Host Specificity and Ecology of Digenean Parasites of Nassariid Gastropods in Central Queensland, Australia, with Comments on Host-Parasite Associations of the Nassariidae

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INTRODUCTION

The Nassariidae Iredale, 1916 (1835) is a large family of marine gastropods containing approximately 442 valid extant species [1] in the Superfamily Buccinoidea Rafinesque, 1815 of the Order Neogastropoda [2]. Nassariids are primarily carnivorous scavengers and are found predominantly in estuarine or shallow marine soft substrates [3].

Digenean trematode parasites typically have a three host life cycle, involving a vertebrate definitive host and two intermediate hosts; the first intermediate host is most often a mollusk [4]. The parasite fauna of only...
a relatively small number of the 442 species of nassariid gastropods has been thoroughly studied (see Table 1); these gastropods include *Tritia obsoleta* (Say) [syn. *Ilyanassa obsoleta* (Say); *Nassarius obsoletus* (Say)], an intertidal gastropod found along the east and west coasts of North America [5], and *Tritia reticulata* (Linnaeus) [syn. *Nassarius reticulatus* (Linnaeus)], common to the north-eastern Atlantic and the Mediterranean, Black, and Azov Seas [6].

The Nassariidae is well represented in Australia [7], with *Nassarius dorsatus* (Röding), *Nassarius olivaceus* (Bruguière), and *Nassarius pullus* (Linnaeus) common inhabitants in the intertidal mangroves of the Capricornia region in Central Queensland, Australia. Knowledge of larval digenean fauna infecting gastropods in Australian marine environments is broadly lacking. To date, few surveys of the digenean fauna in marine gastropods have been conducted in Australia, and only one comprehensive taxonomic survey of the cercariae of a gastropod species has been undertaken. A study of *Clypeomorus batillariaeformis* Habe and Kosuge reported infections with cercariae of eleven species in eight families [8]. This study aimed to document and characterize the trematode fauna infecting *N. dorsatus*, *N. olivaceus*, and *N. pullus* in mangroves in Central Queensland, Australia.

**MATERIALS AND METHODS**

Host gastropod and parasite collection. Gastropods were collected by hand from mudflats at Sandy Point, Corio Bay (22°58′ S, 150°46′ E), Ross Creek, Yeppoon (23°8′ S, 150°45′ E), and the mouth of Cawarral Creek, Keppel Sands (23°19′ S, 150°47′ E) in Central Queensland, Australia. Totals of 1766 *N. pullus* (4.3% of 1614) were collected (no *N. olivaceus* or *N. dorsatus*). Previous reports in the literature were collated to provide a list of cercariae reported from nassariid gastropods (see Table 1) and to derive a matrix of families reported from nassariids (see Table 2).

**RESULTS**

Cercariae of 12 species from six families were found from *N. olivaceus*, *N. dorsatus*, and *N. pullus* (Table 3). Of these, six were attributed to the family Acanthocolpidae Lühn, 1906 and comprised three unusual cercariae and three similar to known *Stephanostomum* spp. cercariae. Of the others, there was one species of each of the families Lepocreadiidae Odhner, 1905, Opecoelidae Ozaki, 1925, Zoogonidae Odhner, 1902, and Microphallidae Ward, 1901 and two of the family Himasthliidae Odhner, 1910 (both were morphologically similar to reported Himasthla spp.). The cercariae from the Lepocreadiidae, Microphallidae, and Himasthliidae and one of the *Stephanostomum* sp. cercaria are yet to be formally described.

A total of 115 infections were identified by cercarial emergence from the 5288 gastropods observed, and a further eleven were identified by dissection. Of the 1667 gastropods dissected, 16 infections were found, four in *N. dorsatus* and 12 in *N. olivaceus*. Of these, 11 were able to be identified as the opecoelid cercaria, whereas the four infections in *N. dorsatus* and one in *N. olivaceus* could not be identified by dissection as the cercariae were too immature and the rediae were not sufficiently distinctive.

Cercariae of eight species were found only in a single gastropod species and only four infected more than one host species (Table 3). No cercaria infected all three species studied. Of the four infections with two host species, three involved *N. olivaceus* and *N. dorsatus* (the acanthocolpids *Cercaria capricornia* III and *Cercaria capricornia* VII (a *Stephanostomum* sp.), and the lepocreadiid cercaria) and the other involved *N. olivaceus* and *N. pullus* (one himasthiid cercaria). For the two-host species, there was generally a higher prevalence of infection in one nassariid species than in the other. For the acanthocolpid *C. capricornia* III, infection was more prevalent in *N. olivaceus* (0.4%) than in *N. dorsatus* (<0.1%). Similarly, the lepocreadiid cercaria was more...
Table 1. Digenean parasites (cercariae) reported from nassariid gastropods.

