

Digenean parasites of deep-sea teleosts: A progress report

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ABSTRACT

The developments in the study of digeneans of deep-sea fish in the 21st Century are documented and discussed. Most recent work has been on the bathyal fauna (i.e. 1,000m-2,999 m depth), with virtually nothing on the abyssal fauna (i.e. deeper than 3,000 m). The one study on hydrothermal vent digeneans has indicated that these regions probably harbour a distinctive fauna. The demarcation of the deep-sea fauna is blurred at the poles, where the cold-adapted fauna appears similar to the shallower bathyal fauna. The abyssal fauna, however, appears distinct, possibly due to adaptations to variable or ultra-high pressures. The digenean fauna of bathypelagic fishes is depauperate. Recent phylogenetic studies reinforce the view that the typical deep-sea fauna has radiated in the deep-sea. Encroachment into the deep from shallow water is relatively rare. Overall, the digenean fauna in the deep-sea is distinctly less diverse than the equivalent fauna in shallow waters. A major conclusion is that our understanding of the deep-sea digenean fauna is poor, and that much further work over a much wider area is needed.

1. Introduction

In a review article we (Bray et al., 1999) in summary posed the question ‘How much do we really know about deep-sea digeneans?’ and answered it with ‘very little’. Have the 20 years since this was written changed this assessment?

1.1. The deep-sea

The term ‘deep-sea’ is customarily considered to cover the areas of the ocean beyond the edge of the continental shelf, which is usually at about 200 m depth, but varies down to about 500 m in the Antarctic. The nomenclature of the zones in the deep-sea is not uniform in the literature, but here the system proposed by Priede (2017) is followed (Table 1). In terms of surface area, most of the sea (over 70%) is the abyssal zone (the average depth of the sea is about 3,700 m), and most of this zone is abyssal plain. The topography of the ocean basins is, of course, more complex than can be summarised readily and consists not only of slopes and plains, but of seamounts, mid-ocean ridges, ‘hydrothermal vents, cold seeps, soaring massive carbonate towers, frozen methane hydrates, asphalt, mud volcanos ... cold-water coral reefs’ (Rex and Etter, 2010), canyons and mid-ocean ridges. The deep-sea is characterised by the relative scarcity of energy availability. ‘Food supplies to the benthos occupying the vast soft sediment environment of the deep-sea is derived ultimately from surface production. ... Patterns of surface production are translated down through the water column to

the seabed as particulate organic carbon (POC) flux’ (Rex and Etter, 2010). Scientific submariners consider that this descending particulate matter can be described as ‘marine snow’ (Gage and Tyler, 1991). As the deep-sea is mostly reliant on the seasonal production of, in particular, phytoplankton in the photic zone, the deep-sea reflects these fluctuations, but the fairly steady standing stock mitigates against dramatic seasonal effects (Rex and Etter, 2010). It should also be noted that bacterial chemosynthesis of organic matter at hydrothermal vents and cold seeps decouples some parts of the deep-sea from surface photosynthesis (see McNichol et al., 2018 and references therein).

There is clearly a close similarity between the fauna of polar waters and the deep-sea fauna, particularly that of the upper bathyal regions, such that it is not straightforward to distinguish the fauna where these regions meet (see Klimpel et al., 2009 and further discussion below). This correlation is probably dictated by adaptation to similar temperatures. The fauna of the Arctic region merges with the upper bathyal fauna, with the same species often occurring in both. The similarity of the Antarctic fauna and the deep-sea fauna is generally at the generic level, with perhaps a barrier formed by the Southern Ocean currents or the Antarctic Convergence.

2. Constraints

Conditions in the deep-sea place constraints on the organisms that live in it (Bray et al., 1999). Below 1,000 m sunlight disappears entirely and light is restricted to bioluminescence and the dim glow from black

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Table 1
Zones of the deep-sea (after [Priede, 2017](#)).

Name	Description and comparison with other usages	depths
Continental shelf	Continental shelf	< 200 m (variable)
Bathyal zone	The continental slope and shallower part of the rise	200–3,000 m
Abyssal zone	Deeper part of continental rise and the abyssal plain	3000–6,000 m
Hadal	Deep trenches	> 6,000 m
Pelagic	Pelagic over the continental shelf	< 200 m (variable)
Mesopelagic		200–1,000 m
Bathypelagic		1000–3,000 m
Abyssopelagic		3000–6,000 m
Hadopelagic		> 6,000 m

smoker vents. Pressure increases at 1 atm every 10 m, such that at the average depth of about 3,800 m the pressure is 381 atm. This amount of pressure affects the tertiary structure of enzymes and structural proteins, so that organisms that survive at these depths must be adapted to avoid protein denaturation ([Gibbs, 1997](#)). The oxygen concentration at depth is thought to be adequate, although it decreases rapidly in the sediment. Temperature below the thermocline (c. 800–1,300 m) is stable at just below 4 °C, so the deep-sea fauna must be adapted to cold. Salinity at depth is stable at about 35‰. Energy may be a problem as most is derived from surface production ('particulate organic carbon (POC) flux') and is seasonal and may be moved around and concentrated by currents. Large food falls, such as whale carcasses, concentrate scavengers such as amphipods and fish and may be prime regions for parasite transmission ([Kemp et al., 2006](#)). Nevertheless, the 'deep-sea is an extremely energy-deprived environment, and energy constraints become more severe with increasing depth' ([Rex and Etter, 2010](#)). The seabed topography and composition, hard surface and, mainly sediment, are not considered particular constraints in the deep-sea.

3. Deep-sea fishes

About 150 families are listed in recent summaries of the deep-sea fish fauna, which is about 30% of the known fish families, and they are mostly those that are considered 'primitive' ([Merrett and Haedrich, 1997](#); [Priede, 2017](#); [Weitzman, 1997](#)). More 'derived' orders such as the Perciformes, are relatively poorly represented. The gadiform family Macrouridae is often dominant in the deeper regions and a high proportion of parasitological investigations have involved members of this family. All reports of abyssal plain digeneans are from members of the macrourid genus *Coryphaenoides*, 'the deepest living genus of macrourids' ([Priede, 2017](#)), and mostly from the wide-spread species *C. armatus* (Hector). In a series of tables, [Priede \(2017, chapter 5\)](#) displayed the composition of various deep-sea faunas from mesopelagic to hadal (see [Table 1](#)) ecoregions, and that chapter should be consulted for detailed information, as it is clear that each ecoregion has its own distinctive fauna. For example, it is striking that such a dominant deep-sea family as the Macrouridae is not reported at hydrothermal vents or cold seeps.

4. Collecting

[Bray et al. \(1999\)](#) listed 19 'landmark papers' on deep-sea parasites, with three in the nineteenth century and only three in the first half of the twentieth century. The first report of an abyssal parasite was not until 1991 and the first use of molecular techniques 1993. The fact that abyssal plain parasites were only explored in the later twentieth century is explained by the expense and difficulty of collection of hosts at these depths. Collection from the upper bathyal can be considered an extension of commercial fishing and, indeed, several recent surveys have relied on by-catches of commercial fisheries ([Nacari and Oliva, 2016](#);



Fig. 1. Photographs of deep-sea collecting. a. Fishing deck in rough weather. b. Bag of deep-sea fishes. c. Emptying net on side trawler. d. Emptying bag on stern trawler. e. Dissection station at sea. f. Winch console, with 10,607 m of trawl wire out at depth of 4775 m. g. RRS *Discovery* at Fairlie, Scotland. h. *Trachyrincus murrayi* from the Goban Spur, depth 1360–1,240 m.

[Pardo-Gandarillas et al., 2007](#); [Salinas et al., 2008](#)). On the other hand, collection of abyssal fishes needs dedicated equipment such as a ship 'with a winch capacity containing the 15,000 m or so of trawl wire necessary to fish below 4,000 m depth. The attendant operating costs are high and often limit the available ship time' ([Merrett and Haedrich, 1997](#)) ([Fig. 1f](#) and [g](#)). The actual collecting of parasites at sea presents several difficulties. It is greatly time consuming. For example, the nearest region of the abyssal plain to the British mainland is the Porcupine Abyssal Plain, several days steam from a home port. This gives time to recover from seasickness and set up collecting gear, but weather may and often does intervene ([Fig. 1a](#)). The apparatus utilised for our abyssal trawling was an OTSB (semi-balloon otter trawl) with a single warp (see [Priede, 2017 Fig. 1.42](#)). When recovered, the fish are not usually in the best of condition having been hauled through the water for several hours at decreasing pressures ([Fig. 1b, c, d, h](#)). The stomach is usually everted through the mouth, due to the pressure changes, probably leading to the loss of some stomach parasites. In some cases, the rectum is prolapsed, possibly also leading to loss of parasites. To collect worms in reasonable condition for morphological and molecular studies the fish must be examined quickly and the gut-wash method as outlined by [Cribb and Bray \(2010\)](#) is most effective. The examination of host tissues (mainly the alimentary canal) and the washes under a dissecting microscope are not straightforward on an actively moving ship ([Fig. 1e](#)). The fixation of worms in hot fixative, the recommended method, is not practical on a ship rolling and pitching in the high seas, so Berland's fluid may be used as the fixative for morphological

Table 2
Deep-sea digeneans omitted from the checklist of Klimpel et al. (2009) or described since.

Family	Species	Host	Locality	Depth	reference
Fellodistomidae	<i>Benthotrema synaphobranchi</i> Machida et al. (2007)	<i>Synaphobranchius affinis</i> Günther, <i>Synaphobranchius</i> <i>Breviodorsalis</i> Günther	Suruga and Tosa Bays, Japan	Not given	Machida et al. (2007)
	<i>Lomasoma japonicum</i> Machida et al. (2007)	<i>Ateleopus japonicus</i> Bleeker, <i>Polymixia japonica</i> (Günther)	Suruga Bay, Japan	Not given	Machida et al. (2007)
Gonoceridae	<i>Megenteron synaphobranchi</i> Kuramochi (2005)	<i>Dysomma anguillare</i> Barnard	East China Sea	205 m	Kuramochi (2005)
Lecithasteridae	<i>Sterngophonus merretti</i> Bray and Waeschenbach (2020)	<i>Caraetx laticeps</i> Koefoed	Goban Spur, NE Atlantic	1,654 m	Bray and Waeschenbach (2020)
	<i>Gonocerca pectoralis</i> Shvetsova, 2013	<i>Albatrossia pectoralis</i> (Gilbert)	Kuril Island	Not given	Shvetsova (2013)
	<i>Lecithophyllum euzeti</i> Gibson and Bray (2003)	<i>Notacanthus chemnitzii</i> Bloch, <i>Polyacanthonotus challengeri</i> (Vaillant)	Porcupine Sea Bight	2400–3,718 m	Gibson & Bray (2003)
Lepidapedidae	<i>Lepidapedon sereti</i> Bray et al. (2013)	<i>Coelornichus sereti</i> Iwamoto & Merrett	off Vanuatu	Not known	Bray et al. (2013)
	<i>Neolepidapedon smithi</i> Bray and Gibson, 1989 ^a	<i>Mura moro</i> (Risso)	Off NE Scotland	910–1,060 m	Bray and Gibson (1989)
	<i>Paralepidapedon variabile</i> Sokolov and Gordeev (2015)	<i>Muraenolepis marmoratus</i> Günther	Amundsen Sea	605–1,632 m	Sokolov & Gordeev (2015)
Opicoelidae	<i>Profundivermis intercalarius</i> Bray and Gibson, 1991 ^a	<i>Coryphaenoides armatus</i> (Hector)	Porcupine Abyssal Plain	4850 m	Bray and Gibson (1991)
	<i>Bathycercadium brayi</i> Pérez-del-Olmo et al., 2014 ^a	<i>Physcis blennoides</i> (Brünnich)	Western Mediterranean Sea	600–647 m	Pérez-del-Olmo et al. (2014)
	<i>Bathypodocotyle enkaimeshi</i> (Blend, Kuramochi & Dronen, 2015a,b)	<i>Nezamia proxima</i> (Smith & Radcliff)	Segami Bay, Japan	681–1,061 m	Blend et al. (2015a)
	<i>Buticulotrema thermichthysi</i> Bray et al., 2014 ^a	<i>Thermichthys hollisi</i> (Cohen, Rosenblatt & Moser)	South East Pacific Rise region	2,598 m	Bray et al. (2014)
	<i>Caudostes ventichthys</i> Bray et al. (2014)	<i>Ventichthys biospeedoi</i> Nielsen, Møller & Segonzac	South East Pacific Rise region	2,586 m	Bray et al. (2014)
Zoogonidae	<i>Helicometra overstreeti</i> Blend & Dronen, 2015a,b	<i>Luciobrotula corethronycter</i> Cohen	Gulf of Mexico	1,280 m	Blend and Dronen (2015b)
	<i>Podocotyle bathyhelminthos</i> Blend & Dronen, 2015a,b	<i>Luciobrotula corethronycter</i>	Gulf of Mexico	622–1,280 m	Blend and Dronen (2015a)
	<i>Podocotyle ninoyi</i> Blend et al. (2016)	<i>Sphagmacrurus grenadae</i> (Parr) <i>Nezamia aequalis</i> (Günther)	Gulf of Mexico	534–995 m	Blend et al. (2016)
	<i>Pseudopocotyle mcauleyi</i> Blend et al. (2017)	<i>Lycodes cortezianus</i> (Gilbert)	off Oregon and British Columbia	depth 200–800 m	Blend et al. (2017)
	<i>Tellurotrema katadara</i> (Kuramochi, 2001)	<i>Gadomus colletti</i> Jordan & Gilbert	off Pacific coast of southern Japan	500–582 m	Kuramochi (2001)
	<i>Brachyenteron dextroporus</i> Kuramochi (2005)	<i>Dysomma anguillare</i>	East China Sea	205 m	Kuramochi (2005)
	<i>Koitea notocanthi</i> (Korotaeva, 1994) Bray, 2008	<i>Notacanthus macrorhynchus</i> Matsubara	High Seas of SE Pacific Ocean	580–630 m	Korotaeva (1994)
	<i>Neosteganoderma physiculi</i> Machida et al. (2006)	<i>Physiculus japonicus</i> Hilgendorf	Suruga Bay and Sagami Sea, Japan	Not given	Machida et al. (2006)
	<i>Proctopiantastes neitastomatis</i> Machida et al. (2006)	<i>Nettastoma parviceps</i> Günther	Suruga Bay, Japan	Not given	Machida et al. (2006)
Family not yet determined	<i>Biospeodrema biospeodio</i> Bray et al., 2014 ^a	<i>Thermichthys hollisi</i>	South East Pacific Rise region	2,598 m	Bray et al. (2014)
	<i>Biospeodrema jolliveti</i> Bray et al., 2014 ^a	<i>Thermichthys hollisi</i>	South East Pacific Rise region	2,598 m	Bray et al. (2014)
	<i>Caudostes dobrovol'ski</i> Sokolov, Lebedev, Shchenkov and Gordeev, 2019 ^a	<i>Ventichthys biospeedoi</i> <i>Liparis</i> sp., <i>Eumicrotremus fedorovi</i> Mandrytsa	South East Pacific Rise region Simushir Island, North Pacific	2,586 m 150–400 m	Bray et al. (2014) Sokolov et al. (2019c)
	<i>Zditovickitrema incognitum</i> Sokolov, Lebedeva, Gordeev & Khasanov, 2019 ^a	<i>Muraenolepis marmorata</i> Günther	Antarctic waters	1193–1,453 m	Sokolov et al. (2019b)

^a molecular data available.

