynchus gracilis, Floriceps minacanthus, Pseudotobothrium dipsacum, Pseudolacistorhynchus heroniensis and Ps. shipleyi, were particularly common and exhibited low host specificity. Limited data suggested a higher diversity of larval trypanorhynchs in larger piscivorous fish families. Several fish families surveyed extensively (Blenniidae, Chaetodontidae, Gobiidae, Kyphosidae and Scaridae) yielded no trypanorhynch larvae. The overall similarity between the fauna of the Great Barrier Reef and New Caledonia was 45%. Where available, information on the adult stages in elasmobranchs has been included.

Key words: Trypanorhyncha, Metacestodes, Great Barrier Reef, New Caledonia, Teleosts.

Résumé – Diversité des métacestodes de Trypanorhynques chez les téléostéens des récifs coralliens de l’est de l’Australie et de la Nouvelle-Calédonie. Les métacestodes de Trypanorhynques de téléostéens des récifs coralliens de l’est de l’Australie et de Nouvelle-Calédonie ont été examinés. À partir de plus de 12,000 poissons examinés, 33 espèces nommées de Trypanorhynques ont été collectées ainsi que trois espèces de Tentacularioidea qui sont décrites mais non nommées. Des listes hôtes-parasites et parasites-hôtes sont fournies, et incluent plus de 100 nouvelles mentions d’hôtes. Les taxa appartenant aux Lacistorhynchoidea et Tentaculariioidea étaient moins nombreux. Cinq espèces, Callitetrarhynchus gracilis, Floriceps minacanthus, Pseudotobothrium dipsacum, Pseudolacistorhynchus heroniensis et Ps. shipleyi étaient particulièrement fréquentes et montraient une faible spécificité d’hôte. Des données limitées suggèrent une plus grande diversité de Trypanorhynques larvaires dans les familles de poissons piscivores de grande taille. Plusieurs familles de poissons étudiées intensivement (Blenniidae, Chaetodontidae, Gobiidae, Kyphosidae et Scaridae) n’avaient pas de larves de Trypanorhynques. La similitude globale entre les faunes de la Grande Barrière de Corail et de la Nouvelle-Calédonie était de 45 %. Des informations sur les stades adultes chez des élasmostrachelques ont été incluses quand disponibles.

Introduction

The identification of significant threats to the coral reefs of the world [9, 17] has been partly responsible for focussing attention on the full diversity of reefs rather than simply on the diversity of fish and corals, the most obvious examples of reef diversity. The contributions of other groups of invertebrates to diversity on reefs have been largely overlooked in the past [7, 32]. Part of this “hidden” invertebrate diversity includes the endoparasites of vertebrates.

In recent years, teleost fish occurring on coral reefs have been recognised as harbouring a particularly diverse array of parasites [20]. Studies to date have focussed either on specific parasite groups such as the Monogenea (e.g. [33]) or Digenea (e.g. [13]), or more recently have examined the diversity of all
helminth parasites found in or on specific families of fish such as the Lethrinidae or Serranidae [21–23].

Teleosts found on coral reefs are commonly infected with the larval stages (plerocerci, merocerci or plerocercoids – for terminology see Chervy, 2002 [12]) of cestodes of the order Trypanorhyncha, the adults of which are found in the stomach or spiral valves of elasmobranchs. Larval stages occur most commonly in the body cavity but may also be found in the musculature or other sites such as the gill arches [27]. They constitute a significant component of parasite diversity but have frequently been overlooked because of taxonomic difficulties in identification [27]. However, unlike other orders of cestodes found in marine fish, the larval stages have scolex features, including the distinctive tentacular armature, which are identical to those found in the adult and which allow specific morphological identification. Although taxonomic studies of this group of parasites are frequent, ecological studies are few, and while systematic collecting has been undertaken in several parts of the world (Gulf of Mexico, Gulf of California, Java, Borneo, Australia and Hawaii), there are few published descriptions of the faunas encountered in these areas (see Jensen, 2009 [19] for Gulf of Mexico and Palm and Bray, 2014 [29] for Hawaii). Some species of trypanorhynchs (e.g. Grillotia (Christianella) minuta van Beneden, 1858; Gilquinia squali Fabricius, 1794) have also been used as biological tags in teleosts [25] because the larval stages are readily identifiable and because they are long-lived in the intermediate host. However, such ecological studies of these species are limited.

In this study, we examined the larval trypanorhynch cestode parasites of teleosts, and where applicable the corresponding adults in elasmobranchs, from the Great Barrier Reef (GBR) and compared them with those from similar reef environments in New Caledonia (NC). New Caledonia is separated from the GBR by about 1200 km of deep oceanic waters.

**Materials and methods**

**Great Barrier Reef (GBR)**

Teleosts and elasmobranchs were collected opportunistically between 1986 and 2010. The two main collecting sites were Heron Island in the southern Great Barrier Reef and Lizard Island in the Northern Barrier Reef. Small numbers of parasites were collected on reefs between these two sites (Mossman, Townsville) and in these instances, the nearest geographical feature on the coast was recorded rather than the specific reef near which the collection was made (Fig. 1).

Metacestodes were collected mainly from body cavities of teleosts, although in some instances they were sought in regions of the body such as the gill arches and musculature. Metacestodes were removed from surrounding cysts (in the case of plerocerci) and the eversion of tentacles was achieved either by shaking vigorously or by applying pressure under a coverslip. Cestodes were fixed in 70% ethanol or 10% formalin and were stained with Celestine blue or carmine (Palm, 2004) [27], dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam. All specimens were identified by IB and have been deposited in either the British Museum (Natural History) (BMNH), the Queensland Museum, Brisbane (QM) or the South Australian Museum, Adelaide (SAM). Some of the records used in this compilation have been published previously in Beveridge & Campbell, 1996, 2001 [1, 3], Beveridge et al., 2000, 2007 [4, 5], Campbell & Beveridge, 1996 [8], Palm, 2004 [27], Palm & Beveridge, 2002 [28] and Sakanari, 1989 [34].

Records of adults from elasmobranchs are included only for species in which larval stages have been identified in teleosts; these are based on both published data and specimens held in museum collections. Additional species of trypanorhynch cestodes from elasmobranchs have been found and their larval stages may be found in the future, but for the present study, these records have not been added.

**New Caledonia (NC)**

Fish were collected opportunistically between 2003 and 2009 generally by line fishing, occasionally by spear fishing and on occasions supplemented by fish obtained from a market. Collections were mainly off Nouméa (Fig. 1). All fish were measured, weighed and photographed. Methods for collection from several host families have been explained elsewhere [21–23]. Trypanorhynch plerocerci were opened and compressed between two slides or immersed in hot saline to evert tentacles. Plerocercoids found in the body cavity were also fixed under pressure to evert tentacles. Metacestodes were fixed in 70% ethanol or 10% formalin and were stained with Celestine blue or carmine (Palm, 2004) [27], dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam. All specimens were identified by IB and have been deposited in the Muséum national
Results

Species found and other data

Larval trypanorhynchs were recovered primarily from the body cavities of the teleosts examined (Figs. 2–7). Plerocerci were usually encountered attached to the mesentery enclosed within white envelopes (Fig. 2), although in some hosts melanisation of the cyst wall had occurred rendering the cysts brown (Fig. 3). Some brown or even black envelopes contained only remnants of plerocerci (Fig. 4). Plerocercoids of tentaculariids were found either in the body cavity or in the gastrointestinal lumen; the latter were not contained within a "cyst". Occasionally, plerocerci were found in the musculature and in the gill arches (Fig. 7), although there was no systematic search of such sites for plerocerci. Merocerci of *Molonica hordidas* occurred in the livers of a limited number of species of teleosts, but the intensity of infection was high and the infections were readily observable at autopsy (Fig. 6).

Species of larval trypanorhynch cestodes found in both teleost (as larvae) and elasmobranch (as adult) hosts at sites along the GBR and off NC are shown in Tables 1 and 2.

