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Red algal parasites: a synopsis of described species, their hosts, distinguishing characters and areas for continued research

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Abstract: Red algal parasites are diverse organisms that are unusual due to the fact that many are closely related to their hosts. Parasitism has developed many times within different red algal groups, but the full extent of parasite biodiversity is unknown, as parasites are easily overlooked due to their small size and often low abundance. Additionally, the literature on red algal parasites is dispersed and has not been compiled in over 30 years. Although criteria have been proposed to define what constitutes a red algal parasite, many parasites are poorly described, and the cellular interactions with their host are poorly known. A few studies have demonstrated that parasites transfer organelles to host cells, which can alter the physiology of the host to the benefit of the parasite. Here, we apply a set of defining criteria for parasites to a compiled list of all described red algal parasites. Our results highlight the lack of knowledge of many key parasitic processes including early parasite development, host cell "control", and parasite origin. Until the biology of more parasites is studied, generalisations on the processes of parasitism in red algae may be premature. We hope this synopsis will stimulate research into this fascinating group.

Keywords: biodiversity; development; host switching; parasitism; taxonomy.

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Introduction

Parasitism is defined as a relationship that is beneficial for the parasite but harms the host and is a common lifestyle in organisms. Approximately 40% of all known species across all phyla are parasitic, and the actual number of parasites is thought to be higher than the number of free-living organisms (Dobson et al. 2008). The parasitic lifestyle occurs in a wide range of organisms such as fish (Le Roux and Avenant-Oldewage 2010), flatworms (Cribb et al. 2002), fungi (Quandt et al. 2015), plants (Westwood et al. 2010), "protozoa" (Keeling and Rayner 2015), and algae (Blouin and Lane 2012, 2016). The importance that parasites have for the ecology, behaviour, and evolution of free-living organisms (e.g. Poulin 1995, Hudson et al. 1998) and biodiversity (e.g. Karvonen and Seehausen 2012) are well documented.

Red algal parasites are common on other red algae (Goff 1982) and are known from eight orders as follows: Ceramiales, Corallinales, Gigartinales, Gracilariales, Halymeniales, Palmariales, Plocamiales, and Rhodymeniales (Salomaki and Lane 2014, Blouin and Lane 2016). The majority of red algal parasites are taxonomically closely related to their hosts (designated as "adelphoparasites"), while a lesser number are more distantly related to their hosts (designated "alloparasites"; Goff 1982). While this dichotomy has been used in the past, there appears to be a continuum from closely related to more distantly related parasite-host combinations (Zuccarello et al. 2004, Blouin and Lane 2012). However, only a few red algal parasites have been investigated phylogenetically.

Red algal parasites are unique in that they transfer organelles (e.g. nuclei, mitochondria, plastids) into host cells, via host-parasite cell fusion by secondary pit connection formation (Goff and Coleman 1985, Salomaki et al. 2015) and thereby "control" host cells for their benefit. A recent study showed that in one parasite these heterokaryotic cells not only contain the host plastid but also retain their own plastid ("ghost plastid") (Salomaki et al. 2015). The process of parasite-host cell fusion is unique to red algal parasite-host interactions and has led to speculation as to their origin and how complete the “control” is (Blouin and Lane 2012). The outcome of parasite organelles being transferred to host cells and the details of parasite development have been studied in very few parasites. However, the establishment of secondary pit connections appears to be essential for parasite development, and host resistance can occur as a response to incompatibility in parasite-host cell fusion (Zuccarello and West 1994a,b,c).

The descriptions of red algal parasites have been problematic for decades, in part because of the size of the parasite thallus and the infrequency with which they have been collected. Some described parasites have later been shown to be misidentifications of small red algal epiphytes, or bacterial infections, or even parts of the host thallus (Table 1). Given these problems, Setchell (1918) attempted to develop a set of characters to be used to characterise red algal parasites and to distinguish them from epiphytes and host outgrowths. This set of characters was: (1) penetration beyond the superficial layer of the host, (2) reduction in the size of the thallus, and (3) loss of colour. These characters were later reviewed and modified by Wynne and Scott (1989) to: (1) reduction in size, (2) reduction in pigmentation, (3) the formation of secondary pit connections between the parasite and the host cells, and 4) the presence of both gametophytes and sporophytes on the same host stage. Most of these criteria, if taken alone, would not be sufficient to confirm that a red algal species was a

Table 1: Alphabetical list of original name of species misidentified as red algal parasites, with changed name (if applicable), and current understanding of the described structure.

