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1 **Trematodes of the Great Barrier Reef, Australia: emerging patterns of diversity and**
2 **richness in coral reef fishes**

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22

23 **Abstract**

24 The Great Barrier Reef (GBR) holds the richest array of marine life found anywhere in
25 Australia, including a diverse and fascinating parasite fauna. Members of one group, the
26 trematodes, occur as sexually mature adult worms in almost all GBR bony fish species.
27 Although the first reports of these parasites were made 100 years ago, the fauna has been
28 studied systematically for only the last 25 years. When the fauna was last reviewed in 1994
29 there were 94 species known from the GBR and it was predicted that there might be 2,270 in
30 total. There are now 326 species reported for the region, suggesting that we are in a much
31 improved position to make an accurate prediction of true trematode richness. Here we review
32 the current state of knowledge of the fauna and the ways in which our understanding of this
33 fascinating group is changing. Our best estimate of the true richness is now a range, 1,100–
34 1,800 species. However there remains considerable scope for even these figures to be
35 incorrect given that fewer than one-third of the fish species of the region have been examined
36 for trematodes. Our goal is a comprehensive characterisation of this fauna, and we outline
37 what work needs to be done to achieve this and discuss whether this goal is practically
38 achievable or philosophically justifiable.

39

40 *Keywords:* Trematoda, richness, diversity, Great Barrier Reef, host-specificity, cryptic
41 species

42

43

44 **1. Introduction**

45 The Great Barrier Reef (GBR) is arguably Australia's greatest natural asset. It is the
46 largest coral reef system globally, stretching for some 1,800 km, and its remarkable
47 complexity harbours the greatest diversity of fishes seen in Australian waters. These fishes
48 are, of course, infected by a significant range of parasites. Rohde (1976) was the first to
49 postulate quantitatively on possible parasite richness of the GBR. He suggested that the (then)
50 1,000 known fish species of the region were likely to have in the order of 20,000 parasite
51 species. Since this first dramatic prediction, there has been a series of analyses of the possible
52 richness for different components of the parasite fauna in different parts of the tropical Indo-
53 West Pacific (TIWP) (Cribb et al., 1994b; Whittington, 1998; Justine, 2010; Palm and Bray,
54 2014). Recently Justine (2010) reviewed patterns of richness for a wide range of metazoan
55 parasite groups and suggested that the 1,700 New Caledonian reef fishes are likely to harbour
56 some 17,000 parasite species (excluding protists) of which just 2% are known to science.
57 When such a high proportion of a predicted fauna remains unknown it is difficult to predict
58 the final number accurately. Ironically, predictions of richness generally gain the greatest
59 attention when there is the greatest proportional difference between the known and unknown;
60 few headlines are made by a suggestion that a fauna of 250 species may rise to 252!
61 However, rather prosaically, it is only when a fauna is relatively well known that the
62 predictions or extrapolations of true richness become relatively reliable.

63 The trematodes of GBR fishes have now been studied for just over a century. The first
64 reports from the region were by S.J. Johnston (1913). In the following 75 years there was a
65 handful of studies by T.H. Johnston, W. Nicoll, W.O. Durio, H.W. Manter, J.C. Pearson and
66 a few others. By 1988 just 30 trematode species had been reported from GBR fishes. In that
67 year systematic study of the fauna began when R.J.G. Lester led the International Congress of
68 Parasitology (ICOPA) parasitological workshop to Heron Island on the southern GBR (Lester
69 and Sewell, 1990). Since 1988 the present authors and colleagues have been involved in a
70 sustained study of this fauna. We calculate that there are now 326 species known from the
71 bony fishes of the region. Cribb et al. (1994b) predicted that GBR fishes may have a fauna of
72 2,270 trematode species. In the 20 years that followed, much has changed in our
73 understanding of this fauna.

74 Here, in what is essentially the 100th anniversary of commencement of work on this
75 fauna and the 20th anniversary of the last overview of its overall composition, we review the

76 nature of progress towards the biodiversity goal of “understanding the system”. Analyses
77 such as this frequently focus on the generation of a headline figure of predicted true richness
78 for the fauna. Such predictions typically demonstrate that a vast amount of work remains to
79 be done (e.g. Appeltans et al., 2012; Nabout et al., 2013), although we note that Strona and
80 Fattorini (2014) argue that such estimates are frequently overblown. Here, we will attempt to
81 produce such a figure, but we do so with some reticence. This reticence relates partly to the
82 inherent difficulties of such predictions and partly to the emptiness of such attempts (Poulin,
83 2014). Is it ultimately of importance as to whether there are 1,000 or 2,000 trematodes in
84 GBR fishes, or is what matters the identity of those trematodes, their life-cycles and how they
85 interact with their various hosts? We suspect the latter, but understand the general interest in
86 the former.

87

88 **2. GBR fish trematode fauna**

89 *2.1. The data set*

90 Analyses and remarks made here are based on the parasitological examination of
91 9,295 individual GBR bony (actinopterygian) fishes belonging to 505 species and 60
92 families. Although chondrichthyans (sharks, rays and chimaeras) do harbour digeneans,
93 infections are so infrequent that we find that we cannot justify sampling these animals.
94 Collection of trematodes from chondrichthyans is dependent on them being found by workers
95 seeking other groups of parasites (especially cestodes which have radiated widely with the
96 elasmobranchs). Our target fish were caught by line, seine net, barrier net, anaesthetic and
97 spear guns. Over time our approach to the examination of fish has evolved from one that
98 emphasised just the intestinal tract to one that searches for infections under the scales, in the
99 urinary bladder, the circulatory system and the tissues; we can only speculate on how many
100 infections were overlooked in our early years. These fishes were collected almost entirely at
101 Heron Island (5,931 individuals) on the southern GBR and Lizard Island (3,293 individuals)
102 on the northern GBR. Depth of examination of the 505 species has varied dramatically in line
103 with collecting priorities and the ease with which species can be collected. A total of 98 fish
104 species have been sampled at least 30 times but, at the other end of the spectrum, 140 species
105 have been examined only once or twice. Our data set of published reports covers all marine
106 fishes from eastern Queensland, Australia, north of the Tropic of Capricorn. Some of the host
107 fishes reported are not strictly coral reef species but rather than engaging in a complex and

108 subjective classification of reef and non-reef species, we have analysed all the records of
109 which we are aware from this region.

110 Table 1 summarises the present state of knowledge of trematodes of the bony fishes of
111 the GBR by family, the numbers of additional species estimated to have been collected by us
112 but not yet reported, and the known level of global richness for the families (including those
113 not yet known from the GBR). Fig. 1A shows the accumulation of trematode species for the
114 fauna over time, Fig. 1B the accumulation of genera, and Fig. 1C the accumulation of new
115 host/parasite species combinations. In total 326 fully identified species from 32 families have
116 been reported and are currently considered valid. The fauna comprises just one species from
117 the subclass Aspidogastrea, *Lobatostoma manteri*, as reported in detail by Rohde (1973); the
118 remaining 325 species belong to the subclass Digenea. The 326 species have been reported in
119 814 unique host/parasite combinations.

120

121 2.2. Characteristics of the fauna

122 Several features emerge from the data set. First, the figures of 326 species and 814
123 unique host/parasite combinations are substantial ones, comprising approximately 7.5% of
124 the global fauna of trematodes of marine fishes. Tellingly, all three accumulation curves (see
125 Fig. 1) have been almost straight lines for the last 25 years. The fact that there is no hint of a
126 plateau effect (except perhaps for the accumulation of genera) suggests that the end of these
127 accumulations can in no way be considered to be close. A striking feature of the fauna is its
128 taxonomic/phylogenetic diversity as opposed to simple richness (i.e. the number of species).
129 The 326 species are distributed among 156 genera, a mean of only 2.1 species per genus. Of
130 course, the size of a genus is somewhat in the eye of the beholder and in the hands of others
131 the number of genera might be either reduced (lumpers) or increased (splitters), but we think
132 that any such effect could only be marginal. Presently, a remarkable 99 genera are
133 represented by just a single known species on the GBR and a further 33 by just two. Thus,
134 85% of trematode genera have just one or two species known on the GBR. Despite this,
135 several genera are rich in GBR fishes. The richest genera are *Transversotrema*
136 (*Transversotrematidae*), *Prosorhynchus* (*Bucephalidae*), *Stephanostomum* (*Acanthocolpidae*),
137 *Retrovarium* (*Cryptogonimidae*), and *Hurleytrematoides* (*Monorchiidae*) with 14, 12, 11, 11
138 and 11 species recorded from the region, respectively. However, these numbers are relatively
139 low in comparison with richness in genera of some other coral reef fish parasites. For

140 example, there are already 36 species known for the myxosporean genus *Ceratomyxa* on the
141 GBR (Gunter et al., 2009; Heiniger and Adlard, 2013). In New Caledonia, studies by J.-L.
142 Justine have shown that the monogenean genus *Pseudorhabdosynochus* is exceptionally rich
143 on serranids, including eight species on a single fish species (Justine, 2007). Certainly
144 parasite richness is distributed differently for every major group of parasites in coral reef
145 fishes.

146 From the data reviewed above, the GBR trematode fauna contains a contrast between
147 a relatively small number of genera that have undergone significant radiations and the vast
148 majority that have not. On the basis of our unpublished collections we predict that this overall
149 pattern will not change with further study. The handful of highly radiated genera have
150 achieved their richness in different ways. *Hurleytrematoides*, *Prosorhynchus* and
151 *Retrovarium* have radiated within narrow host ranges, being found only in chaetodontids and
152 tetraodontids (McNamara and Cribb, 2009; McNamara and Cribb, 2011), serranids (e.g. Bott
153 et al., 2013), and the closely related haemulids and lutjanids (Miller and Cribb, 2007),
154 respectively. In contrast, the genus *Stephanostomum* is known from six families (e.g. Bray
155 and Cribb, 2003, 2008) and *Transversotrema* from a remarkable 11 (Hunter et al., 2010;
156 Hunter and Cribb, 2012; Hunter et al., 2012). These distributions are at least partly explicable
157 a posteriori in terms of host diet and physiological compatibility, and suggest that speciation
158 has tracked these resources.

159 In contrast to the few highly radiated genera, most GBR trematode genera have only
160 one or two species. Where such genera are composed of multiple species they are often in
161 hosts that are not closely related, and are often seemingly absent from hosts that would
162 appear to be suitable. For example, the two reported species of the bivesiculid genus
163 *Bivesicula* infect serranids and a pomacentrid (Cribb et al., 1994a). The four species of the
164 lepocreadiid genus *Lepotrema* have been found in five species of pomacentrids, two
165 monacanthids, two balistids and a single blenniid (Bray et al., 1993; Bray and Cribb, 1996,
166 1998, 2002). In addition, seemingly suitable fishes often lack infections. For example, of 35
167 pomacentrid species we have examined on the GBR, only one is infected by a bivesiculid
168 (Cribb et al., 1994a) and only one is infected by a gymnophalloid (Sun et al., 2014). These
169 apparently haphazard distributional patterns leave us unable to either explain the distributions
170 or to predict in what other fishes related species might be found in the future.