From the GBR, the specimens examined were obtained from the dissection of more than 9000 fish, although not all were specifically examined for trypanorhynch cestodes. Likewise, from NC, approximately 3800 fish were examined but the body cavity was not examined in every fish, as explained by Justine et al. [21–23]. Consequently, prevalence data were available for some species only and abundance data were not available; for most species only presence-absence data were available (with one exception from Lizard Island).

No trypanorhynch metacestodes were found in the families Blenniidae (*n* = 215), Chaetodontidae (*n* = 1638), Gobiidae (*n* = 183), Kyphosidae (*n* = 30) and Scaridae (*n* = 147) from the GBR. Likewise, no metacestodes were found in the families Atherinidae (*n* = 13), Apogonidae (*n* = 19), Echeneidae (*n* = 10) and Haemulidae (*n* = 10) in NC. In addition, although the families Serranidae, Lethrinidae and Lutjanidae were frequently infected with trypanorhynch metacestodes, this pattern was not uniform across all species within these families and in NC, no trypanorhynch metacestodes were found in *Epinephelus areolatus* (*n* = 12), *E. merro* (*n* = 18), *Leithrinus atkinsoni* (*n* = 12), *L. nebulosus* (*n* = 14), *Lutjanus fulviflamma* (*n* = 10) and *L. kasmira* (*n* = 14).

Members of the Tentacularioidea differ from other trypanorhynch metacestodes as they are present as plerocercoids (= post-larvae) rather than plerocerci [14] and may be found in intestinal contents as well as in the viscera. In New Caledonia, tentacularioids were frequently found in smaller schooling fishes, often being the only trypanorhynchs encountered in these fishes.

In total, 33 named species were found (Tables 1 and 3) as well as three species of tentaculariid cestodes to which no current name could be applied. Lacistorhynchoid and tentacularioid trypanorhynchs dominated the fauna in terms of numbers of species recovered (Table 3), with the otobothrioid and gymnorhynchoid trypanorhynchs being less numerous.

Prevalence data were obtained from 182 fish from various families collected during a single collecting trip to Lizard Island. The prevalence of trypanorhynch larvae was: 4/6 (77%) in scombrids, 5/7 (71%) in lethrinids, 2/13 (15%) in lutjanids, 8/9 (89%) in serranids and 1/109 (0.9%) in apogonids. Other fish families were represented by smaller numbers and were excluded.

Tentacularioid metacestodes of uncertain identity

Superfamily Tentacularioidae Poche, 1926

Family Tentaculariidae Poche, 1926

1. *Nybelinia* sp. A (Fig. 8)

Material examined: plerocercoids from *Herklotsichthys quadrimaculatus* (Rüppell, 1937), New Caledonia, MNHN JNC2669C1, 2671A1.

Scolex length 1200, pars bothralis 580, pars vaginals 520; bulbs ovoid, bulb length 250; velum 160; metabasal hooks: length 15, base 10.

Remarks

This species is similar to *N. queenslandensis*, but all measurements including those of the hooks are substantially smaller. In addition, the shape of the hooks differs (Fig. 8). The hook shape aligns the species with *N. lingualis* (Cuvier, 1817), *N. bisulcata* (Linton, 1889), *N. anthicosum* Heinz & Dailey, 1974 and *N. hemipristis* Palm & Beveridge, 2002, but *N. lingualis* and *N. bisulcata* differ in having much larger scoleces (2025–2700 and 2500, respectively) and bulbs (365–425 and 450–505, respectively) while the latter two species have much larger hooks (25–40). Consequently, these
Table 1. Parasite-host list. Species of trypanorhynch cestodes collected from teleosts and elasmobranchs on the Great Barrier Reef, Australia and from New Caledonia. Authorities of cestodes are included and host species are listed in alphabetical order without authorities.

| Authoritative | Great Barrier Reef | New Caledonia |
|---------------|-------------------|---------------|
| **GYMNORHYNCHOIDEA** | | |
| Molicola horridus (Goodsir, 1841) | | |
| Larval | Diodon hystrix | H QM G206954, SAM 44079 |
| | | Diodon hystrix MNHN JNC2977D1, 3199C |
| | Diodon liturosus* | L QM G232552 |
| Pterobothrium lintoni MacCallum, 1916 | | |
| Larval | Choerodon venustus | H SAM 40480 |
| Pterobothrium acanthotrunccatum Escalante & Carvajal, 1984 | | |
| Larval | Plectropomus maculatus* | H QM G217640 |
| | Scomberomorus commerson | H, L QM G217628 |
| Adult | Pristis zijsron* | Tv G SAM 35749 |
| Pterobothrium australiense Campbell & Beveridge, 1996 | | |
| Larval | Halichoeres trimaculatus* | H QM G217629 |
| Adult | Pristis zijsron | Tv SAM 23898 |
| Pterobothrium pearsoni (Southwell, 1929) | | |
| Larval | Sphyraena jello* | L QM G233646 |
| **LACISTORHYNCHOIDEA** | | |
| Bombycirhynchus sphaerenaicum (Pintner, 1930) | | |
| Larval | Sphyraena jello* | L QM G233583 |
| **Callitetrarhynchus gracilis** (Rudolphi, 1819) | | |
| Larval | Abudadfuf whitleyi* | H QM G212162 |
| | Apogon poecilopterus* | H QM G217587 |
| | Caesto cuning* | H QM G217593 |
| | Cephalopholis miniata | H QM G232625 |
| | Cephalopholis cyanostigma* | H, L QM G217575 |
| | Cheroodon cyanodus* | H BM 1980.7.10.148-9 |
| | Cromileptes altivelis* | H QM G217592 |
| | Johnius borneensis* | H QM G217602 |
| | Lotella rhacina* | H QM G217574 |
| | Lutjanus carponotatus* | L QM G233588 |
| | Johnius borneensis* | H QM G217602 |
| | Epinephelus fasciatus* | L QM G233588 |
| | Epinephelus retouti* | MNHN JNC2977D1, 3199C |