| Host species                | Parasite family      | Parasite species                                                                 | Region                      | Sources |
|-----------------------------|----------------------|----------------------------------------------------------------------------------|-----------------------------|---------|
| Family Nassariidae          |                      |                                                                                  |                             |         |
| Subfamily Buccinanopsinae   |                      |                                                                                  |                             |         |
| *Buccinanops cochlidium*    | Lepocreadiidae       | *Opechona* sp.                                                                   | South America               | [44]    |
| (Dillwyn)                   |                      |                                                                                  |                             |         |
| *Buccinanops globulosus*    | Zoogonidae           | *Diptherostomum* sp.                                                              | South America               | [45]    |
| (Kienener)                  |                      |                                                                                  |                             |         |
| *Buccinanops monilifer*     | Lepocreadiidae       | *Opechona* sp.                                                                   | South America               | [44,46] |
| (Kienener)                  |                      |                                                                                  |                             |         |
| Subfamily Bullinae          | Microphallidae       | *Cercaria hastata* [Webb, 1991]                                                 | South Africa, Atlantic & Indian Oceans | [47,48] |
| *Bullia digitalis*          | Zoogonidae           | *Cercaria hapax* [Brown & Webb, 1994] [probable *Zoogonoides* sp.]                |                             |         |
| (Dillwyn)                   |                      | *Cercaria bulliae* [Brown & Webb, 1994] [uncertain placement, tailless cercaria]  |                             |         |
| Subfamily Nassariinae       | Cyathocotylidae      | *Longifurcate-pharyngeate cercaria* [Cyathocotylidae]                            | Indian Ocean                | [49]    |
| *Nassarius arcularia plicatus* | Opecoelidae         | *Cotylomicrocerous cercaria* [Opecoelidae]                                     |                             |         |
| (Röding)                    |                      |                                                                                  |                             |         |
| *Nassarius circumcinctus*   | Lepocreadiidae       | *Cercaria levantina* [2 Lengy & Shchory, 1970]                                   | Indian Ocean & Mediterranean Sea | [30]    |
| (A. Adams)                  |                      |                                                                                  |                             |         |
| *Nassarius dorsatus*        | Acanthocolpidae      | *Cercaria capricornia* [I Barnett, Smales & Cribb, 2008]                          | Pacific Ocean               | [10,31] |
| (Röding)                    |                      | *Cercaria capricornia* [VI Barnett, Smales & Cribb, 2008]                         |                             |         |
|                             |                      | *Cercaria capricornia* [VII Barnett, Miller & Cribb, 2010] [probable *Stephanostomum* sp.] |                             |         |
| *Nassarius olivaceus*       | Acanthocolpidae      | *Cercaria capricornia* [I Barnett, Smales & Cribb, 2008]                          | Pacific Ocean               | [10,31,33,43] |
| (Bruguière)                 |                      | *Cercaria capricornia* [III Barnett, Smales & Cribb, 2008]                        |                             |         |
|                             |                      | *Cercaria capricornia* [III Barnett, Smales & Cribb, 2008]                        |                             |         |
|                             |                      | *Cercaria capricornia* [VII Barnett, Miller & Cribb, 2010] [probable *Stephanostomum* sp.] |                             |         |
| *Nassarius orissaensis*     | Acanthocolpidae      | *Cercaria capricornia* [XII Barnett & Miller, 2014]                               | Indian Ocean                | [50,51] |
| (Preston)                   |                      |                                                                                  |                             |         |
|                             | Opecoelidae          | *Cercaria cloacum* [Srivastava, 1938] Manter & Van Cleave, 1951                   |                             |         |
|                             | Zoogonidae           | *Cercaria chilkaensis* II, Madhavi & Shameem, 1991                               |                             |         |
### Table 1. cont’d

