

**A taxonomic revision of the genus *Dictyota*
(Dictyotales, Phaeophyceae) in South Africa**

Mila B. Geldenhuys

24261898

Submitted in fulfilment of the academic requirements for the degree of

Master of Science in Biochemistry

in the

School of Biological and Chemical Sciences, University of Galway

December 2025

Supervised by Dr Maggie M. Reddy

TABLE OF CONTENTS

TITLE PAGE.....	i
TABLE OF CONTENTS.....	ii
ABSTRACT.....	iv
DECLARATION.....	vi
ACKNOWLEDGEMENTS.....	vii
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
1. Literature review.....	1
1.1. Seaweeds and their identification.....	1
1.1.1. An introduction to seaweeds.....	1
1.1.2. The importance of species identification, using South African flora as examples.....	2
1.1.3. Historical approaches: morphology-based classification.....	5
1.1.4. Contemporary approaches: DNA-based classification.....	7
1.1.5. Emerging approaches: Integrative taxonomy.....	11
1.2. A closer look at the study group: <i>Dictyota</i>	13
1.2.1. The Phaeophyceae.....	13
1.2.2. The genus <i>Dictyota</i>	14
1.3. A closer look at the study site: South Africa.....	18
1.3.1. Biogeography of South Africa.....	18
1.3.2. Seaweed diversity in South Africa.....	20
1.3.3. <i>Dictyota</i> in South Africa.....	22
2. Rationale.....	27
3. Materials and methods.....	29
3.1. Sample collection and processing.....	29
3.2. Morpho-anatomical analysis.....	32
3.2.1. Morphological analysis.....	32
3.2.2. Anatomical analysis.....	33
3.3. Phylogenetic analysis.....	34
3.3.1. Molecular work.....	34
3.3.2. Phylogenetic analysis.....	41
3.3.3. Haplotype network for <i>Dictyota dichotoma</i>	41
4. Results.....	43
4.1. Taxonomic treatment.....	43
4.1.1. Species descriptions.....	43
4.1.2. Topotype sequencing.....	51

4.2.	Morphology of South African <i>Dictyota</i>	52
4.2.1.	Gross morphology of samples.....	52
4.2.2.	Key for the South African <i>Dictyota</i>	55
4.3	Phylogenetics data	56
4.3.1.	Species diversity and distribution in South Africa	56
4.3.2.	Biogeography notes.....	62
4.3.3.	Haplotype network for <i>Dictyota dichotoma</i>	63
5.	Discussion.....	65
5.1.	Biodiversity assessment.....	65
5.2.	Misapplied names	66
5.2.1.	Misapplied names of morphologically similar species	66
5.2.2.	Other possible misapplications.....	67
5.2.3.	The importance of type and topotype material.....	68
5.3.	Distribution ranges and biogeography.....	69
5.4.	Morphological notes.....	74
5.5.	Notes on the molecular data	77
5.6.	Broader implications of these findings.....	78
5.7.	Future research	80
6.	Conclusion	82
7.	References.....	83
8.	Supplementary material	105

ABSTRACT

The genus *Dictyota* is a widely distributed group of brown algae occurring in temperate and tropical environments. Species of *Dictyota* are ecologically important and are known for their rich diversity of secondary metabolites that have been shown to have potential applications in the blue bioeconomy. This genus, however, is taxonomically challenging due to morphological plasticity, and the presence of morphologically similar species, highlighting the need for integrative approaches in taxonomic revisions. This study aimed to clarify the species diversity and distribution of *Dictyota* in South Africa, an understudied region that may harbour substantial undiscovered diversity. A total of 83 specimens were collected over 2 000 km of coastline, spanning over four marine provinces, that differ widely in temperature. An integrative taxonomic approach combining molecular and morphological data was employed, targeting three genetic markers: the plastid photosystem II protein D1 (*psbA*) and ribulose-1,5-biphosphate carboxylase/oxygenase large subunit (*rbcL*), and the mitochondrial cytochrome c oxidase subunit I (*cox1*). The results revealed eight previously undescribed species, four of which are formally described in this study (*D. virilabris* nom. prov. *D. caerulea* nom. prov., *D. variolata* nom. prov. and *D. natalensis* nom. prov.), as well as two new distribution records – *D. stolonifera* in South Africa and *D. dichotoma* in Tristan da Cunha. The study did, however, fail to confirm the presence of four species that have previously been recorded in South Africa based on morphology (*D. friabilis*, *D. implexa*, *D. bartayresiana* and *D. ceylanica*), with contemporary results suggesting these might have been historical misidentifications due to morphological similarities with several new species reported in South Africa or that these species are not present anymore. In addition, the assumption that *Dictyota dichotoma* is invasive in South Africa is challenged by the presence of multiple haplotypes within the region, suggesting a more complex biogeographic history and species origin. This study makes a substantial contribution to the taxonomy of *Dictyota* by updating the South African species list from 13 to 18 species and revising the known distribution ranges for all studied taxa. This study also illustrates the importance of sequencing type or topotype material, as the newly described *Dictyota variolata* nom. prov. could only be distinguished from *Dictyota liturata* after the designation and sequencing of topotype material during this study. Future research should build on these findings by expanding geographic and seasonal sampling, incorporating deepwater habitats, and

including reproductive material to further refine species boundaries and improve taxonomic resolution.

DECLARATION

I declare that this material, which I now submit for assessment, is my own work and that any assistance I received in its preparation is fully acknowledged and disclosed in the document. To the best of my knowledge and belief, all sources have been properly acknowledged, and the assessment task contains no plagiarism. I understand that plagiarism, collusion, and/or copying are grave and serious offences and am aware that penalties could include a zero mark for this assessment, suspension or expulsion from the University of Galway. I have read the University of Galway code of practice regarding plagiarism at Academic Integrity. I acknowledge that this assessment submission may be transferred and stored in a database for the purposes of data matching to help detect plagiarism. I declare that this document was prepared by me for the purpose of partial fulfilment of requirements for the programme for which I am registered with the AUA. I also declare that this assignment, or any part of it, has not been previously submitted by me or any other person for assessment on this or any other course of study or another college.



Student Name: Mila Bianca Geldenhuys

ACKNOWLEDGEMENTS

I would like to begin by thanking my supervisor, Dr Maggie Reddy. Thank you for giving me the opportunity to study in a country I had never even visited before this year, for teaching me new skills, and for providing guidance throughout this journey. It was truly special to study in Europe while bonding with you over our shared love for our home country. You have given me so much through this master's, and I will forever be grateful. I would also like to thank Dr Reddy, Prof Olivier Thomas, the COMBO project, funded by Horizon Europe, and the BEAP-MAR Interreg Atlantic Area project, for providing me with a scholarship that enabled me to complete my studies at the University of Galway.

I would not have been able to complete this degree without my support system—my family. Paps, you instilled my love for nature and the ocean in me. Thank you for all the adventures and for teaching me how to dream. Your confidence in me is what makes me brave. Mams, you are my rock and the person I will always turn to. Thank you for always being there when I need someone to talk to, and for always calling me higher while remaining compassionate and loving. You have given me my greatest gift. Cara, my *beste maatjie*, you are more than just a big sister. You have always been, and will forever be, my role model. Your drive to do extraordinary work and your ability to handle whatever life throws at you are things I deeply admire. Thank you for setting such a good example and for always looking out for me.

