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Invited Review

Recent advances in our knowledge of Australian anisakid nematodes



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ABSTRACT

Anisakidosis is an emerging infection associated with a wide range of clinical syndromes in humans caused by members of the family Anisakidae. Anisakid nematodes have a cosmopolitan distribution and infect a wide range of invertebrates and vertebrates during their life cycles. Since the first report of these parasites in humans during the early 60s, anisakid nematodes have attracted considerable attention as emerging zoonotic parasites. Along with rapid development of various molecular techniques during last several decades, this has caused a significant change in the taxonomy and systematics of these parasites. However, there are still huge gaps in our knowledge on various aspects of the biology and ecology of anisakid nematodes in Australia. Although the use of advanced morphological and molecular techniques to study anisakids had a late start in Australia, great biodiversity was found and unique species were discovered. Here an updated list of members within the family and the current state of knowledge on Australian anisakids will be provided. Given that the employment of advanced techniques to study these important emerging zoonotic parasites in Australia is recent, further research is needed to understand the ecology and biology of these socio economically important parasites. After a recent human case of anisakidosis in Australia, such understanding is crucial if control and preventive strategies are to be established in this country.

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1. Introduction

Members of the family Anisakidae infect animals of almost all phyla, and are particularly prevalent in fish and aquatic associated animals. In the northern hemisphere, interest in these organisms grew tremendously following the discovery that larval stage of *Anisakis* from the North Sea herring, *Clupea harengus*, are able to infect humans (Van Thiel et al., 1960). Since then there have been many

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studies carried out that increased awareness, improved diagnostic techniques and broadened our knowledge about various aspects of their biology and pathogenicity. Anisakid nematodes are regarded as economically important parasites that are recognised as emerging seafood borne parasites with unique characteristics. It is known that even one single dead anisakid larva in properly cooked seafood may cause serious disease in humans (Audicana et al., 2002); anisakid larvae do not die immediately after the host's death, migrating instead from internal organs to the flesh of the host, where they are more likely to be transferred to the definitive host(s). Unlike many other common parasitic diseases of humans,

anisakidosis is not a problem of developing countries only (Gorokhov et al., 1999; Smith, 1999; Lopez-Serrano et al., 2000; Chai et al., 2005; Kapral et al., 2009; Shamsi and Butcher, 2011) (Fig. 1). Hence, it is not surprising that a review of the literature found a sharp increase in the number of publications since the 1960s (Fig. 2). However, to date only 2% of these publications are about Australian anisakids. In the Northern Atlantic and Northern Pacific, the economic importance of the fishing industry has prompted research on the parasites of marine fauna and as a result, many aspects of the biology and ecology of these parasites have been studied, but the parasites of Australian marine animals are poorly known.

The history of studies of anisakids in Australia shows a controversial taxonomy. Australian anisakids are known mostly by the works of Johnston and Mawson in the 1940's but since then there has been no review on importance of those findings and the current status of taxa reported by them. In some recent publications on Australian anisakids wrong taxonomy, old nomenclature and assignment of species to wrong families occur, possibly due to the lack of compact information on changes to the taxonomy and nomenclature of Australian species of anisakids. For example, a common confusion relates to the genus *Hysterothylacium* which was resurrected in 1981 to include those species previously considered as *Thynnascaris* and *Contracaecum* (Deardorff and Overstreet, 1981) and is now classified under family Raphidascarididae (Fagerholm, 1991; Nadler and Hudspeth, 2000) instead of Anisakidae. However, literature review shows there are still 47 publications worldwide, some from Australia, in which *Thynnascaris* has been reported from various hosts or studied, without referring to its significant morphological features in details. Therefore, one cannot draw conclusions about the host, geographical distribution and pathogenic aspects of the specimens reported in these articles. More importantly, *Hysterothylacium* is still reported as an anisakid nematode instead of raphidascarids in some publications. For decision makers in the seafood industry, health sectors and fisheries in several parts of the world, it makes a significant difference in how they deal with anisakids versus raphidascarids. *Hysterothylacium* larvae are very abundant in fish (Shamsi et al., 2013) but they are not as harmful as members of anisakid nematodes for human health. An article that states fish are infected with

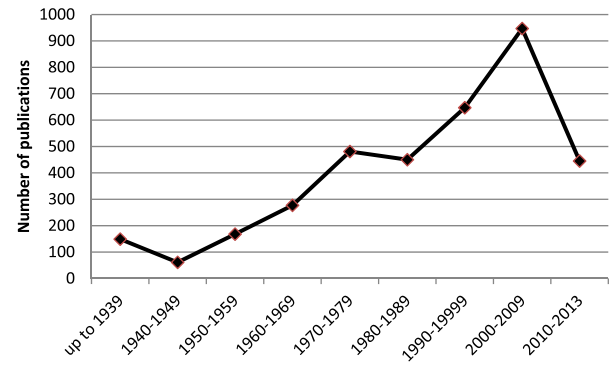


Fig. 2. Number of published articles on anisakid nematodes (key word: Anisakidae) until 2013; based on the search on Web of Science and CABI (Gorokhov et al., 1999; Smith, 1999; Lopez-Serrano et al., 2000; Chai et al., 2005; Kapral et al., 2009; Shamsi and Butcher, 2011).