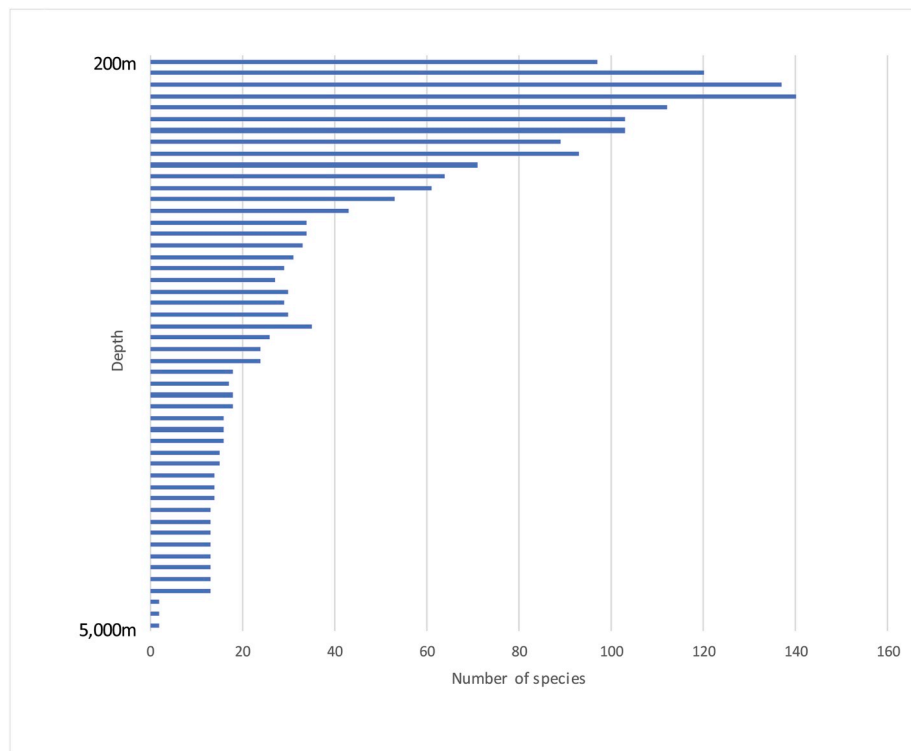


Fig. 2. Graph showing the number of species reported at each 100 m depth sector.

specimens and molecular samples should be placed directly into ethanol.

Trawling is practical for collecting on smooth surfaces such as abyssal sediment but is crude and damaging to the seafloor and it is known that many of the nimbler creatures can avoid it. It is also possible that a few fishes are captured at shallower depths as the trawl is hauled in. To collect from three-dimensionally complex surfaces such as parts of the mid-ocean ridges and hydrothermal vents other techniques are necessary. Pelagic trawling has been used for some studies of the Mid-Atlantic Ridge (Klimpel et al., 2007, 2008a, 2010), fish traps set by a submersible were used to supply hydro-thermal vent worms to Bray et al. (2014) and long-lines were utilised by Nacari and Oliva (2016).

Molecular techniques have been utilised to study the phylogeny of deep-sea forms and aspects of this study in relation to the invasion of, and radiation in, the deep-sea is discussed below. Other aspects of the molecular biology of deep-sea digeneans have not been addressed, apart from the use of ‘metabarcoding’ to explore marine parasite diversity. This study is in its infancy and suffers from the relatively poor sequence library for most groups, notably the Digenea. Mitsi et al. (2019) used 18 S rDNA metabarcoding data to study marine species of Platyhelminthes, including from several deep-sea sites. The Trematoda was found to be distinctly the largest parasitic group, and with the second lowest BLAST identity, after the free-living Proseriata. Scheifler et al. (2019) sampled skin mucus, gill mucus and intestine of fishes and using ‘the hypervariable V4–V5 region of the 16 S rRNA gene’ and employed metabarcoding techniques to indicate what trematodes (*inter alia*) were present on or in these tissues. The results provisionally identified species associated with the tissues including giving some clues to life-cycle stages on gills and skin. This may be a useful technique for deep-sea exploration, with the proviso that enough sequences of well identified taxa must be available.

5. History

The deep-sea has been explored for digenean parasites only intermittently since the first report of a *Stephanostomum* metacercaria in a

macrourid by Wagener (1852). There have been few systematic studies or focussed collecting expeditions until recent years. Early information comes from occasional reports associated with other studies. For example, Bell (1887) described the worm now known as the gorgoderid *Degeneria halosauri* (Bell, 1887) from a halosaur, which was, as far as we are aware, the only digenean collected during the pioneering Challenger expedition (1872–1876). Other early examples are the descriptions of the hemiurid *Dissosaccus laevis* (Linton, 1898) from a macrourid off Woods Hole, Massachusetts (Linton, 1898) and of *Proctophantastes abyssorum* Odhner (1911) also from a macrourid off Norway (Odhner, 1911). The first systematic attempt to study deeper water forms was by Manter (1934) who reported on worms as deep as 1,064 m from off Florida. The first notable ecological study was by Campbell et al. (1980) who studied at worms from fishes that reach to abyssal depths. Our deep-sea cruises in the NE Atlantic in the 1980s, 1990s and early 2000s yielded collections which enabled the first description of worms from an abyssal plain (Bray and Gibson, 1991, 1995) and the first molecular studies of deep-sea digeneans (Bray et al., 1999; Lumb et al., 1993). Review papers by Noble (1973) and Campbell (1983) and the checklist of deep-sea fish parasites by Klimpel et al. (2009) summarised most of the knowledge to that date. The major contributions after that date are discussed when the features they studied are addressed later in this paper.

6. Diversity

Bray (2004) listed just 18 digenean families that had been reported in deep-sea fishes - a small fraction of the about 150 known families. With recent changes in digenean systematics stimulated by molecular phylogenetic inferences the number is now 20, namely the Accacoeiliidae, Acanthocolpidae, Aporocotyliidae, Bivesiculidae, Bucephalidae, Bunocotyliidae, Cryptogonimidae, Derogenidae, Faustulidae, Fellostomidae, Gonocercidae, Gorgoderidae, Hemiuridae, Hirudinellidae, Lecithasteridae, Lepidapedidae, Lepocreadiidae, Monorchidae, Opecoelidae and Zoogonidae. These can be divided into the groups that encroach deep into the bathyal or into the abyssal, and

those that only pass over the edge of the continental shelf into about the first 1,000 m. The groups reported from the lower bathyal and abyssal regions are: Fellodistomidae, Gonocercidae, Gorgoderidae, Hemiuridae, Lecithasteridae, Lepidapedidae, Opecoelidae and Zoogonidae. The checklist of Klimpel et al. (2009) added mentions of the families Azygiidae (with reports down to < 1,200 m; recently *Otodistomum* Stafford, 1904 has been reported in sharks to 2,200 m, see Espinola-Novelo et al., 2018), Didymozoidae (< 600 m), Ptychogonimidae, Sclerodistomidae and Syncoeliidae (latter three species with no depth data). Since these papers, no additional digenean families have been reported in the deep-sea, but a few notable new taxa have been described and are listed in Table 2. None of these new species has been reported from abyssal depths and relatively few have been subjected to molecular study.

Fig. 2 has been generated using data mainly from Klimpel et al. (2009) with information added from more recent papers. The depth range reported for 246 species has been derived from these sources and the number of species reported at each 100 m depth sector plotted on the graph. Several caveats must be made. In some cases, including in Klimpel et al. (2009) but also in later papers, the depth range quoted is for the catch range of the host and the actual ranges where particular parasites are found is not recoverable. For each parasite the range is taken to include all intermediate 100 m sectors, so that if the occurrence is disjunct, for example, this was not detected. Also, it is presumed that all the species are correctly identified. Perhaps the major problem is the sparsity of studies of the abyssal deep-sea. The apparent increase of richness in the first few depths below 200 m is probably an artefact of the frequent lack of depth information in the literature on shallower species. Nevertheless, the figure illustrates the steady decline in richness with depth which parallels the decrease in richness of Actinopterygii as reported by Priede (2017, p. 68ff), but not that of several invertebrate putative intermediate hosts (Rex and Etter, 2010, p. 80ff). Table 3 lists the worms that have been reported only at greater depths than 3,000 m, 2,000 m, 1,000 m and 500 m. These are mostly genuine deep-sea forms, which may complete their life-cycle at depth, whereas most of the worms in waters shallower than 1000 m are probably the spill-over from the shelf fauna.

7. Phylogeny

A noteworthy aspect of studies of molecular phylogenies of deep-sea digeneans is the evidence they can demonstrate of the relationships of the deep-sea taxa and whether they are likely to have radiated in deep water or have separately invaded deep water. Rex and Etter (2010) stated that the ‘prevailing view is that the modern deep-sea fauna inhabiting soft sediments originated in coastal waters’. These authors also pointed out that this is not universally accepted, and that convincing evidence has been provided of groups of corals and isopods originating in deep water and invading coastal environments. In addition, these authors point out that the homogeneity of the deep-sea environment

provides theoretical problems for the ‘canonical allopatric speciation model’. This applies more to the topologically uniform abyssal region than to the more complex bathyal region intersected by numerous canyons and gullies where, perhaps, sympatric speciation is possible. Rex and Etter (2010), therefore, hypothesised ‘that the bathyal zone is the center of evolution, with the abyss playing only a minor role’. The deep-sea is, however, not stable over geological time and regional catastrophes and global anoxia episodes indicate that much of the deep-sea diversity arose recently during the Cenozoic era (Jacobs and Lindberg, 1998).

In our 1999 paper (Bray et al., 1999) we presented early attempts at molecular phylogenies of members of two predominant deep-sea families, the Lepidapedidae (as Lepocreadiidae) and Fellodistomidae. The molecular phylogeny of digeneans has developed to a significant extent in the last twenty years (e. g. Olson et al., 2003; Pérez-Ponce de León and Hernández-Mena, 2019) and although most species included in these and many more focussed studies are parasites of terrestrial, freshwater and shallow water marine hosts, a few deep-sea forms have been included and have clarified some issues relating to invasion of, or radiation in, the deep-sea.

The family Lepidapedidae was raised to this rank from subfamily by Bray and Cribb (2012) based on a molecular phylogeny proposed by Bray et al. (2009). This family contains mainly deep-sea forms along with a few morphologically disparate forms from shallow water, but the deep-water forms are monophyletic and morphologically similar. The tree presented by Bray et al. (2009) supports the findings of Bray et al. (1999) providing further evidence of the radiation of *Lepidapedon* Stafford, 1904 and its relatives in deep-water. Faltýnková et al. (2017) added the Antarctic species *Lepidapedon garrardi* (Leiper & Atkinson, 1914) to the phylogeny, finding it a sister species to *L. beveridgei* Campbell and Bray (1993) an abyssal macrourid parasite. This furnishes further evidence of the close relationship of polar and deep-water forms as suggested by Bray et al. (1999) and Klimpel et al. (2009). Dallarés et al. (2013) added further specimens of *L. desclersae* Bray and Gibson (1995) and Pérez-del-Olmo et al. (2019) added specimens of *L. guevarai* Lopez-Roman & Maillard, 1973 and further specimens of *L. desclersae* to the analysis and also found the monophyly of the group (*Lepidapedon/Neolepidapedon/Profundivermis*). The relationships of the genera *Neolepidapedon* Manter, 1954 and *Profundivermis* Bray and Gibson, 1991 remain controversial as whereas Bray et al. (2009) and Pérez-del-Olmo et al. (2019) found them embedded in the genus *Lepidapedon*, Faltýnková et al. (2017), having added the Antarctic species *Neolepidapedon trematomi* Prudhoe and Bray (1973) to the analysis, and Sokolov et al. (2018c), having added the Antarctic deep-sea species *Muraenolepitrema magnatestis* Gaevskaya & Rodjuk, 1988 to the analysis, found the *Neolepidapedon/Profundivermis* clade sister to a monophyletic *Lepidapedon*.

The phylogeny in Bray et al. (2009) found the deep-sea lepopocreadiid *Prodistomum priedei* Bray & Merrett, 1998 from the epigonid *Epigonus*

Table 3

Species restricted to below stated depths (according to Bray, 2004; Klimpel et al., 2009 and numerous subsequent publications).