To my friends back home—Fran, Jadie, Cam, Chels, Alex, Markus, Jaco, and Maric—thank you for always being in my corner and cheering me on from the other side of the planet. I love you all. To my roommates, thank you for making me feel at home from the very start—you made me love Ireland. Svenja, thank you for taking on this experience with me, and for every shared adventure and sweet treat along the way. Catherine, thank you for taking turns picking each other up when we needed it; tea with you kept me going on more than a few occasions. Shane, thank you for sharing your love of science with me and for being the friend I needed—I am so grateful that our paths crossed. To my lab mates—Gaelle, Dualta, Shauna, Memo, and Juanito—I loved working with you and am thankful to leave this master's a few friendships richer.

Above all else, I thank my Creator, who is the reason I take on anything in my life. You have given me the passion, strength, and tenacity to pursue every dream. I would not have made it this far without You, and I am grateful that I get to share every moment with my Father.

LIST OF TABLES

Table 1. Taken from De Clerck *et al.* (2006) identifying the type specimen, defining characters and numbers of species of the different genera of the tribe Dictyoteae.

Table 2. Summary of the *Dictyota* species previously recorded in South Africa, with available South African barcodes. *Rugulopteryx suhrii* and *Canistrocarpus cervicornis* are included in this table as they were previously described as *Dictyota suhrii* and *Dictyota cervicornis*.

Species and genera names are in alphabetic order.

Table 3. Specimen list of *Dictyota* along the South African coast including new and historic collections.

Table 4. Thermal profile for the PCR amplification of genes *cox1* and *rbcL*. Adapted from Delva *et al.* (2024).

Table 5. Thermal profile for the PCR amplification of *psbA* gene. Adapted from Delva *et al.* (2024).

Table 6. All accepted species of *Dictyota* with the type locality, whether there are any sequences available for the species, and the accession numbers of sequences from- or close to the type locality.

Table 7. Morphological traits of South African *Dictyota* species. The table includes information from South African previous records as well as newly generated data. Columns highlighted in green depict newly described species.

Supplementary Table 1. Samples used in phylogenetic analysis, with accession numbers and sampling locations

Supplementary Table 2. Accession numbers of samples analysed during this study.

LIST OF FIGURES

Figure 1. Taken from Bogaert *et al.* (2020) showing the apical meristem of a *Dictyota* species with a recently divided lens-shaped apical cell.

Figure 2. Taken from De Clerck *et al.* (2006) showing the morphological characters historically used to distinguish between the genera of the tribe Dictyoteae.

Figure 3. Map taken from Anderson *et al.* (2009) showing the different Marine Bioregions in South Africa

Figure 4. Map of South Africa showing all the sampling localities for this study. The colours show the different marine provinces of Anderson *et al.* (2009); Purple: Benguela Marine Province, Blue: Western Transition Zone, Green: Agulhas Marine Province, Orange: Eastern Transition Zone, Red: Indo-west Pacific Marine Province.

Figure 5. Picture of a *Dictyota* sample, showing the measurement of the interdichotomies.

Figure 6. Photograph showing the (a) surface view, and (b) cross section of a *Dictyota* specimen. The medullary cells are the larger cells, and the cortical cells are the smaller cells surrounding the medullary cells in the cross section.

Figure 7. Distribution of *Dictyota variolata nom. prov.* in South Africa

Figure 8. General morphology of *Dictyota variolata nom. prov.* (a) Habit *in situ*. (b-c) Cross-section of the thallus. (d-e) Sporangia. (f) Apical point of the thallus. (g) Surface view of cells.

Figure 9. Distribution of *Dictyota caerulea nom. prov.* in South Africa.

Figure 10. General morphology of *Dictyota caerulea nom. prov.* (a) Habit *in situ*. (b) Cross-section of the thallus. (c) Apical point of the thallus. (d-e) Surface view with (e) showing sporangia.

Figure 11. Distribution of *Dictyota natalensis nom. prov.* in South Africa.

Figure 12. General morphology of *Dictyota natalensis nom. prov.* (a) Habit *in situ*. (b-c) Apical section of the thallus. (d) Surface view of the cells. (e) Cross-section of the thallus.

Figure 13. Distribution of *Dictyota virilabris nom. prov.* in South Africa.

Figure 14. General morphology of *Dictyota vililabris* nom. prov. (a) Habit *in situ*. (b-c) Apical section of the thallus. (d) Cross-section of the thallus. (e) Surface view showing the cortical cells. (f) Surface view showing the medullary cells.

Figure 15. Updated distribution of *Dictyota liturata* in South Africa. Confirmed distribution is shown in blue, while historically recorded distribution is shown with red dots.

Figure 16. Phylogenetic tree of *Dictyota* species inferred from Bayesian- and Maximum likelihood analyses of *psbA* sequences. The tree was rooted with *Canistrocarpus cervicornis*, *Styopodium multipartitum*, and *Stoecho spermum polypodioides* (Family Dictyotaceae). Tip labels show the accession number, sampling country, and originally recorded species name. Brackets indicated clades supported by the data and are annotated with the accepted species names. Specimen sampled in South Africa are indicated in bold, and sequences generated during this study is indicated in blue, together with their associated sample code and sampling location. Bayesian posterior probabilities are shown at nodes when ≥ 0.75 , and maximum likelihood bootstrap percentages are shown when $\geq 65\%$.

Figure 17. Phylogenetic tree of *Dictyota* species inferred from Bayesian- and Maximum likelihood analyses of *rbcL* sequences. The tree was rooted with *Canistrocarpus cervicornis*, *Styopodium flabelliforme*, *Styopodium hawaiiensis*, *Rugulopteryx suhrii*, and *Taonia atomaria* (Family Dictyotaceae). Tip labels show the accession number, sampling country, and originally recorded species name. Brackets indicated clades supported by the data and are annotated with the accepted species names. Specimen sampled in South Africa are indicated in bold, and sequences generated during this study is indicated in blue, together with their associated sample code and sampling location. Bayesian posterior probabilities are shown at nodes when ≥ 0.8 , and maximum likelihood bootstrap percentages are shown when $\geq 65\%$.

Figure 18. Phylogenetic tree of *Dictyota* species inferred from Bayesian- and Maximum likelihood analyses of *cox1* sequences. The tree was rooted with *Canistrocarpus cervicornis*, *Styopodium multipartitum*, *Styopodium flabelliforme*, and *Taonia atomaria* (Family Dictyotaceae). Tip labels show the accession number, sampling country, and originally recorded species name. Brackets indicated clades supported by the data and are annotated with the accepted species names. Specimen sampled in South Africa are indicated in bold, and sequences generated during this study is indicated in blue, together with their associated sample code and sampling location. Bayesian posterior probabilities are shown at nodes when ≥ 0.8 , and maximum likelihood bootstrap percentages are shown when $\geq 65\%$.

Figure 19. Median-joining haplotype network for *Dictyota dichotoma* using the *cox1* gene. The number of hatch marks indicate the number of mutations between haplotypes.