171

172 2.3. *Host specificity*

173 A key biological attribute of any parasite is its host specificity. Host specificity of
174 GBR fish trematodes was reviewed relatively recently by Miller et al. (2011) who showed
175 that trematode specificity in GBR fishes is overwhelmingly high – either oioxenous (a single
176 host species) or stenoxenous (taxonomically related host species); euryxenous distributions
177 (hosts related only by ecology) are exceptional. Indeed, Miller et al. (2011) found this pattern
178 of oioxenous or stenoxenous specificity to be so strong that they cautioned against the
179 acceptance of any pattern of euryxenous specificity without corroborating evidence from
180 molecular analysis. Two subsequent studies have shown that certain transversotrematid and
181 monorchiid trematodes do indeed have stenoxenous rather than euryxenous specificity as
182 originally reported (Hunter and Cribb, 2012; Searle et al., 2014).

183 Host specificity takes on great importance if the richness of a parasite fauna is being
184 assessed. Where host specificity is absolutely strict (e.g. most but not all monogeneans), it is
185 plausible to determine mean richness for known host species and extrapolate it to the
186 remainder of the fauna. Where a proportion of the species is shared, it becomes important to
187 understand the rate and nature of sharing. For the trematodes of GBR fishes, the 326 species
188 have been reported in 814 unique host/parasite combinations at a mean of 2.5 hosts per
189 species. The number of hosts ranges from 24 for the lecithasterid *Thulinia microrchis* to only
190 one known host for 175 species. Perhaps the most important aspect of host-specificity is its
191 nature when a large number of closely related host taxa are present. The cases of *Chaetodon*
192 and *Lutjanus* (for which 24 and 17 species have been investigated for trematodes on the
193 GBR, respectively) are instructive in this respect. For the intensively studied monorchiid
194 genus *Hurleytrematoides*, no species has been found in more than six species of *Chaetodon*
195 (McNamara and Cribb, 2011). For the complex of 21 species of cryptogonimids known from
196 species of *Lutjanus*, the cryptogonimid with the lowest known specificity is *Variavirus*
197 *charadrus*, which has been found in eight *Lutjanus* spp. (Miller et al., 2010b). Thus, even
198 where multiple closely related potential hosts are available, GBR fish trematodes tend to
199 infect only a proportion of the available hosts.

200

201 2.4. *Endemism*

202 Despite its great overall richness, the fish fauna of the GBR has remarkably low
203 endemism. In the context of his estimate that the fish fauna incorporated 1,500 species,

204 Allen (2008) noted that only 34 were endemic to the region (2.3%). On this basis it might be
205 predicted that the parasite fauna would have similarly low endemicity. Although several
206 species have been shown to have wide distributions in the TIWP on the basis of combined
207 morphological and molecular studies (e.g. Lo et al., 2001; Chambers and Cribb, 2006; Miller
208 and Cribb, 2007), according to our records, a remarkable 45% of GBR fish trematodes have
209 not been reported elsewhere. In addition, there are numerous reports of trematodes from fish
210 species that occur on the GBR but that we have not detected there. For example, the well-
211 studied lutjanid species *Lutjanus fulviflamma* is reported to have six species of
212 Cryptogonimidae on the GBR (Miller and Cribb, 2007, 2008; Miller et al., 2010a; Miller et
213 al., 2010b), but a further five have been reported from it elsewhere (Hafeezullah and Siddiqi,
214 1970; Gu and Shen, 1979; Srivastava, 1982; Saoud et al., 1988; Nahhas et al., 1998). In
215 combination, these data might suggest that trematode endemism for the GBR is much higher
216 than for their hosts. However, we suspect that the disparity in proportions of endemism
217 between host and parasite relates significantly to the overall inadequacy of reporting of
218 trematodes throughout the TIWP. We note in particular that reported endemism is
219 exceptionally high for aporocotylids (84%) and transversotrematids (80%). In contrast, GBR
220 Lepocreadiidae have much lower reported endemism (31%). The distinction between these
221 taxa is consistent with the status of the Aporocotylidae and Transversotrematidae as perhaps
222 the least well-studied taxa in the TIWP, and the Lepocreadiidae being one of the best-studied.
223 The system best studied to explore endemism is that of the 20 species of the monorchiid
224 genus *Hurleytrematoides* in chaetodontids in the TIWP. In intensive study at six major
225 localities across the TIWP (McNamara et al., 2012), eight species were found at only one
226 site, however the 10 found on the GBR were all shared with other locations in the TIWP.
227 Overall, it is not yet possible to characterise the level of endemism of trematodes of GBR
228 fishes relative to the remainder of the TIWP except to note that distributions appears to be
229 highly variable and that the field needs attention.

230

231 2.5. Family level patterns

232 A handful of trematode families account for well over half of all the richness known
233 from the GBR. Patterns of distribution and richness vary strikingly between these families
234 and here we review what we consider five of the best-known families.

235

236 2.5.1. *Lepocreadiidae*

237 The family Lepocreadiidae has the richest known fauna (42 species, 19 genera) of any
238 family of trematodes on the GBR. This relates to its diversity of host families (15 at present)
239 and the fact that the family has received continual attention as new taxa have been found
240 during the last 20 years. The 15 host families represent just two orders, the Perciformes, with
241 74% of host/parasite records, and the Tetraodontiformes with 26%. It is of interest to note
242 that the taxa in tetraodontiforms appear to form a clade whereas those of perciforms do not
243 (Bray and Cribb, 2012). Lepocreadiids are certainly abundant on the reef, with major reef fish
244 families well represented as hosts. Chaetodontids (16% of records), balistids and acanthurids
245 (each 16%), pomacentrids and serranids (each 8%), ehippids and lutjanids (each 6%) are the
246 major host families. In fact, the only host families which are not always so closely associated
247 with the reef are the Sillaginidae and Carangidae (each 3%) and the Echeneidae (1%). The
248 factor in common for these fishes is their diet of invertebrates. However, in turn this makes it
249 surprising that other such fishes (e.g. Lethrinidae and Nemipteridae) appear to lack species of
250 this family entirely.

251

252 2.5.2. *Cryptogonimidae*

253 The family Cryptogonimidae has the second greatest reported richness (38 species, 12
254 genera) for the GBR. A unique attribute of this family is that, for its richness, it has by far the
255 smallest host range, being known from only three fish families in the region. Of these, the
256 Serranidae has a single species, the Haemulidae six and the Lutjanidae a remarkable 31. No
257 other fish/trematode family in this system approaches such richness. This concentration is not
258 an artefact of reporting; we are aware of no cryptogonimid species in any other GBR fish
259 families sampled by us. Concentration of this kind renders targeted collecting far more
260 feasible than for most taxa. The depth of knowledge of this group relates almost entirely to
261 the PhD studies of T.L. Miller (e.g. Miller and Cribb, 2007, 2008; Miller et al., 2010a).
262 Despite the richness characterised to date, we have samples of at least another six species and
263 five genera yet to be reported. Our targeted sampling of lutjanids on the GBR has neglected
264 deep-water inhabiting species of the genera *Etelis* and *Pristipomoides* associated with coral
265 reefs throughout the TIWP. At least seven cryptogonimid species have been reported from
266 these species in other localities in the TIWP, suggesting that the deep-water lutjanids of the
267 GBR may harbour a similarly rich fauna. Overall there remain at least a further 23 lutjanid

268 species (including Caesioninae) known from the GBR (Randall et al., 1997) which are
269 entirely unsurveyed for cryptogonimids.

270

271 2.5.3. *Bucephalidae*

272 Twenty-two species of bucephalids (from five genera) have been reported from fishes
273 of the GBR, and we know of at least another 40 species that have been collected but not
274 formally reported. The family occurs only in piscivores which is explained by the apparent
275 complete restriction of its metacercariae to fishes. On present indications, the Bucephalidae
276 will ultimately prove to be the richest family in GBR fishes. Current knowledge of
277 bucephalids from GBR fishes is mainly a result of PhD research by N.J. Bott and colleagues
278 (Bott and Cribb, 2005b, c, a; Roberts-Thomson and Bott, 2007; Bott and Cribb, 2009; Bott et
279 al., 2013) who reported bucephalids from six teleost families. The greatest reported
280 bucephalid richness on the GBR is that in epinepheline serranids, a dominant and speciose
281 host group. This is especially true of the four species of *Plectropomus*, which are reported to
282 harbour 10 prosorhynchine bucephalid species from two genera (*Neidhartia* and
283 *Prosorhynchus*) (Bott et al., 2013). Several further piscivorous families are known, but yet to
284 be reported, as hosts. A continuing anomaly is that the Lutjanidae, comprising many large
285 and dominant piscivores on the GBR, does not harbour any bucephalid species despite
286 extensive investigation. The reasons for this remain unclear, especially when bucephalids
287 have clearly exploited recent dietary changes to piscivory in families not previously (or not
288 commonly) associated with bucephalids i.e. apogonids (Bott and Cribb, 2005a), labrid
289 cleaner fish (Jones et al., 2004) and blenniid mimic cleaner fishes (Roberts-Thomson and
290 Bott, 2007). Bucephalids from this region appear to be host-specific, at least to the level of
291 host family. We have examined more than 1,500 GBR fishes from families known to be
292 infected with bucephalids (globally), and no bucephalid species have been found in more than
293 one host family.

294

295 2.5.4. *Aporocotylidae*

296 The Aporocotylidae, the fish blood flukes, are perhaps the most cryptic of all the
297 trematode taxa found in marine teleosts. They currently comprise eight genera and 25 species
298 in GBR fishes. As adults they occur principally in the circulatory system of the host. Most

329 species are reported from the heart, but they are also seen in the gills, the body cavity, the
330 kidney and the cephalic blood vessels. The first reports of an aporocotyloid from a GBR fish
331 were only published in 1989 (Overstreet and K oie, 1989; Overstreet and Thulin, 1989). A
332 glimpse of the true richness of the group emerged as the result of systematic search in the
333 PhD studies of M.J. Nolan (Nolan and Cribb, 2004, 2006b, a), which reported 20 species
334 (from five genera), and alluded to the presence of a further seven species. This work
335 illustrated that several host groups, most notably the Siganidae, have supported remarkable
336 radiations of two lineages of species whereas many other families remain seemingly free of
337 infection, or almost so. However, infections are often difficult to find and are often only
338 detectable by the discovery of eggs trapped in tissues (Yong et al., 2013). Notably, the
339 uneven host distribution of aporocotylids remains unexplained because, as for all blood
340 flukes, transmission in this group is by direct penetration. It is opaque to us as to why some
341 taxa escape infection from these parasites.