Hysterothylacium spp. and places them under anisakids can potentially lead to raising a false alert among decision makers who are not necessarily taxonomists at potentially tremendous cost to the Australian fishing industry.

This review presents the history of research on Australian anisakid nematodes, a list of taxa reported in Australia followed by their current taxonomic status, the current state of knowledge on life cycle and health impacts of Australian anisakids, and the questions these findings raise.

2. History of study of anisakid nematodes in Australia

There is a paucity of information on anisakid nematodes in Australia. Australian anisakids are known principally from early works by Johnston and Mawson (Johnston, 1910, 1913, 1937, 1938; Johnston and Mawson, 1939, 1940a,b, 1941a, 1942b,c,d, 1943a,b, 1944, 1945a,b, 1947a, 1949, 1951a, 1952, 1953; Mawson, 1953, 1957, 1969). These authors reported and described 32 species of anisakid nematodes, from a broad range of Australian animals. Although their contribution to our knowledge on anisakid nematodes in Australia is significant, most of these early reports of the



Fig. 1. Countries where human cases of anisakidosis have been reported (Gorokhov et al., 1999; Smith, 1999; Lopez-Serrano et al., 2000; Chai et al., 2005; Kapral et al., 2009; Shamsi and Butcher, 2011).

species were poorly described, so that the differentiation among closely related species is not possible.

Many of these species are unidentifiable by current standards, with brief and sometimes unillustrated descriptions. Sometimes new species have been described based on a single specimen, such as is the case for *Contracaecum gypsophocae* (Johnston and Mawson, 1941c,e) or based on immature parasites such as *Phocascaris hydrurgae* (Johnston and Mawson, 1941c). Some of the nomenclature has not been used by other authors for 50 years, such as the case of *Stomachus* which had been used rather than *Anisakis* (Johnston and Mawson, 1953). For many of these species, such as *Contracaecum bancrofti*, *C. clelandi*, *C. sinulabiatum* and *C. magnicollare*, there was no information on the location of the type material in the original paper (Johnston and Mawson, 1941d). Later, a list of type specimens of animal parasites held in Australian institutions was published (Spratt, 1983). Subsequent re-examination of some of these materials by other authors showed that in some cases, hosts or parasites were misidentified. For example, specimens from the fishes, *Stegostoma fasciatum* (Hermann) and *Orectolobus maculatus* (Bonnaterre), recorded as *Terranova galeocerdonis* (Johnston and Mawson, 1951a) were later identified as *Terranova ginglymostomae* (Bruce and Cannon, 1990). Some of these species have only been reported from Australia, such as *Contracaecum bancrofti*, *C. clelandi*, *C. eudyptes*, *C. eudyptulae*, *C. heardi*, *C. magnicollare*, *C. nycticoracis*, *C. podicipitis* and *C. sinulabiatum*, and doubts have been raised concerning their validity (Hartwich, 1963, 1964b).

Some of the species, e.g., *Anisakis simplex*, *Contracaecum osculatum* and *C. spiculigerum* have been also reported from other parts of the world and their taxonomic status have been changed based on evidence provided by molecular studies. It is important to investigate the relationship between Australian taxa and conspecific parasites from elsewhere and to know where Australian species stand based on new evidences. Therefore, since 2009, Shamsi et al. have employed a combined morphological (light and scanning electron microscopy) and molecular (based on the first and second ribosomal internal transcribed spacers (ITS-1 and ITS-2)) approach and have evaluated the taxonomic status of some anisakid species in Australia (Shamsi et al., 2008; Shamsi et al., 2009a,b; Shamsi et al., 2012). This was the first step toward clarifying the taxonomic status of Australian anisakids using advanced techniques.

3. List of anisakid nematodes reported in Australia and their current taxonomic status

Before providing a list of Australian anisakid nematodes it is worth mentioning that the systematics and classification of these parasites and the relationships of genera and species have been the subject of extensive debate (e.g., Gibson, 1983; Sprent, 1983). Until the early 21st century, the proposed classifications were based primarily on an analysis of morphological features of high systematic significance. The lack of sufficient numbers of such characteristics and subjective interpretations of them have also led to considerable controversy over the classification of the Ascaridoidea and position and validity of the family Anisakidae within Ascaridoidea (e.g., Mozgovoi, 1953; Hartwich, 1957, 1964b, 1974; Yamaguti, 1961; Gibson, 1983; Sprent, 1983; Fagerholm, 1991). Since the early 21st century, various molecular approaches have been employed to investigate taxonomic and systematic questions, such as the characterisation of distinct species and detection of genetic variation among anisakid nematodes. Nadler and Hudspeth (2000) used mitochondrial gene cytochrome oxidase subunit 2, small- and large-subunit nuclear rDNA sequences and

morphological data, to produce a phylogenetic hypothesis for representatives of the superfamily Ascaridoidea. Their results were consistent with Fagerholm's 1991 classification of anisakid nematodes. Based on these works, currently *Anisakis*, *Contracaecum*, *Ophidascaris*, *Paranisakiopsis*, *Peritrachelius*, *Phocascaris*, *Pseudanisakis*, *Pseudoterranova*, *Pulchrascaris*, *Raillietascaris*, *Sulcascaris*, *Terranova* are genera to be considered within family Anisakidae. Based on this classification, below is a list of reported species from Australia.