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| Table 1. (continued) |
|----------------------|
|                      | Great Barrier Reef | New Caledonia          |
| **Naso vlamingii**    | H QM G217598       | *Lethrinus miniatus*   |
|                      | MNHN JNC2113A      |                       |
| **Ostorhinchus fasciatus** | H QM G217486     | *Lutjanus vitta*       |
|                      | MNHN JNC1186, 1188 |                       |
| **Plectropomus maculatus** | H QM G217641     | *Megalaspis cordyla*   |
|                      | MNHN JNC2596       |                       |
| **Polyenemus hepatus** | H QM G217591       | *Nemipterus furcatus*  |
|                      | MNHN JNC435        |                       |
| **Pomatomus saltatrix** | H QM G217583       | *Scomberomorus commerson* |
|                      | MNHN JNC2984       |                       |
| **Scomberomorus commerson** | H, L QM G212163   | *Triodon macropterus*  |
|                      | MNHN JNC2984       |                       |
| **Scomberomorus queenslandicus** | H QM G217588   | *Variola louti*        |
|                      | MNHN JNC2596       |                       |
| **Sphyraena obtusata** | H QM G217590       |                       |
|                      |                       |                       |
| **Adult**             |                       |                       |
| **Carcharhinus melanosilus** | H QM G217581   | *Carcharhinus leucas*  |
|                      | MNHN JNC2856       |                       |
|                      |                       |                       |
| **Carcharhinus amblyrhynchoideis** |                       |                       |
|                      |                       |                       |
| **Callitetrarhynchus speciosus** (Linton, 1897) |                       |                       |
| **Larval**            |                       |                       |
| **Dasyiurhynchus basipunctatus** (Carvajal, Campbell & Cornford, 1976) |                       |                       |
| **Fistula commersonii** | H QM G232633       | *Abalistes filamentosus* |
|                      | MNHN JNC2193       |                       |
|                      |                       | *Abalistes stellatus*  |
|                      | MNHN JNC2163, 2926, 2914 |                       |
|                      |                       | *Diodon hystrix*       |
|                      | MNHN JNC2977       |                       |
|                      |                       | *Lagocephalus sceleratus* |
|                      | MNHN JNC2942       |                       |
|                      |                       | *Pseudobalistes fuscus* |
|                      | MNHN JNC1680E, 2164, 2940 |                       |
|                      |                       | *Triodon macropterus*  |
|                      | MNHN JNC2989       |                       |
|                      |                       |                       |
| **Adult**             |                       |                       |
| **Carcharhinus brachyurus** | L QM G232540   | *Carcharhinus amblyrhynchos* |
|                      | MNHN JNC435, 1111 |                       |
|                      |                       | *Carcharhinus plumbeus* |
|                      | MNHN JNC442        |                       |
|                      |                       |                       |
| **Diesingium et lomentaceum** (Diesing, 1850) |                       |                       |
| **Larval**            |                       |                       |
|                      |                       | *Carangoides fulvoguttatus* |
|                      | MNHN JNC3169       |                       |
|                      |                       | *Epinephelus chlorostigma* |
|                      | MNHN JNC3142       |                       |
|                      |                       |                       |
| **Floreces minacanthus** Campbell & Beveridge, 1987 |                       |                       |
| **Larval**            |                       |                       |
| **Cephalopholis boenak** | H QM G212151–3     | *Cephalopholis miniata* |
|                      | MNHN JNC2627       |                       |
| **Cephalopholis cyanostigma** | L QM G233613     | *Cephalopholis sonnerati* |
|                      | MNHN JNC2934, 2935, 2936, 3029 |                       |
| **Cephalopholis miniata** | H QM G217615       | *Cephalopholis urodeta* |
|                      | MNHN JNC3257       |                       |
| **Epinephelus quoyanus** | H SAM 44083       | *Epinephelus coioides* |
|                      | MNHN JNC3198       |                       |
| **Euthynnus affinis** | H QM G217612, 7   | *Epinephelus cyanopodus* |
|                      | MNHN JNC1998       |                       |
| **Euthynnus alleteratus** | H SAM 44082       | *Epinephelus maculatus* |
|                      | MNHN JNC2937, 3061, 3062, 3066 |                       |
| **Grumamocytas bicarinatus** | H, L QM G217613 | *Lethrinus miniatus* |
|                      | MNHN JNC2706A      |                       |
| **Lethrinus miniatus** | H QM G233554       | *Nemipterus furcatus*  |
|                      | MNHN JNC3019       |                       |
| **Lethrinus macroplatus** | L QM G233626       | *Plectropomus leopardus* |
|                      | MNHN JNC2585A      |                       |
| **Plectropomus areolatus** | H, L QM G217611, SAM 32139 | *Plectropomus laevis* |
|                      | MNHN JNC1887       |                       |
| **Plectropomus leopardus** | H QM G217616       | *Sphyraena putnamae*  |
|                      | MNHN JNC3035       |                       |
| **Sphyraena flavicauda** | H QM G233610       | *Tylosurus crocodilus* |
|                      | MNHN JNC1262C, 1263A |                       |
| **Sphyraena jello**   | H QM G217614       | *Variola louti*        |
|                      | MNHN JNC1859B, 3037 |                       |

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| Table 1. (continued) | Great Barrier Reef | New Caledonia |
|----------------------|-------------------|--------------|
| **Adult** Carcharhinus amboinensis | StL³ SAM 22652 | Carcharhinus leucas* MNHN |
| | | Triaenodon obesus* MNHN |
| **Florileps saccatus** (Cuvier, 1817) | | |
| **Larval** | | |
| Diodon hystrix | H SAM 44081 | Caranx papuensis* MNHN JNC3209 |
| Diodon liturosus* | L QM G232554 | Diodon hystrix MNHN JNC22343, 2977, 3199 |
| **Grillotiella exile** (Linton, 1909) | | |
| **Larval** | | |
| Scomberomorus commerson | L QM G233632 | Galeocerdo cuvier MNHN JNC1414 |
| **Adult** Microbothriorynchus coelorhynchi Yamaguti, 1952 | | |
| **Larval** | | |
| Lethrinus atkinsoni* | L QM G233653 | Lethrinus miniatus* MNHN JNC2113 B1, 2158C |
| Lethrinus nebulosus* | L QM G233654 | |
| **Pseudogilquinia microbothri** (MacCallum, 1917) (= Ps. magna; = Dasyrhynchus magna) **Larval** | | |
| Lethrinus atkinsoni | L QM G233653 | Epinephelus coioides MNHN JNC1535, 3140, 3265B |
| Lethrinus miniatus | H BM 2004.3.18.98-99 | Plectropomus laevis MNHN JNC1865, 1887 |
| Lethrinus nebulosus | L QM G233653 | Epinephelus malabaricus MNHN JNC1536 |
| **Pseudogilquinia pillersi** (Southwell, 1929) | | |
| **Larval** | | |
| Lethrinus atkinsoni | H BM 2004.3.18.97 | |
| Lethrinus miniatus | L QM G233653 | |
| Lethrinus nebulosus | | |
| Plectropomus leopardus | H QM G212146 | Abalistes filamentosus* MNHN JNC2724 |
| | | Abalistes stellatus* MNHN JNC2163, 2914, 2926 |
| | | Cephalopholis boenak MNHN JNC2288, 2890, 3205 |
| | | Cephalopholis sonnerati* MNHN JNC2934 |
| | | Gymnocranius grandoculis* MNHN JNC1726 |
| | | Epinephelus chlorostigma MNHN JNC2446C, 3141 |
| | | Epinephelus coioides* MNHN JNC3257 |
| | | Epinephelus cyanopodus [20]² |
| | | Epinephelus fasciatus MNHN JNC1636A, 1758, 1791, 1792, 3039 |
| | | Epinephelus howlandii* MNHN JNC2768 |
| | | Epinephelus polyphekadion MNHN JNC1915C, 3036 |
| | | Epinephelus rivulatus MNHN JNC1545C |
| | | Lethrinus miniatus* MNHN JNC2161C |
| | | Lutjanus vitta* [22]² |
| | | Plectropomus leopardus MNHN JNC3279 |
| | | Pseudobalistes fuscus* MNHN JNC2164, 2940B |
| | | Stegostoma fasciatum MNHN JNC1529 |