342

343 2.5.5. *Transversotrematidae*

344 Transversotrematids are exceptional trematodes, occupying a unique habitat, the
345 space under the scales of bony fishes. Perhaps because of this, this family seems to have been
346 sought rarely from tropical marine fishes. When the first three transversotrematids were
347 reported from the GBR in 1992 (Cribb et al., 1992), only three transversotrematids were
348 known from marine fishes globally (Witenberg, 1944; Angel, 1969; Manter, 1970). Since
349 then, reported richness on GBR teleosts has grown to 15 as a result of the PhD study of J.A.
350 Hunter (Hunter et al., 2010; Hunter and Cribb, 2012; Hunter et al., 2012). The family is
351 especially rich on lutjanid, mullid and nemipterid fishes. Notably, all but one species belongs
352 to a single genus, *Transversotrema*, which is presently the richest single genus known in the
353 fauna. This richness is completely unparalleled in waters outside Australia but almost
354 certainly this relates to a failure to seek these distinctive parasites elsewhere.

355

356 2.5.6. *Understudied taxa*

357 On the basis of their proportion of the known global trematode fauna, several families
358 in our data set appear to be strikingly under-represented. Two effects are concealed here.
359 First, three families, the Derogenidae, the Fellodistomidae and the Lepidapedidae, appear to

330 be genuinely depauperate in this region – all three are encountered more frequently in colder
331 and deeper waters (e.g. Campbell and Bray, 1993; Bray and Campbell, 1995; Bray, 2004). In
332 contrast, several other families, the Didymozoidae, Haploporidae, Haplospalchnidae, and
333 Opacoelidae, are indeed rich in our collections and have simply not received sustained study.
334 The Didymozoidae is perhaps the most glaring case. On the basis of superficial analysis, we
335 have collected perhaps 20 species, in contrast to the six species formally reported from the
336 region. Notably, Yamaguti (1970) reported a remarkable 78 didymozoid species from Hawaii
337 alone. A high proportion of these are parasites of pelagic fishes (especially scombrids) which
338 occur in the waters of the GBR and are likely to be found there as well, should they be sought
339 systematically.

340

341 *2.6. Cryptic species and the molecular revolution – a slow burn*

342 At the time of the last review of the trematodes of GBR fishes (Cribb et al., 1994b),
343 molecular approaches to taxonomy had yet to be applied to any problems of trematode
344 identity in the region. Since then the use of molecular data has increased dramatically and is
345 changing our understanding of many aspects of parasite identity and relationships (Nadler
346 and Perez-Ponce De Leon, 2011). For trematodes of GBR fishes, molecular data have now
347 been applied to a wide range of taxa for the testing of identification hypotheses, inference of
348 phylogenetic relationships, and linking of life-cycle stages. Sequences have been derived
349 from ribosomal (ITS1, ITS2, 18S, 28S) and mitochondrial (*coxI*) DNAs.

350 Molecular data have become essential to the process of distinguishing species that
351 have limited or no morphological differences for many groups of parasites (e.g. Burger et al.,
352 2007; Jabbar et al., 2013). This cannot, strictly, be said to be the case to date for the
353 trematodes of GBR fishes. In taxonomy, molecular approaches can be said to be at their most
354 powerful when they identify combinations of cryptic species which are either entirely
355 unknown or only suspected. Molecular studies of GBR fish trematodes (based mainly on
356 ITS2 rDNA sequences but also on *coxI* sequences) have, by-and-large, confirmed
357 expectations based on morphological examination rather than revolutionising them (e.g.
358 Nolan and Cribb, 2004; Chambers and Cribb, 2006; Nolan and Cribb, 2006a; Hall and Cribb,
359 2008; Cutmore et al., 2010; Downie et al., 2011; Rohner and Cribb, 2013). In part this may
360 relate to the observation that so much of the diversity of the fauna is at the genus rather than
361 the species level. Are molecular data thus unimportant? The answer is resoundingly ‘no’ for

362 three reasons. First, and perhaps most importantly, morphological, biological (especially host
363 identity and geographical source) and molecular data now tend to be gathered and considered
364 almost simultaneously; this approach is at the heart of the so-called “integrative taxonomy”
365 approach (Dayrat, 2005). Such an approach means that the question of whether the species
366 being recognised are only recognised because of the availability of molecular data becomes
367 moot – all the data is used simultaneously (and iteratively) to generate the final taxonomic
368 hypothesis. Second, the molecular data used for identification can also be used for
369 phylogenetic analysis (e.g. Bray and Cribb, 2012; Cutmore et al., 2013) and the matching of
370 life-cycle stages (e.g. Cribb et al., 1998; Lucas et al., 2005; Miller et al., 2009). Third, in
371 several cases molecular data has indeed produced evidence of genuinely cryptic species in
372 GBR fishes (Nolan and Cribb, 2006b; Miller et al., 2010a; Hunter and Cribb, 2012; Cribb et
373 al., 2014; McNamara et al., 2014). The alarming aspect of these latter findings is that the
374 occurrence of cryptic species remains so unpredictable, even with the benefit of hindsight.
375 Poulin (2011) showed that the discovery of cryptic species was proportional to the number of
376 sequences generated, essentially the effort put into finding it, and doubtless there remain
377 more combinations of cryptic trematode species to be found on the GBR as sequences
378 accumulate.

379

380 2.7. Location, location

381 The GBR is a nearly continuous group of coral reefs extending from just south of the
382 Tropic of Capricorn and merging north to the reefs of the Coral Sea. The fish composition of
383 the GBR remains similar along its length; richness increases to the north (Russell, 1983), but
384 many species occur essentially everywhere. How are parasites distributed in this huge
385 potential habitat? Our evidence to answer this question is manifestly inadequate as we have
386 only sampled in any detail at two localities, Heron Island in the south and Lizard Island in the
387 north. Of the total of 326 species reported from the GBR, just 66 (20%) have been reported
388 from both sites, although many more remain to be formally reported from the second site or
389 have not been sought there in the appropriate hosts. There is, however, a significant subset of
390 species for which there is positive evidence (from substantial collecting) of restricted
391 distributions. For example, *Phyllodistomum hoggettae* and *Lepocreadium oyabitcha* are both
392 known only from Lizard Island (Bray and Cribb, 1998; Ho et al., 2014) despite the
393 examination of a large sample of their host species at Heron Island. Even more strikingly,

394 Hunter and Cribb (2012) and Diaz et al. (2013) showed that, in some fish species, species of
395 Faustulidae and Transversotrematidae in the south are replaced by congeners in the north. In
396 both of these cases the two species were readily distinguished by morphology. It remains to
397 be seen whether cryptic variation related to geographic locality on the GBR will prove
398 important.

399 Overall, our data set is too limited to allow comprehensive analysis of the nature of
400 geographical distribution of trematodes of fishes within the GBR. Importantly, we cannot
401 identify whether differences between the two main collecting sites relate to major paradigms
402 such as latitudinal gradients (Kamiya et al., 2014) or glaciation refugia (van Oppen et al.,
403 2011), or simply to sampling bias that would disappear with more extensive collecting along
404 the length of the GBR. We can certainly conclude, however, that sampling at a single site is
405 inadequate to develop a general understanding of the richness of the whole region.

406

407 **3. A richness prediction = Known + Collected + Unknown**

408 Predictions of richness often invoke three categories of knowledge of species. Those
409 that are known and characterised (here 326 species), those that are known (collected) but not
410 characterised, and those that have not yet been detected on any level but are suspected to be
411 present. How does our knowledge for GBR fish trematodes relate to the two categories of
412 uncharacterised species?

413

414 *3.1. Collected but uncharacterised richness*

415 The first category, collected but uncharacterised species, might be expected to be
416 simple to estimate because the specimens already exist in our collection. This is not the case.
417 Until specimens are stained and mounted, ideally sequenced, and compared carefully with
418 other relevant material, we cannot be certain about how many species are in the collection. In
419 essence, if we had managed to analyse the specimens to that extent we could have written the
420 formal accounts of the species. Thus, for only those few taxa that are under active
421 consideration can we make reliable predictions of the level of uncharacterised richness in our
422 collection. Thus for the Apocreadiidae, six species have been characterised but we are aware
423 of a further 12 and for the Bivesiculidae we are confident that the three known species will
424 rise to eight on the basis of existing collections. Not all taxa will increase so impressively; we

425 are aware of no further species of Enenteridae, Gorgocephalidae, Hirudinellidae,
426 Sclerodistomidae or several other families. The greatest difficulty arises in the larger, most
427 poorly studied taxa (e.g. Bucephalidae, Didymozoidae, Haploporidae, Monorchiidae and
428 Opencoelidae). For these taxa the projections of uncharacterised species held in our collection
429 can only be considered educated guesses based on preliminary sorting and sequencing. In
430 total, our estimates of held but uncharacterised species add an extra 240 GBR trematode
431 species (Table 1). This number suggests that we have characterised approximately 58% of the
432 species known to us.

433 Published reports of the 326 GBR trematode species have now been made from 265
434 fish species, a rate of 1.23 species per fish species. Our complete collection of 566 trematode
435 species (published + unpublished) have been from 504 species, a rate of 1.12 per fish species.
436 Given that 28% of the fish species that we have examined have been sampled no more than
437 twice, we conclude that there is significantly more richness to be identified in these species
438 than we have seen to date. Thus, for the fishes that we have examined to date a mean richness
439 of 1.2 trematode species per fish seems conservative. This rate of richness would suggest that
440 the fishes that have been examined (at least to some extent) harbour a minimum of 600
441 species.

442

443 3.2. *Unseen richness*

444 How many trematode species in GBR fishes have never been knowingly seen by us or
445 anyone else? Hoese et al. (2006) stated that the total fish richness of the GBR stands at 1,625
446 species. If we suppose that approximately 100 of these are elasmobranchs (and thus beyond
447 our remit), then perhaps there are approximately 1,000 GBR fish species awaiting assessment
448 for their trematode fauna. The fact that we can begin to use such round numbers hints at the
449 level of inexactitude in the calculations in the remainder of this analysis. What trematodes
450 can be expected in these 1,000 fish species?