Depth	Species
> 4,000 m	0
> 3,000 m	<i>Panopula cavernosa</i> , <i>Proctophantastes gillissi</i>
> 2,000 m	<i>Biospeedotrema biospeedoi</i> , <i>B. jolliveti</i> , <i>B. parajolliveti</i> , <i>Brachyenteron rissouanum</i> , <i>Buticulotrema thermichthysi</i> , <i>Caudotestis ventichthysi</i> , <i>Lecithophyllum euzeti</i> , <i>Lepidapedon cascadenis</i> , <i>L. discoveryi</i> , <i>L. filiformis</i> , <i>L. gaevskayae</i> , <i>L. oregonensis</i> , <i>L. zubchenkoi</i> , <i>Steringophorus haedrichi</i> .
> 1,000 m	<i>Bathypodocotyle margolisi</i> , <i>Brachyenteron campbelli</i> , <i>Degeneria halosauri</i> , <i>Dinosoma oregonensis</i> , <i>D. pectoralis</i> , <i>D. ventrovesicularis</i> , <i>Halosaurotrema halosauropsis</i> , <i>Helicometra overstreeti</i> , <i>Lepidapedon beveridgei</i> , <i>L. sommervilleae</i> , <i>Olssonium turneri</i> , <i>Paralepidapedon williamsi</i> , <i>Podocotyle schistotesiculata</i> , <i>Profundivermis intercalarius</i> , <i>Steringophorus dorsolineatus</i> , <i>S. margolisi</i> , <i>S. merretti</i> , <i>S. thulini</i> , <i>Steringovermes notacanthi</i> , <i>Tellervotrema beringi</i> , <i>Zdzitowieckitrema incognitum</i> .
> 500 m	<i>Bathycreadium biscayense</i> , <i>B. nanaflexicollis</i> , <i>Bathypodocotyle enkaimushi</i> , <i>Chimaerohemecus trondheimensis</i> , <i>Dinosoma rubrum</i> , <i>D. synaphobranchi</i> , <i>D. sulca</i> , <i>D. tortum</i> , <i>Koiea notacanthi</i> , <i>Lepidapedon blairi</i> , <i>L. coelorhynchi</i> , <i>L. desclersae</i> , <i>L. desotoensis</i> , <i>L. guevarai</i> , <i>L. nezumiatis</i> , <i>L. zaniophori</i> , <i>Macrourimegatrema brayi</i> , <i>M. gadomi</i> , <i>Macvicaria selachophidii</i> , <i>Megenterum manteri</i> , <i>Mesobathylebouria lanceolata</i> , <i>Myzoxenus occidentalis</i> , <i>Neolepidapedon smithi</i> , <i>Opegaster caulopsetta</i> , <i>Otodistomum plunketi</i> , <i>Panopula bridgeri</i> , <i>P. spinosa</i> , <i>Paraccacladium jamiesoni</i> , <i>Paralepidapedon variabile</i> , <i>Podocotyle bathyhelminthos</i> , <i>P. harrisae</i> , <i>P. nimoyi</i> , <i>P. pearsei</i> , <i>Proctophantastes brayi</i> , <i>P. nettastomatis</i> , <i>Prodistomum priedei</i> , <i>Prolethochirium pterois</i> , <i>Prudhoeus nicholsi</i> , <i>Steganodermatoides agassizi</i> , <i>S. maceri</i> , <i>Steringophorus congeri</i> , <i>S. pritchardae</i> , <i>Tellervotrema katadara</i> , <i>Trifoliovarium allocytti</i> , <i>T. antimorae</i> .

telescopus (Risso) in the north-eastern Atlantic, embedded within shallow water, mainly reef, species. A closely related and very similar worm, *P. hynnodi* (Yamaguti, 1938) is reported from the epigonid *E. atherinoides* (Gilbert) in Japanese waters. Epigonids are known as ‘Deep-water cardinalfishes’ which may reach to 3,000 m, and are one of the few perciform families to extend into the deep-sea (Priede, 2017). It may be, therefore, that a small clade of leptocephalids has invaded the deep-sea with their perciform hosts. Other *Prodistomum* Linton, 1910 species are from shallow water and the phylogeny of Bray et al. (2009) shows that the genus is not monophyletic.

The other family studied by Bray et al. (1999) was the Fellodistomidae, in particular the relationships of members of the genus *Steringophorus* Odhner, 1905, finding evidence of deep-sea radiation in the genus. *Steringophorus* has been resolved as monophyletic, usually in a clade with the deep-sea genus *Olssonium* Bray & Gibson, 1980 and the cold-water genus *Fellodistomum* Stafford, 1904, in that and most later studies (Cribb et al., 2014; Sun et al., 2014; Wee et al., 2017). On the other hand, Pérez-Ponce de León et al. (2018) added *Steringotrema robertpoulini* Pérez-Ponce de León, Anglade & Randhawa, 2018 from a shallow water pleuronectid to the phylogeny, finding it a sister species to *S. dorsolineatus* (Reimer, 1985) from deep sea ipnopids, which together form a clade sister to the remaining members of *Steringophorus*. Bray and Waeschenbach (2020) produced a phylogenetic tree which also placed *Steringotrema robertpoulini* within the genus *Steringotrema*, but not as sister to *S. dorsolineatus*. They found that the family divided distinctly into two well supported clades, one of parasites of shallow and warm water fishes and the other of deep-sea or cold-water fishes, with the pattern spoiled by the position of *Steringotrema robertpoulini*. It is likely that the genus *Steringophorus* has radiated in deeper water, but that some members have moved into shallow water. The commonly reported species *Steringophorus furciger* (Olsson, 1868) is often found in neritic pleuronectids, but is also reported as reaching well into the bathyal zone (> 2,000 m) (Bray, 2004; Bray and Campbell, 1995; Gordeev et al., 2019). It may be a particularly eurybathic species or a cryptic species group. Understanding of the status of *Steringotrema* awaits further study of multiple species.

All species reported so far from the abyssal plain are either leptocephalids, fellodistomids or ‘derogenids’. The ‘derogenid’ is *Gonocerca phycidis* Manter, 1925 which is now considered a member of the family Gonocercidae (Sokolov et al., 2016a, 2018a, 2019a). The sequences of *G. phycidis* and two other *Gonocerca* Manter, 1925 species in Sokolov’s study (*G. crassa* Manter, 1934 and *G. muraenolepisi* Parukhin & Lyadov, 1979) are derived from Antarctic fishes and a close relationship is found between these species and *G. oshoro* Shimazu, 1970 from a macrourid in the northern Pacific Ocean giving further evidence of the relationship of Antarctic and deep-sea forms. Sokolov et al. (2019a) found the Gonocercidae to be the basally derived group of the Hemiuroida. This study presents a superfamily-wide molecular phylogeny which includes only a few deep-sea forms. Apart from the monophyly of the Gonocercidae, it is notable that the two deep-sea (but not abyssal) hemiuroids in the tree are not monophyletic. The position of *Merlucciottrema praeclarum* (Manter, 1934) is puzzling as it is resolved as sister to a group of shallow water leptocephalids. The sequenced specimen is derived from the deep-sea bythiid *Cataetx laticeps* Koefoed at a depth of 1,654 m, and the species is reported as deep as 2,784 m (Bray, 1996). The other deep-sea hemiuroid in the tree is *Dinosoma synaphobranchi* Yamaguti (1938) originally reported in the synaphobranchid eel *Synaphobranchus affinis* Günther off Japan, with no depth data (Yamaguti, 1938). In the tree it is sister to the shallow-water form *Brachyphallus crenatus* (Rudolphi, 1802). The sequenced specimen is from the deep-sea morid *Antimora microlepis* Bean from the Sea of Okhotsk, but with no depth data given. The only bathymetric information we have for this species is the 644–828 m range reported by Kuramochi (2011). Thus, with the very limited sample available, there is no evidence of deep-sea radiation in the Hemiuroida.

On the other hand, evidence is accumulating of radiation of

opcoelids in deeper waters. Only one species of this large family has been definitely reported as reaching into the abyssal zone (see below), but many more species are reported in bathyal depths. Several of these have been included in molecular phylogenetic inferences. Bray et al. (2016) found a monophyletic group of ‘deep-sea and freshwater ‘Plagioporinae’ in their preliminary study of the family. Later studies included many more freshwater species (Fayton et al., 2018; Martin et al., 2019) and found the freshwater species monophyletic and not close to the deep-sea forms. Martin et al. (2019) found one well resolved clade of (mainly) deep-sea opcoelids which they called the Podocotylineae, including *Bathypodocotyle margolisi* (Gibson, 1995) reported down to 2,220 m (Gibson, 1995) and possibly 3,050 m (Kellermanns et al., 2009), *Buticulotrema thermichthysi* reported at depth 2,598 m (Bray et al., 2014) and *Halosaurotrema halosauropsi* (Bray and Campbell, 1996) reported as deep as 2,670 m (Klimpel et al., 2008b). The other two species resolved in this clade were *Neolebouria georgiensis* Gibson, 1976 from the Antarctic region and *Podocotyle atomon* (Rudolphi, 1802) from the White Sea. The findings of Sokolov et al. (2018b) reinforce the monophyly of this group, whilst lacking the *N. georgiensis* sequence. Other deep-sea opcoelids are scattered throughout the tree: i.e., *Bathycreadium brayi* reaches 1,000 m (Constenla et al., 2015; Dallarés et al., 2016) and *Mesobathylebouria lanceolata* (Price, 1934) reaches 500 m (Reimer, 1987). *Abyssopedunculus brevis* (Andres and Overstreet, 2013) has been considered a deep-water form, but only reaches to 200 m, illustrating the problem of definition of the deep-sea according to different authors (Andres and Overstreet, 2013). Overall, however, the proportion of deep-sea, and indeed shallow water, opcoelids sequenced so far is minute and these results are preliminary.

When the genus *Biospeedotrema* Bray, Waeschenbach, Dyal, Littlewood & Morand (2014) was erected the number of opcoelid sequences available was limited and the genus was considered, based on its basally derived position in the phylogenetic tree and the morphology of the ‘suboptimally preserved’ specimens, to belong to the opcoelid subfamily Stenakrinae. This position was questioned by Shedko et al. (2015) and later studies by Sokolov et al. (2019b; 2019c) have shown that it is sister to *Caudotestis dobrovoltski* Sokolov, Lebedev, Shchenkov & Gordeev, 2019 forming a clade which, with *Zdzitowieckitrema incognitum* Sokolov, Lebedeva, Gordeev & Khasanov, 2019, may be a sister clade to the Opcoeloidea, although resolution of this relationship is poor.

The family Zoogonidae contains many deep-sea species but the recent molecular phylogeny produced by Sokolov et al. (2016a,b) included only one deep-sea species, and only 6 species in all, so no data are available on possible deep-sea radiation in this family.

Degeneria halosauri is the only gorgoderid species has been reported from the deep-sea and molecular evidence suggests that it is not closely related to other gorgoderids. This species has been considered worthy of its own subfamily, as the most basally derived gorgoderid (Cutmore et al., 2013) or as sister to the Anaporrhutinae (Urabe et al., 2015).

8. Bathypelagic Digenea

Bray et al. (1999) pointed out that the few studies on meso or bathypelagic fishes (e. g. Collard, 1970; Gartner and Zwerner, 1989) have shown a low prevalence and intensity of digeneans and other helminth parasites. Later studies have confirmed this finding. Klimpel et al. (2006) made a direct comparison between the parasite burdens of pelagic and demersal deep-sea Arctic fishes and found the demersal macrourid *Macrourus berglax* Lacepède harboured 20 metazoan parasite species, including 7 digeneans, whereas 5 species of bathypelagic and mesopelagic species between them harboured three species. They found that the parasite fauna of six deep-sea fishes in the East Greenland and the Irminger Seas corroborates the statement by Marcogliese (2002) that diversity decreases with depth but increases again close to the sea floor. The dearth of nutrients in these regions restricts the richness of

potential first intermediate hosts, resulting in low prevalence even of ‘widely distributed, non-specific parasites’. Klimpel et al. (2007) compared the parasites of *Maurolicus muelleri* (Gmelin) from the Mid-Atlantic Ridge and the Norwegian Deep, finding digeneans, at relatively low prevalences, but only at the latter locality. Both species recovered, *Brachyphallus crenatus* and *Lecithaster confusus* Odhner, 1905, are hemiuroids with low host specificity and are most common in demersal species, which may act as reservoirs for the occasional invasion of benthopelagic species. Similarly, Klimpel et al. (2008a) found low prevalence of the non-specific hemiuroids *Gonocerca phycidis* and *Lethadena* Manter, 1947 sp. from two myctophids at the Mid-Atlantic Ridge. *Lethadena* sp. was the only digenean found in 247 specimens of 7 mesopelagic and bathypelagic fish species from the Mid-Atlantic Ridge by Klimpel et al. (2010), with a single specimen reported in *Myctophum punctatum* Rafinesque. Andres et al. (2016) found a single immature *Brachyphallus* Odhner, 1905 specimen in the stomach of *Polyipnus clarus* Harold at a depth of 419 m from a sample of 2968 individual stomiiform fishes in the northern Gulf of Mexico. On the other hand, Houston and Haedrich (1986) looked at feeding habits of demersal fishes and found that those which fed on both pelagic and benthic prey had a higher prevalence of digeneans than those whose prey was entirely benthic.

9. Hydrothermal vents and cold seeps

de Buron and Morand (2004) posed the question: why do we not find more deep-sea hydrothermal vent parasites? The main reason is probably the difficulty of sampling at these localities. It is difficult enough to sample from the abyssal plain, where trawling is possible, but the terrain around hydro-thermal vents is not suitable for this relatively crude and damaging practice. These authors mention two unidentified digeneans, one from the ‘Snake Pit’ vent in the north Atlantic and one from the East Pacific Rise in the Pacific Ocean. The *Biospeedo* oceanographic cruise collected a few digeneans from two fish species from the East Pacific Rise in April/May 2004 (Jollivet et al., 2004). The fishes were caught using a fish cage trap deposited near vent fields using the submersible *Nautilie* and the digestive tract was opened and the fluid from the lumen containing the parasites was retained. The worms were washed in saline and fixed in 70% ethanol, giving rise to ‘suboptimally’ fixed specimens. Bray et al. (2014) studied these worms and, with the aid of serial sectioning and molecular sequencing, described a new genus and five new species, all of which they considered to belong in the family Opecoelidae. These species are *Biospeidotrema biospeidoi*, *B. parajolliveti* and *Buticulotrema thermichthysi* from the bythitid *Thermichthys hollisi* at depth 2,598 m and *Biospeidotrema jolliveti*, *Caudotestis ventichthys* and a possible juvenile *B. thermichthysi* in the ophiidiid *Ventichthys biospeidoi* at depth 2,586 m. Three of the species provided useable sequences, while the other two were spoiled by fungal contamination. Nevertheless, these are the only digeneans so far described from a hydrothermal vent and indicate that these vent regions harbour a unique digenean fauna worthy of much further investigation, particularly as the recognition of *Biospeidotrema* as an opecoelid is no longer sustainable and its phylogenetic position remains unresolved (see Sokolov et al., 2019b, 2019c).

