Parasites of cartilaginous fishes (Chondrichthyes) in South Africa – a neglected field of marine science

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Abstract: Southern Africa is considered one of the world’s ‘hotspots’ for the diversity of cartilaginous fishes (Chondrichthyes), with currently 204 reported species. Although numerous literature records and treatises on chondrichthyan fishes are available, a paucity of information exists on the biodiversity of their parasites. Chondrichthyan fishes are parasitised by several groups of protozoan and metazoan organisms that live either permanently or temporarily on and within their hosts. Reports of parasites infecting elasmobranchs and holocephalans in South Africa are sparse and information on most parasitic groups is fragmentary or entirely lacking. Parasitic copepods constitute the best-studied group with currently 70 described species (excluding undescribed species or nomina nuda) from chondrichthyans. Given the large number of chondrichthyan species present in southern Africa, it is expected that only a mere fraction of the parasite diversity has been discovered to date and numerous species await discovery and description. This review summarises information on all groups of parasites of chondrichthyan hosts and demonstrates the current knowledge of chondrichthyan parasites in South Africa. Checklists are provided displaying the host-parasite and parasite-host data known to date.

Keywords: Elasmobranchii, Holocephali, diversity, host-parasite list, parasite-host list

The biogeographical realm of Temperate Southern Africa (sensu Spalding et al. 2007) is dominated by two major ocean currents – the Benguela Current and the Agulhas Current – separating the realm in two distinct marine provinces, the Benguela and Agulhas provinces (sensu Spalding et al. 2007), respectively. The Agulhas province comprises the eastern and most of the southern coastline of South Africa. The marine waters of this province are subject to the warm, fast-flowing Agulhas Current, running southward from the equatorial Indian Ocean along the East-African coastline towards Cape Point (Briggs 1995, Van As et al. 2012). The Benguela province encompasses the marine environment of Namibia and the western coastline of South Africa in the south-eastern Atlantic Ocean. This province is influenced by the cold and slow-flowing Benguela Current, flowing northwards from the Antarctic towards Angola (Briggs 1995). The Temperate Southern African realm exhibits a rich ichthyofauna (Heemstra and Heemstra 2004, Branch et al. 2016, Nelson et al. 2016).

The marine environment of southern Africa is considered one of the most biodiverse regions for chondrichthyan fishes on this planet (Ebert and van Hees 2015, Weigmann, 2016). Chondrichthyans are cartilaginous fishes, uniting the elasmobranchs (i.e. modern sharks and rays) and holocephalans (i.e. chimaeras). The first treatise for the identification of cartilaginous fishes in southern Africa (Compagno et al. 1989) listed a total of 171 species (i.e. 100 sharks [S], 64 rays [R], seven chimaeras [C]). Since then, the number of known species increased and new species discoveries in this charismatic group are frequent. Two recent studies on the chondrichthyan fauna of southern Africa reported c. 210 (i.e. 118 S, 82 R, 10 C; Compagno 1999) and c. 204 (i.e. 119 S, 79 R, 8 C; Ebert and van Hees 2015) species of chondrichthyan. This vast diversity of species accounts for roughly 17% of all chondrichthyans known worldwide (Ebert and van Hees 2015).

The level of endemicity is relatively high, with c. 13% of species restricted to the waters of southern Africa (Ebert and van Hees 2015). Interestingly, the fauna is not equally distributed (Compagno 1999, Ebert and van Hees 2015) and the geographical distribution of most chondrichthyan is limited to either biogeographical province (Ebert and van Hees 2015). The chondrichthyan fauna in the warmer Agulhas province is significantly more diverse, with 175 predominantly tropical and warm-temperate species (Ebert and van Hees 2015). In contrast, the chondrichthyan fauna of the Benguela province in the south-eastern Atlantic consists of only 96 temperate species (Ebert and van Hees 2015). A smaller proportion of chondrichthyan species share an extended distribution over both biogeographical provinces (i.e. 62 species; Ebert and van Hees 2015).
At present, the diversity, biogeography and biology of cartilaginous fishes in southern Africa is reasonably well documented. However, very little is known about their parasites. In South Africa, marine parasitology has a long history, dating back about 200 years, since Leach (1818) described the first parasitic organism, a fish parasitic isopod, *Anilocra capensis* Leach, 1818 (Crustacea: Isopoda), from Cape Town (see Smit and Hadfield 2015). Until now, numerous parasite species have been described, predominantly from teleost fishes (e.g. Fantham 1918, Barnard 1955a, Kensley and Grindley 1973, Kensley 1978, Bray 1984, 1985, 1986, 1987, 1990, 1991, Oldewage 1992a, 1993a, Oldewage and Avenant-Oldewage 1993, Oldewage and Smale 1993, Dippenaar 2004). Only a minor proportion of the marine parasite diversity of South Africa has been explored and taxonomic groups that are covered by experts are limited (Griffiths et al. 2010).

Parasitic copepods represent the best-studied and documented group (e.g. Barnard 1955a, Kensley and Grindley 1973, Oldewage and Avenant-Oldewage 1993, Oldewage and Smale 1993, Dippenaar 2004, 2009, Dippenaar and Jordaan 2007, Dippenaar et al. 2010), mainly due to the personal preferences and expertise of a small number of aquatic parasitologists working in this region. Other parasitic groups (e.g. Annelida, Myxozoa, Platyhelminthes, parasitic protists), especially from poorly-studied hosts (i.e. certain elasmobranch families), are in need of taxonomic evaluation.

Chondrichthyans host a wide range of parasitic organisms (Cheung 1993, Benz and Bullard 2004, Caira et al. 2012). However, relatively few parasite species are documented from this host group in South Africa. To our knowledge, not a single, large-scale systematic survey on the parasite fauna of cartilaginous fishes from South Africa has been undertaken and reports of individual parasite species are based solely on opportunistic findings. The first parasite recorded from a chondrichthyan host in South Africa was a fluke (Digenea) detected in the body cavity of an unidentified species of catshark (Scyliorhinidae) from the southeastern Atlantic off Cape Town (see von Ofenheim 1900). Specimens described by von Ofenheim (1900) were obtained from the Natural History Museum in Berlin and were considered conspecific with *Probolitrema richiardii* (López, 1888), a species described earlier from the Mediterranean Sea (von Ofenheim 1900).

The current knowledge of the parasite fauna of chondrichthyans from South Africa is dominated by parasitic copepods. Although few scientists dedicated much of their scientific career to the exploration of parasitic copepods, only a fraction of potential chondrichthyan hosts have been investigated and the species currently known from South Africa might represent only the ‘tip of the iceberg’. The second largest group of parasites reported from this host group are tapeworms (Cestoda). However, information on this group of internal parasites is based on just nine independent studies.

In a recent report on parasites of elasmobranchs, Caira et al. (2012) stated that the cestode diversity “exceeds that of all of the other metazoan groups parasitising elasmobranchs combined”. On a global scale, ten out of the 19 known orders of cestodes infect chondrichthyans, with a total of 1,044 species most cestodes parasitise elasmobranchs as definitive hosts (Caira and Jensen 2017). Relatively few cestodes are found in holoccephalans; one of the smallest cestode orders, the Gyrocotylidea with a total of 10 species, and certain members of the Phyllobothriidea (Caira and Jensen 2017). The most recent estimate on the global diversity of cestodes infecting elasmobranchs is 5,126 species (see Caira and Jensen 2017). With 1,269 species of elasmobranchs currently known worldwide, this represents an average of four cestode species per elasmobranch host (Caira and Jensen 2017).

Although cestodes currently constitute the second largest group of known chondrichthyan parasites in South Africa, merely 18 of 204 potential host species have been examined for cestode infections. We assume that the diversity of cestodes in South Africa is at least equal to, if not larger than, the diversity of chondrichthyan hosts. Predicting the number of cestodes infecting chondrichthyans in South Africa would be purely hypothetical. However, it is clear that a potentially large proportion of the actual diversity still remains to be discovered. The remaining parasitic groups known to infect chondrichthyans are very poorly explored. Overall, a total of 19 species of six parasite groups (i.e. trypanosomes, ciliates, monogeneans, trematodes, nematodes and isopods) were reported from South Africa. Information on the remaining 12 groups (i.e. amoebae, sporozoans, myxozoans, planarians, acanthocephalans, hirudineans, gastropods, mites, ostracods, amphipods, brachiurans and barnacles) is entirely absent.

The aim of this study is to provide an overview of parasite infection of elasmobranchs and holoccephalans and comprehensive information on the current knowledge from South Africa. In addition, parasite-host and host-parasite checklists are provided for the first time, summarising records of chondrichthyan and parasite species, their classification and the respective literature.

### PARASITE GROUPS INFECTING CHONDRICHTHYANS

**Trypanosomes** (Protozoa, Eozoa, Euglenozoaa, Kinetoplastea, Trypanosomatida)

On a global scale, only relatively few trypanosomes have been reported from chondrichthyan hosts (Burreson 1989, Aragort et al. 2005, Davies et al. 2012). The first trypanosome species from this host group in South Africa was reported by Fantham (1918), who found an unidentified species of *Trypanosoma* Gruby, 1843 in the onefin electric ray, *Narke capensis* (Gmelin) (Narkidae), which until now remains undescribed.

Almost 90 years later, Yeld and Smit (2006) reported a second trypanosome species, *Trypanosoma haploblephari* Yeld et Smit, 2006, from the peripheral blood of two endemic species of catsharks, *Haploblepharus pictus* (Müller et Henle) and *Haploblepharus edwardsii* (Schinz), with a prevalence of 100% of 143 specimens examined. Infection by trypanosomes is greatly increased with sedentary, bot-
tom-dwelling hosts in colder climates (Khan et al. 1980). The known host spectrum of trypanosomes recorded from chondrichthyan hosts is comprised of elasmobranches, predominantly of the families Rajidae and Scyliorhinidae, but also Hemiscylliidae, Dasyatidae, Torpedinidae, Narkidae, Odontaspidae and Rhinobatidae. Holocephalans were thus far not reported to host trypanosomes. The mode of transmission of marine fish trypanosomes involves piscicolid leeches as vectors (Karslbakk 2004, Hayes et al. 2014).

**Ciliates** (Chromista, Harosa, Ciliophora)

Trichodinid ciliophorans are a poorly studied group of parasites that most commonly occur on the gills and skin of teleosts in freshwater and marine environments (Lom 1970, Lom and Dyková 1992, Van As and Basson 1996, Xu et al. 2001). Several species were also reported as endosymbionts occurring in the urinary system and intestinal tract of fishes (Mueller 1932, Basson et al. 1990). Very few species (Evdokimova et al. 1969, Khan 1972, Van As and Basson 1996) reported species of *Trichodina* Ehrenberg, 1830 from the oviducts, genital and urinary systems of rajid and rhinobatid hosts.

The only species known from cartilaginous fishes in South Africa was described by Van As and Basson (1996). *Trichodina rhinobatae* Van As et Basson, 1996 was found in the urogenital tract of *Acroteriobatus annulatus* (Müller et Henle) (Rhinobatidae) collected at the mouth of the Olifants River in the Western Cape Province. Van As and Basson (1996) assumed transmission could be linked to the reproductive behaviour of the elasmobranch hosts, since a number of trichodinid endosymbionts were also encountered on external gill filaments of embryos *in utero* (Van As and Basson 1996).