1. Literature review

1.1. Seaweeds and their identification

1.1.1. An introduction to seaweeds

Algae are photosynthetic organisms found in marine, estuarine, interterrestrial and aquatic environments (Round, 1981; Tschaikner *et al.*, 2007; El Gamal, 2010). They are broadly divided into microalgae and macroalgae, the latter commonly referred to as seaweeds which occurs in marine and estuarine habitats (Chapman & Chapman, 1980). Seaweeds have long attracted scientific interest; for example, the first International Seaweed Symposium was held in Scotland in 1952 (Chan *et al.* 2006). The historical study of seaweeds led to the formation of the International Phycological Society in 1960, an organisation established to promote the global development of phycological research and to facilitate international collaboration and knowledge exchange (Silva, 1961).

More than 12 000 species of seaweeds have been formally described to date (Corrigan *et al.*, 2025), though global diversity is estimated to be as high as 16 000 species (Guiry, 2024). Seaweeds are divided into three evolutionarily distinct groups, namely, red (Rhodophyta), green (Chlorophyta), and brown (Heterokontophyta) algae (Guiry, 2024). Historically blue-green algae (Cyanophyta) were grouped with seaweeds, but these are now recognized as cyanobacteria (Diaz-Pulido & McCook, 2008; Palinska & Surosz, 2014).

Seaweeds occupy a large proportion of the world's coastline and rocky reef habitats, making them foundational components of coastal ecosystems (Corrigan *et al.*, 2025). Consequently, seaweeds provide critical ecological and economical functions, that support both marine biodiversity and human well-being (Corrigan *et al.*, 2025). Ecologically, seaweeds create three-dimensional structure including canopy forming kelp forests and furoid beds, meadows of calcified green algae such as *Halimeda* species, and reef-building crustose coralline algae and rhodolith beds (Corrigan *et al.*, 2025). These habitats serve as biodiversity hotspots, serving as food resources and refuge to numerous species (Cheminée *et al.*, 2017; Dunne *et al.*, 2023; James & Whitfield, 2023). Seaweeds also contribute to ecosystem functioning. Their high primary production fuels marine ecosystems and supports secondary productions directly or through detrital pathways (Duggins *et al.*, 1989). In some regions, seaweeds

contribute to carbon sequestration through carbon burial and export (Duarte *et al.*, 2005; Filbee-Dexter *et al.* 2024).

Depth is greatly correlated with light penetration and can therefore be a limiting factor for seaweed occurrence. All seaweeds are found in the photic zone, with very few species occurring past about 30 m (Anderson *et al.*, 2016). However, in some areas like the tropics light can penetrate more deeply, leading to deepwater populations of seaweed. For example, *Ecklonia radiata* has been recorded on the coast of Mozambique at a depth of 29-35 m where light could penetrate deeper due to clearer water (Coleman *et al.*, 2022).

Economically, macroalgae can be harvested for direct human consumption or feed, aquaculture, and numerous commercial products (e.g. hydrocolloids, cosmetics, and fertilizers) (Mac Monagail *et al.*, 2017; Porse & Rudolph, 2017; Pereira, 2018). Seaweed-dominated habitats also underpin local fisheries supporting commercially valuable species and enhance coastal economies via tourism from activities like diving and ecotourism (Eger *et al.*, 2023; Corrigan *et al.*, 2025). Recent global synthesis estimate kelp forests alone generate ecosystem service worth around \$500 billion USD annually (Eger *et al.*, 2023). Together these ecological and economic contributions demonstrate that seaweed-dominated habitats are foundation to the health, function, and resilience of coastal marine ecosystems.

1.1.2. The importance of species identification, using South African flora as examples

To conserve and manage seaweed diversity and bioresources, it is essential to accurately identify and document species (Brodie *et al.*, 2009). Historically, macroalgae were often neglected in extinction-risk assessments. Their ubiquity in coastal ecosystems has created the impression they were buffered from extinction. However, many species have narrow distributions – for example *Postelsia palmiformis*, *Vanvoorstia bennettiana*, and *Dictyota naevosa* (Guiry & Guiry, 2025) – or occupy environments with tight physiological constraints, such as temperature-restricted kelps (Bolton *et al.*, 2012; Reddy *et al.* 2024).

Narrow distributions and tight physiological boundaries make these species susceptible to climate change and other anthropogenic stressors (Brodie *et al.*, 2009). Documented cases of macroalgal decline illustrate this vulnerability. For example, the only population of *Ecklonia radiata* in the northern hemisphere has recently disappeared, likely due to ocean warming and

reduced upwelling (Coleman *et al.*, 2022). This population harboured a unique haplotype not found elsewhere, demonstrating how local losses can erase genetic diversity (Coleman *et al.*, 2022). Similar collapses have been reported for temperate kelp forests worldwide and certain tropical algae such as coralline algae have been shown to have narrow thermal tolerances that could make them sensitive to heatwaves, rapid ocean warming, and other anthropogenic stressors (Filbee-Dexter *et al.*, 2020; Krieger *et al.*, 2023).

A major challenge in documenting and protecting macroalgal diversity is the prevalence of cryptic species – genetically distinct lineages that are morphologically indistinguishable (Bickford *et al.*, 2007). Species that have narrow distributions are especially vulnerable to habitat loss (Brodie *et al.*, 2009), and this vulnerability is compounded when cryptic or morphologically similar species complexes are mistaken for a single, widespread taxa. For example, studies have revealed extensive diversity in *Dictyota*, *Ulva*, Bangiales and *Cladophoropsis* (Van Der Strate *et al.*, 2002; Hofmann *et al.*, 2010; Tronholm *et al.*, 2010a, Reddy *et al.* 2018, 2020). In each case, morphologically similar “species” consisted of multiple lineages with distinct biogeographic ranges, suggesting localised environmental change could eliminate entire lineages that were previously unknown. Recognising morphologically similar but genetically distinct species can also clarify endemism, showing that species once thought to be widespread are actually endemic. Such information directly informs which habitats should be prioritised for conservation (Bickford *et al.*, 2007).

Similarly, species that are morphologically similar, differing only subtly in appearance, can pose significant taxonomic challenges. Molecular systematics and DNA barcoding have led to the discovery of numerous species that were previously misidentified as more widespread or well-known taxa. This trend is especially prevalent in understudied areas, where local species have often been identified as European species. For example, research has shown that specimens identified as *Plocamium microcladioides* (Type locality: New Zealand) and *Plocamium mertensii* (Type locality: Western Australia) collected in South Africa do not represent these species and group separate from specimens sequenced from the type locality (Reddy *et al.*, 2023a). This suggest these species do not occur in South Africa but that these names have been misapplied to undescribed South African species (Reddy *et al.*, 2023a). However, misidentifications do not only occur between local and non-native species. In some cases, more than one endemic occurs within the same region, and one is mistaken for the other. For example, Reddy *et al.* (2020a) demonstrated that the species *Callithamnion*

africanum was misidentified as *Callithamnion collabens*, the former occurring in the Western Cape while the latter is restricted to the south and east coast of South Africa.

Similar to studies on cryptic species, resolving the misapplication of species names has also led to the recognition of endemic taxa. For example, De Clerck *et al.* (2005b) demonstrated that *Gratelpupia filicina*, previously thought to have a cosmopolitan distribution, is endemic to the Mediterranean. Furthermore, other specimens identified as *G. filicina* from regions outside of the Mediterranean were shown to represent distinct species with restricted distributions, including the newly described *Grateloupia capensis* which represents a South African endemic (De Clerck *et al.*, 2005b). In the previously mentioned example, it was also shown that instead of a single *Callithamnion* endemic, two endemics were present on the coast of South Africa (Reddy *et al.*, 2020a).

