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 that 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 benthoes 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
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 sediments. 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 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; Pardo-Gandiarillas 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

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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           | Pelagic                                     | 200-1,000 m |
| Bathypelagic          | Pelagic                                     | 1000-3,000 m |
| Abyssopelagic         | Pelagic                                     | 3000-6,000 m |
| Hadopelagic           | Pelagic                                     | > 6,000 m  |

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

| Family                  | Species                                          | Host                          | Locality                  | Depth   | reference                           |
|-------------------------|-------------------------------------------------|-------------------------------|---------------------------|---------|-------------------------------------|
| **Fellodistomidae**     | **Benthotrema synaphobranchi** Machida et al. (2007) | Syphophanchnus affinis Günther, | Suruga and Tosa Bays, Japan | Not given | Machida et al. (2007)               |
| Lomosoma japonicum Machida et al. (2007) | Atelopus japonicus Bleeker, Polymixia japonica (Günther) | Syphophanchnus affinis Günther, | Suruga Bay, Japan | Not given | Machida et al. (2007)               |
| Megateron synaphobranchi Kuramochi (2005) | Dynomma anguillare Barnard | Synaphobranchus Brevidorsalis Günther, | East China Sea | 205 m | Kuramochi (2005)                    |
| **Gonocercidae**        | **Gonoeca peccatorii** Shvetsova, 2013          | Atabrusia peccatoralis (Gilbert) | Gobun Spur, NE Atlantic | 1,654 m | Bray and Wiesenberg (2020)          |
| **Lecithasteridae**     | **Lecithophyllum euzeti** Gibson and Bray (2003) | Notacanthus chemnitzii Bloch, Polycanthorhous challengeri (Vaillant) | Kuril Island | Not given | Shvetsova (2013)                   |
| **Lepidapedidae**       | **Lepidapedon serreti** Bray et al. (2013)      | Albatrossia pectoralis (Gilbert) | Off NE Scotland | 1,060 m | Bray and Gibson (1989)              |
| Neolepidapedon smithi Bray and Gibson, 1989 | Mora mori (Bisso) | Muraenolepis marmoratus Günther | Amundsen Sea | 605–1,632 m | Sokolov & Gordeev (2015)           |
| Parapapalpedon variabilis Sokolov and Gordeev (2015) | Corphias pectoralis (Hector) | Polyacanthonotus challengeri (Vaillant) | Porcupine Abyssal Plain | 1,654 m | Bray and Gibson (2015)              |
| Profundivermis intercalatus Bray and Gibson, 1991 | Thermichthys hollisi (Cohen, Rosenblatt & Moser) | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| **Opecoelidae**         | **Bathycreadium braii** Perez-del-Olmo et al., 2014 | Thermichthys hollisi (Cohen, Rosenblatt & Moser) | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| Butyrocotyle enkaimushi (Blend, Kuramochi & Dronen, 2015a,b) | Ventichthys biospeidoi Nielsen, Møller & Segonzac | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| **Helmintidae**         | **Polycotyle bathyhelmintos** Blend & Dronen, 2015a, | Lusibrotula corethromycter Cohen | Gulf of Mexico | 1,280 m | Blend and Dronen (2015a)           |
| Podoocotyle bathyhelmintos Blend & Dronen, 2015a,b | Lusibrotula corethromycter | Gulf of Mexico | 622–1,280 m | Blend and Dronen (2015a)           |
| Podoocotyle nimmori Blend et al. (2016) | Sphagmatoranae gregariae (Parn) | Gulf of Mexico | 534–995 m | Blend and Dronen (2016)           |
| **Pseudope celus mcanlepsi** Blend et al. (2017) | Nezamia acufula (Günther) | Thermichthys hollisi | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| **Tellonatera katadae** (Kuramochi, 2001) | Lycodes cortezianus Gilbert | Thermichthys hollisi | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| **Zoogonidae**          | **Brachyenteron dextroporus** Kuramochi (2005) | Thermichthys hollisi | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| Korea nootoizumi (Korotaea, 1994) Bray, 2008 | Notozamia macrochyla Matsuura | Thermichthys hollisi | South East Pacific Rise region | 2,598 m | Bray et al. (2014)                  |
| Neoestegonodermus pascualis Machida et al. (2006) | Zdasht above kolovnik Sokolov, Lebedev, Shchenkov and Gordeev, 2019 | Lypourc sp., Eumicrostomus fedori Mandytysa | Simushir Island, North Pacific | 150–400 m | Sokolov et al. (2019c)             |
| **Prochepheustas neotomasmati** Machida et al. (2006) | Eumicrotremus fedori Mandytysa | Muraenolepis marmorata Günther | Antarctic waters | 1193–1,453 m | Sokolov et al. (2019b)             |