Original name of species	Changed name	Current understanding	References
Actinococcus aggregatus F. Schmitz	*Gymnogongrus griffithsiae* (Turner) Martius	Nemathecium	Gregory 1930
Actinococcus chiton Howe	*Fredericqia chiton* (Howe) Maggs, Le Gall, Mineur, Provan *et* Saunders	Nemathecium	McCandless and Vollmer 1984
Actinococcus latior F. Schmitz	*Gymnogongrus dilatatus* (Turner) J. Agardh	Tetrasporangial outgrowth	Silva et al. 1996
Actinococcus peltaeformis F. Schmitz	*Gymnogongrus crenulatus* (Turner) J. Agardh	Nemathecium	McCandless and Vollmer 1984
Actinococcus subcutaneus (Lyngbye) Rosenvinge	*Coccotylus trunacates* (Pallas) Wynne *et* Heine	Carpotetrasporangial outgrowth	Dixon and Irvine 1995
Callilithophytum parcum (Setchell *et* Foslie) Gabrielson, Adey, Johnson *et* Hernández-Kantún	–	Epiphyte	Adey et al. 2015
Catenellocolax leeuwenii Weber-van Bosse	–	Fungal infection	Zuccarello 2008
Choreocolax cystoclonii Kylin	–	Bacterial infection	Dixon and Irvine 1995
Choreocolax delesseriae Reinsch	*Neuroglossum delesseriae* (Reinsch) Wynne	Early stages in lateral branch formation	Wynne 2013
Colacolepsis decipiens F. Schmitz	*Phyllophora herediae* (Clemente) J. Agardh	Nemathecium	Goff 1982
Colacolepis incrustans F. Schmitz	*Phyllophora crispa* (Hudson) Dixon	Cystocarpic outgrowth	Dixon and Irvine 1995
Entocolax rhodymeniae Reinsch	–	Fungal infection	Edelstein 1972
Erythrocystis saccata (J. Agardh) P. C. Silva	–	Epiphyte	Melchionna and De Masi 1977
Fosliella paschalis (Me. Lemoine) Setchell *et* N. L. Gardner	–	Epiphyte	Setchell and Gardner 1930
Lobocolax deformans Howe	–	Bacterial infection	McBride et al. 1974, Ashen and Goff 1998
Loranthophycus californicus (Dawson) Dawson[a]	*Loranthophycus californicus* Dawson	Tetrasporophytic outgrowth	Dawson 1945, Goff 1982, Wynne 2013
Neopolyporolithon reclinatum (Foslie) Adey *et* Johansen	–	Epiphyte	Adey et al. 2015
Phaeocolax kajimurae Hollenberg	–	Epiphyte	Apt 1984a
Pleurostichidium falkenbergii Heydrich	–	Epiphyte	Phillips 2000
Rhodymeniocolax austrina	*Halopeltis austrina* (Womersley) Saunders	Epiphyte	Saunders and McDonald 2010
Sterrocolax decipiens F. Schmitz	*Ahnfeltia plicata* (Hudson) Fries	Gametangial outgrowth	Dixon and Irvine 1995

[a]Described as an outgrowth on *Holmesia californica* (Dawson) Dawson.

parasite. For example, some parasites are pigmented during certain stages of their life cycle (Nonomura and West 1979, Goff and Coleman 1995).

Much of the current knowledge of red algal parasite species' diversity is based on old lists and general statements. Setchell (1918) created the first list of described red algal parasites, and further lists followed (Evans et al. 1978, Goff 1982), while subsequent reviews have focused on general knowledge of red algal parasite biology (Blouin and Lane 2012, 2016, Salomaki and Lane 2014). The percentage of parasitic red algal genera has been estimated at 15% of all red algal genera by Goff (1982) or 8% of all florideophyte genera by Blouin and Lane (2012). The estimated number of red algal parasite species has more than doubled since Setchell's (1918) initial list of about 50 species to over a 100 species (Goff 1982, Salomaki and Lane 2014), 116 species (Blouin and Lane 2012), or 121 species (Blouin and Lane 2016).

The aim of this study was to create a comprehensive list of red algal parasite species, with associated primary literature, as such a list has not been produced for over 30 years. This paper (1) summarises the current understanding of the diversity of red algal parasites and (2) provides an analysis of whether existing descriptions meet the criteria for defining parasites. This synopsis highlights the lack of documentation available for many parasite species, as well as the scarcity of data about many key parasitic characters and processes (i.e. host cell "control", parasite origin), which may alter our notions of parasite biology, and suggest areas for future targeted research.