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| Table 1. (continued) | Great Barrier Reef | New Caledonia |
|----------------------|-------------------|--------------|
| **Pseudolacistorhynchus shipleyi** (Southwell, 1929) (= Grillotia overstreeti Sakanari, 1989) | | |
| Larval | | |
| Cephalopholis boenak* | H QM G232626 | Cephalopholis sonnerati* | MNHN JNC3032 |
| Cephalopholis cyanostigma* | H, L QM G214957 | Cephalopholis urodeta | [20] |
| Choerodon cyanodon | H SAM 17416, QM G212160 | Epinephelus polyhekaidion* | MNHN JNC3036 |
| Choerodon fasciatus* | H QM G217519 | Sufflamen fraenatus* | MNHN JNC1421C, 1797, 1798A, 1946, 2928, 3034 |
| Epinephelus ongus* | H QM G212161 | Epinephelus ongus* | MNHN JNC3275 |
| Lotella rhacina* | H QM G214995 | | |
| Rhinecanthus aculeatus* | L QM G232542 | | |
| Sufflamen fraenatus* | H QM G217520 | | |
| **OTOBOTHRIOIDEA** | | |
| **Otobothrium alexanderi** Palm, 2004 | | |
| Larval | | |
| Tylosurus crocodilus | L QM G232555 | Tylosurus crocodilus | MNHN JNC1968 |
| **Otobothrium parvum** Beveridge & Justine, 2007 | | |
| Larval | | |
| | | Epinephelus maculatus* | MNHN JNC1405 |
| | | Lethrinus rubrioperculatus* | MNHN JNC1635A |
| | | Carcharhinus amblyrhynchos | MNHN JNC1111 |
| | | Triakodon obesus | MNHN JNC2109 |
| **Otobothrium penetrans** Linton, 1907 | | |
| Larval | | |
| | | Tylosurus crocodilus | MNHN JNC1968 |
| **Proemotobothrium southwelli** Beveridge & Campbell, 2001 | | |
| Larval | | |
| **Johnius borneensis** | H QM G217939 | | |
| **Pseudotobothrium dipsacum** (Linton, 1897) | | |
| Larval | | |
| Abalistes stellatus | H QM G217928–32 | Abalistes filamentosus* | MNHN JNC2724 |
| Cephalopholis cyanostigma | H QM G214959 | Abalistes stellatus | MNHN JNC2914 |
| Cheilinus trilobatus | L QM G233555 | Cephalopholis miniata* | MNHN JNC2627 |
| Epinephelus coioides | Tv SAM 31342 | Cephalopholis sonnerati* | MNHN JNC1616, 2934–6 |
| Lethrinus obsoletus | H QM G233888 | Cephalopholis urodeta | MNHN JNC2750 |
| Latjumas gibbus | L QM GL 10508 | Cymbacephalus beauforti* | MNHN JNC1833A |
| Naso vlamingii | H QM G214960 | Epinephelus coioides | MNHN JNC1535, 3257 |
| Plectropomus leopardus | H, L QM G217936 | Epinephelus fasciatus* | MNHN JNC1791, 3039 |
| Plectropomus maculatus | H QM G206964 | Epinephelus malabaricus | [20] |
| Pseudocaranx dentex | H QM G214961 | Epinephelus retouti* | MNHN JNC2179 |
| Rhinecanthus aculeatus | L QM G232590 | Plectropomus laevis* | MNHN JNC1865, 1887 |
| Rhinecanthus rectangularis | H QM G217934 | Plectropomus leopardus | MNHN JNC2126 |
| | | Pseudobalistes fuscus* | MNHN JNC2927, 2940 |
| | | Variola louti | MNHN JNC1629, 1662, 1756–7, 1859, 2116–7, 2301, 3037, 3069 |

(continued on next page)
| Specimen | Great Barrier Reef | New Caledonia |
|----------|------------------|---------------|
| **Symbothriorhynchus tigaminacanthus** | | |
| Palm, 2004 | | |
| Larval | Nemipterus furcosus* | MNHN JNC2586, 2610 |
| | Saurida undosquamis* | MNHN JNC2079 |
| | Sphyra lewini | MNHN JNC1628 |
| Adult | | |
| TENTACULARIOIDEA | | |
| **Hepatoxyton trichiuri** | | |
| Larval | Diodon hystrix* | MNHN JNC2977, 3199D |
| | Tetrapterus angustirostris* | MNHN JNC1399 |
| | Thunnus obesus* | MNHN JNC1398 |
| Adult† | | |
| **Heteronybelinia estigmena** (Dollfus, 1960) | | |
| Larval | Sarda australis | H QM G218042–6 |
| | Atule mate* | MNHN JNC2963–5 |
| | Herklotsichthys quadriraculatus* | MNHN JNC2669B, 2673, 2943, 2949 |
| | Selar crumenophthalmus | MNHN JNC3043–4, 3126 |
| | Sphyraena putnamae* | MNHN JNC3035 |
| | Trichiurus lepturus* | MNHN JNC3045–6, 3048 |
| Adult | Carcharhinus sp. | Qld SAM 18322 |
| **Heteronybelinia sp. C** | | |
| Larval | Safflamen fraenatus | MNHN JNC3034 |
| **Myxonybelinia southwelli** (Palm & Walter, 1999) | | |
| Larval | Choerodon venustus | H QM G218062 |
| | Stegostoma fasciatum | MNHN JNC1529 |
| Adult | Dendrochirus zebra* | QM G218031 |
| **Nybelinia aequidentata** Shipley & Homell, 1906 | | |
| Larval | | |
| **Nybelinia basimegacantha** Carvajal, Campbell & Cornford, 1976 | | |
| Larval | Parupeneus bifasciatus* | L QM G232545 |
| | Neoniphon sammara* | MNHN JNC2552 |
| | Parupeneus multifasciatus | MNHN JNC2111 |
| **Nybelinia goreensis** Dollfus, 1960 | | |
| Larval | Lethrinus genivittatus* | MNHN JNC2033 |
| | Lethrinus rubrioculatus* | MNHN JNC1148 |
| | Nemipterus furcosus | MNHN JNC2612 |
| | Parupeneus barberinus* | MNHN JNC1838B |
| | Parupeneus multifasciatus* | MNHN JNC2112 |

(continued on next page)
| Table 1. (continued) | Great Barrier Reef | New Caledonia |
|----------------------|---------------------|---------------|
| **Nybelinia indica** Chandra, 1986 |
| (= *Nybelinia scoliodoni* Vijayalakshmi, Vijayalakshmi & Gangadharam, 1996) |
| Larval | Diodon hystrix | H QM G218034–41 |
| | Caranx sexfasciatus | MNHN JNC3194 |
| | Diodon hystrix | MNHN JNC2977F |
| | Lagocephalus sceleratus* | MNHN JNC2982 |
| | Leiognathus fasciatus* | MNHN JNC2921 |
| | Nemipterus furcosus* | MNHN JNC2288, 2611, 3016 |
| Adult | Taeniura lymma | H SAM 17646 |
| | Triaenodon obesus* | MNHN JNC2109B1 |
| **Nybelinia queenslandensis** Jones & Beveridge, 1998 |
| Larval | Ostorhinchus cookii* | H QM G232539 |
| | Ostorhinchus properuptus* | L QM G2336644 |
| Adult | Carcharhinus melanopterus | H, L QM G217521–31 |
| **Nybelinia strongyla** Dollfus, 1960 |
| Larval | Johnius borneensis | H QM G218109 |
| **Nybelinia sp. A** |
| Larval | | |
| **Nybelinia sp. B** |
| Larval | | |

† Reported in the literature from Australia but outside the region of the Great Barrier Reef.
* New host records.
A Heron Island, Great Barrier Reef.
B Lizard Island, Great Barrier Reef.
C Queensland Museum, Brisbane.
D Muséum national d’Histoire naturelle, Paris.
E South Australian Museum, Adelaide.
F British Museum, Natural History, London.
G Townsville, Queensland.
H Snapper Island, Mossman.
I St Lawrence, Queensland.
J Published report not supported by museum specimen.
Table 2. Species of trypanorhynch cestodes collected from teleosts on the Great Barrier Reef, Australia and from New Caledonia. Authorities of fish are included and cestodes are listed in alphabetical order without authorities. GBR: Great Barrier Reef; NC: New Caledonia.