Priede (2017, p. 360) reported that zoarcids of the genera *Pachycara* Zugmayer and *Thermarces* Rosenblatt & Cohen are the only fishes so far found associated with cold seeps. Nothing is known of their parasites at these sites. Powell et al. (1999) and Tyler et al. (2007) found that mussels of the genus *Bathymodiulus* Kenk & Wilson were heavily infected with ‘*Bucephalus*-like’ parthenitae at petroleum seeps in the northern Gulf of Mexico off Louisiana at various sites varying between 535 and 649 m deep. Powell et al. (1999) found 100% prevalence at one site. The identification of the digenean was based on similarities to bucephalid infection of shallow water mussels. The only digenean reported from either *Pachycara* or *Thermarces* is the lepidapedid *Neolepidapedon trematomi* from *Pachycara brachycephalum* (Pappenheim) in

Antarctic waters off Queen Mary Land (Prudhoe and Bray, 1973). There are no records of bucephalids in these host genera. In fact, bucephalids are not common parasites of zoarcids, with just three reports of *Prosorhynchus squamatus* Odhner, 1905 in *Zoarces viviparus* (Linnaeus), *Lycodes eudipleurostictus* Jensen and *L. mcallisteri* Møller in Arctic waters down to 1,337 m (Chambers, 2008; Shulman and Shulman-Albova, 1953). Powell et al. (1999) pointed out that the use of the term *Bucephalus*-like was a convenience and that they ‘have not been unequivocally assigned to that genus’. It is conceivable that the parthenitae belong to another of the digenean families that utilize bivalves as first intermediate hosts, such as the Fellodistomidae or Gorgoderidae (Cribb et al., 2003; Køie, 1980), the former of which is a major component of the deep-water digenean fauna.

10. Mid ocean ridges

Mid-ocean ridges are difficult to sample and as far as I am aware only a few studies have been made, all restricted to the Atlantic Ocean. Kellermanns et al. (2009) obtained their fish, *Coryphaenoides mediterraneus* (Giglioli) by trawling in the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge at 1700 to 3,500 m. Seven digenean species were recovered, some at fairly high prevalence, but detailed depth data of each digenean species was not given, so it is not possible to be certain which enter the abyssal zone (i.e. below 3,000 m). Klimpel et al. (2008b) also used bottom trawling to study the parasites of *Halosaurusopsis macrochir* (Günther) from the Mid-Atlantic Ridge, finding 5 species, one of which, the gorgoderid *Degeneria halosauri*, was found at 100% prevalence. Other studies of Mid-Atlantic Ridges have used pelagic trawling (Klimpel et al., 2007, 2008a, 2010) showing the low level of digenean parasitization generally exhibited by pelagic hosts (see above). It is not clear whether there are any digeneans particularly associated with the Mid-Ocean Ridge. Kellermanns et al. (2009) reported ‘Digenea indet.’ and an unnamed *Steringotrema* species from *Coryphaenoides mediterraneus*, Klimpel et al. (2008b) reported an unnamed *Steringophorus* species from *H. macrochir* and Klimpel et al. (2008a; 2010) reported an unnamed *Lethadena* species in myctophids. Without taxonomic studies of these worms it is not possible to assess the possible endemicity of some of the Mid-Ocean Ridge fauna.

11. Polar regions

The cold waters of the polar regions apparently harbour similar digenean communities to cold deep waters at lower latitudes. In the Arctic this means that many of the studies are not clearly demarcated as deep-sea. Some recent studies of the Arctic fauna have been designated as deep-sea, including Chambers (2008) who studied a large number of hosts at depth to 1,468 m and Klimpel et al. (2006) who studied pelagic and demersal fishes in the Arctic Ocean, collecting pelagic fishes down to 708 m (over depth down to 3200 m) and demersal fishes only as deep as 387 m. Both studies found many species which are also found at upper bathyal depths at lower latitudes.

In the discussion of phylogeny above, evidence is presented of the generally close phylogenetic relationship of Antarctic and deep-water digenean faunas. On the other hand, Münster et al. (2016) compared the parasite fauna of *Macrourus whitsoni* (Regan), from off King George and Elephant Islands close to the Antarctic Peninsula, a region south of the Antarctic Convergence and south of the Atlantic Ocean, with the parasites of related macrourids from deep-waters elsewhere and found high levels of endemicity at the specific level in the Antarctic. The fauna, however, was dominated by such typical deep-sea genera as *Lepidapedon*, *Paralepidapedon* Shimazu & Shimura, 1984 and *Gonocerca*. The digenean fauna of *M. whitsoni* clustered with that of two sub-Antarctic macrourids *M. carinatus* (Günther) and *M. holotrachys* (Günther), and this cluster was closest to the two north Atlantic species *M. berglax* and *Coryphaenoides rupestris* Gunnerus. The similarity of the Antarctic fauna and the deep-sea fauna is, therefore, mainly at the generic level

and it appears likely that the Southern Ocean currents or the Antarctic Convergence represent a barrier.

12. Pacific Ocean

Northern cold and temperate parts of the Pacific Ocean are quite well explored in terms of the faunistics of the deep sea digenean fauna. An early example is Yamaguti (1938) who reported several digenean species from macrourids in Japanese waters. Many other reports from both the western and eastern parts of the northern Pacific are listed in Klimpel et al. (2009). A few recent reports refer to digeneans from this region (e. g. Blend et al., 2012; Blend et al., 2017; Blend et al., 2015b; Kuramochi, 2011).

Manter (1954) described some macrourid worms from the waters of New Zealand. Three papers have addressed the systematics of the deep-sea digenean fauna of the waters around Vanuatu (Bray et al., 2013; Mouahid et al., 2008, 2012).

Two recent papers have reported on deep-sea digeneans from the Southeastern Pacific Ocean, both relying on by-catches of commercial fisheries. Nacari and Oliva (2016) explored the parasite fauna of three macrourids, a morid and a synphobranchid caught as by-catch of the Patagonian toothfish (*Dissostichus eleginoides* Smitt) from Chilean waters at depths between 1000 and 2,000 m. They found the macrourids, especially *Macrourus holotrachys*, harboured many digeneans, mostly unidentified. Pardo-Gandarillas et al. (2007) studied the parasites of *Coelorinchus chilensis* Gilbert & Thompson and *Notacanthus sexspinis* Richardson from the by-catch of a shrimp fishery off the Juan Fernández Archipelago, Chile. Both species harboured two digenean species, identified only to genus and none were shared. No digeneans have been reported from the vast Pacific Abyssal Plain.

13. Indian Ocean

A few digeneans of deep-sea fishes have been reported in the Indian Ocean, mainly from macrourids off the Mozambique coast (Klimpel et al., 2009; Parukhin, 1976, 1989; Reimer, 1981, 1984, 1985). Nothing is known from the Abyssal Plain.

14. Abyssal regions

Rex and Etter (2010) reckoned that ‘Many abyssal populations appear to be too sparsely distributed to be reproductively viable. They are primarily deeper range extensions for a subset of bathyal species’. The small amount of evidence available for digeneans supports this view in that reports are rare and all the species have also been reported at bathyal depths. Few digeneans have been reported from the abyssal zone (i.e., deeper than 3,000 m).

Five species are reported at abyssal depths but not, so far, on the abyssal plain.

- 1 *Glomerocirrus macrouri* (Gaevskaya, 1975) (Hemiuridae) was reported at depth 4,057 m in *Coryphaenoides armatus* in the NE Atlantic by Bray et al. (1999).
- 2 *Neolebouria merretti* Gibson and Bray (1982) (Opecoelidae) was reported at depth 2,985–3,311 m off the Canary Islands from the ipnoid *Bathytyphlops sewelli* (Norman) by Gibson and Bray (1982). This appears to be the deepest report of an opecoelid.
- 3 *Lecithophyllum euzeti* Gibson and Bray (2003) (Lecithasteridae) was reported at depth 2,400–3,718 m from the Porcupine Sea Bight in two notacanthid species by Gibson and Bray (2003). This appears to be the deepest report of a lecithasterid.
- 4 *Panopula cavernosa* Overstreet and Pritchard (1977) (Zoogonidae) was reported at depth ‘approximately’ 3,173–3,208 m from the ophidiid *Enchelybrotula paucidens* Smith & Radcliffe from the Gulf of Panama by Overstreet and Pritchard (1977).
- 5 *Proctophantastes gillissi* (Overstreet and Pritchard, 1977)

(Zoogonidae) was reported at depth ‘approximately’ 3173–3,208 m from the synphobranchid *Synphobranchus bathybius* (Günther) from the Gulf of Panama by Overstreet and Pritchard (1977). Specimens identified as this species are reported from the deep-sea Antarctic species *Dissostichus eleginoides* and *Muraenolepis marmoratus* Günther from the Ross and Amundsen Seas without detailed bathymetric data (Gordeev and Sokolov, 2016, 2017; Sokolov et al., 2016b)

Campbell et al. (1980) studied 1,712 fish specimens from the ‘deep benthic community’ of the New York Bight, in the north-western Atlantic Ocean. Three host species reached into the abyssal zone, the macrourids *Coryphaenoides armatus* (to 4,815 m) and *C. leptolepis* Günther (to 4,639 m) and the halosaurid *Halosauropsis macrochir* (to 5,179 m). Most parasites were not fully identified or named in this paper, but some were in later publications. For example, Campbell and Munroe (1977) described new hemiurids from macrourids, morids and alepocephalids from this collection. The species are: *Glomerocirrus macrouri* (syn. *G. ulmeri* Campbell and Munroe, 1977), *Gonocerca minuta* Campbell and Munroe (1977), *G. phycidis*, *C. haedrichi* Campbell and Munroe (1977), *Trifoliovarium* [*Pseudolecithaster*] *antimorae* (Campbell and Munroe, 1977), *Dinosoma sulca* Campbell and Munroe (1977), *D. triangulatum* Campbell and Munroe (1977), *Lecithophyllum botryophoron* (Olsson, 1868) [as *L. anteroporum* Margolis 1958]. They did not specify collection depth for individual species, but it is possible that some of their species, in addition to *G. phycidis*, reach into the abyssal region.

Kellermanns et al. (2009) reported the species *Bathypodocotyle margolisi* (Gibson, 1995), *Glomerocirrus macrouri*, *Gonocerca minuta*, *Steringotrema* sp. and *Steringophorus thulini* Bray & Gibson, 1980 from *Coryphaenoides mediterraneus* from the Charlie-Gibbs Fracture Zone a part of the Mid-Atlantic Ridge at depth 1,700–3,050 m. They did not specifically connect any particular parasite species with any particular depth, but it possible that some of these species, in addition to *S. thulini*, may sneak into the upper reaches of the abyssal zone.

Five species are reported from the abyssal plain.

1. *Profundivermis intercalarius* (Lepidapedidae) was described in *Coryphaenoides armatus* at the depth of 4,850 m on the Porcupine Abyssal Plain by Bray and Gibson (1991) and the sample sequenced by Bray et al. (1999) was from the same host species on the Porcupine Abyssal Plain at 4,143 m. This species was known only from abyssal regions until Nacari and Oliva (2016) reported it from *Macrourus holotrachys* off northern Chile at 1,000–2,200 m. This record needs verification.
2. *Lepidapedon beveridgei* Campbell and Bray (1993) (Lepidapedidae) was described in *C. armatus* from 2,481 to 3,470 m from the New York Bight by Campbell and Bray (1993). Bray and Gibson (1995) reported it from the same host at 4,000 m, close to the Porcupine Bank in the north-eastern Atlantic. Bray et al. (1999) found low levels of prevalence at 4,847 m on the Porcupine Abyssal Plain.
3. *Lepidapedon discoveryi* Bray and Gibson (1995) (Lepidapedidae) was reported in *C. armatus* at the depth of 4,847–4,850 m on the Porcupine Abyssal Plain by Bray and des Clers (1992), Bray and Gibson (1995) and Bray et al. (1999).
4. *Lepidapedon zubchenkoi* Campbell and Bray (1993) (Lepidapedidae) was reported as deep as 4,877 m in *Coryphaenoides leptolepis* Günther and *C. profundiculus* (Nybelin) on the Porcupine Abyssal Plain by Bray and Gibson (1995) and 4,100 m on the Goban Spur by Bray et al. (1999).
5. *Gonocerca phycidis* (Gonocercidae) was reported in *C. armatus* at the depth of 4,847–4,850 m on the Porcupine Abyssal Plain by Priede (1994) and Bray et al. (1999).
6. *Steringophorus thulini* Bray & Gibson, 1980 (Fellodistomidae) was reported as deep as 4,865 m and 4,854 m in *Coryphaenoides leptolepis* and *C. profundiculus* (Nybelin), respectively, on the Porcupine Abyssal Plain by Bray (1995) and samples from *C. leptolepis* at

4,100 m on the Porcupine Abyssal Plain were sequenced by Bray et al. (1999).

As stated above, Campbell et al. (1980) reported the halosaurid *Halosauropsis macrochir* to 5,179 m deep in the New York Bight region and reported the species *Plagioporus* sp. from this host. When Bray and Campbell (1996) described *Halosaurotrema halosauropsi* from the same host at shallower depths they considered *Plagioporus* sp. of Campbell et al. (1980) a synonym. It is likely that this species reaches to abyssal depths. The other species mentioned in this host by Campbell et al. (1980) were *Gonocerca phycidis* and *Degeneria halosauri*.

The following species of fish have been examined by us on the Porcupine Abyssal Plain but no digeneans were found; the synbranchid *Histiobranchus bathybius* (Günther) (n = 6), the alepocephalids *Conocara salmoneum* (Gill & Townsend) (n = 2) and *Xenodermichthys copei* (Gill) (n = 2), the stomiid *Malacosteus niger* Ayres (n = 1), the macrourid *Echinomacrus mollis* Roule (n = 1), the gonostomatid *Gonostoma elongatum* Günther (n = 1), the ophiidiid *Bassozetes compressus* (Günther) (n = 1), the melamphaid *Scopeloberyx robustus* (Günther) (n = 1) and an unidentified nemichthyid eel (n = 1) (new data). These samples are small and *H. bathybius* and *X. copei* are known to harbour digeneans at shallower depths.