451 A few of the unexamined 1,000 fish are species that we see but have never attempted
452 to collect. However, after 25 years of consistent collecting by a range of methods it becomes
453 increasingly unusual for us to collect previously unexplored fish species. Why is this when
454 there are evidently 1,000 species yet to be examined? The explanation lies in a combination
455 of effects. Several fishes have special conservation protection (e.g. Queensland groper,
456 Barramundi cod, Hump-Headed Maori wrasse and Steep-head parrot fish). Although we are

457 certainly interested to understand their parasites, we see no special need to seek to sample
458 these species. A second category is fish that are simply rare at the sites that we study (Heron
459 and Lizard Islands). For example, we have only ever seen a single individual of *Chaetodon*
460 *reticulatus* on the GBR and we did not examine it; we see no prospect that we will ever
461 understand its parasites on the GBR (whereas it is abundant and has been examined in depth
462 in French Polynesia). The third and most important category is fishes that are not rare but are
463 difficult to collect. This category has at least three sub-categories. A number of large taxa are
464 simply difficult and sometimes even dangerous to collect. Preeminent among these are the
465 moray eels (Muraenidae) of which there are at least 29 species known for the GBR (Randall
466 et al., 1997). From examination of just 13 individuals of six species of this family on the
467 GBR we know that they have a rich and distinctive trematode fauna, but their aggression and
468 cryptic habits render them especially poorly known and difficult to collect. In a separate sub-
469 category, there are large numbers of small species (especially gobiids) that are difficult to
470 collect because they live deep amongst coral, in crevices, sand and rubble. Such species are
471 typically collected by ichthyologists by the use of rotenone fish poison at ichthyocide
472 stations. This chemical kills and drives fishes from their habitat, allowing them to be
473 collected with relative ease. Species such as the serranid *Pseudogramma polyacanthum* are
474 often collected abundantly at rotenone stations but J.E. Randall, the doyen of Pacific
475 ichthyologists, comments that he has never observed it alive (Randall et al., 1997). We have
476 never seen this species on the GBR but we have examined specimens that were collected at
477 rotenone stations elsewhere in the tropical Pacific Ocean and have found them to be infected
478 with interesting trematodes. However, the use of rotenone is not permitted on the GBR; we
479 wonder how the parasites of such species will ever be characterised while a prohibition on the
480 use of this effective technique (Robertson and Smith-Vaniz, 2008) remains in place. Finally,
481 those fish species that are found below our effective SCUBA diving [define or insert
482 descriptive words] limit of approximately 20 metres remain inaccessible to us. An important
483 part of this deeper water fauna is the inter-reef fauna — fishes typically only collectable by
484 trawling. We note that of the 172 species of bony fishes listed in the report on seabed
485 biodiversity on the continental shelf of the GBR World Heritage Area (Pitcher et al., 2007),
486 only 10 have been examined by us on coral reefs.

487 Thus, the unexamined fishes are a complex mix of rare and hard to collect taxa. The
488 many small species can be expected to have low trematode richness, but there remain many

489 large species to be examined as well. We can predict that the inter-reef fishes will have a
490 fauna quite distinct from that of the more strongly reef-associated species.

491

492 *3.3. An estimate of GBR fish trematode richness*

493 Our final richness estimate comprises two key components – one in which we are
494 confident, and one of which we are quite uncertain. We think that richness in the fishes
495 already studied to some extent is certain to reach 600 species, and perhaps as high as 800
496 species if sources of richness such as cryptic species and geographical localisation are greater
497 than presently understood. Richness in the 1,000 unexamined fish species is far more difficult
498 to predict. We think it unlikely that mean richness in these fishes will equal that of those
499 already examined because, on average, they are smaller and rarer and these characteristics are
500 important drivers of parasite richness (Kamiya et al., 2014). We thus suggest that richness per
501 species for these fishes will be in the range of 0.5–1.0. In combination, these figures (600–
502 800 + 500–1,000) suggest that the fauna might comprise 1,100–1,800 trematode species.
503 Although there remains great scope for error in these predictions, it seems unlikely to us that
504 the fauna comprises fewer than 1,000 species or more than 2,000. Notably, this range is
505 below the 2,270 suggested by Cribb et al. (1994b).

506 Calculation of mean trematode richness for the GBR species has implications for the
507 total mean richness of 20 (all parasites) and 10 (Metazoa only) species per fish species
508 invoked by Rohde (1976) and Justine (2010), respectively, for coral reef fishes. In our
509 experience, trematodes are one of the “big four” in terms of parasite richness in GBR bony
510 fishes. The other highly abundant and rich taxa are the Copepoda, the Monogenea and the
511 Myxozoa. In our experience, other taxa present as adult parasites (acanthocephalans,
512 cestodes, isopods, leeches and nematodes) are relatively minor in their abundance and
513 richness. Given that we find that GBR fishes have a mean trematode richness of ~ 1.2
514 species, we find ourselves with reservations that the remaining parasite taxa contribute, on
515 average, a further eight to nine metazoan species (Justine, 2010) or 18–19 metazoans and
516 protists (Rohde, 1976) for every fish species.

517

518 **4. The task ahead**

519 On the basis of the estimates made above, perhaps 19–30% of the GBR reef fish
520 trematode fauna has now been characterised. This leaves a substantial task, one that might
521 take 60–120 years to complete at the present rate of progress depending on how many species
522 are really there to be found. Given the size of the task it is worth considering the value of the
523 exercise.

524

525 *4.1. Should we even try?*

526 As species represent the basic unit of evolutionary biology and indeed of natural
527 history, we think that it is critical to know what species of trematodes (and indeed all the
528 other groups of parasites) occur on the GBR as a basis for scientific enquiry. We support the
529 standard argument that naming the species is a first critical step in characterising any
530 biological system, although we do appreciate that it is possible to do significant work without
531 having names on all taxa. From our perspective, we therefore see no reason not to
532 characterise this fauna and every reason to do so. However, as we pull back the view of
533 Google Earth™ from Heron or Lizard Island on the GBR to first see the rest of the GBR, and
534 then progressively the reefs of the rest of the TIWP, we are very much aware of the size of
535 the task of characterising the parasite fauna of all the major sites in this region. In our view,
536 that is presently an unarguably impossible task. Whether it is justifiable or not becomes moot
537 when it is first impossible. We therefore make a case here for a continued concentration on
538 the characterisation of the parasite fauna of the GBR with the intention of achieving some
539 kind of completion.

540 Our case has two components. First, we think that the GBR offers the best prospects
541 for achieving something close to completion, and as such forming a basis for comparison
542 with other sites in the TIWP. Australia, by way of the GBR, is one of 13 TIWP nations with a
543 bony fish fauna of over 1,000 coral reef species (Allen, 2008). Of these 13, probably only
544 Japan also has the scientific infrastructure to be able to aspire to comprehensive study its
545 parasitic fauna. In terms of the extent to which other sites have been characterised, the only
546 other coral reef sites that can be considered at all well-known are Hawaii and southern Japan.
547 The extent to which the fauna of Hawaii is characterised is especially due to the work of H.
548 Manter, W.E. Martin, M. Pritchard (née Hanson) and particularly S. Yamaguti. However, the
549 work on this fauna was published almost entirely between 1955 (Hanson, 1955) and 1970
550 (Yamaguti, 1970). As a result none of the species have been characterised by molecular data,

551 which is now a prerequisite for comparison of species occurring over wide ranges. The fauna
552 of Japan, including that of fishes of the more southerly coral reefs, has also been worked on
553 appreciably, again by S. Yamaguti, but also by S. Kamegai, M. Machida, K. Ogawa, Y.
554 Ozaki, T. Shimazu and others. This fauna is not as clearly a fauna of coral reefs as that of the
555 GBR and also awaits the application of molecular approaches.

556 The second argument is that we should attempt to characterise the fauna before it
557 disappears. Although some authors are relatively positive about the prospects for the
558 description of the world fauna and flora (e.g. Costello et al., 2013), coral reefs do appear to be
559 especially threatened by environmental change. Coral reefs face threats globally from coral
560 bleaching, ocean acidification, eutrophication, over-fishing, crown-of-thorns starfish, storms
561 and a range of other threats (Lewis et al., 2009; Munday et al., 2010; e.g. Kayal et al., 2012).
562 We note that despite this, the GBR remains one of the healthiest and best protected of the
563 world's reefs and thus remains an excellent study site. It is possible that the fauna that we
564 find so fascinating, ultimately dependent on the existence of healthy coral reefs, is threatened
565 by large-scale extinction locally and globally.

566

567 **5. How to get there from here**

568 If we accept that characterising this fauna has value, then there are a number of issues
569 to be considered in attacking the task. Here we review issues affecting the implementation of
570 an effective approach.

571

572 *5.1. Every fish species?*

573 First we can consider whether we need to examine every fish species. As discussed
574 above, trematode specificity in GBR fishes is overwhelmingly high. This means that
575 comprehensive surveying for trematodes requires examination of, effectively, all the fish
576 species present. For example, possibly the most thoroughly collected taxon in our dataset is
577 the butterflyfishes (family Chaetodontidae). We have reported 23 trematodes from 35 species
578 of this family and are aware of at least 10 more in our collection. These trematode species are
579 almost all shared by at least two chaetodontid species and the maximum number found in any
580 one host species is nine (*Chaetodon ulietensis*). Such understanding can only be reached by
581 comprehensive sampling, and we thus see no case for selectively excluding fish species from

582 analysis. We do see, however, a case to be made that the parasite fauna of representatives of
583 the most characteristic and prominent fishes on the reef should be especially well
584 characterised as a priority.

585

586 5.2. Prevalence - how many fish?

587 No GBR fish that we have sampled at least 20 times has been infected with the same
588 trematode species in every individual. Thus, in the search for trematodes and a deeper
589 understanding of their distribution, it is necessary to dissect multiple host individuals, but
590 how many? The issue is of importance because there are matters of efficiency, expense and
591 ethics. Fig. 2 shows randomised species accumulation curves and species richness predictors
592 for real data for seven diverse GBR fish species (Chaetodontidae: *Chaetodon lunulatus*;
593 Labridae: *Thalassoma lunare*; Lutjanidae: *Lutjanus carponotatus*; Nemipteridae: *Scolopsis*
594 *bilineatus*; Pomacentridae: *Acanthochromis polyacanthus*; Siganidae: *Siganus lineatus*), each
595 sampled 30 times at Heron Island. A sample of 30 gives, statistically, a 95% probability of
596 finding any parasite present in the population at a prevalence of 10% or greater (Post and
597 Millest, 1991). Two observations emerge from these curves. First, the overall combined
598 observed accumulation curve has begun to plateau and to converge with the two richness
599 predictors, suggesting that for these fish we have collected most, but perhaps not quite all, of
600 the trematode species present. The small upward trend evident in two of the curves relates to
601 the fact that the data set contains a number of singleton and doubleton infections. The
602 richness predictors effectively treat these as evidence that there may be undiscovered richness
603 in the system. Second, the effect of the law of diminishing returns is severe. On average, after
604 just two fish have been examined, > 50% of the actual and predicted richness has been
605 discovered. This pattern generates a clear tension in approaches to collecting. Examination of
606 a small number of host individuals will find most of the trematode species; however, a much
607 larger number is required before all of them are found.