| Order          | Family         | Host species                | Parasites                                                | Location |
|----------------|----------------|-----------------------------|----------------------------------------------------------|----------|
| Anguilliformes | Congridae      | Conger cinereus Rüppell, 1830 | Microbothriorhynchus coelorhynchi                        | NC       |
|                |                |                             | Symbiotheriorhynchus tigaminacanthus                     | NC       |
|                |                |                             | Floriceps minacanthus                                   | GBR, NC  |
|                |                |                             | Otobothrium alexandri                                  | GBR, NC  |
|                |                |                             | Otobothrium penetrans                                   | NC       |
|                |                |                             | Nybelinia basingegantha                                  | NC       |
| Aulopiformes   | Synodontidae   | Saurida undosquamis (Richardson, 1848) | Symbothriorhynchus tigaminacanthus                      | NC       |
| Beloniformes   | Belonidae      | Tylosurus crocodilus (Pérón & Lesueur, 1821) | Otobothrium alexandri                                  | NC       |
|                |                |                             | Otobothrium penetrans                                   | NC       |
|                |                |                             | Nybelinia sp. A                                         | NC       |
|                |                |                             | Callitetrarhynchus granilis                             | GBR      |
| Beryciformes   | Holocentridae  | Neoniphon sammara (Forsskål, 1775) | Callitetrarhynchus granilis                             | GBR      |
| Clupeiformes   | Chirocentridae | Chirocentrus dorab (Forsskål, 1775) | Callitetrarhynchus granilis                             | NC       |
|                | Clupeidae      | Herklotsichthys quadrimaculatus (Rüppell, 1837) | Heteronybelinia estigmena                               | NC       |
| Gadiformes     | Moridae        | Lotella rhacina (Forster, 1801) | Callitetrarhynchus granilis                             | GBR      |
| Perciformes    | Acanthuridae   | Naso vlamingii (Valenciennes, 1835) | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Apogonidae     | Apogon poecilopterus Cuvier, 1828 | Pseudotobothrium dipsacum                               | GBR      |
|                |                |                             | Nybelinia basingegantha                                  | NC       |
|                |                |                             | Callitetrarhynchus granilis                             | GBR      |
|                |                |                             | Heteronybelinia estigmena                               | NC       |
| Carangidae     | Atule mate (Cuvier, 1833) |                             | Callitetrarhynchus granilis                             | GBR      |
|                |                |                             | Heteronybelinia estigmena                               | NC       |
|                |                |                             | Callitetrarhynchus granilis                             | NC       |
|                |                |                             | Dieningsium cf lomentacum                                | NC       |
|                |                |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                |                |                             | Pseudotobothrium dipsacum                               | GBR      |
|                |                |                             | Nybelinia indica                                         | NC       |
|                |                |                             | Callitetrarhynchus granilis                             | GBR      |
|                |                |                             | Floriceps saccatus                                       | NC       |
|                | Megalaspis cordyla (Linnaeus, 1758) |                             | Callitetrarhynchus granilis                             | GBR      |
|                | Pseudocaranx dentex (Bloch & Schneider, 1801) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Selar crumenophthalmus (Bloch, 1793) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Tetrapterus angustirostris Tanka, 1915 |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
| Labridae       | Cheilinus trilobatus (Lacépède, 1801) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Halichoeres trimaculatus (Quoy & Gaimard, 1834) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Choerodon cyanodus (Richardson, 1843) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Choerodon fasciatus (Günther, 1867) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Choerodon venustus (De Vis, 1884) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Leiogathus fasciatus (Lacépède, 1803) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
| Leiognathidae  | Leiognathus atkinsoni Seale, 1910 |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lethrinus atkinsoni Seale, 1910 |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
| Lethrinidae    | Lethrinus atkinsoni Seale, 1910 |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lethrinus genivittatus Valenciennes, 1830 |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lethrinus miniatus (Forster, 1801) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lethrinus nebulosus (Forsskål, 1775) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lethrinus obsoletus (Forsskål, 1775) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lethrinus rubrioperculatus Sato, 1978 |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Gymnocranius grandoculis (Valenciennes, 1830) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
| Lutjanidae     | Caesio cuning (Bloch, 1791) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lutjanus carponotatus (Richardson, 1842) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lutjanus gibbus (Forsskål, 1775) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
|                | Lutjanus vittae (Quoy & Gaimard, 1824) |                             | Pseudolacistorhynchus shipileyi                         | GBR      |
| Order     | Family                | Host species                        | Parasites                           | Location |
|-----------|-----------------------|-------------------------------------|-------------------------------------|----------|
| Mullidae  | *Parupeneus barberinus* (Lacépède, 1801) | *Nybelinia goreensis*               | NC                                  |          |
|           | *Parupeneus bifasciatus* (Lacépède, 1801) | *Nybelinia basimegacantha*          | GBR                                 |          |
|           | *Parupeneus multifasciatus* (Quoy & Gaimard, 1825) | *Nybelinia basimegacantha*          | NC                                  |          |
|           |                       | *Nybelinia goreensis*               | NC                                  |          |
|           |                       | *Nybelinia sp. B*                   | NC                                  |          |
| Nemipteridae | *Nemipterus furcatus* (Valenciennes, 1830) | *Callitetrarhynchus gracilis*      | NC                                  |          |
|           |                       | *Floriceps minacanthus*             | NC                                  |          |
|           |                       | *Nybelinia indica*                  | NC                                  |          |
|           |                       | *Nybelinia goreensis*               | NC                                  |          |
|           |                       | *Nybelinia queenslandensis*         | NC                                  |          |
|           |                       | *Symbothriorhynchus tigamucanthis*  | NC                                  |          |
| Polynemidae | *Polynemus heptadactyla* (Cuvier, 1829) | *Callitetrarhynchus gracilis*      | GBR                                 |          |
| Pomacentridae | *Abudefdyf whitleyi* Allen & Robertson, 1974 | *Callitetrarhynchus gracilis*      | GBR                                 |          |
| Pomatomidae | *Pomatomus saltatrix* (Linnaeus, 1766) | *Callitetrarhynchus gracilis*      | GBR                                 |          |
| Sciaenidae | *Johnius borneensis* (Bleeker, 1851) | *Callitetrarhynchus gracilis*      | GBR                                 |          |
|           |                       | *Nybelinia strongyla*               | GBR                                 |          |
|           |                       | *Proemotobothrium southwelli*       | GBR                                 |          |
| Scombridae | *Euthynnus affinis* (Cantar, 1849) | *Callitetrarhynchus gracilis*      | GBR, NC                             |          |
|           | *Euthynnus allletteratus* (Rafinesque, 1810) | *Callitetrarhynchus gracilis*      | GBR                                 |          |
|           | *Grammatocyclus bicornatus* (Quoy & Gaimard, 1825) | *Callitetrarhynchus gracilis*      | GBR, NC                             |          |
|           | *Sarda australis* (Maclay, 1881) | *Heteronybelinia estigma*           | GBR                                 |          |
|           | *Scomberomorus commerson* (Lacépède, 1800) | *Callitetrarhynchus gracilis*      | GBR, NC                             |          |
|           |                       | *Grillostella exile*                | GBR                                 |          |
|           |                       | *Ptero bothrium acanthotracatum*    | GBR                                 |          |
|           | *Scomberomorus queenslandicus* Munro, 1943 | *Callitetrarhynchus gracilis*      | GBR                                 |          |
|           |                       | *Hepatoxyron trichiuri*             | NC                                  |          |
| Serranidae | *Cephalopholis boenak* (Bloch, 1790) | *Callitetrarhynchus gracilis*      | NC                                  |          |
|           |                       | *Floriceps minacanthus*             | NC                                  |          |
|           |                       | *Pseudolacistorhynchus heroniensis* | NC                                  |          |
|           |                       | *Pseudolacistorhynchus shiplei*     | GBR                                 |          |
|           | *Cephalopholis cyanostigma* (Valenciennes, 1828) | *Callitetrarhynchus gracilis*      | GBR, NC                             |          |
|           |                       | *Floriceps minacanthus*             | GBR                                 |          |
|           |                       | *Pseudolacistorhynchus shiplei*     | GBR                                 |          |
|           |                       | *Floriceps minacanthus*             | GBR                                 |          |
|           | *Cephalopholis miniata* (Forsskål, 1775) | *Pseudolacistorhynchus heroniensis* | GBR, NC                             |          |
|           | *Cephalopholis sonnerati* (Valenciennes, 1828) | *Pseudolacistorhynchus shiplei*     | GBR                                 |          |
|           |                       | *Pseudolacistorhynchus heroniensis* | GB, NC                              |          |
|           | *Cephalopholis spiloparanea* (Valenciennes, 1828) | *Pseudolacistorhynchus shiplei*     | GBR, NC                             |          |
|           | *Cephalopholis urodet* (Schneider, 1801) | *Pseudolacistorhynchus shiplei*     | GBR                                 |          |
|           |                       | *Pseudolacistorhynchus shiplei*     | GBR, NC                             |          |
|           | *Cromileptes alvelis* (Valenciennes, 1828) | *Callitetrarhynchus gracilis*      | GBR                                 |          |
|           | *Epinephelus cooides* (Hamilton, 1822) | *Dasyrhyhanchus pacificus*          | NC                                  |          |
|           |                       | *Floriceps minacanthus*             | NC                                  |          |
|           |                       | *Pseudogilquinia pillersi*          | NC                                  |          |
|           | *Epinephelus chlorostigma* (Valenciennes, 1828) | *Pseudolacistorhynchus heroniensis* | NC                                  |          |
|           |                       | *Dasyrhyhanchus pacificus*          | NC                                  |          |
|           |                       | *Diesingium cf lomentaceum*         | NC                                  |          |
|           |                       | *Pseudolacistorhynchus heroniensis* | NC                                  |          |
|           | *Epinephelus cyanopodus* (Richardson, 1846) | *Floriceps minacanthus*             | NC                                  |          |
|           |                       | *Pseudolacistorhynchus heroniensis* | NC                                  |          |