| Nassarius protrusidens  | Opecoelidae | Cotylomicro cercous cercaria 1 | Indian Ocean | [49] |
|-------------------------|-------------|--------------------------------|--------------|-----|
| Nassarius stolatus (Gmelin) | Acanthocolpidae | Cercaria bengalensis VII Gna Mani, 1994 [similar to Stephanostomum spp.] | Indian Ocean | [52] |
| Phrontis vibex (Say) [syn. Nassarius vibex (Say)] | Himasthidae | Himasthla quissetensis (Miller & Northup, 1926) Stunkard, 1938 | Caribbean Sea | [34,53,54] |
| Phrontis vibex (Say) | Acanthocolpidae | Cercaria bengalensis | | |
| Phrontis vibex (Say) [syn. Nassarius vibex (Say)] | Lepocreadiidae | Lepocreadium album (Stossich, 1890) Stossich, 1903 | North Atlantic | [44,55-58] |
| Tritia corniculum (Oliv) [syn. Nassarius mutabilis (Linnaeus)] | Lepocreadiidae | Lepocreadium album (Stossich, 1890) Stossich, 1903 | North Atlantic | [55,56,58-61] |
| Tritia mutabilis (Linnaeus) | Lepocreadiidae | Lepocreadium album (Stossich, 1890) Stossich, 1903 | North Atlantic | [55,56,58-61] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Lepocreadiidae | Lepocreadium album (Stossich, 1890) Stossich, 1903 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Acanthocolpidae | Stephanostomum tenuis (Linton, 1898) Linton, 1934 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Diplostomidae | Stephanostomum dentatum (Linton, 1900) Linton, 1940 [syn. Cercaria diperocercata Miller & Northup, 1926] | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Himasthidae | Diplostomum massa (Martin, 1945) Stunkard, 1973 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Lepocreadiidae | Himasthla quissetensis (Miller & Northup, 1926) Stunkard, 1938 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Microphallidae | Lepocreadium setiferoides (Miller & Northup, 1926) Martin, 1938 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Pronocephalidae | Gynaecotyla aduca (Linton, 1905) Yamaguti, 1939 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Schistosomatidae | Pleurogonius malaclemys Hunter, 1961 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Austrobilharzia variglandis (Miller and Northup, 1926) Penner, 1953 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Zoogonus lasius (Leidy, 1891) Stunkard, 1938 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Zoogonus lasius (Leidy, 1891) Stunkard, 1938 | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Distomum lasium Leidy, 1891; Zoogonus rubellus (Olsson, 1868) of Stunkard (1938) in part | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Distomum lasium Leidy, 1891; Zoogonus rubellus (Olsson, 1868) of Stunkard (1938) in part | North Atlantic | [62-68] |
| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Distomum lasium Leidy, 1891; Zoogonus rubellus (Olsson, 1868) of Stunkard (1938) in part | North Atlantic | [62-68] |
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| Tritia obsoleta (Say) [syn. Ilyanassa obsoleta (Say); Nassarius obsoletus (Say)] | Zoogonidae | Distomum lasium Leidy, 1891; Zoogonus rubellus (Olsson, 1868) of Stunkard (1938) in part | North Atlantic | [62-68] |

Barnett and Miller: Cercariae in nassariid gastropods
| Genus and Species                        | Family          | Description                                                                 | Location       | Reference          |
|-----------------------------------------|-----------------|-----------------------------------------------------------------------------|----------------|--------------------|
| *Tritia pygmaea* (Lamarck)              | Lepocreadiidae  | *Opechona bacillaris* (Molin, 1859) Dolfus, 1927                            | North Atlantic | 71                 |
| *Tritia reticulata* (Linnaeus) [syn. *Nassarius reticulatus* (Linnaeus)] | Acanthocolpidae | *Cercaria pontica* Dolgikh, 1965 [similar to *Stephanostomum* spp.]         | North Atlantic | 6, 14, 44, 47, 57, 60, 61, 70-73 |
|                                          | Himasthidae     | *Himasthla quissetensis* (Miller & Northup, 1926) Stunkard, 1938            |                |                    |
|                                          | Lepocreadiidae  | *Lepocreadium album* (Stossich, 1890) Stossich, 1903                        |                |                    |
|                                          | Microphallidae  | *Cercaria fasicularis* Villot, 1875                                          |                |                    |
|                                          |                 | *Cercaria sebapoli* Dolgikh, 1965 [similar to *Lepocreadium* sp.]           |                |                    |
|                                          | Microphallidae  | *Gynaeotyla longiintestinata* Leonov, 1958 [syn. *Cercaria sevillana* Russell-Pinto & Bartoli, 2002; *Cercaria misenensis* Dolgikh, 1965] |                |                    |
|                                          | Strigeidae      | *Cardiocephalus longicollis* Szidat, 1928 [syn. *Cercaria nassae* Dolgikh, 1965] |                |                    |
|                                          | Zoogonidae      | *Dipterostomum brusinae* (Stossich, 1888) Stossich, 1903; *Dipterostomum brusinae* (Stossich, 1888) Stossich, 1903; *Distomum brusinae* Stossich, 1888; *Cercaria crispata* Pelseneer, 1906; *Cercaria inconstans* Sinitsin, 1911 |                |                    |
|                                          |                 | *Zoogonus rubellus* (Olsson, 1868) Odhner, 1902 [syn. *Cercaria reticulata* Stunkard, 1932; *Zoogonus mirus* Looss, 1901] |                |                    |
|                                          |                 | An unidentified zoogonid cercaria                                             |                |                    |
| *Tritia trivittata* (Say) [syn. *Ilyanassa trivittata* (Say); *Nassarius trivittatus* (Say)] | Hemiuridae     | *Tubulovesicula pinguis* (Linton, 1940) Manter, 1947                        | North Atlantic | 74, 75             |
|                                          | Lepocreadiidae  | *Lepocreadium areolatum* (Linton, 1900) Stunkard, 1969                      |                |                    |
prevalent in *N. olivaceus* (0.7%) than in *N. dorsatus* (<0.1%), whereas *C. capricornia* VII was more prevalent in *N. dorsatus* (0.6%) than in *N. olivaceus* (0.3%). The himasthlid cercaria was more prevalent in *N. olivaceus* (1.0%) than in *N. pullus* (0.2%).