Materials and methods

This list of red algal parasite species was created by examining recent literature and classifications, reviewing red algal classification for parasitic genera and consulting AlgaeBase (Schneider and Wynne 2007, 2013, Wynne and Schneider 2010, 2016, Guiry and Guiry 2016). Over 200 papers in ten different languages were located, and the species were categorised, and tabulating criteria (i.e. level of pigmentation, reduced thallus, the presence of secondary pit connections, penetration of host tissue, and descriptions of all life cycle stages) were used in defining red algal parasites. The number of these criteria that were met was then used to rank (e.g. all criteria met, only one criterion met) whether there are sufficient data on the described organism to meet the definition of a red algal parasite.

Results

Our list contains 120 species and two invalidly described species (Supplemental Table S1, Figure 1). Supplemental Table S1 combines all available information on red algal parasite species and is organised in systematic order based on the presumed taxonomy of the parasite species. The entries include general information such as host species, year of description, type locality (based on primary literature), and distribution, and whether the criteria used to determine the parasitic status (Goff 1982, Wynne and Scott 1989) were described. The recognised parasites are listed alphabetically in Table 2.

Many red algal parasites were described by Setchell (1914, 1923) and Pocock (1953, 1956). Based on the dates listed in Table 2, approximately 15% of all red algal parasites were described in the 19th century, 80% in the 20th century, and 5% in the 21st century.

Red algal parasites are found in a number of families within the Florideophyceae. Parasitic genera are often small containing 1–4 species. The Pterocladiophilaceae is the only family containing solely parasitic genera (*Gelidiocolax*, *Holmsella* and *Pterocladiophila*).

Approximately 60% of red algal parasites are known from only one host species, 30% have been reported on two or three host species, and only 10% on more than three host species (Figure 1). Four genera, *Gracilaria* (Gracilariaceae), *Gelidium* (Gelidiaceae), *Laurencia*, and *Polysiphonia* (Rhodomelaceae), are the most common hosts of red algal parasites (Supplemental Table S1). Surprisingly,

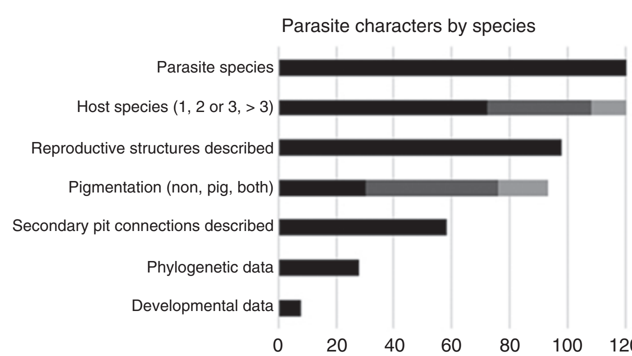

Figure 1: Current knowledge of all 120 red algal parasite species. Host species: number of parasite species which infect one (black bar), two or three (grey bar), or more than three (light grey bar) host species. Reproductive structures described: number of species for which male/female gametophyte and tetrasporophyte described. Pigmentation: none (black), pigmented (grey), both unpigmented and pigmented stages (light grey). Secondary pit connections: number of species for which connections between parasite and host described. Phylogenetic and developmental data: number of species with any phylogenetic or developmental data.

Table 2: Alphabetical list of red algal parasites, year of publication, and family to which they belong. For species authorities, refer to Supplemental Table S1.