Anisakis brevispiculata: This is a recent report from a dwarf whale from New South Wales (Shamsi et al., 2012). *A. brevispiculata* was first described by Dollfus (1966) as a new species but was later synonymised with *A. physeteris* (Davey, 1971). However, recent molecular analysis have shown that *A. brevispiculata* is a valid species, genetically distinct from *A. physeteris* (Mattiucci et al., 2001). No further information has been published regarding its morphological characterisation and the value of different morphological characters for specific identification. In Australia, *A. brevispiculata* was redescribed based on a male specimen and its morphological differentiation from closely related species was discussed (Shamsi et al., 2012). Alignment of ITS-1 and ITS-2 sequences of *A. brevispiculata* found in Australia with those from the northern hemisphere (Nadler et al., 2005) showed that *A. brevispiculata* in Australia is genetically distinct (Shamsi et al., 2012).

A. diomedae: It was first described by Johnston and Mawson (1942b) from albatrosses. The validity of this species is doubtful mainly because the identification and assignment to a new species were based on examination of immature specimens. In addition, members of the genus *Anisakis* do not develop into adults in birds. It was also commented later by one of the authors that these specimens might belong to a new genus and they need to be studied further (Mawson, 1983).

A. kogiae: This species currently considered invalid. *A. kogiae* was first described by Johnston and Mawson (1939) from a pygmy sperm whale from South Australia and Queensland waters but later was synonymised with *A. simplex* by Davey (1971). For further details, see below, under *A. simplex*.

A. marina: (= *Capsularia marina*; *Stomachus marinus*) has been reported from various hosts across Australian coasts (Johnston and Mawson, 1944, 1945b, 1949). In these reports "marina" mostly refers to larval stage of the parasite. Therefore, *A. marina* is not considered a valid taxon but regarded as *Anisakis* larval type. Both *Capsularia* and *Stomachus* have later been synonymised with *Anisakis*.

A. oceanicus: This species was first described from a whale, *Globicephalus melas*, in Australia (Johnston and Mawson, 1951b) but later synonymised with *A. physeteris* (Davey, 1971). Shamsi et al. (2012) raised the possibility that *A. oceanicus* might be a valid species, however examination of additional specimens as well as the type specimen of *A. oceanicus* is required before any conclusion can be drawn.

A. similis (= *Stomachus similis*): This species has been first reported from marine mammals in New South Wales and South Australia (Johnston and Mawson, 1939, 1941c) and then later from Queensland (Cannon, 1977a). Both have been synonymised with *A. simplex* (Davey, 1971). For further details, see below, under *A. simplex*.

A. simplex sensu lato: Currently, based on genetic analysis it is believed that *A. simplex* comprises three genetically distinct species, including *A. pegreffii*, *A. simplex sensu stricto* and *A. simplex C* (Nascetti et al., 1983; Mattiucci et al., 1997). Until recently, these species were considered indistinguishable based solely on morphological characteristics. Mattiucci et al. (2013a) used ventriculus length, tail shape, tail length/total body length ratio, plectane 1 width/plectane 3 width ratio and left and right spicule length/total body length ratios to distinguish these three sibling species and

named *A. simplex* C as *Anisakis berlandi*. In Australia, recently two members of the *A. simplex sensu lato* have been reported, *A. pegreffii* and *A. simplex* C (= *A. berlandi*) from marine mammals (Shamsi et al., 2012). However, due to lack of comparable data, it is not known which species those early reports of *A. simplex sensu lato* (e.g., those reported as *A. similis* or *Stomachus similis*) belong to.

A. typica: In Australia this species was first reported by Cannon (1977a) from the melon-headed whale, in Queensland waters. Larval stages were later identified based on the ITS-1 and ITS-2 sequence data (Jabbar et al., 2012) from various fish species in the same region. In Davey's revision of *Anisakis* spp., *A. typica* was considered a valid species (Davey, 1971). Later, Mattiucci and Nascetti (2006) provided molecular evidence based on the multileucos enzyme electrophoresis and supported validity of the taxonomic status of the species.

Contracaecum bancrofti: This species was first established by Johnston and Mawson (1941b) from Australian pelicans from Queensland and New South Wales in Australia but later Hartwich (1964a) synonymised it with *C. micropapillatum*. Therefore, *C. bancrofti* was treated as a synonym of *C. micropapillatum* in the checklist of parasites of Australian birds by Mawson et al. (1986). Later, Shamsi et al. (2009b) examined more specimens and re-established *C. bancrofti* as a valid species based on the morphological and genetic evidence.

C. clelandi: This species was described from Australian pelicans in Perth (Johnston and Mawson, 1941b) and since then it has not been reported elsewhere. Johnston and Mawson's description of *C. clelandi* is incomplete in several respects but is sufficient to permit the recognition of *C. clelandi* as a valid species. However, an examination of the type specimen deposited in South Australian Museum revealed that the type specimen is female (Shamsi et al., 2008).

C. eudyptulae: This is a well established species which was first described by Johnston and Mawson (1942d) from the little penguin from Western Australia, Victoria, Tasmania and New South Wales. Later, a redescription of the species and genetic characterisation of internal transcribed spacers were provided for this taxon (Shamsi et al., 2009b).