**Coccidians** (Chromista, Harosa, Myxozoa, Apicomplexa, Sporozoa, Conoidasida, Coccidiasina)

Coccidians are apicomplexan parasites of vertebrate and invertebrate hosts, with direct and indirect transmission strategies (Davies and Ball 1993). Xavier et al. (2018) suggested that coccidians follow the evolution of their hosts, with basal lineages infecting chondrichthyans, while more derived lineages are found in higher vertebrates. Although numerous species of coccidians are known to infect fishes, their diversity remains poorly explored (Molnár et al. 2012). Reports of coccidians from chondrichthyan hosts are sparse. Most coccidians reported from this host group belong to the speciose genus *Eimeria* Schneider, 1875 (Eimeriidae) (e.g. Dyková and Lom 1981, Lom and Dyková 1981, 1992), whereas the genus *Goussia* Labbé, 1896 (Eimeriidae) contains only a single species (*Lom and Dyková 1981*). Additional coccidian blood parasites known to infect chondrichthyans are species of *Haemogregarina* Danilewsky, 1885 (Haemogregarinidae) (e.g. Aragort et al. 2005, Davies et al. 2012, Magro et al. 2016). Few studies reported haemogregarines from marine teleost fishes from South Africa (Fantham 1930, Smit and Davies 1999, 2001, 2006, Davies and Smit 2001, Smit et al. 2003, Hayes et al. 2006, Ferreira et al. 2012). However, coccidian infections of chondrichthyans in South African waters have yet to be revealed.

**Myxozoans** (Animalia, Cnidaria, Myxozoa)

Myxozoans are multicellular parasites that have undergone a recent classification change from protists to the animal kingdom, where they are now accepted in the phylum Cnidaria (see Kent et al. 1994, Schlegel et al. 1996, Siddall et al. 1995, Okamura et al. 2015). Many myxozoans infect teleost fishes, but relatively few species are known from chondrichthyans. The primary site of infection is the lumen of the gall bladder (Love and Moser 1983, Cheung 1993). No species has thus far been recorded from chondrichthyans in South Africa.

**Planarians** (Animalia, Platyhelminthes, Rhabditophora, Tricladida)

Planarians are predominantly free-living flatworms. Only very few members adopted a parasitic mode of life. The triclad species, *Micropharynx parasitica* Jägerskiöld, 1896, is the only representative infecting chondrichthyans and has been reported from three species of skates (Rajidae) in the North Atlantic Ocean and the Barents Sea (Jägerskiöld 1896, Awerinzew 1925, Ball and Khan 1976). Although this triclad has not been recorded from South Africa, its occurrence in these waters seems possible, due to the presence of one of its reported hosts. *Raja clavata* Linnaeus is a prominent and widely distributed species in the eastern Atlantic. It ranges from Iceland to South Africa and further into the western Indian Ocean to Madagascar (Froese and Pauly 2018). This species is only one of 26 reported species of rajids present in South African waters, 12 of which are endemic, and, to our knowledge, none of them has ever been examined for parasites.

**Tapeworms** (Lophotrochozoa, Platyhelminthes, Neodermata, Cestoda)

Cestodes or tapeworms are a large group of endoparasitic platyhelmints, which successfully radiated in chondrichthyan hosts and now constitute by far the most diverse group of chondrichthyan parasites. The earliest record of a cestode infection comes from eggs found in a coprolite (fossil faeces) of an elasmobranch that dates back to the middle to late Permian Period, some 270 million years ago (Dentzien-Dias et al. 2013). A total of 19 cestode orders are currently recognised, 10 of which infect chondrichthyans, namely the Catheterophalidea, Diphylidea, Gyrocotylidea (only found in holocelphalans), Lecanicephalidea, Litobothiacea (only found in holocephalans), and Labbéidea.
The diversity of cestodes infecting chondrichthyans is immense, with 203 known genera and 1,044 valid species (Caira et al. 2017). As such, cestodes are far more numerous than all other metazoan parasites infecting chondrichthyans. Within the Cestoda, trypanorhynchs comprise the largest group, with 81 genera and currently 315 recognised species (Beveridge et al. 2017). As mentioned earlier it is estimated that worldwide approximately 1,259 species of cestodes of elasmobranchs remain to be discovered (Caira et al. 2017). Holocephalans are on average less frequently parasitised. Randhawa and Poulin (2010) estimated an even higher species richness of cestodes infecting elasmobranchs. Assessing cestode records of 317 elasmobranch species, Randhawa and Poulin (2010) determined that roughly 3,600 have yet to be described.

Cestodes primarily infect the spiral intestine of their chondrichthyan definitive host. Caira and Healy (2004) stated that “it is very rare to encounter an elasmobranch in nature that does not host at least one species of cestode in its spiral intestine”. On rare occasions, other parts of the chondrichthyan body are infected, such as the stomach and peritoneal cavity. Certain larval stages (mostly of the Trypanorhyncha) were also reported to infest the epidermis, gills, gall bladder, gonads, viscera and the peritoneal cavity. Although cestodes constitute the largest group of metazoan parasites of chondrichthyans, the known fauna from South Africa, at a first glance, seems rather depauperate.

At present, there are 23 species of seven orders recorded from South African waters, including 11 trypanorhynchs, six diphylleids, two tetraphyllideans and one species of gyrocytideans, onchoproteocephalideans, phyllobothrideans and rhinebothrideans, respectively (Linton 1924, Schramm 1889, 1991, Palm 1999, Rodriguez et al. 2011, Caira et al. 2013a, b, Abbott and Caira 2014, Bernt et al. 2015). The first cestode species of chondrichthyans from South Africa was recorded by Linton (1924) from the Cape Province (off Cape Town, Mossel Bay and Table Bay). Linton (1924) described two new species, Gyrocotyle plana (Linton, 1924 (Gyrocotyle) (now G. rugosa Diesing, 1850) and Echeneibothrium australinum Linton, 1924 (Rhinebothriidea), and reported four additional species, namely Acanthobothrium paulum Linton, 1890 (Onchoproteocephalidea), Grillotia erinaceus (van Beneden, 1858), Hepatotyloson trichiuri (Holten, 1902) (both Trypanorhyncha) and Paraoxygnatobothrium angustum (Linton, 1889) (Phyllobothriidea).

Since this first study, only very few scientists contributed to the knowledge of the South African cestode fauna of chondrichthyan hosts and findings from the 1980s until recently were opportunistic and not part of large-scale, systematic investigations. Overall, cestodes were recorded from 18 chondrichthyan host species of seven families, which is merely a fraction of the potential host spectrum of more than 200 chondrichthyan species present in South Africa (Ebert and van Hees 2015). Instead of having a depauperate fauna, it is probable that South Africa might yet reveal its potential of possessing a highly diverse cestode fauna likely to be even greater than the one of their chondrichthyan hosts.

Monogeneans (Animalia, Platyhelminthes, Neodermata, Monogenea)

Monogeneans belong to the flatworm phylum Platyhelminthes and represent a large group of highly host-specific parasites (Bychowsky 1957, Boeger and Krisky 2001). They primarily attach to the gills and external surfaces of teleost fishes in marine and freshwater environments. Certain monogenean families (e.g. Acanthocotylidae, Amphibdellidae, Microbothriidae, Monocotylidae, Chimaericolidae and Hexabothriidae) or members thereof (e.g. Cap-salidae, Diphyllobothriidae, Lophoscolecidae, Udonellidae) parasitise chondrichthyans. The attachment sites on and within their chondrichthyan hosts are diverse and, apart from the gills and epidermis, they may infest the nasal fossae, urogenital system and the body cavity wall (Chisholm and Whittington 1998, Whittington et al. 2000).

In South Africa, research on marine monogeneans started with Manter (1955), who described two species from the Cape elephantfish, Callorhinichus capensis Duméril (Chimaeriformes: Callorhinichidae). At present, nine species of monogeneans belonging to three families have been recorded from eight species of chondrichthyans (Beverley-Burton et al. 1991, Bullard et al. 2004, Vaughan and Chisholm 2010a, b, 2011, Vaughan and Christie 2012, Poddubnaya et al. 2015, Vaughan et al. 2008). Given the high diversity of elasmobranchs and holocelphalans in South African waters, it is expected that a large proportion of the monogenean diversity still remains to be discovered.

Aspidogastreans (Animalia, Platyhelminthes, Neodermata, Trematoda)

Aspidogastreans form a basal group of trematodes (flukes), sister to the Digenea (Rohde et al. 2001). Of the 61 aspidogastrean species known today, only 18 infect marine hosts (Alves et al. 2015), usually with a low intensity. Seven species were reported from chondrichthyans, namely Multicalyx cristata Faust et Tang, 1936, Multicalyx elegans (Olsson, 1869), Multicalyx sp., Rugogaster callorhinchi Amato et Pereira, 1995, Rugogaster hydrologi Schell, 1973, Rugogaster sp. and Stichocotyle nephrops Cunningsham, 1884 (see Alves et al. 2015). Of these, only a single species, M. cristata, was reported from South Africa from the gall bladder and spiral valve of Sphyraena lewini (Griffith et Smith) and the abdominal cavity of Carcharid as taurus Rafinesque (Parukhin and Tkachuk 1980, Bray 1984).

Digeneans (Animalia, Platyhelminthes, Neodermata, Trematoda)

Digeneans are a speciose group of endoparasitic flatworms that are “primitively associated with teleosts” (Bray and Cribb 2003) and which greatly diversified amongst marine fishes. Infections of chondrichthyans, however, are considered a result of several host-switching events from...
teleosts over a long time period (Bray and Cribb 2003, Olson et al. 2003), while others account for accidental infections (see Caira et al. 2012). Overall, the diversity of digeneans in chondrichthyan hosts is rather limited and ranges between 50 and 60 species (Caira et al. 2012), which equals roughly 2.6% of the described digenean fauna (Caira et al. 2012). Among the numerous attachment sites, the preferred locations for digeneans are the body cavities (i.e. buccal, pericardial, and peritoneal cavity), the stomach, and, to a lesser extent, the heart and blood vessels (i.e. members of a single family), liver, oviducts, kidneys, rectum, cloaca and the spiral valve (Cribb et al. 2001, Caira et al. 2012).

Von Ofenheim (1900) was the first to report a species of digeneans from a chondrichthyan host from South Africa. The specimens were recovered from the body cavity of an unidentified cat shark species (Scyliorhinidae) collected in Cape Town. Von Ofenheim (1900) considered them conspecific with Probolitrema richardi (López, 1888) (as Anaporrhutum richardi), a species previously described from Squalus acanthias Linnaeus in the Mediterranean Sea. Soon after, Looss (1902) transferred the species into the newly erected genus Probolitrema Looss, 1902 and considered the specimens of von Ofenheim as a new species, Probolitrema capense Looss, 1902. The same species was later discovered by Gibson (1976) from a white skate, Rostroraja alba (Lacepède). However, Gibson (1976) synonymised nine species, including P. capense, with P. richardi. This decision to synonymise P. capense with P. richardi was later questioned by Yeld (2009), who found specimens allocated to ‘P. capense’ from the dark shyshark, Haplolobephurus pictus (Müller et Henle) off Cape Town. Parukhin (1966) described a second species, Probolitrema callorhynchi Parukhin, 1966, from the Cape elephantfish, Callorhinichus capensis Duméril collected in the southern Atlantic Ocean. At present, knowledge on digeneans infecting chondrichthyans in South Africa is sparse and the two species currently known from the body cavities of a callorhinichid, scylorhinid and rajid host might not represent the actual diversity of digeneans present in these waters.