There were four rare infections with an overall prevalence of infection of ≤0.1%. These were the acanthoceloids *Cercaria capricornia* VI and one *Stephanostomum* sp., and the zoosporid *Cercaria capricornia* XI, each had only a single infection, and the *Stephanostomum* sp. *Cercaria capricornia* VIII, which had two infections. No species occurred at a prevalence of more than 1.4% overall. The most common species were the acanthocelid *Cercaria capricornia* I (27 infections; 1.4%), the *Stephanostomum* sp. *C. capricornia* VII (15 in two host species), the lepocreadiid cercaria (14 in two host species), the opecoelid *Cercaria capricornia* XII (20; 1.0%), and one himasthlid cercaria (24 in two host species).

Some cercarial species were collected only from a single locality (Table 4). For rare infections, this is unlikely to indicate specificity for the locality, but for the two himasthlid and the microphallid cercariae, all infections were restricted to Sandy Point and occurred at locality prevalences of 2.4% (*N. olivaceus*) and 0.4% (*N. pullus*) for one himasthlid, 0.6% for the other himasthlid and 1.0% for the microphallid. Species that were found at all localities included the acanthocelids *C. capricornia* I and *C. capricornia* III, the *Stephanostomum* sp. *C. capricornia* VII, the lepocreadiid cercaria and the opecoelid *C. capricornia* XII, although for the opecoelid, there were more infections at Cawarral Creek than at the other two localities.

The prevalence of infection varied among localities (Table 4). At Cawarral Creek, only the acanthocelid *C. capricornia* I and the opecoelid cercaria were present at prevalences higher than 1.0%. At Sandy Point, *C. capricornia* I and one himasthlid cercaria had prevalences greater than 1.0%. Most parasitized gastropods collected at Ross Creek were infected at prevalences greater than 1.0%, but this was a small area and this may be a result of bias towards collection of larger, older gastropods at that locality. Morphotypes rarely found were *C. capricornia* I, *C. capricornia* V, *C. capricornia* VI, *C. capricornia* VIII, one *Stephanostomum* sp., *C. capricornia* XI, and one of the two himasthlid cercariae.

Overall, *N. olivaceus* had the greatest species richness (8 species from 6 families), followed by *N. dorsatus* (7 species from 3 families), and *N. pullus* (1 species only). *Nassarius olivaceus* also had the highest frequency of infection (102 of 1908; 5.3%), followed by *N. dorsatus* (20 of 1766; 1.1%), and *N. pullus* (4 of 1614; 0.2%).

### DISCUSSION

One interesting feature of the pattern of infection in the three species of *Nassarius* in the present system is the overall low prevalence of infection. Several parasite species had prevalences well under 1% and the highest, *C. capricornia* I, was only 4.3% at Ross Creek. The highest overall prevalence of infection was 5.3% in *N. olivaceus*. These data contrast strikingly with the well-studied nassariid *T. obsoleta*, reported to be generally uninfected until sexual maturity at around three years, incidence of infection then rising exponentially from 5 to 30% at 3 years to 90 to 100% in older individuals [11]. However, the longevity of *T. obsoleta* is remarkable, estimated at 30 to 40 years and, in one population, at 70 years of age [12,13]. Tallmark and Norrgren [14] also found 100% parasitism in older *T. reticulata*, reported to live to 11 years in Portugal [15] and 15 years in Sweden [16]. In addition, spatial heterogeneity of parasitism is seen in *T. obsoleta*, and highly variable results between sample populations were reported from a single sand-flat (infection frequencies of less than 10% as well as 100%) [11]. Similar spatial heterogeneity has been reported in other studies of *T. obsoleta* [13,17]. Curtis [17] admitted that there was considerable variation between sites and that the Delaware regional trematode community had a higher frequency of infection than other studies. In North Carolina, *T. obsoleta* was infected at 6.49% [18] and 4.07% [19], results similar to those seen in *N. olivaceus* in Capricornia.