Parasite	Year	Family	References
Aiolocolax pulchella	1956	Rhodomelaceae	Pocock 1956
Antarctocolax lambii	1953	Rhodomelaceae	Skottsberg 1953
Apoglossocolax pusilla	1993	Delesseriaceae	Maggs and Hommersand 1993
Asterocolax denticulatus	1934	Delesseriaceae	Tokida 1934, Wynne 2013
Asterocolax erythroglossi	1951	Delesseriaceae	Wynne 2013
Asterocolax gardneri	1923	Delesseriaceae	Setchell 1923, Wynne 2013
Asterocolax hypophyllophilus	1970	Delesseriaceae	Wynne 1970
Benzaitenia yenoshimensis	1913	Rhodomelaceae	Kylin 1956
Bostrychiocolax australis	1994	Rhodomelaceae	Zuccarello and West 1994a
Callocolax acicularis	1992	Kallymeniaceae	Wynne and Heine 1992
Callocolax fungiformis	1925	Kallymeniaceae	Abbott and Hollenberg 1992
Callocolax japonica	–	Kallymeniaceae	Goff 1982
Callocolax neglectus	1895	Kallymeniaceae	Batters 1895
Centrocerocolax ubatubensis	1965	Ceramiaceae	Joly 1966
Chamaethamnion pocockiae	1988	Rhodomelaceae	Norris 1988
Chamaethamnion schizandra	1897	Rhodomelaceae	Schmitz and Falkenberg 1897
Champiocolax lobatus	1996	Champiaceae	Womersley 1998
Champiocolax sarae	1985	Champiaceae	Bula-Meyer 1985
Choreocolax americanus	1875	Rhodomelaceae	Reinsch 1875
Choreocolax destructor	1875	Rhodomelaceae	Reinsch 1875
Choreocolax polysiphoniae	1875	Rhodomelaceae	Reinsch 1875
Choreocolax rabenhorstii	1875	Rhodomelaceae	Reinsch 1875
Choreocolax rhodymeniae	1888	Rhodomelaceae	Reinsch 1890
Choreocolax tumidus	1875	Rhodomelaceae	Reinsch 1875
Choreonema thuretii	1889	Hapalidiaceaeae	Womersley 1996
Coccotylus hartzii	1898	Phyllophoraceae	Rosenvinge 1931, Le Gall and Saunders 2010
Colacodasya australica	1998	Dasyaceae	Womersley 1998
Colacodasya californica	1970	Dasyaceae	Hollenberg 1970
Colacodasya inconspicua	1888	Dasyaceae	Reinsch 1890, Kylin 1956
Colacopsis lophurellae	1919	Rhodomelaceae	Kylin and Skottsberg 1919
Colacopsis pulvinata	1897	Rhodomelaceae	Kylin 1956
Colacopsis smitheniae	1988	Rhodomelaceae	Norris 1988
Colacopsis velutina	1953	Rhodomelaceae	Pocock 1953, Norris 1988
Dawsoniocolax bostrychiae	1967	Rhodomelaceae	Joly and Yamaguishi-Tomita 1969
Dipterocolax fernandezianus	1977	Rhodomelaceae	Morrill 1977
Episporium centroceratis	1885	Ceramiaceae	Womersley 1996
Epulo multipedes	2004	Hapalidiaceaeae	Townsend and Huisman 2004
Ezo epiyessoense	1974	Corallinaceae	Adey et al. 1974
Faucheocolax attenuata	1923	Faucheaceae	Setchell 1923
Gardneriella tuberifera	1941	Solieriaceae	Kylin 1956
Gelidiocolax christianae	1963	Pterocladiophilaceae	Feldmann and Feldmann 1963
Gelidiocolax deformans	1982	Pterocladiophilaceae	Seoane-Camba 1982
Gelidiocolax desikacharyi	1970	Pterocladiophilaceae	Ganesan 1970
Gelidiocolax lyndae	1988	Pterocladiophilaceae	Norris 1988
Gelidiocolax mammillatus	1959	Pterocladiophilaceae	Fan and Papenfuss 1959
Gelidiocolax margaritoides	1953	Pterocladiophilaceae	Martin and Pocock 1953, Fan and Papenfuss 1959
Gelidiocolax microsphaericus	1927	Pterocladiophilaceae	Kylin 1956
Gelidiocolax pustulatus	1984	Pterocladiophilaceae	Yoneshigue and de Oliveira 1984
Gelidiocolax suhriae	1953	Pterocladiophilaceae	Martin and Pocock 1953, Fan and Papenfuss 1959
Gelidiocolax verruculatus	–	Pterocladiophilaceae	Ouahi 1993
Gloiocolax novae-zelandiae	1957	Faucheaceae	Sparling 1957
Gonimocolax australis	1919	Delesseriaceae	Kylin and Skottsberg 1919, Kylin 1956
Gonimocolax corymbosus	1941	Delesseriaceae	Baardseth 1946
Gonimocolax roscoffensis	1961	Delesseriaceae	Feldmann and Feldmann 1961
Gonimophyllum africanum	1953	Delesseriaceae	Martin and Pocock 1953

Table 2 (continued)