15. Life-cycles

No life-cycles of deep-sea digeneans have yet been determined, and we do not know to what depth complete life-cycles can function. What is known of the intermediate hosts in the shallow water life-cycles of the families with representatives in the lower bathyal and abyssal regions is summarised in Table 4.

Invertebrate putative hosts are not absent in deeper waters, as is demonstrated by Rex and Etter (2010, Fig. 3.1) who illustrated the species diversity of gastropods, bivalves and polychaetes at various depths in the western North Atlantic Ocean. The figure shows that the diversity peaks at about 2,500 m for gastropods, about 3,000 m for bivalves and just shallower than 2,000 m for polychaetes, but all these taxa have a significant presence down to about 5,000 m. Later (p. 99) they pointed out that harpacticoid copepods ‘increase in diversity from upper bathyal level to 3,000 m and then decrease to 3,940 m in the western North Atlantic Ocean’. It appears, therefore, that potential invertebrate intermediate hosts are present and can be encountered at most depths. On the other hand, teleost fishes decrease in diversity with depth (Priede, 2017) and representatives of families that rely on fish as second intermediate hosts, e.g., Acanthocolpidae, Bucephalidae and Cryptogonimidae, are rare in the deep-sea, where large piscivorous fish such as carangids, serranids, scombrids and lutjanids do not occur. Unsurprisingly, families that are hosted by herbivorous fishes, such as Eenteridae, Gylauchenidae, Haploporidae and Haploplanchnidae, do not occur in the deep sea. It has been suggested (e.g., Marcogliese, 2002) that the difficulty of completing a life-cycle in the deep sea or cold water could lead to abbreviated life-cycles, but the evidence in lists of known abbreviated life-cycles as given in Poulin and Cribb (2002) and Lefebvre and Poulin (2005) suggest the preponderance are in

shallow or freshwater or are terrestrial. This could just be a reflection of our ignorance of deep-sea life-cycles.

Nothing is known of the free-living stages of the deep-sea life-cycle. The miracidium of the major groups of deep-sea digeneans may be ingested with the egg (Hemiuroidea), may hatch and invade the first intermediate host (Fellodistomidae, Lepocreadioidea) or may do either (Xiphidiata) (Cribb et al., 2003). Similarly, the cercarial strategy varies in deep-sea groups, with the cercaria penetrating the second intermediate host in the Xiphidiata and Lepocreadioidea, the cercaria being eaten by the second intermediate host in the Hemiuroidea, and either in the Fellodistomidae (Cribb et al., 2003). Thus, there is no discernible pattern to this aspect of the deep-sea life-cycle.

As far as I am aware, the only evidence of intra-molluscan parthenitae in deep-water are the reports of ‘*Bucephalus*-like’ stages in bivalves at cold-seep sites (see above). The frequent occurrence of polychaetes in deeper-waters indicate the possibility that aporocotylid blood-flukes are more frequent in the deep-sea than at present known, as it is now considered likely that these are the sole intermediate hosts of aporocotylids of marine teleosts (Cribb et al., 2017; Kjøie, 1982). This is a notoriously understudied group (Cribb and Bray, 2011).

Campbell (1983) discussed at length the prey of deep-sea fishes and the indications these data supplied on the possible intermediate hosts, basing assumptions on known life-cycles in shallow water. More recent authors have followed this reasoning and commented on possible life-cycle features. Dallarés et al. (2014), in studying the feeding of *Mora moro* (Risso), thought that polynoid polychaetes could be intermediate hosts of *Lepidapedon desclersae* when consumed accidentally by *M. moro*, although pelagic shrimps preying on chaetognaths or cnidarians is another possibility. According to Dallarés et al. (2016) the occurrence of the opecoelid *Bathycreadium* ‘is associated’ with the consumption of decapod crustaceans and polychaetes. Mateu et al. (2014) found a higher prevalence of *Steringophorus* cf. *dorsolineatus* (Reimer, 1985) in *Bathypterois mediterraneus* Bauchot at Balearic slope sites at 1,400–2,000 m depth than in fish off Barcelona at the same depth range. Mysids were found to be the prey with greatest occurrence in the diet of *Bathypterois mediterraneus* Bauchot from the Balearic Islands slope, and, therefore, may be candidates as intermediate hosts of *Steringophorus* cf. *dorsolineatus*. Marcogliese (1996) produced evidence that in the NW Atlantic at least, the zoogonid *Steganoderma formosum* Stafford, 1904 is specific to its second intermediate host, a hermit crab. If this is the case it is unusual in that this host is often the least specific in the life-cycle.

An interesting observation related to life-cycles in the deep-sea is the finding of didymozoid juveniles in lantern fish at 400–430 m depth by Mateu et al. (2015). Lantern fishes migrate into shallow (about 100 m) water at night (Gastauer et al., 2013) when presumably the parasite is transmitted to the shallow pelagic fishes which commonly have didymozoid infections. No adult didymozoids are reported from deep-water.

The absence of information on life-cycle strategies and intermediate hosts is a highly detrimental deficiency in our knowledge of deep sea digeneans.

Table 4
Summary of known life-cycles in shallow water (Cribb et al., 2003).

Family	First intermediate host	Other intermediate host(s)
Fellodistomidae	Bivalves	None, or ophiuroids, or whelk or fish paratenic host
Gorgoderidae	Bivalves	None, or encysted in bivalves, unencysted in decapods
Gonocercidae	? not known	Not known, probably similar to Hemiuridae
Hemiuridae	Gastropods	Copepods, may use chaetognaths and fish as paratenic hosts
Lecithasteridae	Gastropods or scaphopods	Copepods, possibly scaphopod
Lepidapedidae	Gastropods	Annelids, occasionally molluscs and echinoderms
Opecoelidae	Gastropods	Amphipods, decapods, mysids, fish
Zoogonidae	Gastropods	Brittle stars, polychaetes, bivalves, gastropods

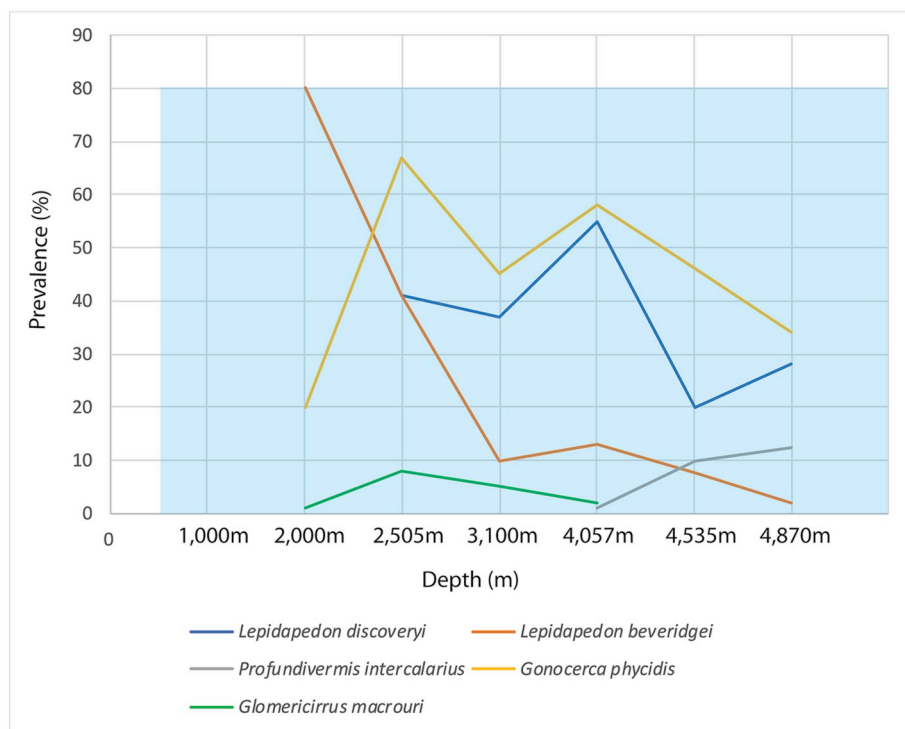


Fig. 3. Depth ranges of five digeneans of *Coryphaenoides armatus* in the NE Atlantic (adapted from Bray et al., 1999). Shaded portion shows depth range of the host, 282–5180 m, according to Froese and Pauly (2019).

16. Bio-indicators

A few authors have attempted to use deep-sea parasites as ‘biological tags’ or have suggested that they might be useful. Mateu et al. (2014) suggested the possible usefulness of two parasites, including *Steringophorus* cf. *dorsolineatus*, as geographical indicators for discriminating discrete stocks of *Bathypterois mediterraneus* in Western Mediterranean waters. Pereira et al. (2015) studied parasites of the phycid *Urophycis brasiliensis* as ecoregion indicators in Atlantic coasts of the South America and considered that parasites are ‘potentially useful as ecosystem indicators.’ Salinas et al. (2008) attempted to use parasites of *Nezumia pulchella* (Pequeño), from the south-eastern Pacific, off Chile as indicators of host populations. No digeneans were fully identified or found useful as indicators.

17. Zoning/Bathymetry

‘In deep-sea soft-sediment habitats, species turnover is nothing like the zonation seen in the more familiar rocky intertidal, where there exist sharply delineated monospecific bands ... The deep-sea patterns are much messier, involving many species with widely overlapping ranges’ (Rex and Etter, 2010). Bray et al. (1999) reported on the depth zones inhabited by five parasites of *Coryphaenoides armatus* in the NE Atlantic. Fig. 3 illustrates the prevalence found at various depths. In this case each parasite has its own depth range, decoupled from the host range and this is believed to be the normal arrangement for most benthic animals including parasites.

Recent reports of well-studied shelf parasites at considerable depths illustrate that certain parasites with low host specificity are capable of invasion of the upper bathyal. Klimpel et al. (2009) reckoned that at high latitudes in particular ‘the typical shelf fauna may inhabit the continental slope to a depth of more than 1,000 m and characteristic deep-sea taxa are found in the polar region at depths of a few hundred meters’. Two examples are the derogenid *Derogenes varicus* (Müller, 1784) and the zoogonid *Zoogonoides viviparus* (Olsson, 1868) which Bray and Kuchta (2006) reported at 1,800 m and 1,000 m, respectively,

off the Outer Hebrides. *D. varicus* has also been reported to 1,513 m off northern Honshu, Japan (Kuramochi, 2009). Manter (1955) pointed out that *D. varicus*, while a shallow-water parasite in polar regions, also occurs in deep water in lower latitudes apparently having a ‘continuous three-dimensional distribution from Antarctic to Arctic’, so-called equatorial submergence (Ekman, 1953).

The digeneans that are found in lower bathyal and abyssal regions appear to have a greater depth range than those in shallower waters, in other words they are eurybathic. The statement by Gibbs (1997) that a ‘general theme appearing in biochemical studies of deep-sea fishes is that adaptation to high and variable pressures has entailed the evolution of pressure-insensitive forms of enzymes, rather than enzymes adapted for function at a specific range of pressures’, also appears to apply to digeneans. These ‘pressure-insensitive’ enzymes do not, however, appear to function throughout the water column, as there is a distinct set of deep-sea digeneans that are not found in shallow waters.

18. Host-parasite relationships

What sorts of host-specificity are exhibited by deep-sea fishes? It is likely that some species and genera are oioxenic, for example *Degeneria halosauri* and *Halosaurotrema halosauropsi* in *Halosauropsis macrochir*. Many *Lepidapedon* spp. are stenoxenic to macrourids, particularly to the genus *Coryphaenoides*. In contrast, the eight *Steringophorus* species for which sequences are available (Bray et al., 1999) are reported in alepocephalids, chlorophthalmids, pleuronectids, ophidiids, bythidiids and macrourids. This array reflects what is found elsewhere and there is no reason as yet to consider that the patterns of host-specificity in deep water digeneans are distinctive.

19. Concluding questions

In our 1999 review (Bray et al., 1999) we posed five concluding questions and it seems appropriate to discuss whether any further progress has been made.

19.1. Is the deep-water fauna smaller than the shallows?

The same problem we found in 1999 still applies. The sampling effort is so skewed to the shallow water forms that it is not surprising that the fauna appears to be smaller in the deep-sea. All recent evidence, however, indicates that this is really the case, but the degree of this distinction is not convincingly demonstrated. It is clear that metazoan faunal biomass decreases with depth (Rex and Etter, 2010, Fig. 1.13), but the deep-sea is such an enormous habitat that the overall biomass of the deep-sea fauna may not be significantly smaller than the shallow fauna.

19.2. Is the deep-sea fauna less diverse than the shallow?

The relatively few digenean families that are represented in the bathyal and abyssal regions indicate that this aspect of diversity is unambiguously depauperate at depth. Most recent reports are of well recognised deep-sea families and the only new information is the discovery of two unattributable genera at hydrothermal vents and deep Antarctic waters (Bray et al., 2014; Sokolov et al., 2019b). According to WoRMS (WoRMS Editorial Board, 2019) 769 new digeneans species have been described this century and 395 since 2009 when Klimpel et al. (2009) produced their checklist. We have listed above the 12 deep-sea species omitted from the checklist and 17 which have been described since 2009. These 17 species constitute about 4% of the species described since 2009: is this a reflection of real depauperate diversity or skewed effort? In terms of new genera 124 have been described this century with 59 since 2009 (WoRMS Editorial Board, 2019). Since 2009 two new deep-sea genera have been described and three new opoecoid genera have been recognised for known species, which represents about 8.5% of the effort in that period. It is significant that all these new genera are based on molecular results, a welcome development. In summary, it appears that the lower diversity reported from the deep-sea reflects a genuine result, but its extent is skewed by sampling effort.

19.3. Are evolutionary transitions from shallow to deep (or vice versa) relatively rare?

It appears that the deep-sea fauna is constituted of a mixture of higher taxa which have radiated in the deep-sea and the occasional taxonomically isolated taxon which has moved into the deep-sea. An example of the latter would be the *Prodistomum* spp. found in epigonids. In this case, the spread into the deep-sea is not profound. All the species reported from abyssal depths belong to higher taxa with most, or at least many, deep sea denizens. Slight spill over from shelf and cold-water regions is apparently common, but adaptation to really deep-sea living seems infrequent.