(continued on next page)
| Order                  | Family                                | Host species                  | Parasites                          | Location |
|------------------------|---------------------------------------|-------------------------------|------------------------------------|----------|
| Epinephelus fasciatus  | Callitetrarhynchus gracilis           | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudotobothrium dipsacum             | NC                            |                                    |          |
| Epinephelus houlandi   | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Floriceps minacanthus                 | NC                            |                                    |          |
| Epinephelus maculatus  | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
| Epinephelus malabaricus| Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus shipleyi        | GBR, NC                        |                                    |          |
| Epinephelus ongus      | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus shipleyi        | GBR, NC                        |                                    |          |
| Epinephelus retouti    | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus shipleyi        | GBR, NC                        |                                    |          |
| Epinephelus quoyanus   | Callitetrarhynchus gracilis           | NC                            |                                    |          |
| Epinephelus rivulatus  | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus shipleyi        | GBR                            |                                    |          |
| Plectropomus areolatus | Floriceps minacanthus                 | NC                            |                                    |          |
|                        | Pseudotobothrium dipsacum             | NC                            |                                    |          |
| Plectropomus leopardus | Floriceps minacanthus                 | NC                            |                                    |          |
|                        | Pseudotobothrium dipsacum             | NC                            |                                    |          |
| Sphyraenidae           | Sphyraena flavicauda                  | GBR                            |                                    |          |
|                        | Sphyraena jello Cuvier, 1829           | GBR                            |                                    |          |
|                        | Bombycirhynchus sphaerenaicum         | GBR                            |                                    |          |
|                        | Floriceps minacanthus                 | GBR                            |                                    |          |
| Sphyraena obtusata     | Callitetrarhynchus gracilis           | GBR, NC                        |                                    |          |
|                        | Pseudolacistorhynchus heroniensis     | GBR                            |                                    |          |
|                        | Pseudolacistorhynchus shipleyi        | GBR                            |                                    |          |
|                        | Pterobothrium acanthotruncatum        | GBR                            |                                    |          |
| Syngnathiformes        | Fistulariidae                         | NC                            |                                    |          |
|                        | Fistularia commersonii                | GBR                            |                                    |          |
|                        | Sphyraena patmamae Jordan & Seale, 1905| NC                            |                                    |          |
|                        | Heteronybelinia estigmata             | NC                            |                                    |          |
| Tetraodontiformes      | Balistidae                            | NC                            |                                    |          |
|                        | Abalistes filamentosus Matsuura & Yoshino, 2004 | NC                  |                                    |          |
|                        | Dasyrhynchus basipunctatus            | GBR                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis NC  | NC                            |                                    |          |
|                        | Pseudotobothrium dipsacum             | NC                            |                                    |          |
| Abalistesstellatus     | Dasyrhynchus basipunctatus            | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis NC  | NC                            |                                    |          |
|                        | Pseudotobothrium dipsacum             | NC                            |                                    |          |
| Pseudobalistes fuscus  | Dasyrhynchus basipunctatus            | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis NC  | NC                            |                                    |          |
| Rhinecanthus aculeatus | Pseudolacistorhynchus shipleyi        | GBR                            |                                    |          |
|                        | Pterobothrium acanthotruncatum        | GBR                            |                                    |          |
| Rhinecanthus rectangulus| Pseudolacistorhynchus heroniensis     | NC                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis NC  | NC                            |                                    |          |
|                        | Pterobothrium acanthotruncatum        | GBR                            |                                    |          |
| Sphyraenidae           | Sphyraena flavicauda                  | GBR                            |                                    |          |
|                        | Sphyraena jello Cuvier, 1829           | GBR                            |                                    |          |
|                        | Floriceps minacanthus                 | GBR                            |                                    |          |
|                        | Pseudolacistorhynchus heroniensis     | GBR                            |                                    |          |
|                        | Pterobothrium acanthotruncatum        | GBR                            |                                    |          |
|                        | Heteronybelinia estigmata             | NC                            |                                    |          |
| Diodontidae            | Diodon hystrix Linnaeus, 1758          | NC                            |                                    |          |
|                        | Floriceps saccatus                    | GBR                            |                                    |          |
|                        | Hepatoxylon trichiuri                 | GBR                            |                                    |          |
|                        | Molicola horridus                     | GBR                            |                                    |          |
|                        | Nybelinia indica                      | GBR                            |                                    |          |
|                        | Pterobothrium acanthotruncatum        | GBR                            |                                    |          |

(continued on next page)
Table 2. (continued)

| Order     | Family          | Host species                       | Parasites                     | Location |
|-----------|-----------------|------------------------------------|-------------------------------|----------|
| Tetraodontidae |                |                                    |                               |          |
|           | Lagocephalus sceleratus (Gmelin, 1789) |                                    | Dasyrhynchus basipunctatus    | NC       |
|           | Nybelinia indica |                                    | Nybelinia indica              | NC       |
|           | Dasyrhynchus basipunctatus |                                    | Dasyrhynchus basipunctatus    | NC       |
| Scorpaeniformes | Platycephalidae | Cymbacephalus beauforti (Knapp, 1973) | Callitetrarhynchus gracilis    | NC       |
|           | Scorpaenidae    | Dendrochirus zebra (Cuvier, 1829) | Pseudotobothrium dipsacum     | NC       |
| Scorpaenidae |                |                                    | Nybelinia aequidentata         | NC       |

Figures 2–7. Metacestodes of trypanorhynch cestodes from teleost fishes. 2. Viable plerocerci of Callitetrarhynchus gracilis in the body cavity of Scomberomorus commerson. 3. Melanised trypanorhynch plerocerci in the body cavity of Epinephelus sp. 4. Melanised and contracted cysts of trypanorhynch metacestodes in the body cavity of Cephalopholis miniata; no viable plerocerci were recovered from these cysts. 5. Plerocerci of Pseudogilquinia spp. (arrows) around the oesophagus of Lethrinus nebulosus. 6. Merocerci of Molicola horridus in the liver of Diodon hystrix. 7. Plerocerci of Grillotiella exile in the gill arches of Scomberomorus commerson (histological section).
plerocercoids most closely resemble *N. lingualis* but cannot be assigned to this species with certainty.

2. *Nybelinia* sp. B (Fig. 9)

Material examined: plerocercoid from *Parupeneus multifasciatus* (Quoy & Gaimard, 1825), New Caledonia, MNHN JNC2172 C4.

Scolex length 1750, pars bothrialis 1100, pars vaginalis 1000, bulbs elongate, 560 long, velum 200, metabasal hooks: length 20, base 14.