Also, the longevity of the infected nassariids in Capricornia was much shorter than that of *T. obsoleta* and *T. reticulatus*; *N. olivaceus* survived for up to ~4.5 years, *N. dorsatus* for up to ~0.8 years and *N. pullus* for only ~0.3 years after collection. Most infected *N. olivaceus* died within the first year (53%), 26% in the second year, 9% in the third and fourth years, and only 3% survived into the fifth year. Although a few infected *N. dorsatus* survived into the second six months after collection, the majority died within the first six months. The longevity of *N. dorsatus* and *N. olivaceus* is unknown. McKillup and McKillup [20] reported that *N. dorsatus* at Cawarral Creek appeared to have a very short life cycle, growing rapidly and surviving for only about 2 months following settlement. They also reported that laboratory maintained specimens of *N. dorsatus* displayed a similar rapid growth [20]. Puturuhu [21] suggested that growth was faster in warm tropical than cool temperate regions, with reduced longevity. A review of published data on 54 species of gastropods found that prevalence was positively correlated with trematode species richness, but found no evidence that longevity was associated with prevalence [22]. However, they warned that their study did not include data from tropical latitudes. A comparison of
Host Specificity

The majority of the cercariae were found in only one host species; only four (the acanthocolpids *C. capricornia* III and *C. capricornia* VII (*Stephanostomum* sp.), the lepocreadiid cercaria and one himasthliid cercaria) infected two species. All three *Stephanostomum* spp. cercariae infected *N. dorsatus*, whereas only one infected *N. olivaceus*, and at a lower prevalence. All other cercariae that infected two host species were more prevalent in *N. olivaceus*. More cercarial species used both *N. olivaceus* and *N. dorsatus* as dual hosts than *N. olivaceus* and *N.
Mollusks living in areas with habitat attractive to birds (e.g., roosting trees or longer tidal exposure) are suggested to have an increased likelihood of infection by bird parasites and a higher diversity [24] or prevalence of infection [24-28]. In Capricornia, bird species infected all three nassariid species, but the diversity and prevalence were highest in *N. olivaceus*. There were two bird parasites in *N. olivaceus*, a himasthlid and a microphallid. Both *N. dorsatus* and *N. pullus* were each infected by a himasthlid but at lower prevalences. Gastropods higher in the intertidal incline potentially emerge earlier and submerge later than those lower in the incline, resulting in longer periods of exposure to infection from birds.

The reason for the depauperate parasite fauna in *N. pullus* is unknown. This nassariid was present at Sandy Point in very high numbers, but was infected by only a single cercaria. This may be linked to the apparent shorter life span of infected *N. pullus* in Capricornia. Although the longevity of *N. pullus* was estimated at 3.85 years in pullus. Both of these gastropods were historically included in the now invalid subgenus *Zeuxis*, whereas *N. pullus* was in the subgenus *Plicarcularia*. This may indicate that more closely related gastropod species may have more shared parasite species than more distantly related species. Further examination of other closely related and sympatric nassariids is needed to test this.

*Nassarius olivaceus* was observed with the highest overall prevalence of infection and the greatest species richness (eight species from all six families) (Table 3). The three gastropod species were closely located at each locality but displayed a degree of zonation. *Nassarius olivaceus* was generally found in shaded pools amongst mangrove trees and in pools adjacent to the trees; and occurred slightly higher in the intertidal zone than *N. dorsatus* and *N. pullus*. There was also some overlap, as all three species were found in the pools along the seaward boundary of the mangroves at Sandy Point, and *N. dorsatus* and *N. pullus* were found together in some areas. Mollusks living in areas with habitat attractive to birds (e.g., roosting trees or longer tidal exposure) are suggested to have an increased likelihood of infection by bird parasites and a higher diversity [24] or prevalence of infection [24-28]. In Capricornia, bird species infected all three nassariid species, but the diversity and prevalence were highest in *N. olivaceus*. There were two bird parasites in *N. olivaceus*, a himasthlid and a microphallid. Both *N. dorsatus* and *N. pullus* were each infected by a himasthlid but at lower prevalences. Gastropods higher in the intertidal incline potentially emerge earlier and submerge later than those lower in the incline, resulting in longer periods of exposure to infection from birds.