19.4. Have most deep-sea digeneans radiated in the deep-sea?

Later molecular studies have, in general, reinforced the view that the genera *Lepidapedon* and its close relatives and *Steringophorus* have substantially radiated in deeper waters. It is also probable that the opoecoid subfamily Podocotylinae as recognised by Martin et al. (2019) and the genus *Gonocerca* have radiated in deep and cold waters. There is little evidence yet that deep-sea species of the well-represented families Hemiuridae and Zoogonidae have radiated in the deep-sea. Nevertheless, it appears that most profoundly deep-sea taxa have radiated in this zone.

19.5. How much do we really know about deep-sea digeneans?

‘Very little’ is still a reasonable answer to this question. In recent years efforts have been made particularly in the Gulf of Mexico, western Mediterranean and the western coastal regions of South America. These

studies have incorporated new species and new faunistic information, but still many studies lack systematic detail. A case in point is the study by Nacari and Oliva (2016) of five deep-sea fishes off Chile. Of the 18 digeneans listed, 6 are identified to species, 5 to genus, 4 to family and 3 are listed as Digenea gen. sp. It is not always clear whether vouchers have been deposited in curated collections. It is clear, however, that many more accurate morphological and molecular systematic investigations are needed for a deeper understanding of deep-sea digenean biology.

19.6. Additional question: how have the constraints encountered in the deep-sea effected digeneans?

Many of the features of the deep-sea, such as salinity, oxygen levels and seabed topography, do not appear to be significant constraints on digeneans. The frequency of invertebrates in the deep-sea suggest that encounters with intermediate hosts restricts the deep-sea digenean fauna to those taxa that rely on invertebrates as second intermediate hosts and precludes those taxa which use fish and algae as sources of intermediate stages. The close similarity of polar and deep-sea digenean faunas suggests that adaptation to cold is a common characteristic of these faunas. The most intriguing and least studied aspect of the deep-sea is the pressure, which in the deepest parts of the ocean is many times greater than at sea level. Small increases in pressure can seriously disrupt the behaviour of shallow-living animals resulting in ‘hyperactivity, convulsions, torpor and eventual death’ (Gibbs, 1997). Clearly many digeneans that reach into the deep-sea have adaptations that prevent such deleterious pressure outcomes. Work on other taxa, often fish, has shown that pressure has significant effects on the structure and function of enzymes, structural proteins and membrane lipids, but nothing is known of these effects in digeneans. When the molecular biochemistry of deep adaptation is better understood, it may be possible to detect these effects in digenean genetics as has been attempted in fishes (e.g. Morita, 2008). At present we know that some currently recognised digenean species, e.g. *Gonocerca phycidis*, *Steringophorus thulini*, *Degeneria halosauri*, may be found at a wide range of depths. It is reckoned that abyssal species are mainly a subset of bathyal species, presumably those that are adapted to tolerance of a greater pressure range. What awaits to be studied is the genetic differences, if any, between members of currently recognised species from different depths.

20. Concluding remarks

Significant studies of deep-sea digeneans have taken place only in the northern Atlantic basin, the North Pacific and the eastern South Pacific Ocean. Nothing is known of the abyssal plain fauna anywhere other than the relatively small area of the Porcupine Abyssal Plain off southwestern Ireland. With the likelihood of imminent deep-sea mining, particularly of hydrothermal vent regions (Thaler and Amon, 2019), it is probable that ‘habitat will be removed, sediment plumes will be created, and some biodiversity loss is inevitable ... A fundamental problem for predicting the impacts of deep-sea mining on hydrothermal vents is our limited knowledge of these ecosystems in general’. These concerns are not solely applicable to hydrothermal vent systems but for the whole deep-sea, indeed the whole ocean. It is to be hoped that in consideration of the moral imperative of good stewardship of the environment, more effort will be made to explore these regions and that parasitologists will be involved so that the large component of the fauna presented by parasites will be integrated into the ecological assessments. At present we are deplorably ignorant of this enormous habitat and its fauna.

Declaration of competing interest

I have no conflict of interests.

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References

- Andres, M.J., Overstreet, R.M., 2013. A new species of *Podocotyloides* (Digenea: Opecoelidae) from the grey conger eel, *Conger esculentus*, in the Caribbean sea. *J. Parasitol.* 99, 619–623.
- Andres, M.J., Peterson, M.S., Overstreet, R.M., 2016. Endohelminth parasites of some midwater and benthopelagic stomiiform fishes from the northern Gulf of Mexico. *Gulf Caribb. Res.* 27, 11–19.
- Bell, F.J., 1887. Description of a new species of *Distomum*. *Ann. Mag. Nat. Hist.* 116–117 Series 5 19.
- Blend, C.K., Dronen, N.O., 2015a. Description of a new species of *Podocotyle* Dujardin, 1845 (Digenea: Opecoelidae: Plagioporinae) from the cusk-eel, *Luciobrotula corethromycter* Cohen, 1964 (Ophidiiformes: Ophidiidae), from the Gulf of Mexico and Caribbean sea. *Acta Parasitol.* 60, 234–243.
- Blend, C.K., Dronen, N.O., 2015b. A review of the genus *Helicometra* Odhner, 1902 (Digenea: Opecoelidae: Plagioporinae) with a key to species including *Helicometra overstreeti* n. sp. from the cusk-eel *Luciobrotula corethromycter* Cohen, 1964 (Ophidiiformes: Ophidiidae) from the Gulf of Mexico. *Mar. Biodivers.* 45, 183–270.
- Blend, C.K., Dronen, N.O., Armstrong, H.W., 2016. *Podocotyle nimoyi* n. sp. (Digenea: Opecoelidae: Plagioporinae) and a re-description of *Podocotyle pearsei* Manter, 1934 from five species of Deep-sea macrourids from the Gulf of Mexico and Caribbean sea. *Zootaxa* 4117, 491–512.
- Blend, C.K., Dronen, N.O., Gardner, S.L., Racz, G.R., Armstrong, H.W., 2012. The Deep-sea fish digenean genus *Tellervotrema* Gibson & Bray, 1982 (Opecoelidae: Plagioporinae): Re-evaluation of the type species, *T. armstrongi* Gibson & Bray, 1982 and *T. beringi* (Mamaev, 1965). *Zootaxa* 3295, 1–29.
- Blend, C.K., Dronen, N.O., Racz, G.R., Gardner, S.L., 2017. *Pseudopecoelus mccauleyi* n. sp. and *Podocotyle* sp. (Digenea: Opecoelidae) from the deep waters off Oregon and British Columbia with an updated key to the species of *Pseudopecoelus* von Wicklen, 1946 and checklist of parasites from *Lycodes cortezianus* (Perciformes: Zoarcidae). *Acta Parasitol.* 62, 231–254.
- Blend, C.K., Kuramochi, T., Dronen, N.O., 2015a. *Allopodocotyle enkatmushi* n. sp. (Digenea: Opecoelidae: Plagioporinae) from the Short-Tail Grenadier, *Nezumia proxima* (Gadiformes: Macrouridae), from Sagami Bay, Japan, with a key to species of this genus and a checklist of parasites reported from this host. *Comp. Parasitol.* 82, 219–230.
- Blend, C.K., Kuramochi, T., Dronen, N.O., 2015b. Re-evaluation of *Tellervotrema katadara* (Kuramochi, 2001) Kuramochi, 2009 (Opecoelidae: Plagioporinae) and supplementary morphological data for *T. beringi* (Mamaev, 1965) Gibson & Bray, 1982 with new host and locality. *Zootaxa* 3986, 435–451.
- Bray, R.A., 1995. *Steringophorus* Odhner, 1905 (Digenea: Fellodistomidae) in deep-sea fishes from the northeastern Atlantic, with the description of *Steringophorus margolisi* n. sp. *Can. J. Fish. Aquat. Sci.* 52, 71–77.
- Bray, R.A., 1996. *Merlucciotrema praeclarum* (Manter, 1934) (Digenea: Hemiuridae) re-described from myctophiform and gadiform fishes of the north Atlantic. *Syst. Parasitol.* 33, 135–141.
- Bray, R.A., 2004. The bathymetric distribution of the digenean parasites of deep-sea fishes. *Folia Parasitol.* 51, 268–274.
- Bray, R.A., Campbell, R.A., 1995. Fellodistomidae and Zoogonidae (Digenea) of Deep-sea fishes of the NW Atlantic Ocean. *Syst. Parasitol.* 31, 201–213.
- Bray, R.A., Campbell, R.A., 1996. New plagioporines (Digenea: Opecoelidae) from Deep-sea fishes of the north Atlantic Ocean. *Syst. Parasitol.* 33, 101–113.
- Bray, R.A., Cribb, T.H., 2012. Reorganisation of the superfamily Lepocreadiioidea Odhner, 1905 based on an inferred molecular phylogeny. *Syst. Parasitol.* 83, 169–177.
- Bray, R.A., Cribb, T.H., Littlewood, D.T.J., Waeschenbach, A., 2016. The molecular phylogeny of the digenean family Opecoelidae Ozaki, 1925 and the value of morphological characters, with the erection of a new subfamily. *Folia Parasitol.* 63, 1–11 013.
- Bray, R.A., des Clers, S.A., 1992. Multivariate analyses of metrical features in the *Lepidapedon elongatum* (Lebour, 1908) species-complex (Digenea, Lepocreadiidae) in deep and shallow water gadiform fishes of the NE Atlantic. *Syst. Parasitol.* 21, 223–232.
- Bray, R.A., Faliex, E., Allienne, J.F., Mouahid, G., 2013. *Lepidapedon sereti* n. sp. (Digenea: Lepidapedidae) in *Coelorrinchus sereti* (Gadiformes: Macrouridae) from deep waters off Vanuatu. *Parasitol. Res.* 112, 3981–3989.
- Bray, R.A., Gibson, D.I., 1989. The Lepocreadiidae (Digenea) of fishes from the north-east Atlantic: review of the genus *Neolepidapedon* Manter 1954, with a description of *N. smithi* n. sp. *Syst. Parasitol.* 13, 11–23.
- Bray, R.A., Gibson, D.I., 1991. The Lepocreadiidae (Digenea) of fishes from the North-east Atlantic: *Profundivermis intercalarius* n. g., n. sp. from the marine fish *Coryphaenoides (Nematonurus) armatus* (Hector) (Macrouridae) from the Porcupine abyssal plain. *Syst. Parasitol.* 18, 121–125.
- Bray, R.A., Gibson, D.I., 1995. The Lepocreadiidae (Digenea) of fishes from the North-east Atlantic: a review of the genus *Lepidapedon* Stafford, 1904. *Syst. Parasitol.* 31, 81–132.
- Bray, R.A., Kuchta, R., 2006. Digeneans from deep-sea marine teleosts off the Outer Hebrides, Scotland, including the description of *Brachyenteron helicoleni* sp. nov. (Zoogonidae). *Acta Parasitol.* 51, 169–175.
- Bray, R.A., Littlewood, D.T.J., Herniou, E.A., Williams, B., Henderson, R.E., 1999. Digenean parasites of deep-sea teleosts: a review and case studies of intrageneric phylogenies. *Parasitology* 119, S125–S144 Supplement.
- Bray, R.A., Waeschenbach, A., 2020. *Steringophorus merretti* n. sp. (Digenea: Fellodistomidae) from the deep-sea fish *Cataetx laticeps* Koefoed (Ophidiiformes, Bythitidae) from the Goban Spur, in the northeastern Atlantic Ocean. *Syst. Parasitol.* (in press).
- Bray, R.A., Waeschenbach, A., Cribb, T.H., Weedall, G.D., Dyal, P., Littlewood, D.T.J., 2009. The phylogeny of the Lepocreadiioidea (Platyhelminthes: Digenea) inferred from nuclear and mitochondrial genes: implications for their systematics and evolution. *Acta Parasitol.* 54, 310–329.
- Bray, R.A., Waeschenbach, A., Dyal, P., Littlewood, D.T.J., Morand, S., 2014. New digeneans (Opecoelidae) from hydrothermal vent fishes in the south eastern Pacific Ocean, including one new genus and five new species. *Zootaxa* 3768, 73–87.
- Campbell, R.A., 1983. Parasitism in the deep-sea. In: In: Rowe, G.T. (Ed.), *The Sea*, vol. 8. John Wiley and Sons, Inc, New York, pp. 473–552.
- Campbell, R.A., Bray, R.A., 1993. *Lepidapedon* spp. (Digenea: Lepocreadiidae) from deep-sea gadiform fishes of the NW Atlantic Ocean, including four new species. *Syst. Parasitol.* 24, 99–110.
- Campbell, R.A., Haedrich, R.L., Munroe, T.A., 1980. Parasitism and ecological relationships among deep-sea benthic fishes. *Mar. Biol. (Berlin)* 57, 301–313.
- Campbell, R.A., Munroe, T.A., 1977. New hemiurid trematodes from deep-sea benthic fishes in the western North Atlantic. *J. Parasitol.* 63, 285–294.
- Chambers, C., 2008. Determining deep-sea fish community structure in the Arctic: using species assemblages, stomach contents, parasite infracommunities and stable isotopes to evaluate trophic interactions. Department of Biological Sciences. University of Manitoba, Winnipeg.
- Collard, S.B., 1970. Some aspects of host-parasite relationships in mesopelagic fishes. In: Sniezko, S.F. (Ed.), *A Symposium on Diseases of Fishes and Shellfishes*. American Fisheries Society, Special Publication 5, Washington, D.C., pp. 41–56.
- Constenla, M., Montero, F.E., Padrós, F., Cartes, J.E., Papiol, V., Carrassón, M., 2015. Annual variation of parasite communities of deep-sea macrourid fishes from the western Mediterranean Sea and their relationship with fish diet and histopathological alterations. *Deep-Sea Res. Part I* 104, 106–121.
- Cribb, T.H., Bray, R.A., 2010. Gut wash, body soak, blender, and heat-fixation: approaches to the effective collection, fixation and preservation of trematodes of fishes. *Syst. Parasitol.* 55, 45–52.
- Cribb, T.H., Bray, R.A., 2011. Trematode families and genera: have we found them all? *Trends Parasitol.* 27, 149–154.
- Cribb, T.H., Bray, R.A., Olson, P.D., Littlewood, D.T.J., 2003. Life cycle evolution in the Digenea: a new perspective from phylogeny. *Adv. Parasitol.* 54, 197–254.
- Cribb, T.H., Chick, R.C., O’Connor, W., O’Connor, S., Johnson, D., Sewell, K.B., Cutmore, S.C., 2017. Evidence that blood flukes (Trematoda: Apocortycylidae) of chondrichthyans infect bivalves as intermediate hosts: indications of an ancient diversification of the Schistosomatoidea. *Int. J. Parasitol.* 47, 885–891.
- Cribb, T.H., Miller, T.L., Bray, R.A., Cutmore, S.C., 2014. The sexual adult of *Cercaria praecox* Walker, 1971 (Digenea: Fellodistomidae), with the proposal of *Oceroma* n. g. *Syst. Parasitol.* 88, 1–10.
- Cutmore, S.C., Miller, T.L., Curran, S.S., Bennett, M.B., Cribb, T.H., 2013. Phylogenetic relationships of the Gorgoderidae (Platyhelminthes: trematoda), including the proposal of a new subfamily (Degeneriinae n. subfam.). *Parasitol. Res.* 112, 3063–3074.
- Dallarés, S., Constenla, M., Padros, F., Cartes, J.E., Sole, M., Carrassón, M., 2014. Parasites of the deep-sea fish *Mora moro* (Risso, 1810) from the NW Mediterranean Sea and relationship with fish diet and enzymatic biomarkers. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 92, 115–126.
- Dallarés, S., Georgieva, S., Kostadinova, A., Carrassón, M., Gibson, D.I., Perez-del-Olmo, A., 2013. Morphometric and molecular characterisation of specimens of *Lepidapedon* Stafford, 1904 (Digenea: Lepidapedidae) from the Deep-sea fish *Mora moro* (Risso) (Teleostei: Moridae) in the western Mediterranean. *Syst. Parasitol.* 85, 243–253.
- Dallarés, S., Moyà-Alcover, C.M., Padrós, F., Cartes, J.E., Solé, M., Castañeda, C., Carrassón, M., 2016. The parasite community of *Phycis blennioides* (Brünnich, 1768) from the Balearic Sea in relation to diet, biochemical markers, histopathology and environmental variables. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 118, 84–100.
- de Buron, I., Morand, S., 2004. Deep-sea hydrothermal vent parasites: why do we not find more? *Parasitology* 128, 1–6.
- Ekman, S., 1953. *Zoogeography of the Sea*. Sidgwick & Jackson, London.
- Espinola-Novelo, J.F., Escribano, R., Oliva, M.E., 2018. Metazoan parasite communities of two deep-sea elasmobranchs: the southern lanternshark, *Etmopterus granulosus*, and the largenose catshark, *Apristurus nasutus*, in the Southeastern Pacific Ocean. *Parasite* 25 (53), 1–8.
- Faltýnková, A., Georgieva, S., Kostadinova, A., Bray, R.A., 2017. Biodiversity and evolution of digeneans of fishes in the Southern Ocean. In: Klimpel, S., Kuhn, T., Mehlhorn, H. (Eds.), *Biodiversity and Evolution of Parasitic Life in the Southern Ocean*. Springer, Switzerland, pp. 49–75.
- Fayton, T.J., McAllister, C.T., Robison, H.W., Connor, M.B., 2018. Two new species of *Plagioporus* (Digenea: Opecoelidae) from the Ouachita madtom, *Noturus lachneri*, and the banded sculpin, *Cottus caroliniae*, from Arkansas. *J. Parasitol.* 104, 145–156.