Clear species boundaries underpin the identification of biodiversity hotspots and areas with increased ecosystem functioning. For example, South Africa has been recognized as a global hotspot of seaweed endemism and phylogenetic diversity, but these patterns only become apparent once cryptic taxa and misapplied names are resolved (e.g. De Clerck *et al.* (2005b), Reddy *et al.* (2018), Reddy *et al.* (2020a), Reddy *et al.* (2023a)). Thus, accurate species inventories form the foundation of regional conservation planning and assessments of ecosystem vulnerability.

Taxonomy is also central to formal conservation frameworks. Many widely used conservation indices, like those applied in the Important Plant Area (IPA) initiative, assumes accurate underlying taxonomy (Bolton, 2020). Likewise, species cannot be evaluated within the IUCN Red List without meeting taxonomic standards (IUCN, 2025). This partially explains why, before 2023 only 75 seaweed species had been assessed for the Red List (Brodie *et al.*, 2023). Without taxonomic clarity, neither risk assessment nor conservation prioritisation can be carried out effectively.

Beyond conservation, reliable species identification is essential for the sustainable exploitation of seaweeds. Research on marine natural products routinely suffers from misidentified specimens (Bolton 2020, Reddy *et al.* 2021), creating uncertainty around commercially important organisms with bioactivity potential. With numerous seaweed species having cryptic diversity (e.g *Dictyota* (Altamirano-Cerecedo *et al.*, 2024), *Ulva* (Hofmann *et al.*, 2010), *Cladophoropsis* (Van Der Strate *et al.*, 2002), Bangiales (Reddy *et al.*, 2018), it is possible that two closely related and morphologically similar species produce

different compounds. For example, in *Dictyota* numerous secondary metabolites – some produced by only one lineage – have been isolated (Chen *et al.*, 2018), yet the genus exhibits extensive morphological plasticity and cryptic diversity (Altamirano-Cerecedo *et al.*, 2024). Misidentification can thus lead to cultivating or harvesting the wrong species, wasting resources and undermining reproducibility. Updating the taxonomy of genera reduces this risk by ensuring that biochemical and ecological research is tied to correctly identified species and facilitating the sustainable use of these species.

Many times, species are referred to by their common names or non-taxonomic terms for groups of organisms (NTGOs). While common names and NTGOs have cultural and practical value (Fraser, 2012), they are often ambiguous and inconsistently applied across regions (Fraser, 2012; Bolton, 2016). For example, “kelp” may be defined strictly as members of Laminariales (e.g. Bolton (2010)) or used more broadly to include other brown algae such as *Saccorhiza* (Order Fucales) or *Desmarestia* (Order Desmarestiales) (e.g. Fraser (2012)). Similarly, common names are often also different between regions, leading to further confusion when used in scientific studies. For example, “Dead Man’s Fingers” refers to *Splachnidium rugosum* in South Africa (Anderson *et al.*, 2016), but also to various *Codium* species in other part of the world (e.g. USA (Goff *et al.*, 1992)). Such inconsistencies can create confusion in scientific communication, reinforcing the need for formal taxonomic names of species.

Thus, a standardised system is used for the naming of species – the Linnaean system. The Linnaean binomial system for naming species is grounded on logical principles and provides a universal language for biodiversity. Standardised taxonomic names enable confident identification, support effective conservation assessments, and ensure that ecological and biotechnological research refers to the correct biological entities. With millions of undescribed species still remaining to be described and an estimated global need for roughly 15 000 taxonomists (Hebert *et al.* 2003), continuing taxonomic work and the accurate identification of organisms is essential to both biodiversity conservation and sustainable resource management.

1.1.3. Historical approaches: morphology-based classification

The taxonomy of seaweeds based on the Linnean system can be traced back to the 1750s, where initial classification and identification was based on morphology (Subbotin *et al.*,

2013; Anderson *et al.*, 2016). For more than two centuries species descriptions were, and currently still are, based on morphological, anatomical and reproductive characters. Although these traits remain valuable, additional methods (molecular, ecological, chemical etc.), have also been used. Each has strengths and limitations, and the most appropriate approach depends on the biology of the group under study, for example, whether a lineage exhibits high morphological plasticity, complex life histories, or substantial cryptic diversity.

Seaweeds present several challenges for morphological-based identification. Firstly, it can be difficult to accurately identify species of seaweeds, as a high level of species exhibit cryptic diversity (as explained above) (e.g Robba *et al.* (2006), Van Der Strate *et al.* (2002)).

Secondly, the complex life histories of many macroalgae complicate identification. Numerous red and brown alga have biphasic and triphasic life cycles in which different stages (e.g sporophyte vs gametophyte) are morphologically distinct despite being genetically identical (Kress & Erickson, 2012). This has historically resulted in different life-history stages being described as separate species. For example, Hughey *et al.* (2002) showed that several seaweeds that were named as different species were all *Gigartina bracteata* and was given different names due to differences in appearance. These differences were caused by different life-history stages, as once the tetrasporangia are released, the sori disintegrate producing a net-like thallus that looks different to a fertile specimen. Thirdly, macroalgae often exhibit strong phenotypic plasticity, producing different morphologies due to varying environmental conditions. For instance, *Sargassum thunbergii* exhibits three distinct morphotypes driven by hydrodynamics, temperature and grazing pressure (Kim *et al.*, 2022). Similarly, environmentally induced morphological variation occurs in *Halimeda* (Pongparadon *et al.*, 2017). Such plasticity can make genetically identical individuals appear to look like different species. Lastly, another limitation of morphological-based taxonomy is that many identification keys were developed by expert taxonomists using highly technical terminology. End users – such as ecologists, chemists, or natural-product researchers – may lack the expertise, training or microscopy equipment required thereby increasing the potential for misidentifications (Hebert *et al.*, 2003; Bolton, 2020, Reddy *et al.* 2021).

Advances in systematics over the past three decades have helped transform seaweed taxonomy. DNA sequencing, molecular systematics, species delimitation models, and integrative taxonomic approaches are new tools which have revealed previously unrecognised diversity, prompted major revisions of numerous groups and is becoming standard practice in the field. These approaches allow taxonomists to distinguish between plasticity and true

speciation, resolve life-history stages, and map genetic lineages onto biogeographic patterns. As Hebert *et al.* (2003) noted, the lack of taxonomists combined with the inherent limitation of morphological identification underscore the need for these other approaches to enable more accurate species identification.

1.1.4. Contemporary approaches: DNA-based classification

Molecular approaches often complement traditional classification methods and play a central role clarifying species boundaries that are difficult to resolve on morphology alone. Modern systematics generally accepts that a species should represent monophyletic groups, following the phylogenetic species concept (Leliaert *et al.*, 2014). DNA barcoding is a molecular method that was originally used to identify specimens of known species by matching their sequence to a curated reference library but has since also been used for flagging potential new species when sequences do not match existing entries (Hebert & Gregory, 2005; Erickson *et al.*, 2008; Saunders & McDevit, 2013).