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**Table 3. Parasite species and first intermediate and definitive hosts for cercariae found in nassariid gastropods in Central Queensland, showing prevalence of infection (%).**

| Digenean species | Likely placement | Host species | Likely definitive host* | Number infected and percentage (%) |
|------------------|-----------------|--------------|------------------------|-----------------------------------|
| *Acanthocolpidae* |                 |              |                        |                                   |
| *Cercaria capricornia* I | Acanthocolpidae | *Nassarius olivaceus* | Fishes | 27 (1.4%) |
| *Cercaria capricornia* III | Acanthocolpidae | *Nassarius olivaceus* | Fishes | 8 (0.4%) |
| *Nassarius dorsatus* |                 |              |                        |                                   |
| *Cercaria capricornia* VI | Acanthocolpidae | *Nassarius dorsatus* | Fishes | 1 (<0.1%) |
| *Cercaria capricornia* VII | *Stephanostomum* sp. | *Nassarius dorsatus* | Fishes | 10 (0.6%) |
| *Cercaria capricornia* VIII | *Stephanostomum* sp. | *Nassarius dorsatus* | Fishes | 5 (0.3%) |
| *acanthocolpid cercaria* 9 |                |              |                        |                                   |
| *Lepocreadiidae* |                 |              |                        |                                   |
| lepocreadiid cercaria | *Prodistomum* sp. | *Nassarius olivaceus* | Fishes | 13 (0.7%) |
| *Nassarius dorsatus* |                 |              |                        |                                   |
| *Zoogonidae* |                 |              |                        |                                   |
| *Cercaria capricornia* XI | Zoogonidae | *Nassarius olivaceus* | Fishes | 1 (<0.1%) |
| *Opecoelidae* |                 |              |                        |                                   |
| *Cercaria capricornia* XII | Opecoelidae | *Nassarius olivaceus* | Fishes | 20 (1.0%) |
| *Himasthliidae* |                 |              |                        |                                   |
| himasthlid cercaria 1 | *Himasthla* sp. | *Nassarius olivaceus* | Birds | 20 (1.0%) |
| *Nassarius pullus* |                 |              |                        |                                   |
| himasthlid cercaria 2 | *Himasthla* sp. | *Nassarius dorsatus* | Birds | 4 (0.2%) |
| *Microphallidae* |                 |              |                        |                                   |
| microphallid cercaria | Microphallidae | *Nassarius olivaceus* | Birds | 8 (0.4%) |
| *Uncertain family* |                 |              |                        |                                   |
| *Nassarius dorsatus* |                 |              |                        |                                   |
| *Nassarius olivaceus* |                 |              |                        |                                   |

*final host details can be obtained from the Keys to the Trematoda Volumes 2 and 3: [76,77].
Table 4. Distribution of infections of each parasite species for each host species at the localities sampled (the percentage of gastropods infected at each locality for each species is shown in brackets).

| Location         | C. capricornia I | C. capricornia III | C. capricornia VI | C. capricornia VII | C. capricornia VIII | acanthocolpid cercaria | lepocreadiid cercaria | himasthrid cercaria | microphallid cercaria | unknown cercariae | Total |
|------------------|------------------|--------------------|-------------------|-------------------|---------------------|-----------------------|-----------------------|---------------------|---------------------|---------------------|-------|
| Ross Creek       |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| N. dorsatus      |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 815)        | 1 (0.1%)         | 1 (0.1%)           | 1 (0.1%)          | 2 (0.2%)          |                     |                       |                       |                     |                     |                     |       |
| N. olivaceus     |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 903)        | 10 (1.1%)        | 1 (0.1%)           | 1 (0.1%)          | 1 (0.1%)          |                     |                       |                       |                     |                     |                     |       |
| N. pullus        |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 623)        | 8 (4.3%)         | 4 (2.2%)           | 3 (2.0%)          | 3 (2.0%)          |                     |                       |                       |                     |                     |                     |       |
| Sandy Point      |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| N. dorsatus      |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 241)        | 4 (1.7%)         | 1 (0.4%)           | 2 (0.8%)          | 3 (1.2%)          |                     |                       |                       |                     |                     |                     |       |
| N. olivaceus     |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 710)        | 1 (0.1%)         | 1 (0.1%)           | 1 (0.1%)          | 1 (0.1%)          |                     |                       |                       |                     |                     |                     |       |
| N. pullus        |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 694)        | 9 (1.3%)         | 3 (0.4%)           | 3 (0.4%)          | 3 (0.4%)          |                     |                       |                       |                     |                     |                     |       |
| Cawarral Creek   |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| N. dorsatus      |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 863)        | 1 (0.1%)         | 1 (0.1%)           | 1 (0.1%)          | 2 (0.2%)          |                     |                       |                       |                     |                     |                     |       |
| N. olivaceus     |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 452)        | 10 (2.2%)        | 1 (0.2%)           | 1 (0.2%)          | 1 (0.2%)          |                     |                       |                       |                     |                     |                     |       |
| N. pullus        |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |
| (n = 472)        | 8 (4.3%)         | 4 (2.2%)           | 3 (2.0%)          | 3 (2.0%)          |                     |                       |                       |                     |                     |                     |       |
| Total            |                  |                    |                   |                   |                     |                       |                       |                     |                     |                     |       |