- Freese, R., Pauly, D., 2019. FishBase. World Wide Web electronic publication. Available on: <http://www.fishbase.org>.
- Gage, J.D., Tyler, P.A., 1991. Deep-sea Biology. A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Cambridge.
- Gartner Jr., J.V., Zwerner, D.E., 1989. The parasite faunas of meso- and bathypelagic fishes of Norfolk Submarine Canyon, western North Atlantic. *J. Fish Biol.* 34, 79–95.
- Gastauer, S., Schaber, M., Fässler, S., Armstrong, E.J., Freijser, J., Keating, J., Brandhof, J., 2013. The distribution and behaviour of mesopelagic fishes west of the British Isles. 20, 1–2 ICES CM 2013/N.
- Gibbs, A.G., 1997. Biochemistry at depth. In: Randall, D.J., Farrell, A.P. (Eds.), *Deep-sea Fishes*. Academic Press, San Diego, pp. 230–277.
- Gibson, D.I., 1995. *Allopodocotyle margolis* n. sp. (Digenea: Opecoelidae) from the deep-sea fish *Coryphaenoides (Chalinura) mediterraneus* in the northeastern Atlantic. *Can. J. Fish. Aquat. Sci.* 52, 90–94.
- Gibson, D.I., Bray, R.A., 1982. A study and reorganization of *Plagioporus* Stafford, 1904 (Digenea: Opecoelidae) and related genera, with special reference to forms from European Atlantic waters. *J. Nat. Hist.* 16, 529–559.
- Gibson, D.I., Bray, R.A., 2003. *Lecithophyllum euzeti* n. sp. (Digenea: Lecithasteridae) from notacanthid fishes in the deep-waters of the Porcupine Sea Bight, north-east Atlantic. In: Combes, C., Jourdan, J. (Eds.), *Taxonomy, ecology and evolution of metazoan parasites*. (Livre hommage à Louis Euzet). Tome I. Presses Universitaire de Perpignan, Perpignan, pp. 347–358.
- Goode, I.L., Sokolov, S.G., 2016. Parasites of the Antarctic toothfish (*Dissostichus mawsoni* norman, 1937) (Perciformes, Nototheniidae) in the Pacific sector of the Antarctic. *Polar Res.* 35, 1–5.
- Goode, I.L., Sokolov, S.G., 2017. Helminths and the feeding habits of the marbled moray cod *Muraenolepis marmorata* Gunther, 1880 (Gadiformes, Muraenolepididae) in the Ross sea (Southern Ocean). *Polar Biol.* 40, 1311–1318.
- Goode, I.L., Sokolov, S., Bañón, R., Morales, X., Orlov, A., 2019. Parasites of the blue Antimora, *Antimora rostrata* and slender codling, *Halargyreus johnsonii* (Gadiformes: Moridae), in the Northwestern Atlantic. *Acta Parasitol.* 64, 489–500.
- Houston, K.A., Haedrich, R.L., 1986. Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, northwest Atlantic Ocean. *Mar. Biol.* 92, 563–574.
- Jacobs, D.K., Lindberg, D.R., 1998. Oxygen and evolutionary patterns in the sea: Onshore/offshore trends and recent recruitment of deep-sea faunas. *Proc. Natl. Acad. Sci. U.S.A.* 95, 9396–9401.
- Jollivet, D., Lallier, F.H., Barnay, A.-S., Bienvu, N., Bonnivard, E., Briand, P., Cambon-Bonavita, M.-A., Comtet, T., Cosson, R., Daguin, C., Donval, J.-P., Fauré, B., Gaillard, M., Glippa, V., Guillou, L., Hourdez, S., Le Bris, N., Morand, S., Pradillon, F., Rees, J.-F., Segonzac, M., Shillito, B., Thiebaut, E., Viard, F., 2004. The BIOSPEEDO cruise: a new survey of hydrothermal vents along the south east Pacific rise from 7°24'S to 21°33'S. *InterRidge* 13, 20–26.
- Kellermanns, E., Klimpel, S., Palm, H.W., 2009. Parasite fauna of the Mediterranean grenadier *Coryphaenoides mediterraneus* (Giglioli, 1893) from the mid-Atlantic Ridge (MAR). *Acta Parasitol.* 54, 158–164.
- Kemp, K.M., Jamieson, A.J., Bagley, P.M., McGrath, H., Bailey, D.M., Collins, M.A., Priede, I.G., 2006. Consumption of large bathyal food fall, a six month study in the NE Atlantic. *Mar. Ecol. Prog. Ser.* 310, 65–76.
- Klimpel, S., Busch, M.W., Kellermanns, E., Kleinert, S., Palm, H.W., 2009. Metazoan deep-sea fish parasites. *Acta Biologica Benrodis* 1–384 Supplementband 11.
- Klimpel, S., Busch, M.W., Sutton, T., Palm, H.W., 2010. Meso- and bathy-pelagic fish parasites at the Mid-Atlantic Ridge (MAR): low host specificity and restricted parasite diversity. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 57, 596–603.
- Klimpel, S., Kellermanns, E., Palm, H.W., 2008a. The role of pelagic swarm fish (Mycetozoa: Teleostei) in the oceanic life cycle of *Anisakis* sibling species at the Mid-Atlantic Ridge, Central Atlantic. *Parasitol. Res.* 104, 43–53.
- Klimpel, S., Kellermanns, E., Palm, H.W., Moravec, F., 2007. Zoogeography of fish parasites of the pearlside (*Maurolicus muelleri*), with genetic evidence of *Anisakis simplex* (s. s.) from the Mid-Atlantic Ridge. *Mar. Biol. (Berlin)* 152, 725–732.
- Klimpel, S., Palm, H.W., Busch, M.W., Kellermanns, E., 2008b. Fish parasites in the bathyal zone: the halosaur *Halosaurus macrochir* (Gunther, 1878) from the Mid-Atlantic Ridge. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* 55, 229–235.
- Klimpel, S., Palm, H.W., Busch, M.W., Kellermanns, E., Ruckert, S., 2006. Fish parasites in the Arctic deep-sea: poor diversity in pelagic fish species vs. heavy parasite load in a demersal fish. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 53, 1167–1181.
- Koie, M., 1980. On the morphology and life-history of *Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911 and *Felodistomum fellis* (Olsson, 1868) Nicoll, 1909 [syn. *S. ovacutum* (Lebour, 1908) Yamaguti, 1953] (Trematoda, Felodistomidae). *Ophelia* 19, 215–236.
- Koie, M., 1982. The redia, cercaria and early stages of *Aporocotyle simplex* Odhner, 1900 (Sanguinicolidae) - a digenetic trematode which has a polychaete annelid as the only intermediate host. *Ophelia* 21, 115–145.
- Korotaeva, V.D., 1994. Two new species of trematodes (Trematoda: Zoogonidae) from fishes of south part of Indian and Pacific Oceans. *Parazitologiya* 28, 248–251 (In Russian).
- Kuramochi, T., 2001. Digenetic trematodes of anguilliform and gadiform fishes from deep-sea areas of Tosa Bay, Japan. In: In: Fujita, T., Saito, H., Takeda, M. (Eds.), *Deep-sea Fauna and Pollutants in Tosa Bay*, vol. 20. National Science Museum Monographs, Tokyo, pp. 19–30.
- Kuramochi, T., 2005. Digenetic trematodes offshores from deep-sea areas off Ryukyu Islands, Southern Japan. *Natl. Sci. Mus. Monogr.* 29, 23–35.
- Kuramochi, T., 2009. Digenetic trematodes of fishes from Deep-sea areas off the Pacific coast of northern Honshu, Japan. In: In: Fujita, T. (Ed.), *Deep-sea Fauna and Pollutants off Pacific Coast of Northern Japan*, vol. 39. National Museum of Nature and Science Monographs, pp. 25–37.
- Kuramochi, T., 2011. Digenetic trematodes of fishes caught in Sagami Bay, off Izu Islands and off Ogasawara Islands. *Mems. Natl. Mus. Nat. Sci., Tokyo* 47, 51–63.
- Lefebvre, F., Poulin, R., 2005. Progenesis in digenetic trematodes: a taxonomic and synthetic overview of species reproducing in their second intermediate hosts. *Parasitology* 130, 587–605.
- Linton, E., 1898. Notes on trematode parasites of fishes. In: *Proc. U. S. Natl. Mus., Washington*, vol. 20. pp. 507–548.
- Lumb, S.M., Bray, R.A., Rollinson, D., 1993. Partial small subunit (18S) rRNA gene sequences from fish parasites of the families Lepocreadiidae and Felodistomidae (Digenea) and their use in phylogenetic analyses. *Syst. Parasitol.* 26, 141–149.
- Machida, M., Kamegai, S., Kuramochi, T., 2006. Zoogonidae (trematoda, Digenea) from fishes of Japanese waters. *Bull. Natl. Sci. Mus., Tokyo. Series A. Zoology* 32, 95–104.
- Machida, M., Kamegai, S., Kuramochi, T., 2007. Felodistomidae (trematoda, Digenea) from Deep-sea fishes of Japan. *Bull. Natl. Sci. Mus., Tokyo. Series A. Zoology* 33, 93–103.
- Manter, H.W., 1934. Some digenetic trematodes from deep-water fish of Tortugas, Florida. *Papers Tortugas Lab* 28, 257–345.
- Manter, H.W., 1954. Some digenetic trematodes from fishes of New Zealand. *Trans. R. Soc. N. Z.* 82, 475–568.
- Manter, H.W., 1955. The zoogeography of trematodes of marine fishes. *Exp. Parasitol.* 4, 62–86.
- Marcogliese, D.J., 1996. Evidence for specificity of *Steganoderma formosum* for its second intermediate host in the Northwest Atlantic. *J. Helminthol.* 70, 215–218.
- Marcogliese, D.J., 2002. Food webs and the transmission of parasites to marine fish. *Parasitology* 124, S83–S99.
- Martin, S.B., Huston, D.C., Cutmore, S.C., Cribb, T.H., 2019. A new classification for deep-sea opecoelid trematodes based on the phylogenetic position of some unusual taxa from shallow-water, herbivorous fishes off south-west Australia. *Zool. J. Linn. Soc.* 186, 385–413.
- Mateu, P., Montero, F.E., Carrasson, M., 2014. Geographical variation in metazoan parasites of the deep-sea fish *Bathypterois mediterraneus* Bauchot, 1962 (Osteichthyes: Ipnopidae) from the western mediterranean. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 87, 24–29.
- Mateu, P., Nardi, V., Fraija-Fernández, N., Mattiucci, S., Gil de Sola, L., Raga, J.A., Fernández, M., Aznar, F.J., 2015. The role of lantern fish (Mycetophidae) in the life-cycle of cetacean parasites from western Mediterranean waters. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 95, 115–121.
- McNichol, J., Stryhanyuk, H., Sylva, S.P., Thomas, F., Musat, N., Seewald, J.S., Sievert, S.M., 2018. Primary productivity below the seafloor at deep-sea hot springs. *Proc. Natl. Acad. Sci. U.S.A.* 115, 6756–6761.
- Merrett, N.R., Haedrich, R.L., 1997. Deep-sea Demersal Fish and Fisheries. Chapman & Hall, London.
- Mitsi, K., Arroyo, A.S., Ruiz-Trillo, I., 2019. A global metabarcoding analysis expands molecular diversity of Platyhelminthes and reveals novel early-branching clades. *Biol. Lett.* 15, 20190182.
- Morita, T., 2008. Comparative sequence analysis of myosin heavy chain proteins from congeneric shallow- and deep-living rattail fish (genus *Coryphaenoides*). *J. Exp. Biol.* 211, 1362–1367.
- Mouahid, G., Faliex, E., Allienne, J.-F., Cribb, T.H., 2008. *Proctophantastes brayi*, n. sp. (Digenea: Zoogonidae) parasite of the deep-sea fish *Polymixia* Lowe, 1838 from Vanuatu. *Parasitol. Int.* 57, 25–31.
- Mouahid, G., Faliex, E., Allienne, J.-F., Cribb, T.H., Bray, R.A., 2012. *Proctophantastes nettastomatis* (Digenea: Zoogonidae) from Vanuatu deep-sea fish: new morphological features, allometric growth, and phenotypic plasticity aspects. *Parasitol. Res.* 110, 1631–1638.
- Münster, J., Kochmann, J., Klimpel, S., Klapper, R., Kuhn, T., 2016. Parasite fauna of Antarctic *Macrourus whitsoni* (Gadiformes: Macrouridae) in comparison with closely related macrourids. *Parasites Vectors* 9, 403.
- Nacari, L.A., Oliva, M.E., 2016. Metazoan parasites of deep-sea fishes from the South Eastern Pacific: exploring the role of ecology and host phylogeny. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 115, 123–130.
- Noble, E.R., 1973. Parasites and fishes in a deep-sea environment. *Adv. Mar. Biol.* 11, 121–195.
- Odhner, T., 1911. Zum natürlichen system der digenen Trematoden. II. *Zool. Anz.* 38, 237–253.
- Olson, P.D., Cribb, T.H., Tkach, V.V., Bray, R.A., Littlewood, D.T.J., 2003. Phylogeny and classification of the Digenea (Platyhelminthes: trematoda). *Int. J. Parasitol.* 33, 733–755.
- Overstreet, R.M., Pritchard, M.H., 1977. Two new zoogonid Digenea from deep-sea fishes in the Gulf of Panama. *J. Parasitol.* 63, 840–844.
- Pardo-Gandarillas, M.C., Gonzalez, K., Ibanez, C.M., George-Nascimento, M., 2007. Parasites of two Deep-sea fish *Coelorynchus chilensis* (Pisces: Macrouridae) and *Notacanthus sexspinis* (Pisces: Notacanthidae) from Juan Fernandez Archipelago, Chile. *JMBA2 - Biodivers. Rec.* 5794, 1–5.
- Parukhin, A.M., 1976. *Assitrema eichleri* gen. et sp. nov., eine neue Trematodenart aus dem indik. *Angew. Parasitol.* 17, 6–9.
- Parukhin, A.M., 1989. [Parasitic Worms of Bottom Fishes of the Southern Seas]. *Naukova Dumka, Kiev* (In Russian).
- Pereira, A.N., Pantoja, C., Luque, J.L., Timi, J.T., 2015. Parasites of *Urophycis brasiliensis* (Gadiformes: Phycidae) as indicators of marine ecoregions in coastal areas of the South American Atlantic. *Parasitol. Res.* 113, 4281–4292.
- Pérez-del-Olmo, A., Dallarés, S., Carrasson, M., Kostadinova, A., 2014. A new species of *Bathycreadium* Kabata, 1961 (Digenea: Opecoelidae) from *Phycis blennoides* (Brünnich) (Gadiformes: Phycidae) in the western mediterranean. *Syst. Parasitol.* 88, 233–244.
- Pérez-del-Olmo, A., Dallarés, S., Georgieva, S., Constenla, M., Kostadinova, A., Carrasson, M., 2019. A new species of *Bathycreadium* Kabata, 1961 (Digenea: Opecoelidae) from *Phycis blennoides* (Brünnich) (Gadiformes: Phycidae) in the western mediterranean. *Syst. Parasitol.* 88, 233–244.

