

Maren Preuss\*, Wendy A. Nelson and Giuseppe C. Zuccarello

# 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.

## 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

\*Corresponding author: Maren Preuss, School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand, e-mail: Maren142@web.de

Wendy A. Nelson: National Institute of Water and Atmospheric Research, Private Bag 14-901, Wellington 6241, New Zealand; and School of Biological Sciences, University of Auckland, Private Bag 92-019, Auckland 1142, New Zealand

Giuseppe C. Zuccarello: School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand

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

<sup>a</sup>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.

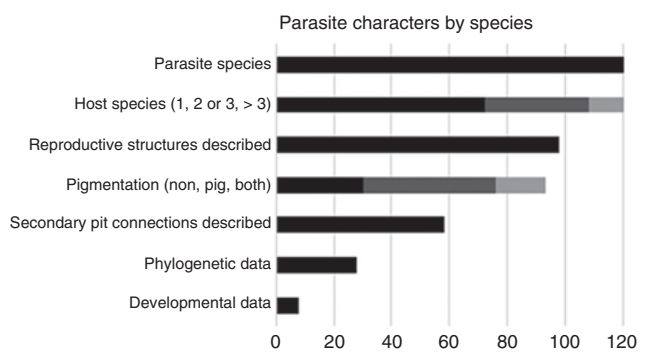
## Results

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



Table 2 (continued)

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

Table 2 (continued)

Parasite	Year	Family	References
<i>Scagelonema parasiticum</i>	1969	<i>Incertae sedis</i>	Norris and Wynne 1969, Wynne and Schneider 2010
<i>Sorellocolax stellaris</i>	1996	Delesseriaceae	Yoshida and Mikami 1996
<i>Sporoglossum lophurellae</i>	1919	Rhodomelaceae	Kylin and Skottsberg 1919
<i>Spyridiocolax capixabus</i>	1966	Ceramiaceae	Joly and de Oliveira 1966
<i>Stromatocarpus parasiticus</i>	1897	Rhodomelaceae	Schmitz and Falkenberg 1897
<i>Symphyocolax koreana</i>	2010	Rhodomelaceae	Kim and Cho 2010
<i>Syringocolax macroblepharis</i>	1875	Ceramiaceae	Reinsch 1875
<i>Tikvahiella candida</i>	1983	Solieriaceae	Kraft and Gabrielson 1983
<i>Trichidium pedicellatum</i>	1983	Rhodomelaceae	Noble and Kraft 1983
<i>Tylocolax microcarpus</i>	1897	Rhodomelaceae	Schmitz and Falkenberg 1897
<i>Ululania stellata</i>	1998	Rhodomelaceae	Apt and Schleich 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 under-reported (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
<i>Aiolocolax pulchella</i>	<i>Polysiphonia caespitosa</i>	Diaz-Tapia and Bárbara 2013
<i>Asterocolax erythroglissi</i>	<i>Erythroglissum laciniatum</i>	Goff et al. 1997
<i>Asterocolax gardneri</i>	<i>Anisocladella pacifica</i>	Goff et al. 1997
	<i>Phycodrys isabelliae</i>	Goff et al. 1997
	<i>Phycodrys setchelli</i>	Goff et al. 1997
	<i>Nienburgia andersoniana</i>	Goff et al. 1997
	<i>Polyneura latissima</i>	Goff et al. 1997
<i>Benzaitenia yenoshimensis</i>	<i>Chondria crassicaulis</i>	Kurihara et al. 2010
<i>Bostrychiocolax australis</i>	<i>Bostrychia radicans</i>	Zuccarello et al. 2004, Zuccarello and West 2006
<i>Choreocolax polysiphoniae</i>	<i>Vertebrata lanosa</i>	Zuccarello et al. 2004, Salomaki et al. 2015
<i>Choreonema thuretii</i>	<i>Jania micrarthrodia</i>	Harvey et al. 2003
<i>Coccotylus hartzii</i>	–	Le Gall and Saunders 2010
<i>Dawsoniocolax bostrychiae</i>	<i>Bostrychia radicans</i>	Zuccarello et al. 2004
<i>Faucheocolax attenuate</i>	<i>Gloiocladia laciniata</i>	Goff et al. 1996
	<i>Gloiocladia fryeana</i>	Goff et al. 1996
<i>Gardneriella tuberifera</i>	<i>Sarcodiotheca gaudichaudii</i>	Goff et al. 1996
<i>Gonimophyllum skottsbergii</i>	<i>Cryptopleura crispa</i>	Zuccarello et al. 2004
<i>Gracilaria babae</i> <sup>a</sup>	<i>Gracilaria salicornia</i>	Ng et al. 2013, Ng et al. 2014, Ng et al. 2015
	<i>Hydropuntia</i> sp.	Ng et al. 2014
<i>Gracilariophila oryzoides</i>	<i>Gracilariopsis lemaneiformis</i>	Goff and Zuccarello 1994, Goff et al. 1996, Hancock et al. 2010
<i>Harveyella mirabilis</i>	<i>Gonimophyllum skottsbergii</i>	Zuccarello et al. 2004
	<i>Odonthalia floccosa</i>	Zuccarello et al. 2004
	<i>Odonthalia washingtoniensis</i>	Zuccarello et al. 2004
	<i>Rhodomela confervoides</i>	Zuccarello et al. 2004
<i>Holmsella pachyderma</i>	<i>Gracilaria gracilis</i>	Zuccarello et al. 2004
	<i>Gracilariopsis longissima</i>	Zuccarello et al. 2004
<i>Holmsella australis</i>	<i>Gracilaria cliftonii</i>	Zuccarello et al. 2004
<i>Hypneocolax stellaris</i> f. <i>orientalis</i>	–	Sherwood et al. 2010
<i>Janczewskia hawaiiiana</i>	<i>Laurencia mcdermidiae</i>	Kurihara et al. 2010
<i>Janczewskia morimotoi</i> <sup>b</sup>	<i>Laurencia nipponica</i>	Kurihara et al. 2010
<i>Kintokiocolax aggregato-ceranthus</i>	<i>Grateloupia angusta</i>	Yang and Kim 2015
<i>Leachiella pacifica</i>	<i>Neosiphonia paniculata</i>	Zuccarello et al. 2004
<i>Plocamiocolax pulvinata</i>	<i>Plocamium cartilagineum</i>	Goff et al. 1996
<i>Rhodophyllis parasitica</i> <sup>a</sup>	<i>Rhodophyllis membranacea</i>	Preuss and Zuccarello 2014
<i>Rhodophysema kjellmanii</i>	–	Clayden and Saunders 2010
<i>Rhodymeniocolax botryoideus</i>	<i>Rhodymenia pacifica</i>	Goff et al. 1996
<i>Tikvahiella candida</i>	<i>Solieria robusta</i>	Saunders et al. 2004
<i>Ululania stellata</i>	<i>Acanthophora pacifica</i>	Kurihara et al. 2010
	<i>Acanthophora spicifera</i>	Kurihara et al. 2010