Remarks

This specimen most closely resembles *N. strongyla* Dollfus, 1960 in scolex length, bulb length and hook size and shape, but differs in the length of the velum (690–830 in *N. strongyla* compared with 200 in the present material).

3. *Heteronybelinia* sp. C (Fig. 10)

Material examined: plerocercoid from *Safflamen fraenatus* (Latreille, 1804), New Caledonia, MNHN JNC3034.

Scolex length 1440, pars bothrialis 770, pars vaginalis 680, bulbs elongate, bulb length 375, velum 125, metabasal hooks on botharial surface: length 17–19, base 8; on bothrial surface: length 25, base 18; basal armature heteromorphous.

Remarks

This specimen clearly belongs to *Heteronybelinia* as the hooks differ markedly in shape on the bothrial versus the anti-bothrial surfaces of the tentacle. Hook sizes are closest to *H. eureia* (Dollfus, 1960), but the specimen differs from this species in the number of hooks per half spiral and by the fact that in this specimen the bulbs are entirely posterior to the pars bothrialis while in *H. eureia*, they do not extend beyond the pars bothrialis. Therefore, this specimen cannot be accommodated within any known species of *Heteronybelinia*.

4. *Nybelinia basimegacantha* Carvajal, Campbell & Cornford, 1976 (Fig. 11)

Material examined: plerocercoid from *Parupeneus multifasciatus* (Quoy & Gaimard, 1825), New Caledonia, MNHN JNC2111 C1; plerocercoid from *Neoniphon sammara* (Forskal, 1775), New Caledonia, MNHN JNC2552.

Specimen from *P. multifasciatus*: Scolex length 2600, pars bothrialis 1400, pars vaginalis 900, bulb length 1060, bulb width 130, velum 90.

Specimen from *N. sammara*: Scolex length 1380, pars bothrialis 840, pars vaginalis 350; bulb length 450, bulb width 70, velum 70.

Remarks

Two specimens have been identified as belonging to this species with its characteristic armature. In spite of the fact that the armature of both specimens is identical, scolex measurements differed substantially and for this reason, the measurements of both specimens are presented. The specimen from *P. multifasciatus* although quite flattened, corresponds more closely with the original description of the species, also from *P. multifasciatus* from Hawaii [10]. In the specimen from *N. sammara*, all measurements are shorter but the tentacular armature is identical.

### Discussion

#### General comments

Although the records of trypanorhynch infections listed here are based on the dissection of thousands of fish from both the GBR and NC, the data collected are based on opportunistic collecting and must be viewed in this light. Few prevalence or intensity data were collected and the data are based largely on the presence of trypanorhynch metacestodes. Fish examined that did not harbour metacestodes were not included in the data presented in the tables but representative examples have been indicated in the results.

In spite of these limitations, the large numbers of metacestodes collected from both regions provide a significant basis for comparing trypanorhynch metacestodes of teleosts inhabiting coral reefs.

Several features are evident from the data presented. In spite of potential differences in the fish faunas between the two regions examined and possible biases in sampling approaches, an extremely large number of fish specimens (thousands) was examined at each locality and even though the methods of examination varied to some degree, the study encompassed a wide range of fish families at both sites. Overall, 45% of the trypanorhynch species recorded here occurred in both regions. In addition, the trypanorhynch species most commonly encountered were similar in both locations. Records of adults from elasmobranchs from both of these regions provided additional information on potential life cycles and the collection included numerous new host and geographical records.

#### Host specificity

Notwithstanding the opportunistic nature of the collecting, several aspects of host specificity are detectable within the data set and are worthy of discussion particularly since Palm & Carra, 2008 [30] have shown that specificity of the larval stages of trypanorhynchas is generally lower than that of the adults. First, it is evident that several fish taxa were rarely infected with trypanorhynchs. Thus, despite examination of substantial...
numbers of Blenniidae, Chaetodontidae, Gobiidae, Kyphosidae and Scaridae, no trypanorhyncs were found in these taxa. Other taxa strikingly underrepresented, though heavily sampled, were the Acanthuridae, Pomacentridae and Echeneidae. We do not suggest that these taxa have been exhaustively examined, but certainly they are depauperate relative to families such as the Balistidae, Lethrinidae, Scombridae and Serranidae.

Among the teleost fishes that were infected, there was evidence of both stenoxenicity (parasitism of closely related

Figures 8–11. Tentacularioid metacestodes incompletely identified. 8. Nybelinia sp. A from Herklotsichthys quadriraculatus (Rüppell, 1937). Scolex, basal and metabasal armature, hook profiles. Scale-bars: scolex and tentacle, 0.1 mm; hooks, 0.01 mm. 9. Nybelinia sp. B from Parupeneus multifasciatus (Quoy & Gaimard, 1825). Scolex, basal and metabasal armature, hook profiles. Scale-bars: scolex and tentacle, 0.1 mm; hooks, 0.01 mm. 10. Heteronybelinia sp. C from Sufflamen fraenatus (Latreille, 1804). Scolex, bothrial metabasal armature and antibothrial metabasal armature. Scale-bars: scolex 0.1 mm; hooks 0.01 mm. 11. Nybelinia basimegacantha Carvajal, Campbell & Cornford, 1976, specimen from Neoniphon sammara (Forsskål, 1775). Scolex, basal and metabasal armature. Scale-bars: scolex 0.1 mm; tentacle 0.01 mm.
species) and euryxenicity (parasitism of distantly or ecologically related species). In the stenoxenous category, *Molicola horditis* was seen in two species of Diodontidae, *Pterobothrium australiense* has been only in labrids (one record), *Pseudogilquinia microbothria* was found only in lethrinids (both in NC and the GBR) and *Dasyrhyynchus basipunctatus* occurred overwhelmingly in tetraodontiforms (five species) although also once in a fustularid. The apparently restricted distributions of such species are doubtless subject to refinement with further collecting but it seems highly unlikely that they will prove to be euryxenous in the same way as are some other species.

We detected some evidence of the absence of trypanorhynch species in particular fish groups. The best evidence comes from the family Serranidae which is probably the most thoroughly characterised for its trypanorhynch fauna. The serranid fishes collected tend to be large and easily examined for trypanorhynchs with which they are often heavily infected. Our results incorporate reports from 25 serranid species and of the 181 host/parasite combinations detected, 55 were from serranids; the next highest number of combinations came from the Lethrinidae with 14. The extent to which the characterisation of this family is comprehensive is demonstrated by the fact that six of the ten trypanorhynch species recorded in this family have been reported from more than one serranid species; three species were found in ten or more serranid species although four species were found in only one. We infer that the true trypanorhynch richness is thus not likely to be very much greater than the 10 species reported so far in this region.

Thus, we predict that species that have been reported relatively frequently in other fishes are genuinely absent, rather than have simply not yet been collected. Most striking in this respect are the species of the Lentacularioidea. Twelve species of this superfamily are reported here in 34 host/parasite combinations, but none in serranids. The apparent absence of a range of species from the Serranidae thus appears consistent with the high host specificity seen for the species described above.

Several species showed remarkably low specificity. Thus, *Callitetrarhynchus gracilis* was reported here from five fish orders and 18 families, *Floriceps minacanthus* from two orders and six families, *Pseudobothrium dipsacum* from three orders and six families, *Pseudolacistorhynchus heroniensis* from two orders and four families and *Pseudolacistorhynchus shipleyi* from three orders and five families. The absence of any detectable specificity in these species leads to the prediction that further sampling will lead to even larger host ranges for these species.

*Callitetrarhynchus gracilis* exhibited the widest host range and has a cosmopolitan distribution [27] with carcharhinid sharks as its primary definitive hosts in the Australian region [1]. Currently recorded in the intermediate stage from approximately 130 species of teleosts [16, 27, 29], 23 new host records have been added in the present study.