* molecular data available.
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 nimble 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, Acanthoccoliidae, Aporocotylidae, Bivesiculidae, Bucephalidae, Bunocotylidae, Cryptogonimidae, Derogenidae, Faustulidae, Fel lodistomidae, 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, Gonocercididae, Gorgoderidae, Hemiuroidae, Lecithasteridae, Lepidapedidae, Opecoelidae and Zoonagonidae. The checklist of Klimpel et al. (2009) added mentions of the families Azygiidae (with reports down to < 1,200 m; recently Ototodistomum Stafford, 1904 has been reported in sharks to 2,200 m, see Espinola-Novelo et al., 2018), Didymozoidea (< 600 m), Ptychogonimidae, Sclerodistomidae and Syncoelidiidae (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 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.

Table 2

| Depth ranges and species reported at greater depths |
|--------------------------------------------------|
| Species                                          |
| > 4,000 m | Panopus cavernosa, P. nettastomatis, Prodistomum priedei |
| > 3,000 m | Biospeedotremabiospeedoi, P. nettastomatis, Prodistomum priedei |
| > 2,000 m | Bathypodocotyle margolisi, Brachyphyllobothrium cercomerulatum, Dinosoma oregonensis, Halosaurotrema halosauropsis, Haloscolex ventricosus, Lepidapedon trematomi, Podocotyle schistotesiculata, Sterigovermes notacanthi, Tellervostra beringi, Zetioscolex microps |
| > 1,000 m | Bathypodocotyle margolisi, Brachyphyllobothrium cercomerulatum, Dinosoma oregonensis, Halosaurotrema halosauropsis, Haloscolex ventricosus, Lepidapedon trematomi, Podocotyle schistotesiculata, Sterigovermes notacanthi, Tellervostra beringi, Zetioscolex microps |
| > 500 m  | Brassicardia caymanensis, B. nanaflexicollis, Bathypodocotyle margolisi, Brachyphyllobothrium cercomerulatum, Dinosoma oregonensis, Halosaurotrema halosauropsis, Haloscolex ventricosus, Lepidapedon trematomi, Podocotyle schistotesiculata, Sterigovermes notacanthi, Tellervostra beringi, Zetioscolex microps |

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-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 Actinopterygi as reported by Priede (2017, p. 68ff), but not that of several invertebrate putative intermediate hosts (Rex and Etter, 2010, p. 80ff).

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 | Panopus cavernosa, P. nettastomatis, Prodistomum priedei                 |
| > 2,000 m | Biospeedotremabiospeedoi, P. nettastomatis, Prodistomum priedei          |
| > 1,000 m | Bathypodocotyle margolisi, Brachyphyllobothrium cercomerulatum, Dinosoma oregonensis, Halosaurotrema halosauropsis, Haloscolex ventricosus, Lepidapedon trematomi, Podocotyle schistotesiculata, Sterigovermes notacanthi, Tellervostra beringi, Zetioscolex microps |
| > 500 m  | Brassicardia caymanensis, B. nanaflexicollis, Bathypodocotyle margolisi, Brachyphyllobothrium cercomerulatum, Dinosoma oregonensis, Halosaurotrema halosauropsis, Haloscolex ventricosus, Lepidapedon trematomi, Podocotyle schistotesiculata, Sterigovermes notacanthi, Tellervostra beringi, Zetioscolex microps |

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 Muraenoleipterum magnatensis 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 lepocreadiid Prodistomum priedei Bray & Merrett, 1998 from the epigonid Epigonus
telescopus (Risso) in the north-eastern Atlantic, embedded within shallow water, mainly reef, species. A closely related and very similar worm, _P. hynodi_ (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 percomorph families to extend into the deep-sea (Priede, 2017). It may be, therefore, that a small clade of lepocreadiids has invaded the deep-sea with their percomorph 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 Feliodistomidae, 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 iopnoids, which together form a clade sister to the remaining members of _Steringophorus_. Bray and Waecchenbach (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 reported species so far from the abyssal plain are either lepocreadioids, felloidistomids 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. osoro_ 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 Hemiuroidae. This study presents a superfamilly-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 _Merrillucteotrema praec slurum_ (Manter, 1934) is puzzling as it is resolved as sister to a group of shallow water lecithasterids. The sequenced specimen is derived from the deep-sea bythid _Cataxetnax laticeps_ Kofeoid 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 _Brachyphyllus 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 bathytypic 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 Hemiuroidae.