Parasite	Year	Family	References
Gonimophyllum buffhamii	1892	Delesseriaceae	Batters 1892
Gonimophyllum insulare	1954	Delesseriaceae	Wagner 1954
Gonimophyllum skottsbergii	1923	Delesseriaceae	Setchell 1923
Gracilaria babae	1986	Gracilariaceae	Yamamoto 1986, Ng et al. 2014
Gracilariocolax deformans	1928	*Incertae sedis*	Weber-van Bosse 1928, Gerung and Yamamoto 2002
Gracilariocolax henriettae	1928	*Incertae sedis*	Weber-van Bosse 1928
Gracilariocolax infidelis	1928	*Incertae sedis*	Weber-van Bosse 1928, Gerung and Yamamoto 2002
Gracilariocolax setchellii	1928	*Incertae sedis*	Weber-van Bosse 1928, Gerung and Yamamoto 2002
Gracilariocolax setchellii var. aggregata	1928	*Incertae sedis*	Weber-van Bosse 1928, Gerung and Yamamoto 2002
Gracilariocolax sibogae	1928	*Incertae sedis*	Weber-van Bosse 1928, Gerung and Yamamoto 2002
Gracilariophila oryzoides	1910	Gracilariaceae	Wilson 1990
Gracilariophila gardneri	1923	Gracilariaceae	Setchell 1923
Grateloupiocolax colombiana	1983	Halymeniaceae	Schnetter et al. 1983
Harveyella mirabilis	1875	Rhodomelaceae	Reinsch 1875, Kylin 1956
Holmsella pachyderma	1875	Pterocladiophilaceae	Fredericq and Hommersand 1990
Holmsella australis	1983	Pterocladiophilaceae	Noble and Kraft 1983
Hypneocolax stellaris	1920	Cystocloniaceae	Børgesen 1920
Hypneocolax stellaris f. orientalis	1928	Cystocloniaceae	Womersley 1994
Janczewskia gardneri	1914	Rhodomelaceae	Setchell 1914
Janczewskia hawaiiana	1987	Rhodomelaceae	Apt 1987
Janczewskia lappacea	1914	Rhodomelaceae	Setchell 1914
Janczewskia meridionalis	1953	Rhodomelaceae	Martin and Pocock 1953
Janczewskia moriformis	1914	Rhodomelaceae	Setchell 1914
Janczewskia morimotoi	1947	Rhodomelaceae	Tokida 1947
Janczewskia ramiformis	1978	Rhodomelaceae	Chang and Xia 1978
Janczewskia solmsii	1914	Rhodomelaceae	Setchell 1914
Janczewskia tasmanica	1897	Rhodomelaceae	Womersley 2003
Janczewskia teysmannii	1923	Rhodomelaceae	Weber-van Bosse 1923
Janczewskia verruciformis	1877	Rhodomelaceae	Setchell 1914
Jantinella sinicola	1924	Rhodomelaceae	Setchell and Gardner 1924, Kylin 1941
Jantinella verruciformis	1911	Rhodomelaceae	McFadden 1911, Morrill 1976a
Kintokiocolax aggregato-ceranthus	1960	Halymeniaceae	Tanaka and Nozawa 1960
Kvaleya epilaeve	1971	Hapalidiaceaeae	Adey and Sperapani 1971
Laurenciocolax polysporus	1964	Rhodomelaceae	Zinova 1967
Leachiella pacifica	1982	Rhodomelaceae	Kugrens 1982
Levringiella gardneri	1923	Rhodomelaceae	Setchell 1923, Kylin 1956
Levringiella microscopica	1941	Rhodomelaceae	Levring 1941, Kylin 1956
Masakiella bossiellae	2007	Corallinaceae	Guiry and Selivanova 2007
Meridiocolax bracteata	1983	Rhodomelaceae	Noble and Kraft 1983
Meridiocolax narcissus	1976	Rhodomelaceae	Morrill 1976b
Meridiocolax polysiphoniae	1973	Rhodomelaceae	De Oliveira-Filho and Ugadim 1973, Noble and Kraft 1983
Microcolax africanus	1953	Rhodomelaceae	Martin and Pocock 1953
Microcolax botryocarpa	1845	Rhodomelaceae	Harvey and Hooker 1845, Schmitz and Falkenberg 1897
Neohalosacciocolax aleutica	1978	Palmariaceae	Lee and Kurogi 1978
Neotenophycus ichthyosteus	2002	Rhodomelaceae	Kraft and Abbott 2002
Onychocolax polysiphoniae	1956	Rhodomelaceae	Pocock 1956
Phitycolax inconspicua	1989	Delesseriaceae	Wynne and Scott 1989
Plocamiocolax pulvinata	1923	Plocamiaceae	Setchell 1923
Plocamiocolax papenfussianus	1953	Plocamiaceae	Martin and Pocock 1953
Polycoryne compacta	1963	Delesseriaceae	Zinova 1963
Polycoryne radiata	1919	Delesseriaceae	Kylin and Skottsberg 1919
Pterocladiophila hemisphaerica	1959	Pterocladiophilaceae	Fan and Papenfuss 1959
Rhodophyllis parasitica	2014	Cystocloniaceae	Preuss and Zuccarello 2014
Rhodophysema kjellmanii	1959	Palmariaceae	Edelstein 1972, Saunders and Clayden 2010
Rhodymeniocolax botryoideus	1923	Rhodymeniaceae	Setchell 1923
Rhodymeniocolax mediterraneus	2005	Rhodymeniaceae	Vergés et al. 2005