C. gypsophocae: Johnston and Mawson (1941c) described it as a new species in the Tasmanian fur seal (*Gypsophoca tasmanica*) from Derwent Heads (Tasmania, Australia) but later re-examined the specimens and synonymised it with *C. osculatum* (Johnston and Mawson, 1945a).

C. heardi: This species was described as a new species from penguins by Mawson (1953) from Heard Island and then later by Fonteneau et al. (2011) from Antarctic.

C. (=Thynnascaris) incurvum: First reported from swordfish in New South Wales by Johnston and Mawson (1943a) but was later synonymised as *Hysterothylacium incurvum* (Deardorff and Overstreet, 1981) and therefore based on the currently accepted classification, it does not belong to the family Anisakidae.

C. (Thynnascaris) legendrei: This species has been reported from various species of fish such as tiger flathead from different locations in Australia (Johnston and Mawson, 1943a, 1944, 1951a). It was later synonymised with *H. incurvum* (Deardorff and Overstreet, 1981) and therefore, based on the currently accepted classification, it does not belong to the family Anisakidae.

C. macquariae: This species was first described as a new species from Macquarie perch from New South Wales (Johnston and Mawson, 1940b). However, the description of excretory pore and morphology of the tail suggest that it should belong to the genus *Hysterothylacium* (Deardorff and Overstreet, 1981) which is no longer considered a member of the family Anisakidae.

C. magnicollare: It was described as a new species by Johnston and Mawson (1941b) from a noddy in Queensland but was later synonymised with *C. magnipapillatum* by Fagerholm et al. (1996).

C. magnipapillatum: Fagerholm et al. (1996) re-examined and redescribed nematode parasites obtained from ulcerated nodules in the proventriculus of the piscivorous black noddy tern, *Anous minutus*, by Johnston and Mawson (1941b) and considered it a senior synonym of *C. magnicollare*.

C. microcephalum: This widely distributed species has been reported from several birds in Australia, e.g., domestic duck and silver gull (Johnston and Mawson, 1941b, 1953). Recently a description of the species and its genetic characterisation from Australian piscivorous birds were published (Shamsi et al., 2009b).

C. multipapillatum: It was reported in Australia for the first time by Shamsi et al. (2008) and was morphologically described and genetically characterised by these authors. Until then, *C. multipapillatum* had only been reported from the Nearctic region (Lucker, 1941a,b; Courtney and Forrester, 1974; Navone et al., 2000; Kinsella et al., 2004).

C. murrayense: This species was described as a new species from various freshwater fish species from Tailm Bend by Johnston and Mawson (1940b). It was later synonymised with *Hysterothylacium murrayense* by Deardorff and Overstreet (1981).

C. (=Thynnascaris) nototheniae: First described in reported in Australia by Johnston and Mawson (1945a) from various fish species and subsequently placed under the genus *Hysterothylacium* (Deardorff and Overstreet, 1981).

C. nycticoracis: It was described as a new species based on the presence of a single male with broken spicule from a heron in New South Wales (Johnston and Mawson, 1941e). The description of this species is very brief and the figures provided in the article do not show sufficient detail of taxonomically important features to differentiate it from other *Contracaecum* spp. Therefore the validity of *C. nycticoracis* is questionable.

C. ogmorhini sensu lato: A few years after the original description of *C. ogmorhini*, by Johnston and Mawson (1941c) from Australia, they synonymised it with *C. osculatum* (Johnston and Mawson, 1945a). It was also considered a synonym of *C. osculatum* by Hartwich (1975). Campana-Rouget and Paulian (1960) considered *C. ogmorhini* a valid species, Fagerholm and Gibson (1987) provided a redescription of the species and recent molecular studies based on allozyme and mtDNA data, have shown that *C. ogmorhini* is a species complex comprised at least two distinct genotypes which cannot be differentiated morphologically; *C. ogmorhini sensu stricto* and *C. margolisi* (Mattiucci et al., 2003) with distinct geographical distribution and host species. *C. ogmorhini sensu stricto* occurs in southern hemisphere while *C. margolisi* occurs in the northern hemisphere.

C. osculatum sensu lato: This species was reported from Australian seals (e.g., Johnston, 1937). Later it was shown *C. osculatum* comprises a number of sibling species that cannot be differentiated from one another morphologically, hence assigned as A to E and *C. osculatum baicalensis* (Nascetti et al., 1993; Orecchia et al., 1994; D'Amelio et al., 1995). Only *C. osculatum* D and E are found in southern hemisphere. Due to lack of comparable data it is not known earlier reports of the species in Australia belong to *C. osculatum* D or E.

C. pelagicum: First described as a new species from albatross in New South Wales (Johnston and Mawson, 1942b) and then it was reported from other countries (e.g., Silva et al., 2005; Garbin et al., 2007).

C. podicipitis: Described as a new species by Johnston and Mawson (1949) from crested grebe in South Australia and its validity has not been criticized since then.

C. pyripapillatum: This species was described morphologically and characterised genetically by Shamsi et al. (2008) for the first

time from Australian pelican. It is morphologically most similar to *C. multipapillatum*, occurring in the same host species/individual (Shamsi et al., 2008) but can be differentiated based on the morphology of pre-anal papillae.

C. radiatum: This anisakid nematode has been commonly reported from the Antarctic Ocean, together with *C. osculatum* from seals (e.g., Johnston and Mawson, 1945a).