Acanthocephalans (Animalia, Syndemata, Acanthocephala)

Acanthocephalans or spiny-headed worms are prominent endoparasites of teleosts (Crompton and Nickol 1985). Adult acanthocephalans possess a spiny, eversible proboscis with which they attach to the intestinal and stomach walls of their definitive hosts. Chondrichthyans are rarely infected and are mostly considered to represent accidental hosts. At present, 18 species were reported from elasmobranches. Four species were exclusively found in elasmobranches (Golvan et al. 1964, Golvan 1969, Bilques and Khan 2005, Weaver and Smales 2014), which might serve as paratenic or even suitable definitive hosts. Infections of holocephalans are unknown. At present, there have been no reports of acanthocephalans parasitising chondrichthyans in South Africa.

Nematodes (Animalia, Ecdysozoa, Nematoda)

Nematodes (roundworms) constitute a large phylum of free-living and parasitic organisms. Between 80 and 100 species of parasitic nematodes are known from chondrichthyan hosts (Benz and Bullard 2004, Caira and Healy 2004). Most species infecting chondrichthyans are endoparasites living in the spiral intestine and stomach, while others occur in the brain, heart, liver, spleen, kidneys, ovaries, uterus, musculature and the body cavity. Very few species were also reported from external body surfaces, such as the gills (Adamson et al. 1987, Cheung 1993, Moravec 2001, Aragort et al. 2002), nasal fossae (Cheung 1993) and from tumors and skin lesions (Adamson et al. 1987, Chabaud 1960, MacCallum 1925, Moravec 2001). A single physaloploid nematode, Proleptus obtusus Dujardin, 1845, has been described from an unidentified species of Rhinobatos Linck from South Africa (Baylis 1933). Moravec et al. (2002) redescribed this species based on material collected from a second host, the puffadder shyshark, H. edwardsii collected off the De Hoop Nature Reserve (Cape Province). Nematodes have never been in the focus of marine parasitological research in South Africa. A single species infecting elasmobranches known to date represents only a mere fraction of the diversity and, as a consequence, many more species await discovery.

Hirudineans (Animalia, Annelida, Clitellata, Hirudinea)

Hirudineans (leeches) of the family Piscicolidae are obligate ectoparasites feeding on the blood of fishes in marine and freshwater systems (Sawyer 1986). Marine hirudineans remain rarely studied in South Africa and the only reports are based on teleost and crustacean hosts (Moore 1958, Utevsky 2004, 2007). The Ph.D. thesis of Eleanor Yeld from the University in Cape Town mentions marine leeches from external surfaces of three species of scylorhinid catsharks, H. pictus, H. edwardsii and Poroderma africanaum (Gmelin) (Yeld, 2009). The piscicolid leeches were tentatively assigned to Stiharobdella macrothela (Schmarda). However, these results have not been formally published. Although piscicolid leeches are known parasites of chondrichthyans (Sawyer 1986), not a single species has been reported from South Africa.

Sea snails (Animalia, Mollusca, Gastropoda, Caenogastropoda, Neogastropoda)

The first and so far only ectoparasitic gastropod, Cancelleria cooperi Gabb, 1865 (Neogastropoda: Cancellariidae), was reported from California (USA) by O’Sullivan et al. (1987). This gastropod species is highly specialised to feeding on the blood of the Pacific electric ray, Tetronarce californica (Ayres) (Torpediniformes: Torpedinidae), and potentially other bottom-dwelling species of rays (O’Sullivan et al. 1987). It is highly unlikely to find this geographically-restricted gastropod species infecting chondrichthyan hosts in South Africa. However, since only limited information on the parasite infections of chondrichthyans is known and previous studies from South Africa only focused on few chondrichthyan hosts and even fewer, selected parasite groups, such an infection might have been
simply overlooked. Moreover, electric rays (Torpedinidae) have never been in the focus of any parasitological study in South Africa.

**Mites** (Animalia, Arthropoda, Chelicerata, Arachnida, Acari)

Benz and Bullard (2004) reported an unidentified species of acariform mite from the heart lumen of a nurse shark collected in Florida Bay in the north-western Atlantic Ocean. Although this has been the first report of acariform mites infecting chondrichthyans, several others have been reported from the swim-bladder, gills, pharynx, oesophagus and the stomach wall of teleosts (Bykhovskaya-Pavlovskaya et al. 1964, Hare and Burt 1975, Ching and Parker 1983, Fain and Belpaire 1985, Fain and Lambrechts 1985). Until now, parasitic infections with acariform mites have neither been reported from chondrichthyan hosts in waters off South Africa in particular, nor the entire southern hemisphere in general.

**Ostracods** (Animalia, Arthropoda, Crustacea, Ostracoda)

Ostracods (seed shrimps) are generally free-living organisms. Only very few species were reported to parasitise the gills and nasal cavities of elasmobranchs (Wilson 1913, Harding 1966, Williams and Bunkley-Williams 1996, Bennett et al. 1997). However, none has been reported from South Africa.

**Isopods** (Animalia, Arthropoda, Crustacea, Malacostraca, Peracarida, Isopoda)

Parasitic isopods almost exclusively occur on external surfaces of the chondrichthyan hosts (i.e. epidermis, nasal fossae, gills, buccal cavity, cloaca; see Brusca 1981, Heupel and Bennett 1999, Smit and Basson 2002, Bunkley-Williams and Williams 1998). Few species are considered as endoparasites, present in the heart (Bird 1981), stomach (van Beneden 1861, Meinert 1877, Hurley 1961) and uterus (Bird 1981, Caira and Healy 2004). The fauna of parasitic isopods of chondrichthyans known from South Africa to date includes only two species; the gnathiid, *Gnathia pantherina* Smitt and Basson, 2002 (see Smitt and Basson 2002, Smit and Davies 2004, Hayes et al. 2007), and the cirolanid, *Natatolana hirtipes* (Milne-Edwards, 1840) (Barnard 1936).

**Amphipods** (Animalia, Arthropoda, Crustacea, Malacostraca, Peracarida, Amphipoda)

Amphipods are malacostracan crustaceans, which have a laterally compressed body lacking a carapace. Although mostly free-living, certain species are facultative ectoparasites on a wide array of hosts (Bousfield 1987). Parasitic amphipods infecting fishes may spend some parts of their lives free in the water column and attach temporarily to the body surfaces of fish hosts to feed on the skin tissue and food items or simply using fishes as a means of transport (‘hitch-hikers’ senseu Bousfield 1987).

Chondrichthyan hosts mostly include species of the deep-sea, e.g. lantern sharks (Etmopteridae) or dogfish sharks (Squalidae), or of colder climates, e.g. rajid skates in the northwestern Atlantic (Vader and Romppainen 1986). The western coastline of South Africa might represent a suitable environment for parasitic amphipods, given the presence of the cold and slow-flowing Benguela Current and the occurrence of a large assemblage of potential etmopterid, dalatid and rajid host species. However, no records of parasitic amphipods infecting chondrichthyans in South Africa can be found in the literature.

**Branchiurans** (Animalia, Arthropoda, Crustacea, Ichthyostega, Branchiura)

Branchiurans (fish lice) of the genus *Argulus* Müller, 1785 are dominant ectoparasites of teleosts, but have also been reported from chondrichthyans (Wilson 1902, 1904, Cresssey 1972, 1978, Ross 1999, Caira and Healy 2004). In South Africa, very few species of *Argulus* are known from marine or brackish water teleost hosts (Barnard 1955a, Avenant-Oldewage 1994, Avenant-Oldewage and Oldewage 1995, Van As et al. 1999, Van As and Van As 2001, Smit et al. 2005), while records of branchiuran infections on chondrichthyans are entirely absent.

**Barnacles** (Animalia, Arthropoda, Crustacea, Hexanauplia, Thecostraca, Cirripedia)

Cirripeds, commonly known as barnacles, are a minor arthropod group of predominantly sessile, suspension-feeding crustaceans. Very few genera of cirripeds made the evolutionary transition to a parasitic mode of life (Newman et al. 1969). Of these, a single species infects vertebrate hosts. The pedunculate barnacle, *Anelasma squalicola* (Lovén, 1845), parasitises several species of deep-sea lantern sharks (Etmopteridae) of the genera *Etmopterus* and *Centroscyllium* (Darwin 1851, Hickling 1963, Leung 2014).

The peduncle of *A. squalicola* is thereby used as a feeding device to absorb nutrients from its squalloid hosts and as a solid anchorage (Ommundsen et al. 2016), deeply embedded into the tissue of the head, abdomen, claspers, dorsal, pectoral and pelvic fins (Kabata 1970, Long and Waggoner 1993, Yano and Musick 2000) and even the buccal cavity (Yano and Musick 2000). As it was shown for other parasitic cirripeds (Reinhard 1956, Hoggarth 1990), *A. squalicola* has negative impacts on the reproductive organs of its hosts, actively impeding the development of testes and ovaries (Hickling 1963). Although *A. squalicola* possesses a cosmopolitan distribution (Yano and Musick 2000), its presence in South Africa infecting etmopterid sharks has never been demonstrated.

**Copepods** (Animalia, Arthropoda, Crustacea, Hexanauplia, Copepoda)

Copepods are the most diverse and by far the best studied group of parasites of chondrichthyans in South Africa. These ectoparasitic arthropods are mostly detected on external surfaces of their hosts, such as the epidermises, gills, branchial chambers, nasal fossae, spiracles, eyes, buccal cavity, cloaca and the acoustic-lateralis system. Rather unusual findings of parasitic copepods were reported from external surfaces of embryos *in utero* (Nagasawa et al. 1998)
and the nasal capsules penetrating into the olfactory lobe of the brain (Diebakate et al. 1997). At present, 70 valid species from 11 families of parasitic copepods are known from chondrichthyans in South Africa. In addition, six species have only recently been considered *nomen nuda*, whereas another 16 could not be identified to species level. This multitude of known species infecting cartilaginous fishes makes South Africa one of the best studied countries for this line of parasite research in the world and new copepod species are described frequently.