608 From the accumulation curves described above we can predict that, at least for these
609 fish, and probably for most, a sample size of 30 is effective in characterising the trematode
610 fauna of GBR fishes at individual localities (providing that there are no dramatic effects from
611 ontogeny, local distribution or season – all entirely possible and all little studied). Infections
612 that are not detected because they are rare remain a distinct problem. An example comes from
613 a faustulid parasite, *Parayamagutia ostracionis*, of the boxfish *Ostracion cubicus*. We have

614 examined a large sample of these fishes on the GBR (91), exploring a range of parasitological
615 questions. The first of these was examined in 1986 and produced a single individual of *P.*
616 *ostracionis*. In a total of 90 further *O. cubicus* examined by us, we have seen only one more
617 infection for an overall prevalence of 2.2%. We conclude that this species is a valid parasite
618 of *O. cubicus* which, for reasons undetectable to us, is strikingly rare. Scarcity of this kind is
619 itself not rare in biology (Jones et al., 2002; Magurran and Henderson, 2003), but for our
620 purposes it poses an essentially insoluble problem.

621 If indeed it is necessary to examine 30 individuals of each fish from at least two sites
622 to get a comprehensive understanding of the fauna, then a further 60,000 fishes (many hard to
623 get) remain to be examined. Sixty thousand fish, at an optimistic rate of an hour per fish to
624 collect and dissect, translates into a figure of 7,500 field days and much more time in the
625 laboratory.

626

627 5.3. What should be done – some priorities

628 If we need to examine another 60,000 fish to characterise the GBR fish trematode fauna
629 then there is certainly room to identify priorities. We think that the best progress might be
630 characterised by

- 631 i) Maintaining continued attention on the best studied families (e.g.
632 Aporocotylidae, Bucephalidae, Cryptogonimidae, Lepocreadiidae and
633 Transversotrematidae) to create a comprehensive basis for comparison with
634 other localities.
- 635 ii) Characterising comprehensively the parasite faunas of key fish species such as
636 the Coral trout (*Plectropomus leopardus*), the Red-throat emperor (*Lethrinus*
637 *chrysostomus*), the Moon wrasse (*Thalassoma lunare*) and other species that
638 have distinctive parasite faunas.
- 639 iii) Attempting to be consistent in accompanying new species descriptions and
640 reports with molecular data and “back-filling” for those already reported
641 without such data.
- 642 iv) Improving characterisation of the level of similarity between different areas of
643 the GBR.
- 644 v) Making a realistic attempt to explore the importance of small fishes in the
645 richness of GBR fish trematodes.

- 646 vi) Making a realistic attempt to sample the neglected inter-reef fauna.
647 vii) Improving the availability of summary information regarding the fauna so as to
648 make the work that has been done more accessible and valuable to others.

649 Seven priorities is perhaps already too many in the context of the workforce available
650 to tackle these tasks, but it is difficult to distinguish between them in terms of importance.
651 We note with interest, that priorities for the study of parasite faunas in different parts of the
652 world may vary. Perez-Ponce de Leon and Choudhury (2010) make a convincing case that
653 the end is in sight for the characterisation of the helminth fauna of Mexican freshwater fish.
654 In that context they argue that, for that fauna, current priorities should be the least studied fish
655 (whereas here almost no species can be considered fully characterised) and the search for
656 cryptic species (which is here considered important but not a dominant issue).

657

658 **6. Conclusions - beyond the numbers**

659 At the head of this review we stated that our goal was to work towards the
660 biodiversity goal of “understanding the system”. Although we have shown that there remains
661 a formidable task to characterise all the species in the system, we do not downplay the
662 progress that has been made. We now have a reasonable understanding of the kinds of
663 trematodes that are likely to be found in the most frequently encountered fishes of the GBR.
664 We also have a broad understanding of patterns of host specificity – largely we know what
665 sorts of trematode families will be found in what sorts of fish taxa, even if the details still
666 have the capacity to surprise us. Indeed, some interesting patterns have been noted in this
667 review, e.g. the apparent lack of aporocotyliids in many reef fish species, and the
668 unpredictable distribution of cryptic trematode species. The most glaring gap in our
669 understanding of this system is knowledge of life-cycles. These parasites all have at least two
670 hosts, most three and some four. Given the profusion of animals available for involvement in
671 these cycles, the task of elucidating them in any detail is considerably more complex than that
672 of characterising the adults. This perhaps explains why there are still only two completely
673 elucidated life-cycles for trematodes parasitic in GBR fishes (Pearson, 1968; Rohde, 1973)
674 although a range of life-cycle connections have been made (Cribb et al., 1996; Cribb et al.,
675 1998; Lucas et al., 2005), especially by the use of molecular approaches. This field perhaps
676 offers the single greatest challenge for the future.

677 The task of characterising the biodiversity of the parasites of coral reef fishes is a
678 daunting yet fascinating one. In 25 years of study, knowledge has evolved from a complete
679 absence of understanding of what to expect to a point where the data now create fascinating
680 biological patterns. After many years in this field we have come to recognise that the two
681 finest moments are when we can look at a trematode and say either “I have no idea what that
682 is!”, or, “I know exactly what that is!” The balance of experience is slowly shifting from the
683 former to the latter, but the former is still very much there to be had!

684 (Board, 2014)

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691

692 **References**

- 693 Allen, G.R., 2008. Conservation hotspots of biodiversity and endemism for Indo-Pacific coral
694 reef fishes. *Aquat. Conserv.-Mar. Freshw. Ecosyst.* 18, 541–556.
- 695 Angel, L.M., 1969. *Prototransversotrema steeri* gen. nov., sp. nov. (Digenea:
696 Transversotrematidae) from a South Australian fish. *Parasitology* 59, 719–724.
- 697 Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R.,
698 Barber, A., Bartsch, I., Berta, A., Błażewicz-Paszkowycz, M., Bock, P., Boxshall, G.,
699 Boyko, C.B., Brandão, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.Y.,
700 Cheng, L.N., Collins, A.G., Cribb, T.H., Curini-Galletti, M., Dandouh-Guebas, F.,
701 Davie, P.J.F., Dawson, M.N., De Clerck, O., Decock, W., De Grave, S., de Voogd,
702 N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald, K., Fautin,
703 D.G., Feist, S.W., Fransen, C., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson,
704 D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D.,
705 Hernandez, F., Hoeksema, B.W., Hopcroft, R.R., Jaume, D., Kirk, P., Koedam, N.,
706 Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B.,
707 Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C.,
708 Mapstone, G., McLaughlin, P.A., Mees, J., Meland, K., Messing, C.G., Mills, C.E.,
709 Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J.,
710 Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh,
711 P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-Salinas, J.I., Scarabino, V.,
712 Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P.,
713 Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr,
714 S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, M.A., Turon, X.,
715 Tyler, S., Uetz, P., van der Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest,

716 R.W.M., Vanaverbeke, J., Walker-Smith, G., Walter, T.C., Warren, A., Williams,
717 G.C., Wilson, S.P., Costello, M.J., 2012. The magnitude of global marine species
718 diversity. *Curr. Biol.* 22, 2189–2202.

719 Board, W.E., 2014. World Register of Marine Species. Available from
720 <http://www.marinespecies.org> at VLIZ. Accessed 06/2014, WoRMS Editorial Board.

721 Bott, N.J., Cribb, T.H., 2005a. First report of a bucephalid digenean from an apogonid
722 teleost: *Prosorhynchoides apogonis* n. sp. from *Cheilodipterus macrodon* on the
723 southern Great Barrier Reef, Australia. *Syst. Parasitol.* 60, 33–37.

724 Bott, N.J., Cribb, T.H., 2005b. *Grammatorcynicola* n. g. (Bucephalidae: Dolichoenterinae)
725 from *Grammatorcynus* spp. (Scombridae) from the Great Barrier Reef, Australia.
726 *Syst. Parasitol.* 61, 93–98.

727 Bott, N.J., Cribb, T.H., 2005c. *Prosorhynchoides lamprelli* n. sp. (Digenea: Bucephalidae)
728 from the brassy trevally, *Caranx papuensis* (Teleostei: Carangidae), from off Lizard
729 Island on the Great Barrier Reef, Australia. *Zootaxa* 1059, 33–38.

730 Bott, N.J., Cribb, T.H., 2009. Prosorhynchine trematodes (Digenea: Bucephalidae) from
731 epinephelins (Perciformes: Serranidae) on the Great Barrier Reef, Australia. *Syst.*
732 *Parasitol.* 72, 57–69.

733 Bott, N.J., Miller, T.L., Cribb, T.H., 2013. Bucephalidae (Platyhelminthes: Digenea) of
734 *Plectropomus* (Serranidae: Epinephelinae) in the tropical Pacific. *Parasitol. Res.* 112,
735 2561–2584.

736 Bray, R.A., 2004. The bathymetric distribution of the digenean parasites of deep-sea fishes.
737 *Folia Parasitol.* 51, 268–274.

738 Bray, R.A., Campbell, R.A., 1995. Fellodistomidae and Zoogonidae (Digenea) of deep-sea
739 fishes of the NW Atlantic Ocean. *Syst. Parasitol.* 31, 201–213.

740 Bray, R.A., Cribb, T.H., 1996. Two *Lepotrema* Ozaki, 1932 species (Digenea:
741 Lepocreadiidae) from marine fishes from the southern Great Barrier Reef,
742 Queensland, Australia. *Syst. Parasitol.* 35, 111–117.

743 Bray, R.A., Cribb, T.H., 1998. Lepocreadiidae (Digenea) of Australian coastal fishes: new
744 species of *Opechona* Looss, 1907, *Lepotrema* Ozaki, 1932 and *Bianium* Stunkard,
745 1930 and comments on other species reported for the first time or poorly known in
746 Australian waters. *Syst. Parasitol.* 41, 123–148.

747 Bray, R.A., Cribb, T.H., 2002. Lepocreadiinae lepecreadiids (Digenea) from tetraodontiform
748 fishes in the waters off Tasmania, Queensland and Moorea, French Polynesia. *Acta*
749 *Parasitol.* 47, 6–13.

750 Bray, R.A., Cribb, T.H., 2003. Species of *Stephanostomum* Looss, 1899 (Digenea:
751 Acanthocolpidae) from fishes of Australian and South Pacific waters, including five
752 new species. *Syst. Parasitol.* 55, 159–197.

753 Bray, R.A., Cribb, T.H., 2008. *Stephanostomum* spp. (Digenea: Acanthocolpidae) from
754 scombrids and carangids (Perciformes) from the Great Barrier Reef, with the
755 description of two new species. *Rev. Mex. Biodivers.* 79, 49S–68S.

756 Bray, R.A., Cribb, T.H., 2012. Reorganisation of the superfamily Lepocreadioidea Odhner,
757 1905 based on an inferred molecular phylogeny. *Syst. Parasitol.* 83, 169–177.