Table 2 (continued)

Parasite	Year	Family	References
Scagelonema parasiticum	1969	*Incertae sedis*	Norris and Wynne 1969, Wynne and Schneider 2010
Sorellocolax stellaris	1996	Delesseriaceae	Yoshida and Mikami 1996
Sporoglossum lophurellae	1919	Rhodomelaceae	Kylin and Skottsberg 1919
Spyridiocolax capixabus	1966	Ceramiaceae	Joly and de Oliveira 1966
Stromatocarpus parasiticus	1897	Rhodomelaceae	Schmitz and Falkenberg 1897
Symphyocolax koreana	2010	Rhodomelaceae	Kim and Cho 2010
Syringocolax macroblepharis	1875	Ceramiaceae	Reinsch 1875
Tikvahiella candida	1983	Solieriaceae	Kraft and Gabrielson 1983
Trichidium pedicellatum	1983	Rhodomelaceae	Noble and Kraft 1983
Tylocolax microcarpus	1897	Rhodomelaceae	Schmitz and Falkenberg 1897
Ululania stellata	1998	Rhodomelaceae	Apt and Schlech 1998

approximately 54% of the parasites found on two or more hosts have host species from different genera (Supplemental Table S1). For example, *Choreocolax polysiphoniae* has been reported from *Cystoclonium purpureum*, *Neosiphonia confusa*, and *Vertebrata lanosa*.

Classifying red algal parasites according to their pigments (Table 1) reveals that 38% are pigmented, 25% are unpigmented, and 14% are described as having both the unpigmented and pigmented stages, whereas no information is available on pigmentation for the remaining 23%. In most cases, it is not possible to determine from the literature if this pigment variation is due to the parasites being on different host species or is a consequence of a developmental stage (i.e. early development, reproductive stage).

Based on an estimate of 861 genera of the Florideophyceae (Schneider and Wynne 2007, 2013, Wynne and Schneider 2010, 2016), slightly over 7% of genera include parasitic species. Fewer than half of the species (approximately 45%) fulfil all the criteria used to define red algal parasites (Goff 1982, Wynne and Scott 1989). Approximately 45% of all descriptions of parasitic species do not mention the secondary pit connections between the parasite and the host, which is a crucial criterion for establishing parasitic status (Goff and Coleman 1985, Blouin and Lane 2012). Much of the missing data on the secondary pit connections can be explained by the fact that many of these parasitic species were described before 1982 when this unusual developmental process was first highlighted (Goff 1982). A smaller percentage of the species' descriptions (approximately 10%) did not supply information on pigmentation or secondary pit connections and lacked description of all reproductive structures (Supplemental Table S1).

The majority of type localities for red algal parasites are in the USA (26), South Africa (13), and Australia (11), and many type localities are on islands. The distribution data available are highly variable, ranging from records of single individuals and their host species to infrequent collections, and thus it is difficult to draw any conclusions about the distribution of most species.

There is limited knowledge of the phylogenetic relationships of red algal parasites. Phylogenetic sequences are available for only 27% of all red algal parasites (Table 3) and, in many cases, their hosts have not been sequenced. Data from all the three genomes (mitochondria, nuclear, and plastid) are only available for a small percentage of parasites (2.5%; Table 3).

Only eight red algal parasites have been investigated with reference to host cell transformation, and in only three species are the nuclei known to divide after transfer into the host cell (Table 4).

Overall there is a great lack of knowledge about red algal parasites. This includes frequently minimal detail in taxonomic descriptions, limited phylogenetic data, and few investigations of the development of parasites on their hosts. Most species have not been studied after their original description.

Discussion

Although it has been stated that red algal parasites have evolved independently over a hundred times (Blouin and Lane 2012), this is based on the current morphological taxonomy rather than on phylogenetic analyses. The origin (i.e. taxonomy) of parasites is complicated by their reduced thalli and consequent lack of diagnostic morphological characters, leading to diversity being underreported (Zuccarello and West 1994a). The ability of many parasites to switch hosts and infect multiple hosts, and the propensity of phycologists to name parasites based on hosts, further complicate the interpretation of their

Table 3: List of red algal parasites (and host species) on which phylogenetic analyses have been conducted.