*Floriceps minacanthus* appears to be limited to the Indo-Pacific region, and again, its known definitive hosts are carcharhinid sharks [26], with adults having been reported from four species of *Carcharhinus*. However, the present record in *Trienodon obesus* is the first from a shark not belonging to this genus. Plerocerci have been reported from 13 species of teleosts [27, 29] from the Red Sea, Australia and off Indonesia and Hawaii while 14 new species of teleosts are reported here as hosts.

*Pseudobothrium dipsacum* was also found in a wide variety of teleosts. It has previously been reported from numerous species of teleosts ranging from the west coast of Africa to Australia [4, 27]. Eight new hosts, all from New Caledonia, have been added in the present study. In spite of its wide host range and distribution, its definitive hosts remain unknown.

*Pseudolacistorhynchus heroniensis* is known only from the GBR and from NC but is found in a wide range of teleosts, with 12 new teleost hosts being added in the current study. The only record of the adult parasite is a single collection from *Stegostoma fasciatum* from New Caledonia [6]. The specimens collected were either immature or hyperapolytic such that some doubt exists as to whether this is the usual definitive host species.

*Pseudolacistorhynchus shipleyi* occurs widely in the Indo-West Pacific, with the adults being found in *Nebrius ferrugineus* off Sri Lanka [2]. In the current study, eleven new intermediate host records are reported.

The above five species occurred in a wide variety of teleost hosts with serranids (25 species), carangids (5), balistids (5), scrombids (5) and sphyraenids (5) being most frequently encountered. The same five species of trypanorhynch were the most commonly encountered species both on the Great Barrier Reef and off New Caledonia in spite of obvious differences in the species of fish infected at the two localities. There was no intentional bias in collecting activities, but it may have been that more of these larger fishes were collected than other smaller taxa.

Other species of trypanorhynch had a more restricted host distribution. Limited data on prevalence based on a single series of collections from Lizard Island suggested that trypanorhynch larvae were prevalent in larger fishes (serranids, sphyraenids, scrombids, lutjanids) but in small fish (a single family, Apogonidae) they occurred at a very low prevalence. However, these data were based on a very small sample of fish and need to be interpreted with caution.

Overall, the patterns of host specificity seen here, a mixture of stenoxenicity and euryxenicity, resemble that reported by Chambers et al., 2000 [11] for tetraphyllidean (*sensu lato*) metacestodes of GBR fishes. In that study, metacestode Type 4 was found in two orders and 12 families, whereas Types 9 and 10 were found only in labrids. However, in the study of tetraphyllidean metacestodes it is often not possible to be confident that a single morphotype represents only one species whereas the complex morphology of trypanorhynch scoleces makes identification to species quite reliable.

**Biogeography**

Of the 33 trypanorhynch species reported here, 15 (45%) were found both in NC and on the GBR. Almost certainly this number underestimates the level of sharing between the two areas. Noticeably, the nine species reported in the largest number of host/parasite combinations were all found at both sites. Of the 21 species found in only one or two host/parasite combinations, only one (*Molicola horditis*) was found both in NC and on the
GBR. It seems likely, or at least possible, that some species are restricted to one or other of the two sites but at present the evidence is generally marginal in this respect. The only robust parasitological study of which we are aware that has previously compared parasites of NC and the GBR is that of McNamara et al., 2012 [26] who analysed monorchiid trematodes of chaetodontids from NC and the GBR (as well as other sites in the Tropical Indo-West Pacific [TIWP]). Thirteen species of Hurleytrematoides Yamaguti, 1953 were found in total for the two sites of which just six were found at both sites for a similarity of 46%; four species were found only from the GBR and three only from NC. In every case, hosts suitable for the species not found in each area had been examined in numbers sufficient to suggest that they would have been found if present. The proportion of monorchiid species shared (46%) is thus remarkably similar to that for the trypanorhynchs. Given the much stricter restriction of monorchiid species shared (46%) is thus remarkably similar to that for the trypanorhynchs.

Of the species found, eight (C. gracilis, F. saccatus, Gr. exile, Heph. trichiuri, Het. estigmia, M. horridus, N. goreensis, O. penetrans) have a cosmopolitan distribution, based on records in Palm, 2004 [27], while ten species are widely distributed in the Tropical Indo-West Pacific (TIWP) (D. pacificus, F. minacanthus, N. basimegacantha, N. indica, Psgi. microbothria, Psgi. pillersi, D. basipunctatus, Psl. shipleyi, Psl. dipsacum, Pt. acanthotruncatum). By contrast, seven species occur only in south-east Asia and Australasia (N. queenslandensis, O. alexanderi, O. purvum, Psl. heroniensis, Psl. nanus, Pt. australiensis, S. tigaminacanthus). Several additional species (e.g. Pt. lintoni) with few, highly disjunct records are difficult to categorise. Nevertheless, with many of the trypanorhynch species encountered having extremely wide geographical distributions [31], it was not surprising that the species found on the GBR and from NC were broadly similar.

Localisation in host

Apart from potential differences in the species of fish present at the two sites studied, or their abundance and hence ease of obtaining a particular species, other factors may be involved such as the location of trypanorhynch metacestodes in the body of the teleost. Most are found in the body cavity and are easily recognised. However, the metacestodes of Gr. exile occur only in the gill arches of Sc. commerson [35] and this site is not always examined for the presence of metacestodes. Similarly, the metacestodes of Psgi. microbothria cluster around the oesophagus of L. nebulosus (unpublished) while those of Pt. lintoni are found in the musculature (unpublished). Failure to examine sites other than the body cavities may lead to differences in the species recovered.

Life cycles

Combining the data obtained here with that available for adult trypanorhynchs in elasmobranchs in the same region has provided some insights into life cycles such as finding the adult of Pt. acanthotruncatum for the first time in Pristis zijsron. In addition, the definitive host range of F. minacanthus is expanded to include the shark Triaenodon obesus. Many life cycles remain to be identified, but broad scale collecting, such as that undertaken in this study, can be useful in identifying both potential intermediate and definitive hosts.

Species of Diodon warrant a particular mention as they are parasitised by several well-recognised trypanorhynch species including Floriceps saccatus and Mollusca horridus. Infections with the latter species are particularly striking as much of the hepatic parenchyma may be replaced by metacestodes (Fig. 5). Species of Diodon are not only highly toxic [36], but can also inflate their bodies when threatened. As adults of these cestodes are found in large sharks such as Prionace glauca (Linnaeus, 1758) (see Dollfus, 1942) [14], it is tempting to assume that only large sharks are able to consume species of Diodon. Alternatively, it may be that the life cycles of these cestodes are completed using alternative intermediate hosts and their presence in species of Diodon indicates an occurrence in “dead-end” hosts. By comparison, in a study of the larval anisakid nematodes of teleosts off Lizard Island, Jabbar et al., 2012 [18] found no larval anisakids in their sample of tetraodontiform fishes, which would potentially be “dead-end” hosts for these nematodes.

Conclusion

This is the first study to attempt to examine the trypanorhynch larval cestode fauna of coral reef teleosts in the west Pacific, examining reefs on the GBR and NC. The trypanorhynch fauna was dominated numerically by a small number of species at both sites with considerable similarity between the two localities examined. Although large numbers of teleosts were examined at both sites, it is most unlikely that the trypanorhynch fauna has been exhaustively surveyed and more detailed comparisons must await much more extensive sampling. Nevertheless, apart from characterising the general features of the fauna, this study has provided additional insights into host specificity and life cycles of these cestode parasites.

Conflict of Interest

The Editor-in-Chief of Parasite is one of the authors of this manuscript. COPE (Committee on Publication Ethics, http://publicationethics.org/), to which Parasite adheres, advises special treatment in these cases. COPE wrote: “Editors should not be denied the ability to publish in their own journal, but they must not exploit their position. The journal must have a procedure for handling submissions from the editor or members of the editorial board that ensures that peer review is handled independently of the author/editor. This process should be detailed once the paper is published.” In this case the peer-review process was handled by Invited Editor Dominique Vuitton.

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