**CHONDРИЧИТЫАНЫ AS HOSTS ОF PARASITES FROM SOUTH AFRICA**

In South Africa, only a mere fraction of the expected parasite diversity has been reported from chondrichthyans hosts and available chondrichthyan parasite records are based on information collected from 90 species, including 24 unidentified ones. Even if the unidentified species are considered as valid host records, less than 50% of the chondrichthyan species known from South Africa have been investigated for parasites. Among the best-studied host species are the great white shark, *Carcharodon carcharias* (Linnaeus), with a total of 30 records (13 species of copepods, followed by the bull shark, *Carcharhinus leucas* (Müller et Henle), with 25 records (10 species of copepods and four species of cestodes) and the dusky shark, *Carcharhinus obscurus* (Lesueur), with 23 records (13 species of copepods and one species of monogeneans and cestodes, respectively). Overall, carcharhiniform sharks make up 50% of all host records. Among the Carcharhiniformes, the requiem sharks (Carcharhinidae) represent the best-studied host group with 125 records (i.e. 30% of all host records). Mackerel sharks (Lamniformes) represent the second-most studied host group, with 83 host records (24 unidentified ones). Even if the unidentified species have only recently been considered, *nomen nuda*, whereas another 16 could not be identified to species level. This multitude of known species infecting cartilaginous fishes makes South Africa one of the best studied countries for this line of parasite research in the world and new copepod species are described frequently.

**PARASITE-HOST LIST**

The classification and nomenclature of parasites follows Ruggiero et al. (2015) and WoRMS Editorial Board (2018). The phyla of Protozoa and Chromista are followed by the sub- and infrakingdom (if available) in parentheses. In Animalia, each class is followed by the subphylum (if available) in parentheses. Orders of Arthropoda, Mollusca, Nematoda and Platyhelminthes are followed by the subclass and superorder (if available) in parentheses. Parasite and host species are listed alphabetically. Host classification follows Last et al. (2016a, b – Batomorphi) and Weigmann (2016 – Selachii and Holocephali). Nomenclature of chondrichthyan species follows Froese and Pauly (2018). Each host species is followed by the order and family, in parentheses, and the respective study, where hosts were listed.

**Kingdom Protozoa**

**Phylum: Euglenozoa (Eozoa: Euglenozoa)**

**Class:** Kinetoplastea

**Order:** Trypanosomatida

**Family:** Trypanosomatidae

*Trypanosoma haploblephari* Yeld et Smit, 2006

*ex.* *Haploblepharus edwardsii* (Schinz) (Carcharhiniformes: Scyliorhinidae); Yeld and Smit (2006)

*Trypanosoma pictus* (Müller et Henle) (Carcharhiniformes: Scyliorhinidae); Yeld and Smit (2006)

*Trypanosoma sp.*

*ex.* *Narke capensis* (Gmelin) (Torpediniformes: Narkidae); Fantham (1918)

**Kingdom Chromista**

**Phylum: Ciliophora (Harosa: Aleolata)**

**Class:** Oligohymenophorea

**Order:** Mobilida (Peritrichia)

**Family:** Trichodinidae

*Trichodina rhinobatae* Van As et Basson, 1996

*ex.* *Acroteriobatus annulatus* (Müller et Henle) (Rhinopristiformes: Rhinobatidae); Van As and Basson (1996)

**Kingdom Animalia**

**Phylum: Platyhelminthes**

**Class:** Monogenea (Neodermata)

**Order:** Dicylobothriidea (Polyopisthocotylea)

**Family:** Hexabothriidae

*Callorhynchicola multitestitculata* Manter, 1955

*ex.* *Callorhinchus capensis* Duméril (Chimaeriformes: Callorhinichidae); Manter (1955), Beverley-Burton et al. (1993)

*Callorhynchicola multitestitculata* Manter, 1955

*ex.* *Callorhinchus capensis* Duméril (Chimaeriformes: Callorhinichidae); Manter (1955), Beverley-Burton et al. (1993)

*Callorhynchicola multitestitculata* Manter, 1955

*ex.* *Callorhinchus capensis* Duméril (Chimaeriformes: Callorhinichidae); Manter (1955), Beverley-Burton et al. (1993)
Branchotenthes robinoverstreeti Bullard et Dippenaar, 2003
ex Rhina acynlostoma Bloch et Schneider (Rhinopristiformes: Rhinidae); Bullard and Dippenaar (2003)

Callorhynchocotyle callorhynchi (Manter, 1955)
ex Callorhinchus capensis Duméril (Chimaeriformes: Callorhinchidae); Manter (1955), Vaughan and Christison (2012), Poddubnaya et al. (2015)

Order: Monocotylidea (Monopisthocotylea)
Family: Monocotylidae

Dendromonocotyle citrosa Vaughan, Chisholm et Christison, 2008
ex Dasyatis chrysonota (Smith) (Myliobatiformes: Dasyatidae); Vaughan et al. (2008)
ex Maculabatis gerrardi (Gray) (Myliobatiformes: Dasyatidae); Vaughan et al. (2008) [in captivity]

Dendromonocotyle ukhatheni Vaughan, Chisholm et Christison, 2008
ex Himantura cf. varnak (Myliobatiformes: Dasyatidae); Vaughan et al. (2008) [in captivity]
ex Maculabatis gerrardi (Gray) (Myliobatiformes: Dasyatidae); Vaughan et al. (2008) [in captivity]

Dermophthirius carcharhini MacCallum, 1926
ex Cararchinus obscurus (Lesueur) (Carcharhiniformes: Cararchinidae); Bullard et al. (2004)

Heterocotyle tokoloshei Vaughan et Chisholm, 2010
ex Bathtyshoa brevicaudata (Hutton) (Myliobatiformes: Dasyatidae); Vaughan and Chisholm (2010a)

Neoheterocotyle robbi Vaughan et Chisholm, 2010
ex Acroteriobatus annulatus (Müller et Henle) (Rhinopristiformes: Rhinobatidae); Vaughan and Chisholm (2010b)

Family: Microbothriidae

Pseudoeleptobothrium christisoni Vaughan et Chisholm, 2011
ex Acroteriobatus annulatus (Müller et Henle) (Rhinopristiformes: Rhinobatidae); Vaughan and Chisholm (2011)

Order: Aspidogastrea (Aspidogastrea)
Class: Trematoda (Neodermata)
Order: Aspidogastrida (Aspidogastrea)
Family: Multicalycidae

Multicalyx cristata Faust et Tang, 1936
ex Cararchias taurus Rafinesque (Lamniformes: Odontaspididae); Bray (1984)
ex Sphyra lewini (Griffith et Smith) (Carcharhiniformes: Sphyridae); Parukhin and Tkachuk (1980), Bray (1984)

Order: Plagiorchida (Digenea)
Family: Gorgoderidae

Probolitrema callorhynchi Parukhin, 1966 nomen nudum (Bray and Cribb, 2003)
ex Callorhinchus capensis Duméril (Chimaeriformes: Callorhinchidae); Parukhin (1966, 1968)

Probolitrema richardi (López, 1888)
ex Rostroarea alba (Lacepède) (Rajiformes: Rajidae); Gibson (1976)
ex Scyliorhiniidae gen. sp. (Carcharhiniformes: Scyliorhinidae); von Oehseniden (1900)

Class: Cestoda (Neodermata)
Order: Gyrocotyliidea (Cestodaria)
Family: Gyrocotyliidae

Gyrocotyle rugosa Diesing, 1850
ex Callorhinchus callorhynchus (Linnaeus) (Chimaeriformes: Callorhinchidae); Linton (1924)

Order: Diphylloidea (Eucestoda)
Family: Echinobothriidae

Andodacronum meganae Abbott et Caird, 2014
ex Leucoraja wallacii (Hulley) (Rajiformes: Rajidae); Abbott and Caird (2014)

Echinobothrium dorotheae Caird, Pickering, Schulman et Hahnessian, 2013
ex Raja straeleni Poll (Rajiformes: Rajidae); Caird et al. (2013a)

Echinobothrium dodgermanni Caird, Pickering, Schulman et Hahnessian, 2013
ex Rhinobatos annulatus Smith in Müller et Henle (Rhinopristiformes: Rhinobatidae); Caird et al. (2013a)

Echinobothrium joshuai Rodriguez, Pickering et Caird, 2011
ex Cruriraja halleyi Aschliman, Ebert et Compagno (Rajiformes: Rajidae); Rodriguez et al. (2011)

Echinobothrium marquesi Abbott et Caird, 2014
ex Leucoraja wallacii (Hulley) (Rajiformes: Rajidae); Abbott and Caird (2014)

Echinobothrium vace Caird, Rodriguez et Pickering, 2013
ex Raja miraletus Linnaeus (Rajiformes: Rajidae); Caird et al. (2013b)

Order: Onchoproteocephalidea (Eucestoda)
Family: Onchobothriidae

Acanthobothrium paulum Linton, 1890
ex Rajidae gen. sp. (Rajiformes: Rajidae); Linton (1924)

Order: Phyllobothriidea (Eucestoda)
Family: Phyllobothriidae

Paraorygmatobothrium angustum (Linton, 1889)
ex Cararchinus melanopterus (Quoy et Gaimard) (Carcharhiniformes: Cararchinidae); Linton (1924)

Order: Rhinebothriidea (Eucestoda)
Family: Echeneibothriidae

Echeneibothrium australium Linton, 1924
ex Rajidae gen. sp. (Rajiformes: Rajidae); Linton (1924)

Order: Tetraphyllidea (Eucestoda)
Family: Calliobothriidae

Calliobothrium ezeeti Bernot, Caird et Pickering, 2015
ex Mustelus palumbes Smith (Carcharhiniformes: Triakidae); Bernot et al. (2015)

Symcallio petersi Bernot, Caird et Pickering, 2015
ex Mustelus palumbes Smith (Carcharhiniformes: Triakidae); Bernot et al. (2015)

Order: Trypanorhyncha (Eucestoda)
Family: Lacistorhynchidae

Grillotia erinaceus (van Beneden, 1858)
ex Rajidae gen. sp. (Rajiformes: Rajidae); Linton (1924)

Pseudogrillotia perelica (Shuler, 1938)
ex Cararchinus leucas (Müller et Henle) (Carcharhiniformes: Cararchinidae); Schramm (1991)
ex Cararchinus plumbeus (Nardo) (Carcharhiniformes: Cararchinidae); Schramm (1991)
Family: Sphyriocephalidae

Hepatoxylon trichiuri (Holten, 1802)

ex Squalus acanthias Limneaus (Squaliformes: Squalidae); Linton (1924)

Family: Tentaculariidae

Heteronybelinia estigmata (Dollfus, 1960)

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Palm (1999)

ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Palm (1999)

Heteronybelinia heteromorphii Palm, 1999

ex Sphyra mokarran (Rüppell) (Carcharhiniformes: Sphyridae); Palm (1999)

Heteronybelinia robusta (Linton, 1890)

ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Palm (1999)

Heteronybelinia yamaguti (Dollfus, 1960)

ex Sphyra lewini (Griffith et Smith) (Carcharhiniformes: Sphyridae); Palm (1999)

Nybelinia africana Dollfus, 1960

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Palm (1999)

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Palm (1999)

ex Scyllilagothes quenetti Boulenger (Carcharhiniformes: Triakidae); Palm (1999)

Nybelinia schmidtii Palm, 1999

ex Prionace glauca (Linnaeus) (Carcharhiniformes: Carcharhinidae); Palm (1999)

Nybelinia scoliidoni (Vijayalakshmi, Vijayalakshmi et Gangdharam, 1996)

ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Palm (1999)

Family: Otobothriidae

Poecilancistrum carophyllum (Diesing, 1850)

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Schramm (1989)

Phylum: Nematoda

Class: Chromadorea

Order: Rabditida (Chromadoria)

Family: Physalopteridae

Proleptus obtusus Dujiardin, 1845

ex Haploblepharus edwardsii (Schinzi) (Carcharhiniformes: Scylliorhinae); Moravec et al. (2002)

ex Rhinobatos sp. (Rhinopristiformes: Rhinobatidae); Baylis (1933) Phylum: Arthropoda

Class: Malacostraca (Crustacea)

Order: Isopoda (Eumalacostraca: Peracarida)

Family: Gnathiidae

Gnathia pantherina Smit et Basson, 2002

ex Acrophyllus annulatus (Müller et Henle) (Rhinopristiformes: Rhinobatidae); Hayes et al. (2007)

ex Haploblepharus edwardsii (Schinzi) (Carcharhiniformes: Scylliorhinae); Smit and Basson (2002), Smit and Davies (2004), Hayes et al. (2007)

ex Poroderma pantherian (Müller et Henle) (Carcharhiniformes: Scylliorhinae); Smit and Basson (2002), Smit and Davies (2004)

ex Torpedo fuscomaculata Peters (Tropidiformes: Torpedinidae); Smit and Basson (2002), Smit and Davies (2004)

Family: Cirolanidae

Natatolana hirtipes (Milne-Edwards, 1840)

ex Carcharias sp. (Lamniformes: Odontaspididae); Barnard (1936)

Class: Hexanauplia (Crustacea)

Order: Siphonostomatoida (Copepoda: Podoplea)

Family: Caligidae

Alebion carchariae Kroyer, 1863

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Kressey (1967b)

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Cresse (1967b)

Alebion sp.