- N. dorsatus
- N. olivaceus
- N. pullus

Barnett and Miller: Cercariae in nassariid gastropods

Indonesia [21], its longevity in the field here is unknown (the longest surviving infected N. pullus lived for only ~0.3 years after collection). If the species lives for a much shorter period in this region, the risk of exposure to infection is reduced. Conversely, if infection markedly reduces longevity, infected N. pullus may not survive for long in the field and would therefore not be available for collection.

Geographic Specificity

As the distribution of infection in first intermediate hosts is expected to reflect the distribution of final hosts, results were examined to see if there was any specificity of infections at these localities. Although these sites flow into Keppel Bay, the localities are geographically separate, and each is part of a discrete coastal wetland habitat.

Species that use fish as their definitive host were distributed across all localities, except for the rare infections, which were present in numbers too low to determine their distribution. The most commonly observed cercariae were the acanthocolpids C. capicornia I, C. capicornia III, and C. capicornia VII, and the lepocreadiid and opecoelid cercariae, although there were many more opecoelid infections collected at Kawaral Creek than at the other two localities. This indicates that the fish hosts of these cercariae visit all three localities. As all three localities connect with the same bay, many adult fish species are expected to move between them.

Both himasthlid and the single microphallid species were found only at Sandy Point. Digeneans of both families generally infect birds as their final hosts, and Sandy Point is listed as important habitat for both domestic and migratory birds. Sandy Point is in the eastern estuaries of the Shoalwater and Corio Bays Ramsar wetland (designated as a site of significant international importance under the Ramsar Convention), an area that provides important roosting sites for local and migratory birds, and the mud and sandflats are feeding sites for a diversity of shorebirds [29]. The Ramsar wetland was reported to have 226 species of birds, representing 32 percent of Australia’s bird fauna [29]. The other localities are of lower importance as bird habitats and have much smaller and less diverse bird populations. These results reflect the relative significance of Sandy Point as an important bird habitat, which has resulted in a higher diversity and prevalence of parasites that use birds as definitive hosts.

Trematode Fauna of Nassariid Gastropods

Sixteen new host-parasite records can now be added for the Nassariidae. No infections were found in N. olivaceus, N. dorsatus, or N. pullus by families that had not been previously reported from other nassariids, although there were six previously reported families that were not found (Table 1).

The Nassariidae contains the subfamilies Buccinanopsinae, Photinae, Cylelleninae, Bullinae, Anentominae, Dorsaninae, and Nassariinae [2]. Of these, no parasites have yet been reported from gastropods of the Dorsaninae, Anentominae, Cylelleninae or Photinae. Parasites are reported from gastropods in the Nassariinae (from Nassarius spp., Phrontis vibex and Tritia spp.), the Bullinae (Bullia digitalis) and the Buccinanopsinae (Buccinanops spp.). Digenean families commonly reported to use nassariids as first intermediate hosts include the Acanthocolpidae, Himasthidae, Lepocreadiidae, Microphallidae, and Zoogonidae (Tables 1 and 2).

The nassariid reported with the highest number of infecting parasite families is T. obsoleta. Tritia obsoleta is indigenous to the Atlantic coast of North America, but was also introduced to the west coast unintentionally via attempted oyster transplantation in the early 1900s [5]. The invasive west coast population was reported to have lost three parasites in the new range, and had not gained any new native west coast parasites [5]. Tritia spp. are generally found in the North Atlantic and West Africa, with two isolated species from Australia and New Zealand [1]. Of the other nassariids that have been reported as hosts, their distribution is geographically restricted: Buccinanops spp. are found in South America, Bullia spp. from the Indian Ocean, Phrontis spp. from the Caribbean Sea and both coasts of the Isthmus of Panama, and Nassarius spp. from the Indo-Pacific Ocean and the coast of Israel on the Mediterranean Sea [1,30].

Of the nassariid hosts that have been studied, the most common family using them as first intermediate host is the Lepocreadiidae (12 host-family records for 16 parasite species), followed by the Zoogonidae (8 for 12), Acanthocolpidae (6 for 13), Himasthidae (6 for 8), Microphallidae (4 for 4), Opecoelidae (3 for 3), Strigeidae (2 for 2), and the rest with single records (Table 2). Nassariid gastropods were also found to be the dominant marine first intermediate hosts for the Acanthocolpidae, Lepocreadiidae, and Zoogonidae.