758 Bray, R.A., Cribb, T.H., Barker, S.C., 1993. The Lepocreadiidae (Digenea) of pomacentrid
759 fishes (Perciformes) from Heron Island, Queensland, Australia. *Syst. Parasitol.* 26,
760 189–200.

761 Burger, M.A.A., Cribb, T.H., Adlard, R.D., 2007. Patterns of relatedness in the Kudoidae
762 with descriptions of *Kudoa chaetodoni* n. sp. and *K. lethrini* n. sp. (Myxosporea:
763 Multivalvulida). *Parasitology* 134, 669–681.

- 764 Campbell, R.A., Bray, R.A., 1993. *Lepidapedon* spp. (Digenea: Lepocreadiidae) from deep-
765 sea gadiform fishes of the NW Atlantic Ocean, including four new species. Syst.
766 Parasitol. 24, 99–110.
- 767 Chambers, C.B., Cribb, T.H., 2006. Phylogeny, evolution and biogeography of the
768 Quadrifoliovariinae Yamaguti, 1965 (Digenea: Lecithasteridae). Syst. Parasitol. 63,
769 61–82.
- 770 Costello, M.J., May, R.M., Stork, N.E., 2013. Can we name earth's species before they go
771 extinct? Science 339, 413–416.
- 772 Cribb, T.H., Adlard, R.D., Bray, R.A., Sasal, P., Cutmore, S.C., 2014. Biogeography of
773 tropical Indo-West Pacific parasites: A cryptic species of *Transversotrema* and
774 evidence for rarity of Transversotrematidae (Trematoda) in French Polynesia.
775 Parasitol. Int. 63, 285–294.
- 776 Cribb, T.H., Anderson, G.R., Adlard, R.D., Bray, R.A., 1998. A DNA-based demonstration
777 of a three-host life-cycle for the Bivesiculidae (Platyhelminthes: Digenea). Int. J.
778 Parasitol. 28, 1791–1795.
- 779 Cribb, T.H., Bray, R.A., Barker, S.C., 1992. A review of the family Transversotrematidae
780 (Trematoda: Digenea) with the description of a new genus, *Crusziella*. Invertebr.
781 Taxon. 6, 909–935.
- 782 Cribb, T.H., Bray, R.A., Barker, S.C., 1994a. Bivesiculidae and Haploplanchnidae
783 (Digenea) from fishes of the southern Great Barrier Reef, Australia. Syst. Parasitol.
784 28, 81–97.
- 785 Cribb, T.H., Bray, R.A., Barker, S.C., Adlard, R.D., 1996. Taxonomy and biology of
786 *Mitotrema anthostomatum* Manter, 1963 (Digenea: Cryptogonimidae) from fishes of
787 the southern Great Barrier Reef, Australia. J. Helm. Soc. Wash. 63, 110–115.
- 788 Cribb, T.H., Bray, R.A., Barker, S.C., Adlard, R.D., Anderson, G.R., 1994b. Ecology and
789 diversity of digenean trematodes of reef and inshore fishes of Queensland. Int. J.
790 Parasitol. 24, 851–860.
- 791 Cutmore, S.C., Bennett, M.B., Cribb, T.H., 2010. *Staphylorchis cymatodes* (Gorgoderidae
792 Anaporrhutinae) from carcharhiniform, orectolobiform and myliobatiform
793 elasmobranchs of Australasia: Low host specificity, wide distribution and
794 morphological plasticity. Parasitol. Int. 59, 579–586.
- 795 Cutmore, S.C., Miller, T.L., Curran, S.S., Bennett, M.B., Cribb, T.H., 2013. Phylogenetic
796 relationships of the Gorgoderidae (Platyhelminthes: Trematoda), including the
797 proposal of a new subfamily (Degeneriinae n. subfam.). Parasitol. Res. 112, 3063–
798 3074.
- 799 Dayrat, B., 2005. Towards integrative taxonomy. Biol. J. Linn. Soc. 85, 407–415.
- 800 Diaz, P.E., Bray, R.A., Cribb, T.H., 2013. *Paradiscogaster flindersi* and *P. oxleyi* n. sp.
801 (Digenea: Faustulidae): overlapping host and geographical distributions in corallivore
802 chaetodontid fishes in the tropical Indo-West Pacific. Syst. Parasitol. 86, 87–99.
- 803 Downie, A.J., Bray, R.A., Jones, B.E., Cribb, T.H., 2011. Taxonomy, host-specificity and
804 biogeography of *Symmetrovvesicula* Yamaguti, 1938 (Digenea: Fellodistomidae) from
805 chaetodontids (Teleostei: Perciformes) in the tropical Indo-west Pacific region. Syst.
806 Parasitol. 78, 1–18.
- 807 Gu, C.D., Shen, J., 1979. Ten new species of digenetic trematodes of marine fishes. Acta
808 Zool. Sin. 4, 342–355.
- 809 Gunter, N.L., Whipps, C.M., Adlard, R.D., 2009. *Ceratomyxa* (Myxozoa: Bivalvulida):
810 Robust taxon or genus of convenience? Int. J. Parasitol. 39, 1395–1405.
- 811 Hafeezullah, M., Siddiqi, A.H., 1970. Digenetic trematodes of marine fishes of India. Part I.
812 Bucephalidae and Cryptogonimidae. Indian J. Helm. 22, 1–22.

- 813 Hall, K.A., Cribb, T.H., 2008. Revision of *Flagellotrema* Ozaki, 1936 (Digenea,
814 Gyliuchenidae Fukui, 1929), including the description of two species from
815 acanthuroid fishes from the Great Barrier Reef, Queensland, Australia. *Zootaxa* 1718,
816 1–35.
- 817 Hanson, M.L., 1955. Some digenetic trematodes of plectognath fishes of Hawaii. *Proc. Helm.*
818 *Soc. Wash.* 22, 75–87.
- 819 Heiniger, H., Adlard, R.D., 2013. Molecular identification of cryptic species of *Ceratomyxa*
820 Thelohan, 1892 (Myxosporea: Bivalvulida) including the description of eight novel
821 species from apogonid fishes (Perciformes: Apogonidae) from Australian waters.
822 *Acta Parasitol.* 58, 342–360.
- 823 Ho, H.W., Bray, R.A., Cutmore, S.C., Ward, S., Cribb, T.H., 2014. Two new species of
824 *Phyllodistomum* Braun, 1899 (Trematoda: Gorgoderidae Looss, 1899) from Great
825 Barrier Reef fishes. *Zootaxa* 3779, 551–562.
- 826 Hoese, D.F., Bray, D.J., Paxton, J.R., Allen, G.R., 2006. Fishes. Zoological Catalogue of
827 Australia Volume 35. ABRS & CSIRO Publishing, Australia.
- 828 Hunter, J.A., Cribb, T.H., 2012. A cryptic complex of species related to *Transversotrema*
829 *licinum* Manter, 1970 from fishes of the Indo-West Pacific, including descriptions of
830 ten new species of *Transversotrema* Witenberg, 1944 (Digenea:
831 *Transversotrematidae*). *Zootaxa* 3176, 1–44.
- 832 Hunter, J.A., Hall, K.A., Cribb, T.H., 2012. A complex of *Transversotrematidae*
833 (Platyhelminthes: Digenea) associated with mullid fishes of the Indo-West Pacific
834 Region, including the descriptions of four new species of *Transversotrema*. *Zootaxa*
835 3266, 1–22.
- 836 Hunter, J.A., Ingram, E., Adlard, R.D., Bray, R.A., Cribb, T.H., 2010. A cryptic complex of
837 *Transversotrema* species (Digenea: *Transversotrematidae*) on labroid, haemulid and
838 lethrinid fishes in the Indo-West Pacific Region, including the description of three
839 new species. *Zootaxa* 2652, 17–32.
- 840 Jabbar, A., Beveridge, I., Mohandas, N., Chilton, N.B., Littlewood, D.T.J., Jex, A.R., Gasser,
841 R.B., 2013. Analyses of mitochondrial amino acid sequence datasets support the
842 proposal that specimens of *Hypodontus macropi* from three species of macropodid
843 hosts represent distinct species. *BMC Evol. Biol.* 13, 259.
- 844 Johnston, S.J., 1913. On some Queensland trematodes, with anatomical observations and
845 descriptions of new species and genera. *Q. J. Microsc. Sci.* 59, 361–400.
- 846 Jones, C.M., Grutter, A.S., Cribb, T.H., 2004. Cleaner fish become hosts: a novel form of
847 parasite transmission. *Coral Reefs* 23, 521–529.
- 848 Jones, G.P., Caley, M.J., Munday, P.L., 2002. Rarity in coral reef fish communities, in: Sale,
849 P.F. (Ed.), *Coral reef fishes: dynamics and diversity in a complex ecosystem*, pp. 81–
850 101.
- 851 Justine, J.-L., 2007. Parasite biodiversity in a coral reef fish: twelve species of monogeneans
852 on the gills of the grouper *Epinephelus maculatus* (Perciformes: Serranidae) off New
853 Caledonia, with a description of eight new species of *Pseudorhabdosynochus*
854 (Monogenea: Diplectanidae). *Syst. Parasitol.* 66, 81–129.
- 855 Justine, J.-L., 2010. Parasites of coral reef fish: how much do we know? With a bibliography
856 of fish parasites in New Caledonia. *Belg. J. Zool.* 140, 155–190.
- 857 Kamiya, T., O'Dwyer, K., Nakagawa, S., Poulin, R., 2014. What determines species richness
858 of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biol.*
859 *Rev.* 89, 123–134.
- 860 Kayal, M., Vercelloni, J., de Loma, T.L., Bosserelle, P., Chancerelle, Y., Geoffroy, S.,
861 Stievenart, C., Michonneau, F., Penin, L., Planes, S., Adjeroud, M., 2012. Predator
862 crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and

863 cascading effects on reef fish and benthic communities. PLoS One 7, e47363.
864 doi:47310.41371/journal.pone.0047363.

865 Lester, R.J.G., Sewell, K.B., 1990. Checklist of parasites from Heron Island, Great Barrier
866 Reef. Aust. J. Zool. 37, 101–128.

867 Lewis, S.E., Brodie, J.E., Bainbridge, Z.T., Rohde, K.W., Davis, A.M., Masters, B.L.,
868 Maughan, M., Devlin, M.J., Mueller, J.F., Schaffelke, B., 2009. Herbicides: A new
869 threat to the Great Barrier Reef. Environ. Pollut. 157, 2470–2484.

870 Lo, C.F., Morgan, J.A.T., Galzin, R., Cribb, T.H., 2001. Identical digeneans in coral reef
871 fishes from French Polynesia and the Great Barrier Reef (Australia) demonstrated by
872 morphology and molecules. Int. J. Parasitol. 31, 1573–1578.