DNA barcoding refers to the use of a short region of the genome, called a gene marker, to identify species (Hebert *et al.*, 2003; Kress & Erickson, 2012). DNA barcodes generally contain 400-800 base pairs – a short enough region that makes the process of DNA extraction and identification of the organism efficient and easy (Hebert *et al.*, 2003). DNA barcodes, however, are not limited to species identification, they can also be used in molecular systematics – which is the use of genomic information to resolve the phylogeny and taxonomy of organisms (Subbotin *et al.*, 2013). DNA barcoding and molecular systematics started to be used for algal systematics in the 1990s (e.g. Freshwater & Rueness (1994); Rousseau *et al.* (1997); Stache-Crain *et al.* (1997); Siemer *et al.* (1998); De Clerck & Coppejans (1999)) and have now become an integral tool for taxonomists documenting the biodiversity of our planet (Kress & Erickson, 2012).

DNA barcoding works by comparing an unknown sequence to a reference library (e.g BOLD or GenBank) using distance metrics or alignment algorithms such as Kimura-2-Parameter, Smith Waterman, or BLAST (Erickson *et al.*, 2008; Kress & Erickson, 2012). The effectiveness of barcoding depends on building accurate reference databases from vouchered specimens, which will enable the identification of new samples and detection of possible undescribed diversity (Erickson *et al.*, 2008; Kress & Erickson, 2012). For example, a barcoding study done in the Canadian subarctic aimed to survey the seaweeds found in the

area, however, it also highlighted a few species that need taxonomic work, and that might be undescribed (Saunders & McDevit, 2013).

a) Genes targeted during molecular studies

Numerous gene regions have been applied to the molecular systematics of algae. For species delimitation, effective DNA barcodes must have substantial genetic variability between species while still having conserved flanking sites that make it possible to create universal PCR primers (Kress & Erickson, 2012). Marker choice is especially important in algae, which are phylogenetically diverse, with no single universal DNA marker that works across all lineages (Leliaert *et al.*, 2014). The following section focuses exclusively on brown algae as this falls within the scope of the present study.

Highly conserved genes, like the Small Subunit ribosomal RNA (SSU) gene, are primarily used for resolving broad phylogenetic relationships at a higher taxonomic level (Rousseau *et al.*, 1997), whereas moderately conserved markers such as the Large Subunit rRNA gene (LSU) gene often provide family and genus level-resolution. (Rousseau *et al.*, 1997). On the other hand, less conservative regions, like the nuclear ribosomal DNA internal transcribed spacer regions (ITS1 and ITS2), are frequently used for population genetics and can be too variable for resolving deeper phylogenetic relationships (Stache-Crain *et al.*, 1997).

The mitochondrial gene cytochrome c oxidase sub-unit 1 (*cox1*) (Hebert *et al.*, 2003; Kress & Erickson, 2012; Leliaert *et al.*, 2014), is the standard barcode for animals, but it evolved too slowly in plants to function as a universal barcode (Chase *et al.*, 2005; CBOL Plant Working Group, 2009). However, *cox1* has been successfully used in combination with other markers to resolve species-level relationships in brown algae (e.g. (Tronholm *et al.*, 2010b; Ni-Ni-Win *et al.*, 2024)). No universal protocol has been created for algae, largely because different laboratories historically used different markers (Saunders, 2005). Commonly used markers for brown algae include the plastid genes *psbA*, *rbcL* and the Rubisco spacer, mitochondrial *cox1* and *cox3*, and nuclear ITS (Leliaert *et al.*, 2014). Within the genus *Dictyota*, the most frequently used markers are *rbcL*, *psbA*, and *cox1* (Altamirano-Cerecedo *et al.*, 2025). Other markers, for example the Internal Transcribed Spacer 1 (ITS1), has been used in the past for the genus but provided poor species-level resolution (De Clerck *et al.*, 2001).

The plastid marker *psbA* is regarded as the reference marker for the genus *Dictyota* (Vieira *et al.* 2025) and is therefore targeted in this study. However, several studies on *Dictyota* and

other brown algae have demonstrated that the use of multiple genetic markers increases confidence in species delimitation, suggesting the use of a multi-locus species delimitation approach (Leliaert *et al.* 2014). Reliance on a single marker may fail to detect hybridisation or introgression events (Mols-Mortensen *et al.*, 2012), while the retention of ancestral polymorphisms can obscure species boundaries in recently diverged taxa, leading to an underestimation of species diversity (Hickerson *et al.*, 2006; Leliaert *et al.*, 2014). For this reason, two additional genetic markers are often recommended.

Recent studies have used *cox1* alongside *psbA* to increase confidence in species identification and to assess genetic diversity within *Dictyota* species (Tronholm *et al.* 2010b; Ni-Ni-Win *et al.* 2014). In addition, *cox1* has been applied to construct haplotype networks, providing insights into both genetic diversity and phylogeographic structure at the species level (Corrales *et al.*, 2025). The complementary use of *cox1*, *rbcL* and *psbA* has been shown to aid in the identification and analysis of phylogeography of *Dictyota* species (Delva *et al.*, 2024). Furthermore, these markers can be used together to make a more robust taxonomic review of species in a region (Vieira *et al.*, 2025b).

b) Advantages of using molecular tools

DNA barcoding and the underlying molecular data allows species to be identified as monophyletic clades based on their genes (Leliaert *et al.* 2014; Bolton, 2020), and not morphological features that could have evolved separately on numerous occasions (convergent evolution) or have led to species with a range of different morphological forms (morphological plasticity e.g. Kim *et al.* (2022)). Barcoding is rapid, reliable, reproducible and broadly applicable, making it a valuable tool for conservation, ecological monitoring and biodiversity assessments (DeSalle, 2006; Kress & Erickson, 2012). When combined with morphological, chemical and ecological data, molecular systematics using DNA barcoding contributes to integrative taxonomy by strengthening species delimitation and clarifying evolutionary relationships among taxa.

A major advantage of using molecular systematics is that all life-history stages share the same DNA sequence – even when morphology differs drastically – allowing identification of microscopic, juvenile, degraded, or fragmented specimens (Kress & Erickson, 2012). Barcoding enables the detection of cryptic species, which is especially important for conservation as mentioned earlier (Bickford *et al.*, 2007). It is also widely applied in food-

web studies, where organisms can be identified from gut contents or faecal material. Finally, when sequences do not match any existing references, this may signal an undescribed species or overlooked taxonomic diversity (Bickford *et al.*, 2007; Kress & Erickson, 2012).

c) Limitations of molecular tools

Molecular data can be hard to obtain due to a range of technical limitations. DNA extracted from older herbarium specimens, for example, is often degraded making it difficult to obtain high quality DNA sequences (Paabo, 1989). In addition, extraction of seaweed DNA can also be challenging due to the presence of specialised metabolites like tannins and polyphenols (Porebski *et al.*, 1997). These technical constraints highlight the risks of relying exclusively on molecular data, as practical difficulties can limit data availability and quality.