On the other hand, evidence is accumulating of radiation of opecoelids in deeper waters. Only one species of this large family has been definitely been 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 ‘Plagioporiinae’ in their preliminary study of the family. Later studies included many more freshwater species (Fayton et al., 2019; Martin et al., 2019) and found the freshwater species monophyletic and close to the deep-sea forms. Martin et al. (2019) found one well-resolved clade of (mainly) deep-sea opecoelids which they called the Podocotylinae, including _Bathypodocotyle margolisi_ (Gibson, 1995) reported down to 2,220 m (Gibson, 1995) and possibly 3,050 m (Kellermanns et al., 2009), _Buitucotylce thermichthysi_ reported at depth 2,598 m (Bray et al., 2014) and _Halosaurotrema halosaurops_ (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 opecoelids are scattered throughout the tree: i.e., _Bathycystidum brayi_ reaches 1,000 m (Constenla et al., 2015; Dallarés et al., 2016) and _Mesobathybourea lanceolata_ (Price, 1934) reaches 500 m (Reimer, 1987). _Abyssopectinula 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, opecoelids sequenced so far is minute and these results are preliminary.

When the genus _Biospeedotrema_ Bray, Waecchenbach, Dyal, Littlewood & Morand (2014) was erected the number of opecoelid 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 opecoelid 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 dobrowolski_ Sokolov, Lebedev, Schchenkov & Gordeev, 2019 forming a clade with, _Zusztowiecktrema incognitum_ Sokolov, Lebedev, Gordeev & Khasanov, 2019, may be a sister clade to the Opecoeloidae, 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, 1976; 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 Magoczi (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 digenaeans, 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 Le-thadena 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 Polypterus clarius 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 digenaeans 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 digenaeans, 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 digenaeans 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 Nautile 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 Opecoeliidae. These species are Biospeedotrematia biospeedei, B. parajolliveti and Buticylostomum thermichthysi from the bythitid Thermichthys hollii at depth 2,598 m and Biospeedotrematia jolliveti, Caudocestis ventichthysi and a possible juvenile B. thermichthysi in the ophidiid Ventichthys biospeedei 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 digenaeans 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 Biospeedotrematia 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 Theramarcus 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 Bathymodiolus Kenk & Wilson were heavily infested 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 Theramarcus is the lepidapedid Neolepiedapedon 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 Pro-sorhynchus squamatus Odhner, 1905 in Zoarces viviparus (Linnaeus), Lycodes eudiopelirustocis Jensen and L. mcallisteri Moller 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 Felodistomatidae or Gorgoderidae (Cribb et al., 2003; Koie, 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 medi terraneus (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 Halosaurus opsis macrochir (Günther) from the Mid-Atlantic Ridge, finding 5 species, one of which, the gorgoderid Degenaria halosaurus, 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 digenaeans 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 Steringotrema 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), off from 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-seas 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, Paralepidaepedon Shimazu & Shimura, 1984 and Gonocerca. The digenean fauna of M. whitsoni clustered with that of two sub-Antarctic macrourids M. carinatus (Günther) and M. holotrichus (Günther), and this cluster was closest to the two north Atlantic species M. berglax and Coryphaenoides rajastris 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 synaphobranchid caught as by-catch of the Patagonian toothfish (Dissostichus eleginoides Smit) from Chilean waters at depths between 1000 and 2,000 m. They found the macrourids, especially Macrourus holotrachys, harboured many digeneans, mostly unidentified. Pardo-Gandarrillas 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 productively viable. They are primarily deeper range extensions for a subset of benthal 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 benthal 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. Glomerictus macrourii (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 ipnopid Bathytyphlops sewelli (Norman) by Gibson and Bray (1982). This appears to be the deepest report of an opecoelid.
3. Lecithophyllum exzeti 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 ophiidid Enchelybrotula paucicdens 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’ 3,173–3,208 m from the synaphobranchid Synaphobranchus bathybius (Günther) from the Gulf of Panama by Overstreet and Pritchard (1977). Specimens identified as this species are reported from the deep-sea Atlantic 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: Glomerictus macrourii (syn. G. ulmeri Campbell and Munroe, 1977), Gonocerca minuta Campbell and Munroe (1977), G. physicus, C. haedrichi Campbell and Munroe (1977), Trifoliovum [Pseudocelestis] antinomea (Campbell and Munroe, 1977), Dinonoma sulca Campbell and Munroe (1977), D. triangulatum Campbell and Munroe (1977), Lecithophyllum botryophoronz (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. physicus, reach into the abyssal region.