C. rudolphii: In Australia, anisakids from various cormorants comply morphologically with the description of *C. rudolphii sensu lato* (Hartwich, 1964a,b). However, morphological examination of Australian specimens followed by characterisation of internal transcribed spacers showed that they could be divided into two groups; *C. rudolphii* D and *C. rudolphii* E. These observations suggested that *C. rudolphii* in Australia consists of two distinct species (Shamsi et al., 2009a). In the northern hemisphere, *C. rudolphii*, has been reported from the stomach of a number of species of pelicans and cormorants (Hartwich, 1964a) where existence of four sibling species within *C. rudolphii sensu lato* named *C. rudolphii* A, *C. rudolphii* B and *C. rudolphii* C and *C. rudolphii* F was revealed (Mattiucci et al., 2002; Li et al., 2005; Zhang et al., 2009; D'Amelio et al., 2012). *C. rudolphii* D and *C. rudolphii* E from Australia are different from *C. rudolphii* A, B, C and F reported from northern hemisphere.

C. sinulabiatum: First described as a new species by Johnston and Mawson (1941b) and reported from various birds in Queensland and South Australia. Since then there has been no further report of this parasite. The location of the type specimen was not known, therefore later Hartwich (1964a) expressed doubt over the validity of the species. Spratt (1983) published the list of type species and it was considered a valid species in the Mawson et al. (1986) checklist.

C. spiculigerum: This parasite was reported from various birds across Australia (e.g., Johnston and Mawson, 1941b). However, Hartwich (1964a) subsequently examined the types of *C. spiculigerum* and found that the type material of *C. spiculigerum* was *C. microcephalum*. Therefore, he referred to this taxon as *C. spiculigerum sensu auctorum* and created the new name *C. rudolphii*.

C. (Thynnascaris) tasmaniense: First described and reported in Australia by Johnston and Mawson (1945a) from various fish species and subsequently placed under the genus *Hysterothylacium* (Deardorff and Overstreet, 1981).

C. variegatum: In Australia, *C. variegatum* was first reported in Australian Pelican and darter (Shamsi et al., 2009b). The taxonomy of this species has seen several major changes mainly due to the type specimen being a female (Rudolphi, 1809) but Hartwich (1964a) redescribed the species. Specimens reported and characterised from Australia show slight difference to previous descriptions of the species (Hartwich, 1964a; Nagasawa et al., 1999). Similar differences were observed between *C. variegatum* from Scottish waters and the type specimen (Fagerholm et al., 1996) suggesting it is likely that *C. variegatum* with a worldwide distribution, does not represent a single species.

Mawsonascaris australis: see *Paranisakis australis*

Ophidascaris varani: see *Raillietascaris varani*.

O. pyrrhus: First described by Johnston and Mawson (1942a) from a black snake and later reported from various species of snakes from several locations in Australia (Jones, 1980).

O. filarial: It was reported from carpet snake in Queensland (Johnston and Mawson, 1942a).

Paranisakiopsis sp.: The only report of this marine fish parasite in Australia is from albatross with a comment by the author that it should have been ingested with food (Mawson, 1953).

Paranisakis australis: It was described as a new species from a ray in Sydney by Johnston and Mawson (1943b) but it was assigned to the new genus *Mawsonascaris* (Sprent, 1990).

P. hydrurgae: The main criticism about *P. hydrurgae* is that it was established based on immature specimens by Johnston and

Mawson (1941c). The taxonomic status of genera *Contracaecum* and *Phocascaris*, both of which have aquatic life cycles and homeothermic final hosts has been the subject of several debates. Hartwich (1974) distinguished them based on morphological characteristics, whereas, Berland (1963) considered species of *Contracaecum* occurring in seals as *Phocascaris* and those species maturing in birds remained in the genus *Contracaecum* which later was supported by (Mattiucci et al., 2008). Since there is no strong evidence for a close relationship between these morphological features and the evolutionary lineages for *Contracaecum* and *Phocascaris*, the taxonomic status of these genera remains unclear (D'Amelio, 2003; Nadler et al., 2000).

Porrocaecum kogiae: It was described as a new species pygmy sperm whale in South Australia and Queensland (Johnston and Mawson, 1939). Members of *Porrocaecum* were later placed under genus *Terranova*.

Pseudoterranova piscicum: Mawson (1953) reported this species from various seals in Macquarie Island as *Terranova piscicum*. Later, those members of the genus *Terranova* that developed into adults in marine mammals were placed into genus *Pseudoterranova* (Gibson and Colin, 1982). Since then there have been several studies on *Pseudoterranova* spp. using advanced molecular approaches and some newly established species, such as *P. decipiens* D and E were reported from Antarctic waters. However the relationship with and/or differentiation from *P. piscicum* has not been discussed.

Raillietascaris varani: It was first described as *Ophidascaris varani* by Johnston and Mawson (1947b) based on a single male from *Varanus varius* in Queensland and subsequently was placed into the new genus, *Raillietascaris* by Sprent (1985).

Stomachus similis: This currently invalid taxon, has been reported from various seals in Australia (Mawson, 1953). See A. simplex for more details.

Terranova crocodyli: It was reported from *Crocodylus johnsoni* in Australia by Baylis (1931) and was redescribed by Sprent (1979).