Even when DNA extraction and amplification is successful, molecular systematics based on DNA barcodes cannot be used in isolation when describing a species (DeSalle, 2006). While molecular data can serve as the primary line of evidence, it must always be complemented by morphological data to support robust species delimitation. Public sequence repositories like GenBank depend on user-submitted identification, which means misidentified specimens can introduce errors that propagate through subsequent studies (Collins & Cruickshank, 2013). Although additional metadata, like morphological characters, can be associated with uploaded sequences to improve confidence in identifications (Collins & Cruickshank, 2013), this functionality is largely restricted to the BOLD platform (Ratnasingham & Hebert, 2007). Together, these limitations underscore the importance of integrative taxonomy, in which molecular data is combined with morphological, ecological and other trait-based evidence to produce robust and reproducible species delimitations.

d) Type specimen

One way to mitigate some of the limitations of molecular systematics is to sequence the type specimens of species and to include these sequences, along with other confidently identified sequences, in phylogenetic studies when identifying or classifying specimens of the same genus (Chakrabarty *et al.*, 2013). Robust taxonomic revision ideally relies on molecular data derived directly from the type material (Tautz *et al.*, 2003; De Clerck *et al.*, 2013), as this increases confidence in the correct application of species names. Sequencing type specimens

allows direct comparison between newly collected material and the specimens on which species descriptions were originally based on.

However, type material is often unavailable for molecular work or yields degraded DNA that is difficult to amplify, limiting its use in molecular studies (Tautz *et al.*, 2003; De Clerck *et al.*, 2013). In such cases, a topotype should be designated by collecting specimens near the type locality (Tautz *et al.*, 2003), that closely match the original morphological description of the species. These specimens can then be barcoded and their sequences used as reference data for the species. The inclusion of type or topotype-derived sequences substantially increases the reliability and stability of molecular taxonomy.

1.1.5. Emerging approaches: Integrative taxonomy

As taxonomic tools continue to advance, seaweed systematics is increasingly moving toward integrative approaches in which morphological, molecular, ecological, and biochemical data are combined to produce more robust species delimitations. Biogeographic and ecological data has been shown to support the divergence of morphologically similar but genetically distinct species (e.g. Reddy *et al.* (2020b), Yang & Kim (2023)). In such cases, molecular divergence is accompanied by consistent differences in geographic distribution, habitat preference, or environmental conditions, providing additional evidence for evolutionary independence.

Consequently, ecological and biogeographic data can serve as supporting lines of evidence in species delimitation, complementing morphological and molecular datasets and increasing the robustness of species descriptions. For example, Reddy *et al.* (2020b) described *Pyropia meridionalis* (now *Neoporphyra*) based on a combination of ecological (habitat preference), molecular and morphological data. In another study, *Callithamnion africanum* was described using morphological, molecular and biogeographical data (Reddy *et al.*, 2020a). Furthermore, a putative species, *Porphyra agulhensis* nom. prov., based on an integrative approach also using biogeographical data has been proposed (Reddy, 2018). Although this taxon has not been formally described or accepted, the study further illustrates how information other than molecular and morphological data can contribute to identifying independent species.

Chemotaxonomy – the use of specialised metabolites as taxonomic markers – is another line of evidence that has long been recognised in botany, where chemical traits such as alkaloids

and terpenes can potentially be used to support the classification of species based on morphology (Fairbrothers *et al.*, 1975; Teixeira & Kelecom, 1988). The term chemotaxonomy itself only gained widespread use from the late 1990s onwards (Ng *et al.*, 2024) and although no species have been formally described based solely on chemical traits as diagnostic characters, chemical data have increasingly been used as supporting evidence in taxonomic studies (e.g. Leal *et al.* (2025)). As analytical techniques continue to improve, chemical traits may play a growing role in seaweed systematics by complementing morphological and molecular data and increasing the robustness of species delimitation.

Recent studies demonstrate that chemical profiles can align closely with evolutionary relationships. For example, chemotaxonomy profiles of *Hibiscus* agree with the phylogenies inferred from traditional morphological traits supporting its utility in species delimitation (Abdelfattah *et al.*, 2024). Scientists have also started to realise the value of chemotaxonomy in the study of marine sponge species. Recently, chemical data has been used to support the description of sponges within the order Haplosclerida based on molecular and morphological data (Leal *et al.*, 2025). Seaweeds have also received growing attention in chemotaxonomy studies (Teixeira & Kelecom, 1988; Simas *et al.*, 2014; Ng *et al.*, 2024). For example, *Dictyota caribea*, produces diterpenes such as dictyol B acetate, pachydictyol A and disopachydictyol A, whereas morphologically similar species of the genus *Canistrocarpus* synthesise only dollabelane and dolastane type skeletons. (Simas *et al.*, 2014). These distinct chemical profiles provide reliable markers separating the genera.

However, chemotaxonomy must be applied with caution. Some compounds are found across multiple related genera as illustrated by Ng *et al.* (2024), who found that halogenated snyderane-type sesquiterpenes in *Laurencia snackeyi* are also produced by species of *Palisada* and *Ohelopapa*, all within the tribe Laurencieae. Such overlap limits their usefulness for species-level resolution diagnostics but suggests value at higher taxonomic ranks. The increasing complexity of chemical datasets also raises opportunities to use suites of metabolites rather than single compounds, an approach used in phytoplankton identification (Peltomaa *et al.*, 2023).

Overall, while chemical, ecological, biogeographical, molecular and morphological data alone cannot resolve all taxonomic questions, their integration provides a powerful framework for accurately describing species, resolving cryptic diversity and refining algal systematics. The red seaweed *Callithamnion africanum* and the green seaweed *Ulva capillata*

have both been described using an integrative approach using multiple lines of evidence (Reddy *et al.*, 2020a; Steinhagen *et al.*, 2022). These successes suggest that brown algae, which often display similar morphological plasticity and cryptic diversity, would also benefit from integrative taxonomic reviews.

1.2. A closer look at the study group: *Dictyota*

1.2.1. The Phaeophyceae

The Phaeophyceae, or brown algae, are one of the most ecologically dominant groups of seaweeds globally, especially in temperate- and polar regions (Hanley *et al.*, 2024). Brown algae were the last of the major algal lineages to diverge, with molecular clock estimates suggesting their origin approximately 450 million years ago (Choi *et al.*, 2024), compared with about ~1 billion for the first green algae (Tang *et al.*, 2020) and over 1.5 billion years for the first reds (Bengtson *et al.*, 2017). Phaeophyceae are morphologically diverse, ranging from large structurally complex kelps to the small morphologically simple filamentous algae such as *Ectocarpus*. The group comprise nearly 300 genera, with wide variation in life cycles, reproductive strategies and thallus forms (Silberfeld *et al.*, 2010; Bogaert *et al.*, 2013; Simas *et al.*, 2014). Their pigmentation is characterised by chlorophylls a, c₁, and c₂, as well as β -carotene, duatoxanthin, and fucoxanthin (De Reviere *et al.*, 2007; Wehr, 2015), the latter being responsible for the brown colouration of the group. Brown algae also produce a suite of bioactive compounds with demonstrated antitumor, anti-inflammatory, antimicrobial and antiviral activity, contributing to growing interest in their biotechnological potential (El Gamal, 2010).

Recent estimates indicate that brown algal forests and beds cover about 2.68 million km² of coastline, out of a total global seaweed cover of 6 to 7.2 million km² (Duarte *et al.*, 2022). However, brown macroalgae contribute disproportionately to the ecosystem services associated with global seaweed assemblages. Their ecological importance stems from their roles in primary production, carbon export, and habitat formation (Steneck *et al.*, 2002; Duarte *et al.*, 2005; Corrigan *et al.*, 2025). Although the vast majority of Phaeophyceae are marine, a small number of freshwater genera are well documented (e.g. *Heribaudiella*, *Pleurocladia*, *Bodanella* (McCauley & Wehr, 2007)).