Kellermanns et al. (2009) reported the species Bathypodocotyle margolisi ( Gibson, 1995), Glomerictus macrourii, Gonocerca minuta, Sterigotrema sp. and Sterigophorus thulini Brig & 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 is 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 Cleres (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. profundicolus (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 physicus (Gonocercididae) was reported in C. armatus at the depth of 4,847–4,850 m on the Porcupine Abyssal Plain by Prieide (1994) and Bray et al. (1999).
6. Sterigophorus thulini Bray & Gibson, 1980 (Fellodistomiidae) was reported as deep as 4,865 m and 4,854 m in Coryphaenoides leptolepis and C. profundicolus (Nybelin), respectively, on the Porcupine Abyssal Plain by Bray (1995) and samples from C. leptolepis at
As stated above, Campbell et al. (1980) reported the halosaurid *Halosaurotrema 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 halosauropterus* 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 *Gonocera 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 synaphrobranchid *Histiorbranchus bathybius* (Günther) (n = 6), the alepocephalids *Conocara salmonae* (Gill & Townsend) (n = 2) and *Xenodermichthys copei* (Gill) (n = 2), the stomiid *Malacosteus niger* Ayres (n = 1), the macrourid *Echinomacraurus mollis* Roule (n = 1), the gonostomatid *Gonostoma elongatum* Günther (n = 1), the ophiid *Bassasetus compressus* (Günther) (n = 1), the lamellid *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., Acanthocarpidae, Bucephalidae and Cryptogonimidae, are rare in the deep-sea, where large piscivorous fish are more frequent in the deep-sea that 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; Kaie, 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. Dallarès 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 crinarians is another possibility. According to Dallarès 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 *Steganocephalus 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.

| Family               | First intermediate host                  | Other intermediate host(s)                                    |
|----------------------|-----------------------------------------|----------------------------------------------------------------|
| Fellodistomidae      | Bivalves                                | None, or ophidianis, or whelk or fish paratenic host          |
| Gorgoderidae         | Bivalves                                | None, or encysted in bivalves, unencysted in decapods         |
| Gonocercidae         | ? not known                             | Not known, probably similar to Hemiuriidae                   |
| Hemiuriidae          | 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              |

Summary of known life-cycles in shallow water (Cribb et al., 2003).
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 Nezumiapulchella (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 Derogenses varius (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. varius has also been reported to 1,513 m off northern Honshu, Japan (Kuramochi, 2009). Manter (1955) pointed out that D. varius, 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 Halosauotrema halosauropsi in Halosauropsis macrochir. Many Lepidopedon 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, ophiidiids, 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 opecoelid 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 Lepidapdon and its close relatives and Steringophorus have substantially radiated in deep waters. It is also probable that the opecoelid 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 affected 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 Podoctoloides (Digenea: Opecoelidae): from the grey conger eel, Conger esculentus, in the Caribbean sea. J. Parasitol. 99, 615–622.

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 Brugia. Ann. Mag. Nat. Hist. 11, 117–119.

Blend, C.K., Dronen, N.O., 2015b. A review of the genus Lepidapedon (Digenea: Opecoelidae) from the cusk-eel, Lycodontia proxima (Manter). Folia Parasitol. 63, 1–11.

Bray, R.A., Gibson, D.I., 1989. The Lepocreadiidae (Digenea) of fishes from the north-east Atlantic: a review of the genus Neolepidapedon Manter 1954, with a description of N. smithi n. sp. Syst. Parasitol. 13, 11–25.