T. galeocerdonis: This species was reported from various species of sharks from Queensland and South Australia (Johnston and Mawson, 1951a; Bruce and Cannon, 1990). Gibson and Colin (1982) considered *T. galeocerdonis* as synonym of *T. pristis*. However, *T. galeocerdonis* was later considered a valid species and distinct from *T. pristis* by various authors (Tanzola and Sardella, 2006).

T. ginglymostomae: It was reported and redescribed from various sharks in Queensland (Bruce and Cannon, 1990).

T. piscicum: see *Pseudoterranova piscicum*.

T. pristis: Reported from elasmobranchs in Queensland water by Bruce and Cannon (1990) who redescribed the species.

A summary of the current taxonomic status of the above mentioned taxa is provided in Table 1.

4. Life cycle of Australian anisakid nematodes

The common life cycle pattern for all genera and species within the family Anisakidae according to (Anderson, 2000) is as follows: eggs pass out in the faeces of the definitive host and enter the water where they embryonate into first stage larvae within the egg (L1). They then develop further and moult to the second stage (L2). Eggs or larvae can be ingested by first intermediate hosts (crustaceans, usually copepods) and then grow in their haemocoel. When infected copepods are eaten by second intermediate hosts, larvae reach the third larval stage (L3). A great variety of teleost fishes can play a role as paratenic hosts. Piscivorous fishes may accumulate enormous numbers of larvae due to preying upon infected small fishes. Larvae in small fishes can infect piscivorous fish without moulting. This general life history pattern is variable and there are differences in the type of intermediate/definitive

Table 1

Summary of the current taxonomic status of the anisakid nematodes reported in Australia. For full report see Section 3. Those taxa previously placed in the family Anisakidae and now in other families are not listed.

Taxa	Current status	Note
<i>Anisakis brevispiculata</i>	Valid	<i>A. brevispiculata</i> in Australia is genetically distinct from those reported previously (Shamsi et al., 2012)
<i>A. berlandi</i>	Valid	Previously known as <i>A. simplex</i> C
<i>A. diomedae</i>	Invalid	
<i>A. kogiae</i>	Invalid	
<i>A. marina</i>	Invalid	
<i>A. oceanicus</i>	Inquirenda	For further information see Shamsi et al. (2012)
<i>A. pegreffii</i>	Valid	Previously known as <i>A. simplex</i> A
<i>A. similis</i>	Invalid	
<i>A. typica</i>	Valid	<i>A. typica</i> in Australia seems to be genetically different from those reported in other countries (Shamsi, 2007)
<i>Contracaecum bancrofti</i>	Valid	
<i>C. clelandi</i>	Inquirenda	Type specimen is female however the description by Johnson and Mawson (1941b) is sufficient to recognize a distinct species
<i>C. eudypulae</i>	Valid	
<i>C. gypsophocae</i>	Invalid	
<i>C. heardi</i>	Valid	
<i>C. magnicollare</i>	Invalid	
<i>C. magnipapillatum</i>	Valid	
<i>C. microcephalum</i>	Valid	
<i>C. multipapillatum</i>	Valid	
<i>C. nycticoracis</i>	Inquirenda	The validity of <i>C. nycticoracis</i> is questionable due to insufficient description as new species based on a single male with broken spicule
<i>C. ogmorhini sensu stricto</i>	Valid	
<i>C. osculatum sensu lato</i>	Valid	Only <i>C. osculatum</i> D and E are found in southern hemisphere. Due to lack of comparable data it is not known earlier reports of the species in Australia belong to <i>C. osculatum</i> D or E
<i>C. pelagicum</i>	Valid	
<i>C. podicipitis</i>	Valid	
<i>C. pyripapillatum</i>	Valid	
<i>C. radiatum</i>	Valid	
<i>C. rudolphii sensu lato</i>	Valid	<i>C. rudolphii</i> D and <i>C. rudolphii</i> E were reported from Australia. They are different from <i>C. rudolphii</i> A, B, C and F reported from northern hemisphere
<i>C. sinulabiatum</i>	Valid	
<i>C. spiculigerum</i>	Invalid	
<i>C. variegatum</i>	Valid	
<i>Capsularia marina</i>	Invalid	
<i>Mawsonascaris australis</i>	Valid	
<i>Ophidascaris filarial</i>	Valid	
<i>O. pyrrhus</i>	Valid	
<i>O. varani</i>	Invalid	
<i>Paranisakis australis</i>	Invalid	
<i>Phocascaris hydrurgae</i>	Inquirenda	
<i>Porrocaecum kogiae</i>	Invalid	
<i>Pseudoterranova piscicum</i>	Inquirenda	
<i>Raillietascaris varani</i>	Valid	
<i>Stomachus marinus</i>	Invalid	
<i>S. similis</i>	Invalid	
<i>Terranova crocodyli</i>	Valid	
<i>T. galeocerdonis</i>	Valid	
<i>T. ginglymostomae</i>	Valid	
<i>T. piscicum</i>	Invalid	
<i>T. pristis</i>	Valid	

hosts among different genera and species of anisakids. Adults of *Anisakis* spp., also known as “whaleworms”, are parasites of the