Gastropods from the superfamily Buccinoidea were the most commonly reported first intermediate hosts for the Acanthocolpidae, with parasites reported from the Buccinidae, Columbellidae, Fasciolariidae and Nassariidae [31]. The majority of infections were in gastropods from the Nassariidae, all in the subfamily Nassariinae. Eight cercariae are now reported from Nassarius spp. and include five Stephanostomum or Stephanostomum-like and three non-Stephanostomum species, compared to only three in Tritia spp., all suggested to be Stephanostomum or Stephanostomum-like.

Huston et al. [32] reviewed the first intermediate hosts for the Lepocreadioida and remarked that, apart from a single exception, the Lepocreadiidae used the Nas-
Nassariidae, Columbellidae, or Conidae as first hosts. Their study found that the Nassariidae was the most common family reported. They included a number of cercariae of uncertain status, also mostly from the Nassariidae or Columbellidae, and noted that these may also be lepocreadiid cercariae. In Tables 1 and 2, these uncertain cercariae have been placed as Lepocreadiidae as they closely resemble other lepocreadiid cercariae. Lepocreadiids have been reported from all three nassariid subfamilies.

For the Zoogonidae, gastropods from the Buccinidae, Columbellidae, Fasciolariidae and Nassariidae, Naticidae (Naticoidea), and Trochidae and Turbinidae (Trochoidea) were the first intermediate hosts for cercariae [33]. The dominant host group for zoogonids was the Buccinoidea, and within that superfamily, the Nassariidae was the most frequently infected family, harboring at least seven species of zoogonid (of 15 described cercariae reported as belonging to the Zoogonidae). Zoogonids are also reported from all three nassariid subfamilies.

Nassariids are also one of the most common first intermediate host families for species of marine Himasthla spp. (Himasthidae) (5 in 6 species of nassariid). Other families hosting marine Himasthla or Himasthla-like cercariae are the Melongenidae (2 in 1) [34], the Littorinidae of superfamily Littorinoidea (5 in 3) [35-39] and a single cercaria is reported to infect the Potamididae (1 from 1) [40]. From the Himasthidae, only Himasthla and Himasthla-like cercariae have been reported from nassariids to date, all in the subfamily Nassariinae.

Microphallid cercariae have been found in only a small number of nassariid gastropods, three from the Nassariidae and one from Bulliniae; these are N. olivaceus, T. obsolete and T. reticulata, and B. digitalis. Adult microphallids infect a variety of vertebrates, mainly birds [41]. Most reports of cercariae are from litorinid and hydroid gastropods [42] and the Nassariidae does not appear to be an important intermediate host for this family.

Opecoelid parasites are reported from a broad range of gastropods. Over 70 cercariae have been reported from at least ten superfamilies of molluskan first intermediate hosts, but only two have been reported from nassariids [43]. These both involved species of Nassarius, and no opecoelid cercariae have been reported from other nassariid genera. Other buccinoid hosts of opecoelids include gastropods from the Buccinidae and Columbellidae. The Opecoelidae has four subfamilies: the Opecoelinae Ozaki, 1925, the Plagioporinae, Manter, 1947, the Stenakrinae Yamaguti, 1970, and the Opecoelininae Gibson & Bray, 1984. The cercaria found here was placed in the Opecoelinae, and the dominant hosts for opecoeline cercariae are columbellids [43].

The most ancient genus of nassariids with reported host-parasite associations was suggested to be Buccinancops [1]; only lepocreadiids and zoogonids are reported from this genus (and from all nassariid subfamilies, as well as from related buccinoid families). This indicates a long-standing relationship between the family and these two parasite families that has potentially co-evolved with the divergence of the Nassariidae from other buccinoids.

Some Tritia spp. were infected rarely by cercariae from the Strigeidae, Pronocephalidae, Diplostomatidae, Schistosomatidae, and Hemiuridae, yet no infections by these families have, as yet, been reported from any other nassariid genera (see Table 2). This could indicate that the host-parasite associations for these parasites are more recent than the divergence of the species, but further examination of other hosts is needed to see if other buccinoid gastropods are common hosts. As well, a cercaria from the Cyathocotylidae was only reported from Nassarius. This may also indicate that this host association has occurred after the divergence of the species. Further examination of more nassariid species will indicate if the host-parasite associations described here are consistent within the Nassariidae.

This work presents a glimpse into the complex ecology and biodiversity of the trematode fauna inhabiting Australian intertidal gastropod communities. Unraveling details of all of the hosts involved in the intricate life-cycles of these trematodes present in gastropods in the region, their host specificity and pathological impacts on their hosts driving selection pressures in these communities awaits further exploration.

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