Parasite	Host	References
Aiolocolax pulchella	*Polysiphonia caespitosa*	Diaz-Tapia and Bárbara 2013
Asterocolax erythroglossi	*Erythroglossum laciniatum*	Goff et al. 1997
Asterocolax gardneri	*Anisocladella pacifica*	Goff et al. 1997
	Phycodrys isabelliae	Goff et al. 1997
	Phycodrys setchelli	Goff et al. 1997
	Nienburgia andersoniana	Goff et al. 1997
	Polyneura latissima	Goff et al. 1997
Benzaitenia yenoshimensis	*Chondria crassicaulis*	Kurihara et al. 2010
Bostrychiocolax australis	*Bostrychia radicans*	Zuccarello et al. 2004, Zuccarello and West 2006
Choreocolax polysiphoniae	*Vertebrata lanosa*	Zuccarello et al. 2004, Salomaki et al. 2015
Choreonema thuretii	*Jania micrarthrodia*	Harvey et al. 2003
Coccotylus hartzii	–	Le Gall and Saunders 2010
Dawsoniocolax bostrychiae	*Bostrychia radicans*	Zuccarello et al. 2004
Faucheocolax attenuate	*Gloiocladia laciniata*	Goff et al. 1996
	Gloiocladia fryeana	Goff et al. 1996
Gardneriella tuberifera	*Sarcodiotheca gaudichaudii*	Goff et al. 1996
Gonimophyllum skottsbergii	*Cryptopleura crispa*	Zuccarello et al. 2004
Gracilaria babae[a]	*Gracilaria salicornia*	Ng et al. 2013, Ng et al. 2014, Ng et al. 2015
	Hydropuntia sp.	Ng et al. 2014
Gracilariophila oryzoides	*Gracilariopsis lemaneiformis*	Goff and Zuccarello 1994, Goff et al. 1996, Hancock et al. 2010
Harveyella mirabilis	*Gonimophyllum skottsbergii*	Zuccarello et al. 2004
	Odonthalia floccosa	Zuccarello et al. 2004
	Odonthalia washingtoniensis	Zuccarello et al. 2004
	Rhodomela confervoides	Zuccarello et al. 2004
Holmsella pachyderma	*Gracilaria gracilis*	Zuccarello et al. 2004
	Gracilariopsis longissima	Zuccarello et al. 2004
Holmsella australis	*Gracilaria cliftonii*	Zuccarello et al. 2004
Hypneocolax stellaris f. orientalis	–	Sherwood et al. 2010
Janczewskia hawaiiana	*Laurencia mcdermidiae*	Kurihara et al. 2010
Janczewskia morimotoi[a]	*Laurencia nipponica*	Kurihara et al. 2010
Kintokiocolax aggregato-ceranthus	*Grateloupia angusta*	Yang and Kim 2015
Leachiella pacifica	*Neosiphonia paniculata*	Zuccarello et al. 2004
Plocamiocolax pulvinata	*Plocamium cartilagineum*	Goff et al. 1996
Rhodophyllis parasitica[a]	*Rhodophyllis membranacea*	Preuss and Zuccarello 2014
Rhodophysema kjellmanii	–	Clayden and Saunders 2010
Rhodymeniocolax botryoideus	*Rhodymenia pacifica*	Goff et al. 1996
Tikvahiella candida	*Solieria robusta*	Saunders et al. 2004
Ululania stellata	*Acanthophora pacifica*	Kurihara et al. 2010
	Acanthophora spicifera	Kurihara et al. 2010

[a]Parasites in which sequences are available from mitochondrial, nuclear, and plastid genomes.

phylogenetic origin (Goff et al. 1996, 1997), and have led to multiple names for some taxa that are found on multiple hosts (Zuccarello and West 1994a). An example is *Asterocolax gardneri* (Setchell) Feldmann et Feldmann, where phylogenetic results indicate that the species has three independent origins from *Phycodrys setchellii*, *Phycodrys isabelliae* and *Polyneura latissima* (i.e. a polyphyletic *A. gardneri*; Goff et al. 1997). Without further information on their phylogeny or more detailed morphological investigations, the origins of parasites and their true diversity remain to be uncovered. The few phylogenetic studies have revealed parasites that are nested within their host genera, requiring taxonomic changes which may involve parasites losing their distinct generic status to maintain monophyly of the host genus (Ng et al. 2014, Preuss and Zuccarello 2014).