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009)

Caligus chrysophrysi Pillai, 1985

ex Mobula alfredi (Krefft) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

Caligus coryphaenae Steenstrup et Lütken, 1861

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)

ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Dippenaar and Jordaan (2007)

ex Squalus acantius Limneaus (Squaliformes: Squalidae); Smit and Basson (2002), Smit and Davies (2004)

ex “shark”; Barnard (1955a), Kressey and Grindley (1973)

Alebion gracilis Wilson, 1905

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Cresse (1967b)

Alebion sp.

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009)

Caligus chrysophrysi Pillai, 1985

ex Mobula alfredi (Krefft) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

Caligus coryphaenae Steenstrup et Lütken, 1861

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)

ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Dippenaar and Jordaan (2007)

ex Squalus acantius Limneaus (Squaliformes: Squalidae); Smit and Basson (2002), Smit and Davies (2004)

ex “shark”; Barnard (1955b)

Euryphorus brachypterus (Gerstaeker, 1853)

ex “shark”; Oldewage and Avenant-Oldewage (1993)

Lepeophtheirus longispinosus Wilson, 1908

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Kressey and Grindley (1973), Dippenaar and Jordaan (2007)

ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)

ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)

ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Oldewage and Avenant-Oldewage (1993)

Lepeophtheirus natatornis Kressey and Grindley, 1973

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Smit and Basson (2002), Smit and Davies (2004)

ex Torpedo fuscomaculata Peters (Tropidiformes: Torpedinidae); Smit and Basson (2002), Smit and Davies (2004)
Families: Carcharhinidae; Kensley and Grindley (1973) Dippenaar and Jordaen (2007)

ex Carcharias taurus Rafinesque (Lamniformes: Odontaspidae); Oliver et al. (2000), Dippenaar and Jordaen (2007), Dippenaar (2009)

Lepeophtheirus sp.
ex Rhinobatos sp. (Rhinopristiformes: Rhinobatidae); Barnard (1955a)

Paralephon elongatous Wilson, 1911
ex Carcharhinus amboinensis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaen (2007)

ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Cressey (1967a, b), Dippenaar and Jordaen (2007), Dippenaar (2009),

ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaen (2007)

ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaen (2007)

Pupulina cliffi Dippenaar et Lebepe, 2013

ex Mobula eregoodoontekte (Bleeeker) (Myliobatiformes: Mobulidae); Dippenaar and Lebepe (2013), Lebepe and Dippenaar (2013)

ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Dippenaar and Lebepe (2013), Lebepe and Dippenaar (2013)

Pupulina meriru Dippenaar et Lebepe, 2013

ex Mobula eregoodoontekte (Bleeeker) (Myliobatiformes: Mobulidae); Dippenaar and Lebepe (2013), Lebepe and Dippenaar (2013)

ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Dippenaar and Lebepe (2013), Lebepe and Dippenaar (2013)

Families: Dichelesthiidae

Anthosoma crassum (Abildgaard, 1794)
ex Carcharias taurus Rafinesque (Lamniformes: Odontaspidae); Dippenaar and Jordaen (2007)

ex Carcharias spp. (Lamniformes: Odontaspidae); Barnard (1955a)

ex Carcharodon carcharias (Linnaeus) (Lamniformes: Lamnidae); Dippenaar and Jordaen (2007), Kensley and Grindley (1973), Oldewage and Smale (1993)

ex Isurus oxyrinchus Rafinesque (Lamniformes: Lamnidae); Dippenaar and Jordaen (2007), Kensley and Grindley (1973), Oldewage and Smale (1993)

ex Isurus sp. (Lamniformes: Lamnidae); Cressey (1967b), Kensley and Grindley (1973)

ex Lamna nasus (Bonnaterre) (Lamniformes: Lamnidae); Barnard (1955a)

ex Mobula alfredi (Krefft) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

ex Mobula birostris (Walbaum) (Myliobatiformes: Mobulidae); Dippenaar and Jordaen (2007)

ex Odontaspis sp. (Lamniformes: Odontaspidae); Kensley and Grindley (1973)

ex Prionace glauca (Linnaeus) (Carcharhiniformes: Carcharhinidae); Kensley and Grindley (1973)

Families: Eudactylinae

Carnifissorius siamensis Deets et Ho, 1988
ex Rhina ancylostoma Bloch et Schneider (Rhinopristiformes: Rhinidae); Dippenaar and Jordaen (2007)

Eudactylinia acanthii Scott, 1901
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Dippenaar and Molele (2015)

Eudactylinia aspera Heller, 1865
ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaen (2007)

ex Sphyra lewini (Griffith et Smith) (Carcharhiniformes: Sphyridae); Dippenaar and Jordaen (2007)

Eudactylinia diabolophila Deets, 1994 (nomen nudum)
ex Mobula alfredi (Krefft) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

Eudactylinia dolfullisi Brian, 1924
ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaen (2007)

Eudactylinia hornostelli Deets, 1994 (nomen nudum)
ex Aetobatus narinari (Euphrasen) (Myliobatiformes: Aetobatidae); Dippenaar and Jordaen (2007)

Eudactylinia oliveri Laubier, 1968
ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Dippenaar and Jordaen (2007), Lebepe and Dippenaar (2013)

ex Mobula eregoodoontekte (Bleeeker) (Myliobatiformes: Mobulidae); Dippenaar and Lebepe (2013), Lebepe and Dippenaar (2013)

Eudactylinia pollex Cressey, 1967
ex Sphyra mokarran (Rüppell) (Carcharhiniformes: Sphyridae); Dippenaar and Jordaen (2007)

Eudactylinia pusilla Cressey, 1967
ex Galeocerdo cuvier (Péron et Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009), Dippenaar and Jordaen (2007), Dippenaar et al. (2009)

Eudactylinia vaquetillae Deets, 1994 (nomen nudum)
ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

Eudactylinia sp.
ex Squalus cf. megalops (Squaliformes: Squalidae); Dikgale and Dippenaar (2010)

Eudactylinoides niger (Wilson, 1905)
ex Carcharias taurus Rafinesque (Lamniformes: Odontaspidae); Dippenaar (2009), Dippenaar and Jordaen (2007)

Nemesis lamna Risso, 1826
ex Carcharodon carcharias (Linnaeus) (Lamniformes: Lamnidae); Cressey (1967b), Kensley and Grindley (1973), Dippenaar et al. (2008), Dippenaar (2009), Mangena et al. (2014)

ex Isurus oxyrinchus Rafinesque (Lamniformes: Lamnidae); Oldewage and Smale (1993), Dippenaar (2009), Mangena et al. (2014)

ex Isurus sp. (Lamniformes: Lamnidae); Cressey (1967b)

Nemesis robusta (van Beneden, 1851)
ex Alopias vulpinus (Bonnaterre) (Lamniformes: Alopiidae); Barnard (1948, 1955a), Kensley and Grindley (1973)

ex Prionace glauca (Linnaeus) (Carcharhiniformes: Carcharhinidae); Kensley and Grindley (1973)

Nemesis sp.
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Dippenaar and Molele (2015)

Nemesis sp. 1
ex Carcharhinus brevipinna (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaen (2007)

DOI: 10.14411/fp.2019.002 Parasite of chondrichthyans in South Africa
forms: Carcharhinidae); Mangena et al. (2014)
ex Sphyrna lewini (Griffith et Smith) (Carcharhiniformes: Sphyridae); Mangena et al. (2014)

* Nemesis sp. 2
  ex Carcharhinus brevipinna (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Mangena et al. (2014)

* Nemesis sp. 3
  ex Alophias vulpinus (Bonnetterre) (Lamniformes: Alopiidae); Dippenaar (2009), Mangena et al. (2014)
ex Carcharhinus limbatis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009), Mangena et al. (2014)
ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009), Mangena et al. (2014)
ex Carcharhinus sealei (Pietschmann) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009)
ex Sphyra lewini (Griffith et Smith) (Carcharhiniformes: Sphyridae); Mangena et al. (2014)

* Nemesis sp. 4
  ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009)

* Nemesis sp. 5
  ex Carcharhinus brevipinna (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009)

Family: Kroyeridae

Kroyerina mobulae Deets, 1987
  ex Mobula kuhlii (Müller et Henle) (Myliobatiformes: Mobulidae); Lebepe and Dippenaar (2013)

Kroyerina scottorum Cressey, 1972
  ex Sphyra lewini (Griffith et Smith) (Carcharhiniformes: Sphyridae); Dippenaar and Jordaan (2007)

Kroyeria carchariaeglauci Hesse, 1878
  ex Carcharhinus amboinensis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Mokumo and Dippenaar (2015)
ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007), Mokumo and Dippenaar (2015)
ex Prionace glauca (Linnaeus) (Carcharhiniformes: Carcharhinidae); Kensisley and Grindley (1973)

Kroyeria decepta Deets, 1994 (nomen nudum)
ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009), Mokumo and Dippenaar (2015)
ex Carcharhinus brevipinna (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar et al. (2000a), Mokumo and Dippenaar (2015)

Kroyeria dispar Wilson, 1935
  ex Galeocerdo cuvier (Péron et Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar et al. (2009), Mokumo and Dippenaar (2015)
ex Carcharhinus brevipinna (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar (2009), Dippenaar et al. (2009), Mokumo and Dippenaar (2015)