873 Lucas, T., O'Brien, E.K., Cribb, T.H., Degnan, B.M., 2005. Digenean trematodes infecting
874 the tropical abalone *Haliotis asinina* have species-specific cercarial emergence
875 patterns that follow daily or semilunar spawning cycles. Mar. Biol. 148, 285–292.

876 Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural
877 species abundance distributions. Nature 422, 714–716.

878 Manter, H.W., 1970. A new species of *Transversotrema* (Trematoda: Digenea) from marine
879 fishes of Australia. J. Parasitol. 56, 486–489.

880 McNamara, M.K.A., Adlard, R.D., Bray, R.A., Sasal, P., Cribb, T.H., 2012. Monorchiids
881 (Platyhelminthes: Digenea) of chaetodontid fishes (Perciformes): biogeographical
882 patterns in the tropical Indo-West Pacific. Parasitol. Int. 61, 288–306.

883 McNamara, M.K.A., Cribb, T.H., 2009. *Hurleytrematoides justinei* n. sp. (Digenea:
884 Monorchiidae) from Valentinni's sharpnose puffer, *Canthigaster valentini* (Bleeker)
885 (Tetraodontiformes: Tetraodontidae) from Heron Island, Queensland, Australia.
886 Zootaxa 2027, 63–68.

887 McNamara, M.K.A., Cribb, T.H., 2011. Taxonomy, host specificity and dietary implications
888 of *Hurleytrematoides* (Digenea: Monorchiidae) from chaetodontid fishes on the Great
889 Barrier Reef. Parasitol. Int. 60, 255–269.

890 McNamara, M.K.A., Miller, T.L., Cribb, T.H., 2014. Evidence for extensive cryptic
891 speciation in trematodes of butterflyfishes (Chaetodontidae) of the tropical Indo-West
892 Pacific. Int. J. Parasitol. 44, 37–48.

893 Miller, T.L., Adlard, R.D., Bray, R.A., Justine, J.-L., Cribb, T.H., 2010a. Cryptic species of
894 *Euryakaina* n. g. (Digenea: Cryptogonimidae) from sympatric lutjanids in the Indo-
895 West Pacific. Syst. Parasitol. 77, 185–204.

896 Miller, T.L., Bray, R.A., Cribb, T.H., 2011. Taxonomic approaches to and interpretation of
897 host-specificity of trematodes of fishes: lessons from the Great Barrier Reef.
898 Parasitology 138, 1710–1722.

899 Miller, T.L., Bray, R.A., Justine, J.-L., Cribb, T.H., 2010b. *Variialvus* gen. nov. (Digenea:
900 Cryptogonimidae), from species of Lutjanidae (Perciformes) off the Great Barrier
901 Reef, New Caledonia and Maldives. Acta Parasitol. 55, 327–339.

902 Miller, T.L., Cribb, T.H., 2007. Coevolution of *Retrovarium* n. gen. (Digenea:
903 Cryptogonimidae) in Lutjanidae and Haemulidae (Perciformes) in the Indo-West
904 Pacific. Int. J. Parasitol. 37, 1023–1045.

905 Miller, T.L., Cribb, T.H., 2008. Eight new species of *Siphoderina* Manter, 1934 (Digenea,
906 Cryptogonimidae) infecting Lutjanidae and Haemulidae (Perciformes) off Australia.
907 Acta Parasitol. 53, 344–364.

908 Miller, T.L., Downie, A.J., Cribb, T.H., 2009. Morphological disparity despite genetic
909 similarity; new species of *Lobosorchis* Miller & Cribb, 2005 (Digenea:
910 Cryptogonimidae) from the Great Barrier Reef and the Maldives. Zootaxa 1992, 37–
911 52.

- 912 Munday, P.L., Dixon, D.L., McCormick, M.I., Meekan, M., Ferrari, M.C.O., Chivers, D.P.,
913 2010. Replenishment of fish populations is threatened by ocean acidification. Proc.
914 Natl. Acad. Sci. U. S. A. 107, 12930–12934.
- 915 Nabout, J.C., Rocha, B.D., Carneiro, F.M., Sant'Anna, C.L., 2013. How many species of
916 Cyanobacteria are there? Using a discovery curve to predict the species number.
917 Biodivers. Conserv. 22, 2907–2918.
- 918 Nahhas, F.M., Sey, O., Nishimoto, R., 1998. Digenetic trematodes of marine fishes from the
919 Kuwaiti Coast of the Arabian Gulf: families Pleorchiidae, Fellodistomidae, and
920 Cryptogonimidae, with a description of two new species, *Neoparacryptogonimus*
921 *sphericus* and *Paracryptogonimus ramadani*. J. Helm. Soc. Wash. 65, 129–140.
- 922 Nolan, M.J., Cribb, T.H., 2004. Two new blood flukes (Digenea: Sanguinicolidae) from
923 Epinephelinae (Perciformes: Serranidae) of the Pacific Ocean. Parasitol. Int. 53, 327–
924 335.
- 925 Nolan, M.J., Cribb, T.H., 2006a. *Cardicola* Short, 1953 and *Braya* n. gen. (Digenea:
926 Sanguinicolidae) from five families of tropical Indo-Pacific fishes. Zootaxa 1265, 1–
927 80.
- 928 Nolan, M.J., Cribb, T.H., 2006b. An exceptionally rich complex of Sanguinicolidae von
929 Graff, 1907 (Platyhelminthes: Trematoda) from Siganidae, Labridae and Mullidae
930 (Teleostei: Perciformes) from the Indo-west Pacific Region. Zootaxa 1218, 1–80.
- 931 Overstreet, R.M., Kjøie, M., 1989. *Pearsonellum corventum*, gen. et sp. nov. (Digenea:
932 Sanguinicolidae), in serranid fishes from the Capricornia section of the Great Barrier
933 Reef. Aust. J. Zool. 37, 71–79.
- 934 Overstreet, R.M., Thulin, J., 1989. Response by *Plectropomus leopardus* and other serranid
935 fishes to *Pearsonellum corventum* (Digenea: Sanguinicolidae), including
936 melanomacrophage centres in the heart. Aust. J. Zool. 37, 129–142.
- 937 Palm, H.W., Bray, R.A., 2014. Marine Fish Parasitology in Hawaii. Westarp & Partner
938 Digitaldruck, Hohenwarsleben.
- 939 Pearson, J.C., 1968. Observations on the morphology and life-cycle of *Paucivitellosus*
940 *fragilis* Coil, Reid & Kuntz, 1965 (Trematoda: Bivesiculidae). Parasitology 58, 769–
941 788.
- 942 Perez-Ponce de Leon, G., Choudhury, A., 2010. Parasite inventories and DNA-based
943 taxonomy: lessons from helminths of freshwater fishes in a Megadiverse country. J.
944 Parasitol. 96, 236–244.
- 945 Pitcher, C.R., Doherty, P., Arnold, P., Hooper, J., Gribble, N., Bartlett, C., Browne, M.,
946 Campbell, N., Cannard, T., Cappo, M., Carini, G., Chalmers, S., Cheers, S.,
947 Chetwynd, D., Colefax, A., Coles, R., Cook, S., Davie, P., De'ath, G., Devereux, D.,
948 Done, B., Donovan, T., Ehrke, B., Ellis, N., Ericson, G., Fellegara, I., Forcey, K.,
949 Furey, M., Gledhill, D., Good, N., Gordon, S., Haywood, M., Jacobsen, I., Johnson,
950 J., Jones, M., Kinninmoth, S., Kistler, S., Last, P., Leite, A., Marks, S., McLeod, I.,
951 Oczkowicz, S., Rose, C., Seabright, D., Sheils, J., Sherlock, M., Skelton, P., Smith,
952 D., Smith, G., Speare, P., Stowar, M., Strickland, C., Sutcliffe, P., Van der Geest, C.,
953 Venables, W., Walsh, C., Wassenberg, T., Welna, A., Yearsley, G., 2007. Seabed
954 biodiversity on the continental shelf of the Great Barrier Reef World Heritage Area.
955 AIMS/CSIRO/QM/QDPI CRC Reef Research Task Final Report. 315 pp.
- 956 Post, R.J., Millest, A.L., 1991. Sample size in parasitological vector surveys. Parasitol. Today
957 7, 141.
- 958 Poulin, R., 2011. Uneven distribution of cryptic diversity among higher taxa of parasitic
959 worms. Biol. Lett. 7, 241–244.
- 960 Poulin, R., 2014. Parasite biodiversity revisited: frontiers and constraints. Int. J. Parasitol. 44,
961 581–589.

- 962 Randall, J.E., Allen, G.R., Steene, R.C., 1997. The Complete Divers' and Fishermen's Guide
963 to Fishes of the Great Barrier Reef. Crawford House Publishing, Bathurst.
- 964 Roberts-Thomson, A., Bott, N.J., 2007. Exploiting mimicry: *Prosorhynchoides thomasi* n. sp.
965 (Digenea: Bucephalidae) from the fang blenny genus *Plagiotremus* (Bleeker)
966 (Blenniidae) from off Lizard Island on the Great Barrier Reef, Australia. *Zootaxa*
967 1514, 61–64.
- 968 Robertson, D.R., Smith-Vaniz, W.F., 2008. Rotenone: An essential but demonized tool for
969 assessing marine fish diversity. *Bioscience* 58, 165–170.
- 970 Rohde, K., 1973. Structure and development of *Lobatostoma manteri* sp. nov. (Trematoda:
971 Aspidogastrea) from the Great Barrier Reef, Australia. *Parasitology* 66, 63–83.
- 972 Rohde, K., 1976. Species diversity of parasites on the Great Barrier Reef. *Z. Parasitenkd.* 50,
973 93–94.
- 974 Rohner, C.A., Cribb, T.H., 2013. Opecoelidae (Digenea) in northern Great Barrier Reef
975 goatfishes (Perciformes: Mullidae). *Syst. Parasitol.* 84, 237–253.
- 976 Russell, B.C., 1983. Annotated checklist of the coral reef fishes in the Capricorn-Bunker
977 group Great Barrier Reef Australia. Great Barrier Reef Marine Park Authority,
978 Mackay.
- 979 Saoud, M.F.A., Ramadan, M.M., Al Kawari, K.S.R., 1988. Helminth parasites of fishes from
980 the Arabian Gulf. 4. On *Allacanthochasmus lutjani* n. sp. and *Metadena leilae*
981 Nagaty, 1957 (Digenea: Cryptogonimidae). *Qatar Univ. Sci. Bull.* 8, 161–172.
- 982 Searle, E.L., Cutmore, S.C., Cribb, T.H., 2014. Monorchiid trematodes of the painted
983 sweetlips, *Diagramma labiosum* (Perciformes, Haemulidae), from the southern Great
984 Barrier Reef, including a new genus and three new species. *Syst. Parasitol.* 88, 195–
985 211.
- 986 Srivastava, C.B., 1982. The fauna of India and the adjacent countries. *Platyhelminthes.*
987 Director, Zoological Survey of India, Calcutta.
- 988 Strona, G., Fattorini, S., 2014. Parasitic worms: how many really? *Int. J. Parasitol.* 44, 269–
989 272.
- 990 Sun, D., Bray, R.A., Yong, R.Q.-Y., Cutmore, S.C., Cribb, T.H., 2014. *Pseudobacciger*
991 *cheneyae* n. sp. (Digenea: Gymnophalloidea) from Weber's chromis (*Chromis weberi*
992 Fowler & Bean) (Perciformes: Pomacentridae) at Lizard Island, Great Barrier Reef,
993 Australia. *Syst. Parasitol.* 88, 141–152.
- 994 van Oppen, M.J.H., Peplow, L.M., Kininmonth, S., Berkelmans, R., 2011. Historical and
995 contemporary factors shape the population genetic structure of the broadcast
996 spawning coral, *Acropora millepora*, on the Great Barrier Reef. *Mol. Ecol.* 20, 4899–
997 4914.
- 998 Whittington, I.D., 1998. Diversity "down under": monogeneans in the Antipodes (Australia)
999 with a prediction of monogenean biodiversity worldwide. *Int. J. Parasitol.* 28, 1481–
1000 1493.
- 1001 Witenberg, G., 1944. *Transversotrema haasi*, a new fish trematode. *J. Parasitol.* 30, 179–180.
- 1002 Yamaguti, S., 1970. Digenetic Trematodes of Hawaiian Fishes. Keigaku Publishing Co.,
1003 Tokyo.
- 1004 Yong, R.Q.-Y., Cutmore, S.C., Miller, T.L., Adlard, R.D., Cribb, T.H., 2013. The ghost of
1005 parasites past: eggs of the blood fluke *Cardicola chaetodontis* (Aporocotylidae)
1006 trapped in the heart and gills of butterflyfishes (Perciformes: Chaetodontidae) of the
1007 Great Barrier Reef. *Parasitology* 140, 1186–1194.