Bray, R.A., Gibson, D.I., 1991. The Lepocreadiidae (Digenea) of fishes from the north-east Atlantic: Profundivermis intercalaris n. g., n. sp. from the marine fish Coryphaenoides rupestris (Nematocidae) 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 Brachycentron helicoleni sp. nov. (Opecoelidae: Distomidae). Acta Parasitol. 51, 169–175.

Bray, R.A., Littlewood, D.T.J., Heroniu, 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., Waenschenbach, A., 2006. Steringocephalus merretti n. sp. (Digenea: Felloidistomidae) from the deep-sea fish Cantherinops koeusoi (Ophiidiphoridae, Bythididae) from the Goban Spur, in the northeastern Atlantic Ocean. Syst. Parasitol. 65, 1–11.

Bray, R.A., Waenschenbach, A., Cribb, T.H., Weedall, G.D., Dyal, P., Littlewood, D.T.J., 2007. The phylogeny of the Lepidocreadiidae (Phylodistomidae: Digenea) inferred from nucleolar and mitochondrial genes: implications for their systematics and evolution. Acta Parasitol. 52, 310–329.

Bray, R.A., Waenschenbach, 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 3758, 73–87.

Campbell, R.A., 1983. Parasitism in the deep-sea. 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: Lepidapedidae) from deep-sea gastropod worms of the NW Atlantic Ocean, including four new species. Syst. Parasitol. 24, 99–110.

Campbell, R.A., Hardrich, R.L., Munroe, T.A., 1980. Parasitism and ecological relationships among sea-bed benthic fishes. Mar. Biol. (Berlin) 57, 301–313.

Campbell, R.A., Munroe, T.A., 1977. New nemuriid trematodes from deep-sea benthic invertebrates of the western North Atlantic Ocean. J. Parasitol. 63, 203–207.

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: Smieszko, S.P. (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., Carrasson, M., 2013. Morphometric and molecular characterisation of specimens of Abrusites apristurus (Risso) (Digenea: Opecoelidae) from the deep-sea fishes of the southeastern Pacific Ocean. Parasite 20, 110–123.

Cribb, T.H., Bray, R.A., 2010. Gut wall ultrastructure, 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., 2010. Evidence that blood flukes (Trematoda: Apoecilocidae) of chondrichthyan infect bivalves as intermediate hosts: indications of an ancient diversification of the Schistosomatidae. Int. J. Parasitol. 40, 885–891.

Cribb, T.H., Miller, S.T., Bray, R.A., 2011. The sexual adult of Circaria praecox Walker, 1971 (Digenea: Felloidistomidae), with the proposal of Oenoma c. 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 Goezia (Digenea: Opecoelidae: trematoda), including the proposal of a new subfamily (Goeziinae n. subfam.). Syst. Parasitol. 112, 3063–3074.

Dallarés, S., Constenla, M., Pedros, F., Cartes, J.E., Solé, M., Carrascó, M., 2014. Parasites of the deep-sea fish Murora 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., Kostadina, A., Carrascó, M., Gibson, D.I., Perez-del-Olmo, A., 2013. Morphometric and molecular characterization of specimens of Lepidapedon Stafford, 1904 (Digenea: Lepidapedidae) from the Deep-sea-gadoids (Risso) (Teleostei: Moridae) in the western Mediterranean Ocean. Syst. Parasitol. 85, 243–253.

Dallarés, S., Moñó-Alcover, C.M., Pedros, F., Cartes, J.E., Solé, M., Castaño, C., Carrascó, M., 2016. The parasite community of Physeter macrocephalus (Bermann, 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, P., 1953. Zoogeography of the Sea. Sidwrick & Jackson, London, Espinola-Novelo, J.F., Escrriano, 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. Parasitol. Res. 117, 1–10.

Fayton, T.J., McAllister, C.T., Robison, H.W., Connior, M.B., 2018. Two new species of Allopodocotyle (Digenea: Opecoelidae) from the deep waters off Oregon and California. Zootaxa 4383, 1–29.

Fayton, T.J, McAllister, C.T., Robison, H.W., Connior, M.B., 2018. Two new species of Allopodocotyle (Digenea: Opecoelidae) from the deep waters off Oregon and California. Zootaxa 4383, 1–29.