Characters used to define the parasitic mode in red algae differ in their utility. Both size and pigmentation are not definitive because small epiphytes do exist, and reproductive structures in some red algae can have lighter pigmentation. The criteria that we feel are the most useful are the cell-cell secondary pit connections between the parasites and the host cells, and finding all life-history stages of parasites on the same host plant,

Table 4: List of species of red algal parasites in which the parasite's development, parasite-host nuclear transfer, and the fate of these parasite nuclei in the host heterokaryotic cell have been documented.

	Host transformation	Parasite nuclear division	References
Bostrychiocolax australis	+	–	Zuccarello and West 1994a
Leachiella pacifica (as *Choreocolax polysiphoniae*)	+	–	Goff and Coleman 1985, Zuccarello et al. 2004
Dawsoniocolax bostrychiae	+	–	Zuccarello and West 1994a
Gardneriella tuberifera	+	+	Goff and Zuccarello 1994
Gracilariophila oryzoides	+	+	Goff and Zuccarello 1994
Harveyella mirabilis	+	?	Goff 1976
Janczewskia gardneri	+	+	Goff and Coleman 1987
Janczewskia morimotoi	+	?	Nonomura 1979

Host transformation: +, changes observed in infected host cells, which can include increased storage products in infected host cells, loss of host plastid fluorescence, host nuclear enlargement, infected host cell division. Parasite nuclear division: +, parasite nuclei known to divide in heterokaryotic host cell; –, parasite nuclei do not divide in heterokaryotic host cell; ?, data not available.

which reduces the chance of mistaking host outgrowths as parasites.

Our summary highlights that our understanding of the parasitic process in these unique organisms is based on only a small handful of species that have been studied intensively (e.g. *Leachiella pacifica* Kugrens). Red algal parasites have been intriguing for scientists as the first reports of nuclear, and organelle, transfer between the parasites and the hosts (Goff 1982, Goff and Coleman 1985). This is a unique phenomenon in eukaryotic parasitism, although in some non-parasitic florideophyte lineages there is nuclear transfer during carposporophyte development (Kugrens and Delivopoulos 1985, Delivopoulos and Diannelidis 1990). Summaries of these processes (early parasite development, host cell "control") have been presented (Graham and Wilcox 2000, Salomaki and Lane 2014) but generalisations about these processes are based on very few examples, and more data may show that different, and novel, infection mechanisms exist.

The classification of red algal parasites as parasites is rarely discussed, but there is evidence that parasites alter hosts and many have detrimental effects on their hosts. This evidence includes the following: degradative changes in infected host cells include plasmolysis and hypertrophy (Goff 1982), host cell death (Goff 1976), breakdown of host nuclei and plastids (Goff 1982), and reduction in host growth (Apt 1984b). Another negative effect for the host is the loss of cell cycle regulation, shown by rapid division of plastids, nuclei, and host cells (Goff 1976, Goff and Coleman 1985), and the infection spreading to surrounding host cells (Goff and Coleman 1995). Few studies have analysed the effects of parasite infection on host fitness, and the results vary from negative effects on the host being either highly localised and minimal (Goff 1982) or appreciable (Martin and Pocock 1953). In contrast to its effects on the host, it is clear that the parasite depends on the host for nutrients (Evans et al. 1973, Goff 1982), for a habitat due to their host specificity (Goff 1982), and for cell-cell interactions during early development (Zuccarello and West 1994b,c). The degree of parasitism (i.e. damage to the host) may therefore vary among host species, but further investigations are needed for a better understanding of parasite-host relationships.

We have produced a comprehensive list of described parasites and characterised the available knowledge about these parasites. It is clear that much information is still lacking. We hope that this list will focus research on poorly studied parasites, and thereby add information about their taxonomy, origins, early development, distribution and effects on host fitness, and will contribute to species discovery. Guiry (2012) estimated that only half of all red algae are described to date. To illustrate this point, many red algal genera and species in New Zealand are continuing to be described (Boo et al. 2015, D'Archino et al. 2015, 2016, Nelson et al. 2015). Currently, there are ten red algal parasites known from New Zealand. In addition, several undescribed parasitic species have been included in compilations of the flora (Dalen and Nelson 2013). We hope that molecular studies, especially studies using molecular markers from all the three genomes, will be stimulated by this study and that further work will also investigate host switching and cell-cell relationships between parasites and hosts. The diversity of parasite development has been barely explored, and current hypotheses about developmental processes need to be tested. We hope that this synopsis will aid and inspire further work on these organisms.

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