- M., 2019. Species of *Lepidapedon* Stafford, 1904 (Digenea: Lepidapedidae) from Deep-sea fishes in the western mediterranean: molecular and morphological evidence. *Syst. Parasitol.* 96, 149–169.
- Pérez-Ponce de León, G., Anglade, T., Randhawa, H.S., 2018. A new species of *Steringotrema* Odhner, 1911 (Trematoda: Fellodistomidae) from the New Zealand sole *Peltorhamphus novaeseelandiae* Gunther off Kaka point in the Catlins, south Island, New Zealand. *Syst. Parasitol.* 95, 213–222.
- Pérez-Ponce de León, G., Hernández-Mena, D.I., 2019. Testing the higher-level phylogenetic classification of Digenea (Platyhelminthes, Trematoda) based on nuclear rDNA sequences before entering the age of the 'next-generation' Tree of Life. *J. Helminthol.* 93, 260–276.
- Poulin, R., Cribb, T.H., 2002. Trematode life cycles: short is sweet? *Trends Parasitol.* 18, 176–183.
- Powell, E.N., Barber, R.D., Kennicutt, M.C., Ford, S.E., 1999. Influence of parasitism in controlling the health, reproduction and PHA body burden of petroleum seep mussels. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 46, 2053–2078.
- Priede, I.G., 1994. Tracking of scavenging fishes in the abyss. *Endeavour (New Series)* 18, 74–79.
- Priede, I.G., 2017. *Deep-sea Fishes. Biology, Diversity, Ecology and Fisheries.* Cambridge University Press, Cambridge.
- Prudhoe, S., Bray, R.A., 1973. Digenetic trematodes from fishes. *B.A.N.Z. Antarctic Research Expedition Reports, Series B (Zoology and Botany)* 8, 199–225.
- Reimer, L.W., 1981. Lepocreadiidae (Digenea) aus Fischen der Kuste von Moçambique. *Angew. Parasitol.* 22, 204–212.
- Reimer, L.W., 1984. Investigations of shallow and deepwater prawns and fishes on parasites and a short note on biomass of plancton of the coast of the P. R. of Mozambique. *Fischerei - Forschung, Wissenschaftliche Schriftenreihe* 22, 27–35.
- Reimer, L.W., 1985. *Ocultacetabulum dorsolineatum* gen. et spec. nov. (Ocultacetabulinae subfam. nov.), ein fellodistomider Digener aus einem Tiefseefisch der Straße von Mozambique. *Angew. Parasitol.* 26, 107–109.
- Reimer, L.W., 1987. Opcoelidae (Trematoda) von Meeresfischen vor Moçambique. *Angew. Parasitol.* 28, 143–158.
- Rex, M.A., Etter, Ron J., 2010. *Deep-sea Biodiversity.* Harvard University Press, Cambridge.
- Salinas, X., González, M.T., Acuña, E., 2008. Metazoan parasites of the thumb grenadier *Nezumia pulchella*, from the south-eastern Pacific, off Chile, and their use for discrimination of host populations. *J. Fish Biol.* 73, 683–691.
- Scheifler, M., Ruiz-Rodríguez, M., Sanchez-Brosseau, S., Magnanou, E., Suzuki, M.T., West, N., Duperron, S., Desdevises, Y., 2019. Characterization of ecto- and endoparasite communities of wild Mediterranean teleosts by a metabarcoding approach. *PLoS One* 14, e0221475.
- Shedko, M.B., Sokolov, S.G., Atopkin, D.M., 2015. The first record of *Dimerosaccus oncorhynchi* (Trematoda: Opcoelidae) in fishes from rivers of Primorsky Territory, Russia, with a discussion on its taxonomic position using morphological and molecular data. *Parazitologiya (St. Petersburg)* 49, 171–189.
- Shulman, S.S., Shulman-Albova, R.E., 1953. Parasites of Fish of the White Sea. *Karelo-Finskii Institut Biologii, Akademii nauk SSSR, Moscow, Leningrad.*
- Shvetsova, L., 2013. A new trematode species, *Gonocerca pectorali* sp. n. (Hemiurata: Derogenidae) from *Albatrossia pectoralis* (Gilbert, 1891) (Gadiformes: Macrouridae). *Parazitologiya* 47, 344–348.
- Sokolov, S.G., Atopkin, D.M., Gordeev II, Shedko, M.B., 2018a. Phylogenetic position of the genus *Gonocerca* Manter, 1925 (Trematoda, Hemiuroidea), based on partial sequences of 28S rRNA gene and a reconsideration of taxonomic status of Gonocercinae Skrjabin et Guschanskaja, 1955. *Parasitol. Int.* 67, 74–78.
- Sokolov, S.G., Atopkin, D.M., Urabe, M., Gordeev, I.I., 2019a. Phylogenetic analysis of the superfamily Hemiuroidea (Platyhelminthes, Neodermata: trematoda) based on partial 28S rDNA sequences. *Parasitology* 146, 596–603.
- Sokolov, S.G., Gordeev, I.I., 2015. *Paralepidapedon variable* sp. n. (Trematoda, Lepocreadioidea, Lepidapedidae) and other representatives of the genus *Paralepidapedon* from Antarctic fish. *Zool. Zh.* 94, 756–763 (In Russian) [English version: *Biol. Bull.* (2016) 43, 2612–2618].
- Sokolov, S.G., Gordeev, I.I., Atopkin, D.M., 2016a. Redescription of trematode *Gonocerca muraenolepsii* Paruchin et Ljadov, 1979 (Hemiuroidea: Derogenidae), a body cavity parasite of Antarctic fishes, with a discussion of its phylogenetic position. *Invert. Zool.* 13, 191–202.
- Sokolov, S., Gordeev, I., Lebedeva, D., 2016b. Redescription of *Proctophantastes gillissi* (Overstreet et Pritchard, 1977) (Trematoda: Zoogonidae) with discussion on the systematic position of the genus *Proctophantastes* Odhner, 1911. *Acta Parasitol.* 613, 529–536.
- Sokolov, S.G., Khasanov, F.K., Gordeev, I.I., 2018c. New data on the morphology and phylogenetic connections of *Postlepidapedon opisthobifurcatum* (Trematoda, Lepocreadioidea: Lepidapedidae), a parasite of Antarctic and sub-Antarctic fishes. *Helminthologia* 55, 95–101.
- Sokolov, S.G., Lebedeva, D.I., Gordeev, I.I., Khasanov, F.K., 2019b. *Zdzitowieckitrema incognitum* gen. et sp. nov. (Trematoda, Xiphidiata) from the Antarctic fish *Muraenolepis marmorata* Günther, 1880 (Gadiformes: Muraenolepidae): ordinary morphology but unclear family affiliation. *Mar. Biodivers.* 49, 451–462.
- Sokolov, S.G., Lebedeva, D.I., Shchenkov, S.V., Gordeev, I.I., 2019c. *Caudotestis dobrowski* n. sp. (Trematoda, Xiphidiata) in North Pacific scorpaeniform fish: a crisis of concept of the opcoelid subfamily Stenakrinae Yamaguti, 1970. *J. Zool. Syst. Evol. Res.* 1–12. <https://doi.org/10.1111/jzs.12359>.
- Sokolov, S.G., Shchenkov, S.V., Gordeev, I.I., 2018b. Records of opcoelid species *Pseudopcoelus cf. vulgaris* and *Anomalotrema koiae* Gibson & Bray, 1984 (Trematoda, Opcoelidae, Opcoelinae) from fish of the north Pacific, with notes on the phylogeny of the family Opcoelidae. *J. Helminthol.* 93, 475–485.
- Sun, D., Bray, R.A., Yong, R.Q., Cutmore, S.C., Cribb, T.H., 2014. *Pseudobacciger cheneyae* n. sp. (Digenea: Gymnophalloidea) from Weber's chromis (*Chromis weberi* Fowler & Bean) (Perciformes: Pomacentridae) at Lizard Island, great barrier reef, Australia. *Syst. Parasitol.* 88, 141–152.
- Thaler, A.D., Amon, D., 2019. 262 Voyages beneath the sea: a global assessment of macro- and megafaunal biodiversity and research effort at deep-sea hydrothermal vents. *PeerJ* 7, e7397.
- Tyler, P., Young, C.M., Dolan, E., Arellano, S.M., Brooke, S.D., Baker, M., 2007. Gametogenic periodicity in the chemosynthetic cold-seep mussel "*Bathymodiolus childressi*". *Mar. Biol.* (Berlin) 150, 829–840.
- Urabe, M., Ishibashi, R., Uehara, K., 2015. The life cycle and molecular phylogeny of a gorgoderid trematode recorded from the mussel *Nodularia douglasiae* in the Yodo River, Japan. *Parasitol. Int.* 64, 26–32.
- Wagener, G.R., 1852. *Enthelminthica* No. III. *Arch Anat., Physiol. wiss. Medicin* 555–569.
- Wee, N.Q.X., Cutmore, S.C., Yong, R.Q.Y., Cribb, T.H., 2017. Two new and one known species of *Tergestia* Stossich, 1899 (Trematoda: Fellodistomidae) with novel molecular characterisation for the genus. *Syst. Parasitol.* 94, 861–874.
- Weitzman, S.H., 1997. Systematics of deep-sea fishes. In: Randall, D.J., Farrell, A.P. (Eds.), *Deep-sea Fishes.* Academic Press, San Diego, pp. 43–77.
- WoRMS Editorial Board, 2019. *World register of marine species.* Available from: <http://www.marinespecies.org.at.VLIZ> Accessed 2019-09-12.
- Yamaguti, S., 1938. Studies on the Helminth Fauna of Japan. Part 21. Trematodes of Fishes, IV. Satyū Yamaguti, Kyoto.