Kroyeria gemursa Cressey, 1967
  ex Sphyra mokarran (Rüppell) (Carcharhiniformes: Sphyridae); Dippenaar and Jordaan (2007), Mokumo and Dippenaar (2015)
ex Mustelus palambe Smith (Carcharhiniformes: Triakidae); Mokumo and Dippenaar (2015)
ex Kroyeria lineata van Beneden, 1853
  ex Mustelus palambe Smith (Carcharhiniformes: Triakidae); Mokumo and Dippenaar (2015)
ex Kroyeria longicauda Cressey, 1970
  ex Carcharhinus limbatus (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007), Mokumo and Dippenaar (2015)
ex Kroyeria papillipes Wilson, 1932
  ex Galeocerdo cuvier (Péron et Lesueur) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007), Mokumo and Dippenaar (2015)
ex Kroyeria procerobscaena Deets, 1994 (nomen nudum)
ex Carcharhinus amboinensis (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007), Mokumo and Dippenaar (2015)
ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007), Mokumo and Dippenaar (2015)
ex Kroyeria rhopemaphaga Deets, 1994 (nomen nudum)
ex Galeorhinus galeus (Linnaeus) (Carcharhiniformes: Triakidae); Mokumo and Dippenaar (2015)
ex Charopinus dalmanni (Retzius, 1829)
ex Haplolepus edwardsii (Schinz) (Carcharhiniformes: Scyliorhinidae); Oldewage (1992a), Oldewage and Av- enant-Oldewage (1993)
ex Squalus acanthias Linnaeus (Squaliformes: Squalidae); Oldewage (1993a)
ex Charopinus dubius Scott, 1901
  ex Raju sp. (Rajiformes: Rajidae); Kensley and Grindley (1973)
ex Rajella caudaspinosa (von Bonde et Swart) (Rajiformes: Rajidae); Kensley and Grindley (1973)
ex Rajella leoparda (von Bonde et Swart) (Rajiformes: Rajidae); Kensley and Grindley (1973)
ex “skate” (Rajiformes: Rajidae); Barnard (1955a)
ex Lernaeopoda galei Kroyer, 1837
  ex Mustelus mustelus (Linnaeus) (Carcharhiniformes: Triakidae); Barnard (1955a), Kensley and Grindley (1973)
ex Rhizoprionodon acutus (Rüppell) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2007)
ex Lernaeopoda sp.
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Dippenaar and Malele (2015)
ex Neocallichima eumittor (Yamaguti, 1939)
ex Etmopterus sp. (Squaliformes: Etmopteridae); Kensley and Grindley (1973)
ex Etmopterus sp. (Squaliformes: Etmopteridae); Kensley and Grindley (1973)
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Dippenaar and Malele (2015)


Folia Parasitologica 2019, 66: 002 Page 11 of 23
Schistobrachia jordaanae Dippenaar, Olivier et Benz, 2004
ex Gymnura natalensis (Gichrist et Thompson) (Myliobatiformes: Gymnuridae); Dippenaar et al. (2004)

Schistobrachia kabata Dippenaar, 2016
ex Dippterus dourei (Cadenat) (Rajiformes: Rajidae); Kessler and Grindley (1973)
ex Leucoraja wallacei (Hulley) (Rajiformes: Rajidae); Dippenaar (2016)
ex Raja straeleni Poll (Rajiformes: Rajidae); Dippenaar (2016)
ex Rostroraja alba (Lacepède) (Rajiformes: Rajidae); Dippenaar (2016)
ex “skate” (Rajiformes: Rajidae); Barnard (1955b)

Vanbenedenia hydrolagae Oldewage, 1993
ex Hydrologus sp. (Chimaeriformes: Chimaeridae); Oldewage (1993b)

Family: Pandaridae

Achtheinus dentatus Wilson, 1911
ex Carcharhinus leucas (Müller et Henle) (Cararchariniformes: Cararcharidae); Cressey (1967a, b), Dippenaar and Jordaan (2007)
ex Cararchinus limbatis (Müller et Henle) (Cararcharidae); Dippenaar and Jordaan (2007)
ex Cararchinus obscurus (Lesueur) (Cararcharhiniformes: Cararcharididae); Cressey (1967b), Dippenaar and Jordaan (2007), Dippenaar (2009)
ex Cararchinus sealei (Pietschmann) (Cararcharhiniformes: Cararcharididae); Dippenaar and Jordaan (2007)
ex Carcharodon carharis (Linnaeus) (Lamniformes: Lamnidae); Kessler and Grindley (1973)
ex Haplobolephas edwardsii (Schniz) (Scyliorhinae; Kessler and Grindley (1973), Oldewage and Aventan-Oldewage (1993)
ex Mustelus canis (Mitchell) (Cararcharhiniformes: Triakidae); Kessler and Grindley (1973)
ex Mustelus mosis Hemprich et Ehrenberg (Cararcharhiniformes: Triakidae); Dippenaar and Jordaan (2007)
ex Mustelus sp. (Cararcharhiniformes: Triakidae); Cressey (1967b), Kessler and Grindley (1973)
ex Mustelus spp. (Cararcharhiniformes: Triakidae); Cressey (1967a)
ex Scoliodon sp. (Cararcharhiniformes: Cararcharididae); Kessler and Grindley (1973)
ex Sphyraena zygaena (Linnaeus) (Cararcharhiniformes: Sphyridae); Kessler and Grindley (1973)
ex Squalus acanthias Linnaeus (Squaliformes: Squalidae); Kessler and Grindley (1973)
ex Squalus blainvillei (Risso) (Squaliformes: Squalidae); Kessler and Grindley (1973)
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Oldewage and Aventan-Oldewage (1993)
ex “shark”; Kessler and Grindley (1973)

Achtheinus oblongus Wilson, 1908
ex Cararcharodon carcharias (Linnaeus) (Lamniformes: Lamnidae); Barnard (1955a), Oldewage and Smale (1993), Dippenaar and Jordaan (2007), Dippenaar (2009)
ex Haplobolephas edwardsii (Schinz) (Cararcharhiniformes: Scyliorhinae); Oldewage (1992a)
ex Hexanchus griseus (Bonnaterre) (Hexanchiformes: Hexanchidae); Oldewage and Smale (1993)
ex Mustelus sp. (Cararcharhiniformes: Triakidae); Barnard (1955a)
ex Pliotrema warreni Regan (Pristiophoriformes: Pristiophoridae); Wilson (1923), Kessler and Grindley (1973), Oldewage and Smale (1993)
ex Squalus acanthias Linnaeus (Squaliformes: Squalidae); Oldewage (1993a), Wilson (1923)
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Oldewage (1992a, 1993a), Oldewage and Smale (1993)
ex “dogfish”; Barnard (1955a)
ex Squalus cf. megalops (Squaliformes: Squalidae); Dikgale and Dippenaar (2010)

Achtheius pinguis Wilson, 1912
ex Cararcharhinus taurus Rafinesque (Lamniformes: Odonotusplididae); Barnard (1955a), Dippenaar and Jordaan (2015)
ex Carcharodon carcharias (Linnaeus) (Lamniformes: Lamnidae); Dippenaar and Jordaan (2015)
ex Galeorhinus galeus (Linnaeus) (Cararcharhiniformes: Triakidae); Dippenaar and Jordaan (2015)
ex Mustelus mustelus (Linnaeus) (Cararcharhiniformes: Triakidae); Oldewage (1992b)
ex Rhizoprionodon acutus (Rüppell) (Cararcharhiniformes: Carcharhinidae); Barnard (1955a)
ex Pliotrema warreni Regan (Pristiophoriformes: Pristiophoridae); Barnard (1955a)
ex Scyliorhinus sp. (Cararcharhiniformes: Scyliorhinae); Barnard (1955a)
ex Squalus acanthias Linnaeus (Squaliformes: Squalidae); Barnard (1955a)
ex Squalus megalops (Macleay) (Squaliformes: Squalidae); Oldewage (1992b), Dippenaar and Molele (2015)
ex Squalus cf. megalops (Squaliformes: Squalidae); Dippenaar and Jordaan (2015)
ex “shark”; Barnard (1955a)

Dinomoura latifolia (Steensstrup et Lütken, 1861)
ex Isurus oxyrinchus Rafinesque (Lamniformes: Lamnidae); Oldewage and Smale (1993)
ex Prionace glauca (Linnaeus) (Cararcharhiniformes: Carcharhinidae); Cressey (1967b), Kessler and Grindley (1973), Oldewage (1992c)
ex Prionace sp. (Cararcharhiniformes: Carcharhinidae); Kessler and Grindley (1973)
ex Echthrogaleus coleoptratus (Guérin-Ménéville, 1837)
ex Carcharodon carcharias (Linnaeus) (Lamniformes: Lamnidae); Oldewage and Smale (1993)
ex Prionace glauca (Linnaeus) (Cararcharhiniformes: Carcharhinidae); Barnard (1955a), Kessler and Grindley (1973)
ex Echthrogaleus denticulatus Smith, 1873
ex Isurus oxyrinchus Rafinesque (Lamniformes: Lamnidae); Oldewage and Smale (1993)
ex Echthrogaleus torpedinis Wilson, 1907
ex Tetranoraca nobiliana (Bonaparte) (Torpediniformes: Torpedinidae); Kessler and Grindley (1973)
ex Torpedo sp. (Torpediniformes: Torpedinidae); Kessler and Grindley (1973)
ex Entepherus laminipes Bere, 1936
ex Mobula alfredi (Krefft) (Myliobatiformes: Mobulidae); Lebbepe and Dippenaar (2013)
Nesippus crypturus Heller, 1868
ex Carcharinus brevipinnus (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2012)

Nesippus tigris Cressey, 1967
ex Galeocerdo cuvier (Péron et Lesueur) (Lamniformes: Sphyridae); Dippenaar and Jordaan (2012)

Nesippus orientalis Heller, 1868
ex Alopias vulpinus (Bonnaterre) (Lamniformes: Alopidae); Dippenaar and Jordaan (2006, 2012)

Nesippus nana Cressey, 1970
ex Carcharinus plumbeus (Nardo) (Carcharhiniformes: Carcharhinidae); Dippenaar and Jordaan (2012)

Nesippus vasca Kirtisinghe, 1964
ex Rhina ancylostoma Bloch et Schneider (Rhinopristiformes: Rhinidae); Dippenaar and Jordaan (2007, 2012), Dippenaar (2009)

Nesippus vespa Kirtisinghe, 1964
ex Rhyynchobatus djiddensis (Forsskål) (Rhinopristiformes: Rhinidae); Dippenaar and Jordaan (2007, 2012)

Paradus bicolor Leach, 1816
ex Carcharhinus sp. (Carcharhiniformes: Carcharhinidae); Kimsel and Grindley (1973)

Paradus carcharini Ho, 1963
ex Carcharhinus leucas (Müller et Henle) (Carcharhiniformes: Carcharhinidae); Cressey (1967a, b)

ex “hammerhead shark” (Carcharhiniformes: Sphyrnidae); Bibby et al. (2011)

ex “grey shark”; Barnes (1955a)

Paradus cranchi Leach, 1819
ex Carcharhinus longimanus (Poe) (Carcharhiniformes: Carcharhinidae); Cressey (1967a, b)

ex Carcharodon carcharias (Linneaus) (Lamniformes: Lamnidae); Cressey (1967b)

ex Poroderma africanum (Gmelin) (Carcharhiniformes: Scyliorhinidae); Barnard (1955a)

ex Sphyra zygaena (Linneaus) (Carcharhiniformes: Sphyridae); Dippenaar and Jordaan (2007, 2012)

ex Squalus acanthias (Linneaus) (Squaliformes: Squalidae); Oldeway and Smale (1993)

ex "dogfish"; Kinsel and Grindley (1973)

ex “grey shark”; Barnes (1955a)