<sup>a</sup>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
<i>Bostrychiocolax australis</i>	+	–	Zuccarello and West 1994a
<i>Leachiella pacifica</i> (as <i>Choreocolax polysiphoniae</i> )	+	–	Goff and Coleman 1985, Zuccarello et al. 2004
<i>Dawsonicolax bostrychia</i>	+	–	Zuccarello and West 1994a
<i>Gardneriella tuberifera</i>	+	+	Goff and Zuccarello 1994
<i>Gracilariophila oryzoides</i>	+	+	Goff and Zuccarello 1994
<i>Harveyella mirabilis</i>	+	?	Goff 1976
<i>Janczewskia gardneri</i>	+	+	Goff and Coleman 1987
<i>Janczewskia morimotoi</i>	+	?	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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## Bionotes



**Maren Preuss**  
School of Biological Sciences, Victoria  
University of Wellington, PO Box 600,  
Wellington, 6140, New Zealand,  
[Maren142@web.de](mailto:Maren142@web.de)

Maren Preuss is interested in evolution, taxonomy and systematics of red algae and especially of red algal parasites. She is a PhD candidate at Victoria University of Wellington in New Zealand under the supervision of Dr. Giuseppe Zuccarello and Dr. Wendy Nelson.



**Wendy A. Nelson**  
National Institute of Water and Atmospheric  
Research, Private Bag 14-901, Wellington  
6241, New Zealand; and School of Biological  
Sciences, University of Auckland, Private Bag  
92-019, Auckland 1142, New Zealand

Wendy A. Nelson specialises in marine phycology, particularly the biosystematics of macroalgae of New Zealand, with research on floristics, evolution and phylogeny, as well as ecology and life history studies. Recently she has worked on the systematics and biology of red algae including corallines, distribution and diversity of seaweeds of the New Zealand region, including the Ross Sea and the Balleny Islands. Wendy leads NIWA's biosystematics research team and holds a joint appointment as a Professor at the University of Auckland in the School of Biological Sciences.



**Giuseppe C. Zuccarello**  
School of Biological Sciences, Victoria  
University of Wellington, PO Box 600,  
Wellington, 6140, New Zealand

Giuseppe C. Zuccarello is interested in the taxonomy, evolution and speciation of algae. His research has focussed on mangrove-associated red algae of the genus *Bostrychia* and *Caloglossa*. He received a PhD degree from the University of California Berkeley. He has been president of the International Phycological Society and is currently an Associate Professor at Victoria University of Wellington and has published over 120 peer-reviewed papers.