stomach of pinnipeds, such as elephant seals, fur seals, grey seals, leopard seals, monk seals, ringed seals, sea lions and walrus as well as cetaceans such as dolphins, narwhals, porpoises and whales (Baker, 1992; Ugland et al., 2004). Marine crustaceans, such as euphausiids, are their first invertebrate intermediate hosts. For *Contracaecum* spp. various species of piscivorous birds and mammals associated with freshwater, brackish and marine environments (such as cormorants, pelicans and seals) are definitive hosts (Kloser et al., 1992) and a broad range of invertebrates, including coelenterates, ctenophores, gastropods, cephalopods, polychaetes, copepods, mysids, amphipods, euphausiids, decapods, echinoderms and chaetognaths can act as first intermediate hosts (Semenova, 1979), although their roles in the natural transmission of the larvae to fish intermediate hosts is not completely clear. Life cycles of the other genera within the family Anisakidae have not been studied as extensively. Species of reptiles and elasmobranchs could act as the definitive hosts for other genera, such as *Terranova* and *Ophidascaris*.

In Australia, our knowledge on the life cycle of various anisakid nematodes is poor mainly because larval stage of anisakids cannot be identified to species based solely on morphological characteristics. Several taxonomically important features, such as spicules, papillae and lips are absent in larval stages. Hence, many aspects of their biology and ecology remain unknown.

Larval stages of anisakid nematodes in Australia were mainly studied by (Cannon, 1977c) who reported, described and illustrated several distinct larval types from marine fishes in south-eastern Queensland including *Anisakis* Type I, *Terranova* Types I and II, and *Contracaecum* Types I and II. He also described *Hysterothylacium* (= *Thynnascaris*) Types I, II, III and IV larvae which now are placed under Raphidascarididae. He also reported and described fourth stage larval ascaridoids found in bivalves, *Pinna menkei*, from Moreton Bay, in *Spondylus ducalis* and *Amusium balloti* from the Bundaberg region as well as a gastropod, *Cypraea tigris*, in Queensland (Cannon, 1978) which he found to be consistent with description of larvae found in pearl oysters, reported previously (Shipley and Hornell, 1906). In his study on the parasites of Queensland marine fishes in Australia, Cannon (1977b) suggested that *Anisakis* is essentially pelagic and has been found in the adult stage in the predators of nektons.

Since, Cannon, there have been few reports of larval anisakids from fishes in Australian waters. Some authors followed Cannon's description to differentiate anisakid larvae occurring in Australian waters at least to different types (Hooper, 1983; Lymbery et al., 2002), whereas others simply placed them into different genera (Doupe et al., 2003).

One of the outcomes of employing molecular techniques to study Australian anisakids was the specific identification of anisakid larvae from a range of hosts, therefore clarifying part of the life cycle. Since larval stages of anisakid nematodes cannot be identified specifically using morphological characters, ITS-1 and ITS-2 sequences of larval stages of anisakid nematodes were compared with ITS-1 and ITS-2 sequences from well described adult stages, which allowed unequivocal identification of anisakid larvae to species (Shamsi et al., 2011b, 2012). Therefore, it was shown that *Anisakis* larval type I in Australia comprises at least three known species, including *A. pegreffii*, *A. simplex* C (= *A. berlandi*) and *A. typica* (Shamsi, 2007). It was also shown that *Contracaecum* larval type I, found in mullet, *Mugil cephalus*, and hardyheads (Atherinidae), were distinct from one another and comprised at least two distinct genotypes. *Contracaecum* larval type I from mullet was matched with adult *C. multipapillatum* and *Contracaecum* larval type I from hardyheads (Atherinidae) was matched with adult *C. pyripapillatum* (Shamsi et al., 2011b). By contrast, *Contracaecum* larval type II, found in two different host species including mackerel, *Scomber australasicus*, and king fish, *Seriola lalandi*, had

identical ITS-1 and ITS-2 sequences to adult *C. ogmorhini sensu stricto* (Shamsi et al., 2011b). Finally, *Contracaecum* larval type III found in flathead, *Platycephalus laevigatus*, had identical ITS-1 and ITS-2 sequences as adults of *C. rudolphii* D (Shamsi et al., 2011b). This partly clarified the life cycle of these species. However, larval characteristics, intermediate hosts and life cycle patterns of other anisakids in Australia remain unclear. Twelve different morphotypes of *Hysterothylacium* larvae were described and genetically characterised from Australian waters (Shamsi et al., 2013) however they are now placed in the family Raphidascarididae and their details will not be discussed here.

5. Public health significance of anisakid nematodes in Australia

Despite the popularity of consuming seafood in Australia as well as the multicultural environment of the country in which different cuisines use raw or undercooked sea foods, there has been (to date) only one report of human anisakidosis acquired in Australia (Shamsi and Butcher, 2011) and two cases were diagnosed in Australia but acquired abroad (unpublished data). The Australian case of anisakidosis was due to *Contracaecum* larval type. The patient's symptoms, vomiting, diarrhoea, abdominal pain, sore throat, rhinorrhoea, nasal congestion and cough lasted about 3 weeks until a larva was passed in a bowel motion. As human infestations occur after eating infested seafood, and the patient had history of eating South Australian mackerel, it is implied that the mackerel eaten by the patient was infected.