Paradus floridanus Cressey, 1967
ex Carcharhinus taurus Rafinesque (Lamniformes: Lamnidae); Oldeway and Smale (1993)

Paradus smithii Rathbun, 1886
ex Carcharhinus obscurus (Lesueur) (Carcharhiniformes: Carcharhinidae); Kinsel and Grindley (1973)

ex Carcharhinus sp. (Carcharhiniformes: Carcharhinidae); Barnard (1955a)

ex Carcharhinus taurus Rafinesque (Lamniformes: Lamnidae); Oldeway and Smale (1993)

ex Carcharhinus sp. (Lamniformes: Lamnidae); Oldeway and Smale (1993)

ex Carcharhinus spp. (Lamniformes: Lamnidae); Oldeway and Smale (1993)

ex Isurus oxyrinchus Rafinesque (Lamniformes: Lamnidae); Oldeway and Smale (1993)
HOST-PARASITE LIST

Higher level classification of the class Chondrichthyes follows Nelson et al. (2016). Ordinal and family level classification within the subclasses Euselachii and Holocephali follows Last et al. (2016a, b) (i.e. Batomorphi) and Weigmann (2016) (i.e. Selachii and Holocephali). Nomenclature of chondrichthyan species follows Froese and Pauly (2016). Parasite species in respective groups are listed alphabetically. Parasite groups are indicated by the following abbreviations: Cestoda – Ce, Ciliophora – Ci, Copepoda – Co, Isopoda – Is, Kinetoplastida – Ki, Monogenea – Mo, Nematoda – Ne, Trematoda – Tr.

Class Chondrichthyes

Subclass: Holocephali

Order: Chimaeriformes
Family: Chimaeridae
Callorhinichus callorhynchus (Linnaeus): Ce – Gyrocoyle rugosa
Callorhinichus capensis Duméril: Mo – Callorhynchocotyle callorhynchi (Manter, 1955); Callorhynchicola multitetes cutulatus Manter, 1955; Tr – Probolitrema callorhynchi Parukhin, 1966 (nomen nudum)

Family: Chimaeridae
Hydrologus sp.: Co – Vanbenedenia hydrologae Oldewage, 1993

Subclass: Euselachii

Infraclass: Elasmobranchii

Division: Batomorphi

Order: Rajiformes
Family: Rajidae

Cruiraja huleyi Aschliman, Ebert et Compagno: Ce – Echinobothrium joshua; Rodriguez, Pickering et Caira, 2011
Dipturus doutei (Cadenat): Co – Schistobrachia kabata Dippenaar, 2016

“skate”: Co – Charopinus dubius Scott, 1901; Schistobrachia kabata Dippenaar, 2016; Trebus caudatus Kroyer, 1838

Order: Torpediniformes
Family: Narkidae

Narke capensis (Gmelin): Ki – Trypanosoma sp.

Family: Torpedinidae

Tetronarce nobiliana (Bonaparte): Co – Echthrogaleus torpedinis Wilson, 1907
Torpedo fusconaculata Peters: Is – Gnathia pantherina Smit et Basson, 2002
Torpedo sp.: Co – Echthrogaleus torpedinis Wilson, 1907

Order: Rhinopristiformes
Family: Rhinidae

Rhina ancylostoma Bloch et Schneider: Co – Carnifossorius siamensis Deets et Ho, 1988; Nesippus vespa Cressey, 1964; Mo – Branchotenthes robinoversreit Bullard et Dippenaar, 2003
Rhynchobatis djiddensis (Forsskål): Co – Nesippus vespa Cressey, 1964

Family: Rhinobatidae

Rhinobatos sp.: Co – Lepeophtheirus sp.; Ne – Proteleus obtusus Dujardin, 1845

Order: Myliobatiformes
Family: Aetobatidae

Aetobatis narinari (Euphrasen): Co – Eudactylina hornbosteli Deets, 1994 (nomen nudum)
Family: Dasyatidae

Bathytoshia brevicaudata (Hutton): Mo – Heterocotyle tokoloshe Vaughan et Chisholm, 2010
Dasylatis chrysonotus (Smith): Mo – Dendromonocotyle citrosa Vaughan, Chisholm et Christison, 2008
Himantura cf. varnak: Mo – Dendromonocotyle ukuthena Vaughan, Chisholm et Christison, 2008

Maculabatis gerrardi (Gray): Mo – Dendromonocotyle citrosa Vaughan, Chisholm et Christison, 2008; D. ukuthena Vaughan, Chisholm et Christison, 2008

Family: Gymnuridae

Gymnura natalensis (Gilechrist et Thompson): Co – Schistobrachia jordanae Dippenaar, Olivier et Benz, 2004

Family: Mobulidae

Mobula alfredi (Krefft): Co – Anthosoma crassum (Abildgaard, 1974); Caligus chrysophyssi Pillai, 1985; Entepheurus laminipes Bere, 1936; Eudactylina diabolophila Deets, 1994 (nomen nudum)

Mobula birostris (Walbaum): Co – Anthosoma crassum (Abildgaard, 1974); Entepheurus laminipes Bere, 1936

Mobula kuhlii (Müller et Henle): Co – Caligus chrysophyssi Pillai, 1985; Caligus coryphaenae Steenstrup et Lütken, 1861; Entepheurus laminipes Bere, 1936; Eudactylina oliveri Laubier, 1968; E. vaquetillae Deets, 1994 (nomen nudum); Kroeyerina mobulae Deets, 1987; Pupulina cliffi Dippenaar et Lebepe, 2013; P. merira Dippenaar et Lebepe, 2013

Family: Myliobatidae

Aetomylaeus bovinus (Geoffroy Saint-Hilaire): Co – Pseudocha-ropinus pteryomylæi Raubert et Essafi, 1979

Division: Selachii

Order: Hexanchiformes
Family: Hexanchidae

Hexanchus griseus (Bonnaterre): Co – Achtheinus oblongus Wilson, 1908

Order: Pristiphoriformes
Family: Pristiphoridae

Pliotrema warreni Regan: Co – Achtheinus oblongus Wilson, 1908; A. pinguis Wilson, 1912

Order: Squaliformes
Family: Squalidae

Squalus acantias Linnaeus: Ce – Hepatosynon trichiuri (Holten, 1802); Co – Achtheinus dentatus Wilson, 1911; A. oblongus Wilson, 1908; Pseudocha-ropinus bicaudatus (Kroyer, 1837); Trebus benzi Dippenaar, 2017; Trebus sp.

Squalus cf. megalops: Co – Achtheinus oblongus Wilson, 1908; A. pinguis Wilson, 1912; Eudactylina acanthi Wilson, 1911

Family: Lepidobatidae

Lepidobatis megalops (Macleay): Ce – Achtheinus dentatus Wilson, 1911; A. oblongus Wilson, 1908; A. pinguis Wilson, 1912; Eudactylina acanthi Scott, 1901; Lepeophtheirus longispinosus Wilson, 1908; Lernaeopoda sp.; Nemesis sp.; Pseudocha-ropinus bicaudatus (Kroyer, 1837); Trebus benzi Dippenaar, 2017; Trebus sp.

Lepidobatis megalops: Co – Achtheinus oblongus Wilson, 1908; A. pinguis Wilson, 1912; Eudactylina acanthi Wilson, 1911