In contrast to most marine taxa, brown algae exhibit their greatest diversity and ecological dominance in cold and temperate regions (De Reviers *et al.*, 2007). Temperate kelp forests, including those formed by *Ecklonia*, *Laminaria* and *Macrocystis*, structure some of the most productive ecosystems on earth (Steneck *et al.*, 2002). However, Phaeophyceae are also key components of tropical and subtropical floras, where they can be abundant or ecologically influential. Genera such as *Dictyota*, *Padina* and *Sargassum* dominate many low-latitude reef and lagoon systems, contributing substantially to tropical benthic diversity and functioning (De Reviers *et al.*, 2007; Ni-Ni-Win *et al.*, 2021). This broad ecological range – from polar kelp forests to tropical algal meadows – underscores the global significance and versatility of the Phaeophyceae.

1.2.2. The genus *Dictyota*

a) Taxonomy

The placement of the family Dictyotaceae within the brown algae group was disputed in the 19th century, with some taxonomists arguing that the group was not part of the Phaeophyceae, but rather a close relative (De Reviers *et al.*, 2007). The advent of molecular techniques, resolved these uncertainties, confirming that the Dictyotales – although an early diverging lineage – belong firmly to the brown algae (Rousseau *et al.*, 2001). The family includes two tribes, Dictyoteae (108 species) and Zonarieae (246 species) (Guiry & Guiry, 2025). The genus *Dictyota* was first described by J.V. Lamouroux in 1809 (Lamouroux, 1809; Guiry & Guiry, 2025; Bogaert *et al.*, 2020), and it forms part of the well-defined order Dictyotales (De Clerck *et al.*, 2006). This order is comprised of only three families, the Dictyotopsidaceae and Scoresbyellaceae (each monogeneric and monospecific), and the Dictyotaceae (De Clerck *et al.*, 2006). The genus *Dictyota* falls under the tribe Dictyoteae, which is distinguished from Zonarieae based on the presence of one apical cell ((De Clerck *et al.*, 2006); Figure 1). Due to the complicated morphology of the Dictyoteae tribe, numerous taxonomic changes have been applied to its genera in the past two centuries (Bogaert *et al.*, 2020).



Figure 1. Taken from Bogaert *et al.* (2020) showing the apical meristem of a *Dictyota* species with a recently divided lens-shaped apical cell.

Species of *Dictyota* were originally classified based on a single-layered medulla and cortex, while other species with a multi-layered cortex or medulla were classified in the genus *Dilophus* or *Pachydictyon* (Figure 2; Table 1). A fourth species, *Glossophora*, was identified based on the presence of surface proliferations (Figure 2; Table 1). The genus *Glossophorella* was later described to classify species that have different number of medullary and cortex layers, along with surface proliferations (Nizamuddin & Campbell, 1995), however, De Clerck *et al.* (2006) synonymised this genus with *Dictyota*. De Clerck *et al.* (2006) further synonymised the genera *Glossophora* and *Pachydictyon* with *Dictyota*, using molecular data. *Dilophus* was synonymised with *Dictyota* after it was discovered that the number of cell layers can change due to external factors (Hörnig *et al.*, 1992). Finally, De Clerck *et al.* (2006) described two new genera supported by DNA data, namely *Rugulopteryx* and *Canistrocapus*. *Canistrocarpus* can be distinguished from *Dictyota* morphologically as they have multicellular paraphyses surrounding the antheridia of the male gametophyte, where *Dictyota* has unicellular paraphyses (Bogaert *et al.*, 2020).

Table 1. Taken from De Clerck *et al.* (2006) identifying the type specimen, defining characters and numbers of species of the different genera of the tribe Dictyoteae.

Genus	Type species	Defining characters	Currently recognized species
<i>Dictyota</i>	<i>D. dichotoma</i> (Hudson) Lamouroux	Medullary layers 1, cortical layers 1	~ 46
<i>Dilophus</i>	<i>Dil. gunnianus</i> J. Agardh	Medullary layers > 1, cortical layers 1	16
<i>Glossophora</i>	<i>G. kunthii</i> (C. Agardh) J. Agardh	Surface proliferations, medullary and cortical layers 1 to variable	3
<i>Glossophorella</i>	<i>G. dhofarensis</i> Nizamuddin and Campbell	Surface proliferations, medullary and cortical layers > 1 near the base	1 (– 2)
<i>Pachydictyon</i>	<i>P. furcellatum</i> J. Agardh [= <i>P. polycladum</i> (Kützinger) Womersley]	Medullary layers 1, cortical layers > 1	4

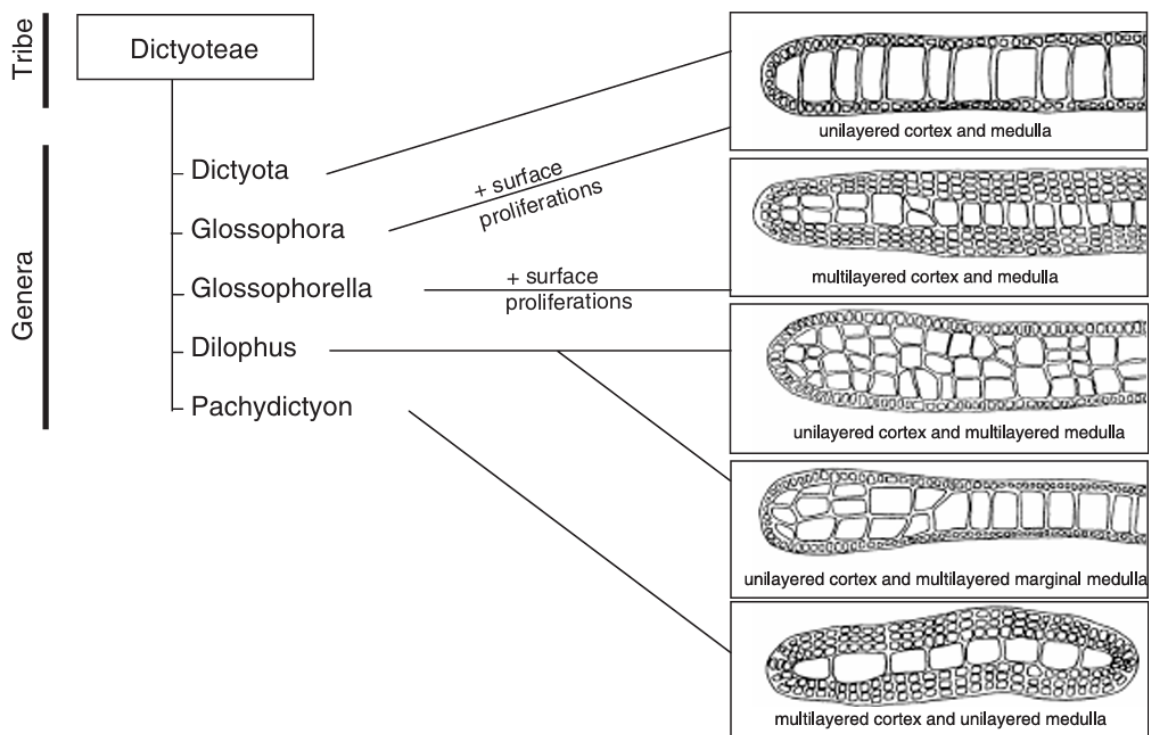


Figure 2. Taken from De Clerck *et al.* (2006) showing the morphological characters historically used to distinguish between the genera of the tribe Dictyoteae.