1008

1009 **Figure legends**

1010 Table 1. Numbers of trematode species reported and collected but not reported from Great
 1011 Barrier Reef (GBR), Australia, fishes. Estimates for known global richness of trematode
 1012 families predominantly or significantly in marine actinopterygian fishes based on counts in
 1013 the World Register of Marine Species (2014) and our records.

Family	Reported GBR genera	Reported GBR species	Collected GBR species	Reported global species	% World fauna
Acanthocolpidae	5	15	1	199	7.5
Accacoeliidae	0	0	1	27	0.0
Aephnidiogenidae	3	4	1	21	19.0
Apocreadiidae	4	6	12	87	6.9
Aporocotylidae	8	25	15	118	21.2
Aspidogastridae	1	1	0	10	10.0
Atractotrematidae	2	2	0	2	100.0
Azygiidae	0	0	0	42	0.0
Bathycotylidae	0	0	0	2	0.0
Bivesiculidae	3	4	5	27	14.8
Botulisaccidae	0	0	0	1	0.0
Bucephalidae	5	23	40	380	6.1
Cladorchiidae	0	0	1	4	0.0
Cryptogonimidae	12	38	6	220	17.3
Derogenidae	1	3	1	132	2.3
Deropristidae	0	0	1	6	0.0
Dictysarcidae	0	0	0	8	0.0
Didymozoidae	5	6	20	280	2.1
Enenteridae	2	4	0	32	12.5
Faustulidae	4	13	10	77	16.9
Fellodistomidae	3	3	3	142	2.1
Gorgocephalidae	1	2	0	3	66.7
Gorgoderidae	2	3	2	85	3.5
Gy liauchenidae	6	10	16	42	23.8
Gymnophalloidea (incertae sedis)	1	1	1	4	25.0
Haploporidae	2	3	15	113	1.8
Haplospalchnidae	2	2	11	47	4.3
Hemiuridae	10	15	5	500	3.0
Hirudinellidae	1	1	0	5	20.0
Lecithasteridae	12	18	5	149	12.1
Lepidapedidae	2	4	0	99	2.0
Lepocreadiidae	19	42	8	270	15.6
Mesometridae	0	0	1	9	0.0
Microscaphidiidae	1	1	6	41	2.4
Monorchiidae	9	23	13	255	9.0
Opecoelidae	19	27	30	680	4.0
Opistholebetidae	2	3	0	26	11.5
Sclerodistomidae	1	1	0	43	2.3
Sclerodistomoididae	0	0	0	1	0.0
Styphlotrematidae	0	0	0	1	0.0
Syncoeliidae	0	0	0	11	0.0
Tandanicolidae	0	0	0	12	0.0
Transversotrematidae	2	15	3	25	60.0
Zoogonidae	6	8	7	123	4.9

Family	Reported GBR genera	Reported GBR species	Collected GBR species	Reported global species	% World fauna
Total	156	326	240	4361	7.5

1014 % World fauna, GBR reported species as a percentage of known world fauna.

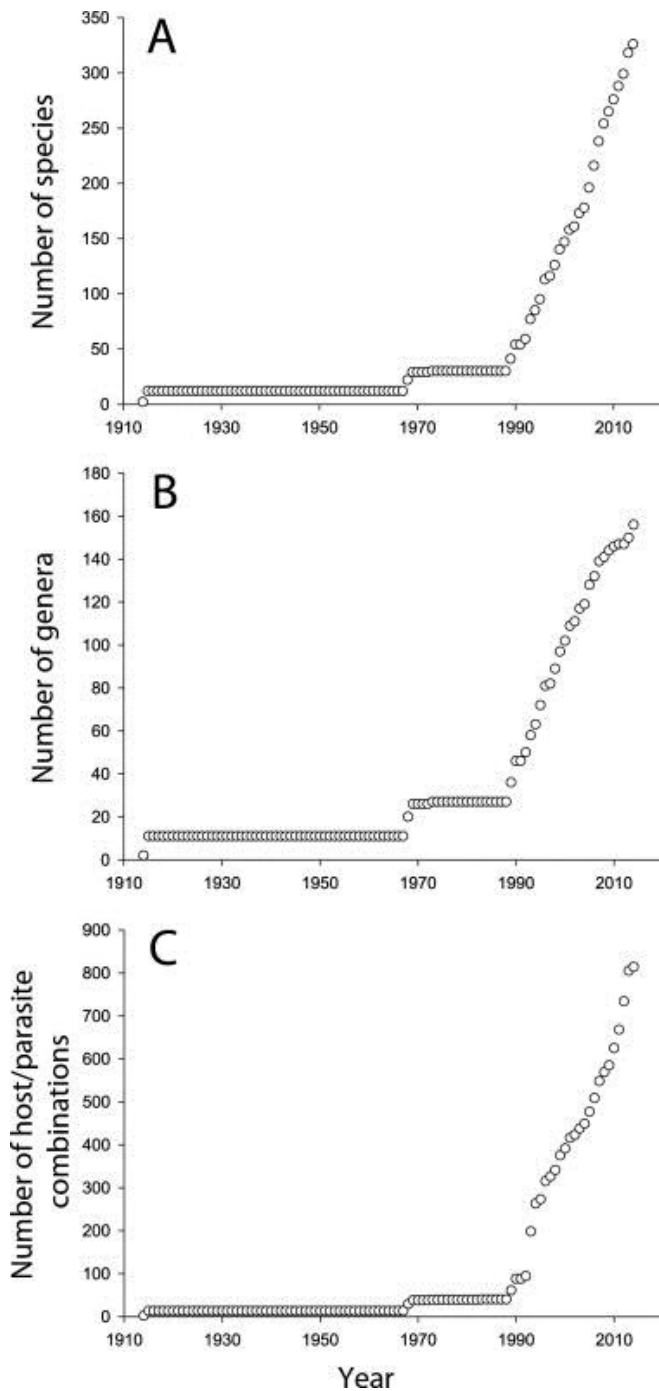
1015

1016 Fig. 1. The study of trematodes from fishes of the Great Barrier Reef, Australia, from 1910.

1017 The International Congress of Parasitology workshop on the parasites of the Great Barrier

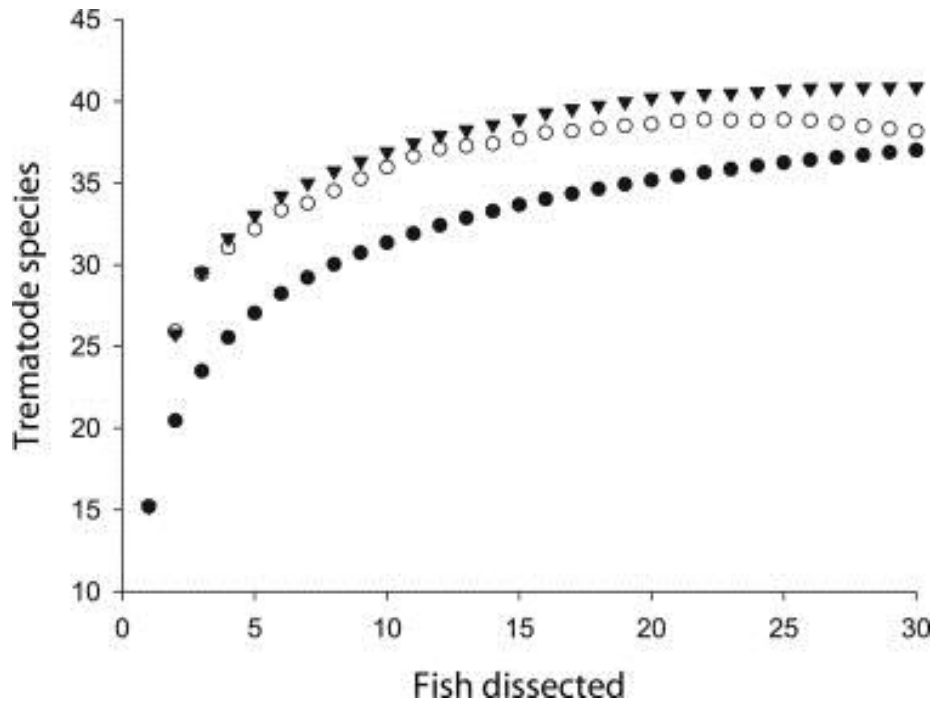
1018 Reef was held in 1988. (A) Accumulation of species; (B) accumulation of genera; (C)

1019 accumulation of unique host/parasite combinations.



1020

1021 Fig. 2. Combined randomised (1,000 randomisations) accumulation of species richness
1022 (actual and predicted) of digenean trematodes in 30 individuals each of seven species (see
1023 Section 5.2) of Great Barrier Reef fishes at Heron Island, Australia. ● Observed, ○



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