Family: Etmopteridae

Etmopterus sp.: Co – Neoalbionella etmopteri (Yamaguti, 1939)
Order: Orectolobiformes
Family: Rhinoconidae
Rhincodon typus Smith: Co – Pandarus smithii Rathbun, 1886
Family: Stegostomatidae
Stegostoma fasciatum (Hermann): Co – Pandarus cranchi Leach, 1819
Stegostoma sp.: Co – Pandarus cranchi Leach, 1819
Order: Lamniformes
Family: Alopiidae
Alopias vulpinus (Bonnaterre): Co – Nemesis robusta (van Beneden, 1851); Nemesis sp. 3; Nesippus orientalis Heller, 1865
Family: Odontaspidae
Carcharias taurus Rafinesque: Co – Acheilinus pinguis Wilson, 1912; Alebion carcharidiae Kroyer, 1863; Anthosoma crassum (Ahlbergd, 1794); Echthrogaleus denticulatus Smith, 1873; Nesippus orientalis Heller, 1865; Pandarus floridanus Cressy, 1967; P. smithii Rathbun, 1886; Pandarus sp. 1; Tr – Multicalyx cristata Faust et Tang, 1936
Carcharias sp.: Co – Anthosoma crassum (Ahlbergd, 1794); Pandarus bicolor Leach, 1816; P. smithii Rathbun, 1886; Is – Natatolana hirtipes (H. Milne-Edwards, 1840)
Odontaspis sp.: Co – Alebion carcharidiae Kroyer, 1863; Anthosoma crassum (Ahlbergd, 1794); Pandarus bicolor Leach, 1816; P. smithii Rathbun, 1886
Family: Lamnidae
Carcharodon carcharias (Linnaeus): Co – Acheilinus dentatus Wilson, 1911; A. oblongus Wilson, 1908; A. pinguis Wilson, 1912; Alebion carcharidiae Kroyer, 1863; Anthosoma crassum (Ahlbergd, 1794); Echthrogaleus coleoptratus (Guérin-Méneville, 1837); Nesippus lamna Risso, 1826; Nesippus crypturus Heller, 1868; N. orientalis Heller, 1868; N. tigris Cressy, 1967; Pandarus cranchi Leach, 1819; P. smithii Rathbun, 1886; Pandarus sp. 3
Isurus oxyrinchus Rafinesque: Co – Alebion carcharidiae Kroyer, 1863; Anthosoma crassum (Ahlbergd, 1794); Dinemoura latifolia (Steinstrup et Lütken, 1861); Echthrogaleus denticulatus Smith, 1873; Nesippus lamna Risso, 1826; Nesippus orientalis Heller, 1865; Pandarus smithii Rathbun, 1886; Phylothryus cornutus (Milne-Edwards, 1840)
Isurus sp.: Co – Anthosoma crassum (Ahlbergd); Nemesis lamna Risso, 1826; Pandarus smithii Rathbun, 1886
Lamna nasus (Bonnaterre): Co – Anthosoma crassum (Ahlbergd, 1794)
Order: Carcharhiniformes
Family: Scyliorhinidae
Haploléphhus edwardsi (Schinz): Co – Acheilinus dentatus Wilson, 1911; A. oblongus Wilson, 1908; Charopinus dalmanni (Retzius, 1829); Ne – Propterygius obtusus Dujardin, 1845; Is – Gnatia pantherina Smith et Basson, 2002; Ki – Trypanosoma haplolephei Yeld et Sm, 2006
Haploléphhus pictus (Müller et Henle): Ki – Trypanosoma haplolephei Yeld et Sm, 2006
Poroderma africam (Gmelin): Co – Pandarus cranchi Leach, 1819
Poroderma pantherium (Müller et Henle): Is – Gnatia pantherina Smith et Basson, 2002
Scyliorhinidae gen. sp.: Tr – Probolitrema richardi (López, 1888)
Scyliorhinus sp.: Co – Acheilinus pinguis Wilson, 1912
Family: Triakidae
Galeorhinus galeus (Linnaeus): Co – Acheilinus pinguis Wilson, 1912; Kroyeria rhophenophaga Deets, 1994 (nomen nudum); Pandarus bicolor Leach, 1816
Mustelus canis (Mitchill): Co – Acheilinus dentatus Wilson, 1911
Mustelus mossus Hemprich et Ehrenberg: Co – Acheilinus dentatus Wilson, 1911; Pseudopandarus gracilis Kirtisinghe, 1950; P. longus (Gnanamuthu, 1951)
Mustelus musculus (Linnaeus): Co – Acheilinus oblongus Wilson, 1908; A. pinguis Wilson, 1912; Lernaeopoda galea Kroyer, 1837; Nesippus orientalis Heller, 1865; Triaphylus beatricea Dippenaar, 2018
Mustelus palumbus Smith: Ce – Calliobothrium eusebi Bernot, Caira et Pickeering, 2015; Symcaecilia peteri Bernot, Caira et Pickeering, 2015; Co – Kroyeria lineata van Beneden, 1853; Triaphylus benzi Dippenaar, 2018
Mustelus sp.: Co – Acheilinus dentatus Wilson, 1911; A. oblongus Wilson, 1908
Scylligaleus queketti Boulenger: Ce – Nybelinia africana Dollfus, 1960
Family: Hemigaliidae
Hemipristis elongata (Kunzinger): Co – Triaphylus lewisi Dippenaar, 2018
Family: Sphyridae
Sphyrida levini (Griffith et Smith): Ce – Heteronybelinia yamaguti (Dollfus, 1960); Co – Eudactylina aspera Heller, 1865; Kroyeria sphyrnae Rangnekar, 1957; Kroyeriana scotorum Cressy, 1972; Nesippus sp. 1; Nesippus sp. 3; Nesippus orientalis Heller, 1865; Pandarus sp. 2; Pansous japonicas (Shino, 1960); Triaphylus vaissieri (Delamare Deboutville et Nuñes-Ruivo, 1954); Tr – Multicalyx cristata Faust et Tang, 1936
Sphyrida zygaena (Linnaeus): Co – Acheilinus dentatus Wilson, 1911; Rangnekar, 1957; Nesippus crypturus Heller, 1868; N. orientalis Heller, 1868; Pandarus cranchi Leach, 1819
Sphyrida sp.: Co – Pandarus cranchi Leach, 1819
“hammerhead shark”: Co – Pandarus cranchi Leach, 1819
Family: Carcharhinidae
Carcharhinus amboinensis (Müller et Henle): Co – Kroyeria procrobesca Deets, 1994 (nomen nudum); Kr. carcharidiae Hesse, 1879; Paralebion elongatus Wilson, 1911
Carcharhinus brachyrurus (Günther): Co – Nesippus orientalis Heller, 1865
Carcharhinus brevipinnus (Müller et Henle): Co – Kroyeria deetsi Dippenaar, Benz et Olivier, 2000; Kroyeria sp.; Nesippus crypturus Heller, 1868; N. orientalis Heller, 1868; Nemesis sp. 1; Nemesis sp. 2; Nemesis sp. 5
Carcharhinus leucas (Müller et Henle): Ce – Heteronybelinia estigmata (Dollfus, 1960); Nybelinia africana Dollfus, 1960; Poecilancistrum caryophyllum (Diesing, 1850); Pseudogrillotia perelica (Shuler, 1938); Co – Acheilinus dentatus Wilson, 1911; Caligus coryphaenae Steenstrup et Lütken, 1861; Kroyeria carcharidiae Hesse, 1878; K. procrobesca Deets, 1994 (nomen nudum); Lepeophtheirus longissinosus Wilson, 1908; L. natalensis Kroyer et Grindley, 1973; Nesippus crypturus Heller, 1868; N. orientalis Heller, 1868; Pandarus carcharini Ho, 1963; Paralebion elongatus Wilson, 1911
Carcharhinus limbatus (Müller et Henle): Ce – Heteronybelinia estigmensia (Dollfus, 1960); H. robusta (Linton, 1890); Nybelinia scoliodoni (Vijayalakshmi, Vijayalakshmi et Gangdharam, 1996); Co – Achteinus dentatus Wilson, 1911; Eudactylina aspera Heller, 1865; Kroyeria longicauda Cressy, 1970; Lepeophtheirus longispinosus Wilson, 1908; Nemesis sp. 3; N. crypturus Heller, 1868; N. orientalis Heller, 1868; Paralebion elongatus Wilson, 1911
Carcharhinus longimanus (Poeyi): Co – Pandarus cranchi Leach, 1819
Carcharhinus melanopterus (Quoy et Gaimard): Ce – Paraorygmatobothrium angustum (Linton, 1889)
Carcharhinus obscurus (Lesseur): Ce – Nybelinia africana Dollfus, 1960; Co – Achteinus dentatus Wilson, 1911; Alebion carcharhini Kraey, 1863; A. gracilis Wilson, 1905; Alebion sp.; Caligus coryphaenae Steenstrup et Lütken, 1861; Eudactylina dolffusi Brian, 1924; Kroyeria decepta Deets, 1994 (nomen nudum); Nemesis sp. 3; Nemesis sp. 4; Pandarus smithii Rathbun, 1886; Paralebion elongatus Wilson, 1911; Pseudopandarus longus (Gnanamuthu, 1951); Triaphylus elongatus (Wilson, 1932); Mo – Dermophthiri us cararchini MacCallum, 1926
Carcharhinus plumbeus (Nardo): Ce – Pseudogrillotia pereli (Shuler, 1938); Co – Eudactylinia dolffusi Brian, 1924; Nesippus nana Cressy, 1970
Carcharhinus sealei (Pietschmann): Co – Achteinus dentatus Wilson, 1911; Nemesis sp. 3; Pseudopandarus longus (Gnanamuthu, 1951)
Carcharhinus sp.: Co – Alebion carcharhini Kraey, 1863; Pandarus bicolor Leach, 1816; Pandarus smithii Rathbun, 1886
Prionace glauca (Linnaeus): Ce – Nybelinia schmidtii Palm, 1999; Co – Anthosoma crassum (Ahlidgaard, 1794); Dinemoura latifolia (Steenstrup et Lütken, 1861); Echthrogaleus coleoptratus (Guérin-Méneville, 1837); Kroyeria carchariae Hesse, 1878; Nemesis robusta (van Beneden, 1851); Pandarus smithii Rathbun, 1886
Prionace sp.: Co – Dinemoura latifolia (Steenstrup et Lütken, 1861)
Rhizoprionodon acutus (Rüppell): Co – Achteinus pinguis Wilson, 1911; Lernaeopoda galei Kraey, 1837; Pseudopandarus longus (Gnanamuthu, 1951)
Sciliodon laticaudus Müller et Henle: Co – Pandarus smithii Rathbun, 1886
Sciliodon sp.: Co – Achteinus dentatus Wilson, 1911
Triaeodon obesus (Rüppell): Co – Pseudopandarus longus (Gnanamuthu, 1951)
“grey shark”: Co – Pandarus bicolor Leach, 1816
“shark”: Co – Euyphrom brachypterus (Gerstaeker, 1853); Achteinus dentatus Wilson, 1911; A. pinguis Wilson, 1912; Alebion carcharhini Kraey, 1863; Caligus coryphaenae Steenstrup et Lütken, 1861

CONCLUSIONS

Marine parasitology has a long history in South Africa dating back almost two centuries. However, information on the parasite fauna was gathered through opportunistic findings, while large-scale systematic attempts on certain host groups or biogeographical regions are lacking. Scientists also displayed a bias towards certain groups of parasitic organisms (e.g., parasitic copepods), while others remained undetected and neglected. This is especially notable for chondrichthyans, a very diverse host group in South Africa. With roughly 200 species of elasmobranchs and few holocephalans known from this biogeographical region (Ebert and van Hees 2015), only a small proportion of species has been observed for parasites. In order to rigorously assess the diversity of chondrichthyan parasites, dedicated biodiversity efforts are essential, with a particular focus on under-represented hosts and regions.

At present, knowledge on the parasites of cartilaginous fishes in South Africa is fragmentary and incomplete. In addition, the chondrichthyan fauna of South Africa contains a high degree of endemism, with approximately 13% of species only present in these waters. Information on parasite assemblages from endemic hosts would significantly expand our knowledge on the co-evolution of hosts and parasites in this region and their host-parasite interactions. Advancement in knowledge on the biology (including parasitism) of endemic host species could also contribute to conservation efforts helping to sustain the unique marine fauna present in South Africa. Information on a molecular level may be used to refine the phylogenetic relationships of parasites from Temperate Southern Africa (sensu Spalding et al. 2007) and those of adjacent biogeographical provinces (e.g., Temperate South America or Western Indo-Pacific; sensu Spalding et al. 2007).

One of the biggest obstacles in marine parasitological research in South Africa, however, seems to be the lack of expertise and systematicists able to assess the diversity of parasitic groups, especially protists, helminths, myxozoans and hirudineans. In order to resolve this issue, educational programs to train future taxonomists and systematists should be implemented. Another major obstacle scientists in this line of research are faced with is the sampling of chondrichthyans for parasitological studies. A total of 29% of all chondrichthyan species present in South African waters, including 13% of the endemic species, are placed in the three highest categories (i.e. vulnerable, endangered, critically endangered) in the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Ebert and van Hees 2015). Apart from certain ectoparasitic groups found on outer surfaces of the host, the assessment of endoparasites requires lethal-sampling of host individuals. Obtaining permits to sample chondrichthyan species solely for the purpose of parasitological work is unlikely being approved. An alternative for this dilemma is to form active collaborations with foundations and organisations focused on chondrichthyan conservation. The host specimen as such represents a pose of parasitological work is unlikely being approved. An alternative for this dilemma is to form active collaborations with foundations and organisations focused on chondrichthyan conservation. The host specimen as such represents a whole ecosystem for parasites. For this reason, some scientists and especially parasitologists argue that conservation efforts should also be expanded from the threatened host species to include its parasites. Implementing parasites as conservation targets and learning more about the unique host-parasite interactions and life histories, we would gain insights into the biology of the host and ultimately help to preserve the biodiversity by protecting the threatened host species and a wide array of parasite species, which may
face extinction together with their host species. This study along with previous reviews (Smit and Hadfield 2015, Reed 2015, Van As 2015) and faunal checklists (e.g. Van As and Basson 1984, Oldewage and Avenant-Oldewage 1993, Dippenaar et al. 2004) illustrates that South Africa boasts a prodigious fauna in both marine and freshwater systems. However, even after centuries of research, the fauna still remains insufficiently explored. Documenting this neglected fauna and describing species new to science could tremendously advance scientific research in South Africa and would also provide opportunities for younger generations of South Africans to pursue a scientific career.

Acknowledgements. This study was financed by the postdoctoral fellowship of the principle author from North-West University.

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Cite this article as: Schaeffner B.C., Smit N.J. 2018: Parasites of cartilaginous fishes (Chondrichthyes) in South Africa – neglected field of marine science. Folia Parasitol. 66: 002.