The Australian case of Anisakidosis was unusual for two reasons. Firstly, infection of humans with *Contracaecum* type larva, as occurred in Australia is very rare. Most cases of anisakidosis around the world are due to *Anisakis* (Fumarola et al., 2009; Mattiucci et al., 2013b) or *Pseudoterranova* larval types (Arizono et al., 2011). Secondly, in most cases the anisakid larvae penetrate patient's gastrointestinal wall. The transient form of the anisakidosis in which larvae pass the alimentary tract and leave it alive, as it happened in Australia, have rarely been reported (Smith, 1999).

In Australia, larval and adult stages of various species of anisakids infest a broad variety of fish, including mackerels (Shamsi et al., 2011a). However, there has been only one human case of anisakidosis in the country. Given that the popularity of consuming raw or undercooked fish (e.g., sushi and sashimi) is increasing, it is possible that anisakidosis is under diagnosed in Australia due to the vague symptoms and limited diagnostic tests, which raises the question as to the extent of hidden cases of anisakidosis in this country. It is important to design and implement strategies to prevent anisakidosis in Australia. Educational campaigns would also be useful to inform the public and medical professionals/practitioners.

6. Significance of anisakid nematodes on Australian wildlife health

It has been shown that anisakid nematodes are relatively prevalent in Australian marine fish (Cannon, 1977c; Shamsi et al., 2011a; Doupe et al., 2003). There is no report on the impact of anisakids on the health of Australian fishes. It is noteworthy that infection of fish with anisakid nematodes is of importance not only because of anisakidosis in humans, but also because of the effect they have on the infected fish. Anisakid larvae, particularly when located in the musculature, can affect the commercial value of fish and thus result in significant economic losses to the fishing industry (Smith and Wootten, 1975; Angot and Brasseur, 1995). Moreover, anisakids can cause disease in fish. The symptoms and severity of disease can vary considerably depending on factors such as the species of fish, species and intensity of infecting parasite in the fish and the particular organ invaded (Woo, 1995). In brief, disease is

most severe when the anisakid larvae infect the liver. Fibrosis of the liver can lead to atrophy of this organ and a significant loss in body weight. Other symptoms can also be granulomata, inflammation and necrosis of the muscularis externa of the pyloric caeca, gallbladder, intestine and body cavity, which can cause substantial mortality in fish (Woo, 1995).

It seems that these parasites may not be host specific at the larval stages which means a wide range of fish species can act as their intermediate or paratenic host. It has been shown that larval anisakids can pass through several fish species via predation and can be accumulated in larger fishes (Jensen, 1997). Hence, fishes of different species can play an important role in the distribution of anisakids in the environment. Different species of fish can be the source of infestation in humans as well as a wide range of marine mammals and piscivorous birds (Shamsi et al., 2011b).

There is controversy about the effect and pathogenicity of anisakid nematodes on marine mammals and piscivorous birds. Whilst some authors believe that infections with anisakid nematodes are not serious in marine mammal hosts (Geraci and St Aubin, 1987), others have stated that anisakids can be quite harmful in the alimentary tract of marine mammals (Stroud and Roffe, 1979; McColl and Obendorf, 1982; Jefferies et al., 1990; Abollo et al., 1998). Anisakids have also been reported from terrestrial mammals, such as dogs and pigs, which are fed fish harbouring anisakid larvae (Usui et al., 1973) with pathological changes resembling those found in marine mammal final hosts but differing in some aspects, for example in fewer macroscopic granulomata in pigs.

In other countries, there are numerous reports of infection of piscivorous birds with anisakid nematodes (e.g., Torres et al., 2005), describing their pathogenicity in different species of birds. Some authors considered large numbers of nematodes in the stomachs of pelecyaniform birds as a benefit for the host, assisting in the digestion of food (Owre, 1962). By contrast, other authors reported immature *Contracaecum* nematodes attached tightly to ulcers in the proventriculus of white pelicans, causing an extensive inflammatory reaction with necrotic debris (Liu and Edward, 1971). In Australia the only study to investigate the impact of anisakids on marine mammals and piscivorous birds is by Norman (2005) who did not find a direct impact on animal health due to infection with anisakids.

In Australia anisakid nematodes have also been reported in reptiles (Glazebrook and Campbell, 1990). *Anisakis* spp. type I in pen-reared green turtles, *Chelonia mydas* caused haemorrhagic ulcers in the lower stomach and upper intestine (Glazebrook and Campbell, 1990). Ulceration of the gastric and intestinal mucosa, as well as visceral adhesions, have also been reported in farmed turtles in northern Australia (due to the migration of larval *Anisakis* from the lumen of the gut to the pleuro-peritoneal cavity) (Glazebrook and Campbell, 1990).

7. Conclusion

Despite considerable past achievements, there are still huge gaps in our knowledge about many aspects of the biology and ecology of these important parasites and huge potential remains for future work. In Australia, it is evident that there is a broad range of anisakid nematodes, infecting a broad variety of invertebrate and vertebrate hosts, however, most species have not yet been adequately described. There is a need to employ tools such as electron microscopy and molecular approaches for a reliable and accurate specific identification and differentiation of species, particularly those that have only been reported from Australia. In spite of a significant increase in the body of the literature on the biology and life cycle of anisakids, many aspects of their developmental stages and life cycle still remain unknown. For example,

the part of the life cycle which occurs in crustaceans is not known. In addition, the specific identity of the larval stages of most species has not been determined. Therefore, the host-specificity of these parasites in different developmental stages, their life history patterns and geographical distributions remain unclear.

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