b) Biogeography, biology and ecology

Dictyota is a globally distributed genus, occurring in tropical, subtropical, and warm-temperate waters across the Atlantic, Pacific, and Indian Oceans (e.g. Hörnig *et al.* (1992), De Clerck (2003), Vieira *et al.* (2025a)). Species occupy a wide range of ecological niches, growing in subtidal areas as well as intertidal rock pools and in a few cases are found in deep-water habitats (Searles & Schneider, 1987; Tronholm *et al.*, 2008; Bogaert *et al.*, 2020). The genus is not uniformly seasonal worldwide – its seasonality varies by species and location. For example, populations of *D. dichotoma* in the Mediterranean regress during the warmest months, while Atlantic populations to the north decline mainly during the coldest months of the year (Steen *et al.*, 2019). *Dictyota dichotoma* occurring in Argentina, on the other hand, are present year-round (Gauna *et al.*, 2013). Furthermore, other species occurring in the Mediterranean do not show seasonal patterns like *D. dichotoma*, with the introduced *D. cyanoloma* occurring year-round in the Mediterranean (Aragay *et al.*, 2016).

Dictyota has a life cycle where the haploid gametophyte and diploid sporophyte phases are morphologically similar (Williams, 1904). Individuals of the genus are dioecious (having

only male or female reproductive organs) (Phillips *et al.*, 1990). Specimens can reproduce both sexually, and asexually through propagation (Herren *et al.*, 2006). These reproductive traits have direct implications for genetic diversity, as vegetative reproduction in seaweeds produces genetically identical clones while sexual reproduction and the recombination of genes increase genetic diversity (Johannesson *et al.*, 2011). Previous studies suggest the low genetic diversity observed in seaweed populations may be partly explained by the asexual reproduction by propagation or fragmentation (Johannesson *et al.*, 2011; Song *et al.*, 2025)

The genus *Dictyota* is ecologically important as it provides shelter, food, and substrate for invertebrates, fishes and microbial epibionts (Azzurro *et al.*, 2007; Carrión-Cortez *et al.*, 2010; McCarty & Sotka, 2013; Boisnoir *et al.*, 2019; Bogaert *et al.*, 2020; Altamirano-Cerecedo *et al.*, 2024). However, *Dictyota* can negatively affect other species, particularly corals. It has been shown that *Dictyota* both inhibits the recruitment of coral larvae and induces tissue mortality in adult corals through allelopathic compounds (Kuffner *et al.*, 2006; Rasher & Hay, 2010). These chemical defences are part of a diverse arsenal of secondary metabolites, which protect *Dictyota* from herbivory, biofouling and competition (Hardt *et al.*, 1996; De Clerck *et al.*, 2005a; Ktari *et al.*, 2010; Siless *et al.*, 2018; Rushdi *et al.*, 2022). This combination of ecological importance, chemical complexity, and broad biogeographic distribution makes *Dictyota* a key component of many tropical and subtropical ecosystems.

c) Applications

The rich secondary metabolite chemistry of *Dictyota*, particularly its diterpenes, has led to substantial interest in its biotechnological potential (Bogaert *et al.*, 2020). Although no *Dictyota*-derived compounds are used commercially, numerous *in vitro* studies demonstrate antimicrobial, antifungal, antiviral, and antitumor activities. Methanol extracts from *Dictyota humifusa* have been shown to have inhibiting acetylcholinesterase activity, which is known to be an effective treatment against Alzheimer's disease (Stirk *et al.*, 2007). Other extracts have been shown to induce apoptosis in cancer cells (Gomes *et al.*, 2015), while extracts from *Dictyota pfaffii* has shown potent anti-HIV-1 effect in cell lines (Pardo-Vargas *et al.*, 2014). These are only a few examples that illustrate that *Dictyota* shows great potential for drug discovery for different diseases.

Recently, research initiatives worldwide have started focusing on identifying novel ways to utilise marine organisms with the aim of developing more sustainable ways to meet the

demands of a growing global population. One such initiative is the COMBO project (Horizon Europe, 2024), an international collaboration funded by Horizon Europe. COMBO aims to identify biologically active compounds produced by a few selected seaweed and sponge taxa, including members belonging to the genus *Dictyota*, and to develop methods for their cultivation and application in the pharmaceutical and cosmetics industries.

The present study forms part of the COMBO and BEAP-MAR projects. Despite the promising findings mentioned above, most pharmacological research on *Dictyota* has occurred in North America, Oceania, and Europe (Altamirano-Cerecedo *et al.*, 2024), highlighting substantial opportunities for discovery in understudied regions. COMBO has identified South Africa as one such region, which may harbour novel species of both seaweeds and sponges with biotechnological and biomedical potential.

1.3. A closer look at the study site: South Africa

1.3.1. Biogeography of South Africa

The distribution of seaweeds is strongly influenced by their physiological tolerances – particularly their thermal tolerances – and therefore by local seawater temperature (Breeman, 1988). Regions that span multiple environmental gradients (temperature, nutrients, etc.) typically support greater species diversity because they provide a wider range of ecological niches and abiotic conditions. South Africa is a prime example: its coastline encompasses distinct oceanographic systems across its western, southern, and eastern shores (Spalding *et al.*, 2007; Griffiths *et al.* 2010; Smit *et al.*, 2013;).

In an attempt to create a biogeographic system to classify the ocean, Spalding *et al.* (2007) proposed the Marine Ecoregions of the World (MEOW) system. Within this framework, South Africa falls entirely within the Temperate Southern African realm, which is subdivided into two provinces and three ecoregions (Spalding *et al.*, 2007). The west coast forms part of the Benguela Province and the Namaqua ecoregion, dominated by the cold, nutrient-rich Benguela Current flowing northward toward the equator (Spalding *et al.*, 2007). The south coast constitutes the Agulhas Bank ecoregion and the east coast forms the Natal ecoregion – both part of the Agulhas Province, a warm-temperate region influenced by the southward-flowing Agulhas Current (Anderson *et al.*, 2009). The region between Cape Agulhas and the Cape Peninsula acts as a transition area between the warm-temperate and cool-temperate

waters, although it is still generally classified as warm-temperate. In contrast the west coast, north of the Cape Peninsula experiences strong environmental variability due to coastal upwelling and is typically regarded as cold-temperate (Stegenga *et al.*, 1997).

Bolton & Stegenga (2002), constructed a finer-scale biogeographic framework by dividing the South African coastline into 50km transects to examine patterns of inshore seaweed diversity (Figure 3). Subsequent analyses revealed that, the south coast, consistently supports the highest average species diversity, whereas the west coast supported the lowest (Bolton & Stegenga, 2002). Patterns within the brown algae mirrored this overall trend in seaweed diversity, with the south coast having slightly higher species diversity than the east coast and the species diversity in the east coast increasing with a decrease in latitude (Bolton & Stegenga, 2002). It is also worth mentioning that Bolton & Stegenga (2002) showed that ~12.5% of the diversity in South Africa consists of brown seaweeds, while ~18.5% is greens and the remaining ~69% is reds.

Finally, Anderson *et al.* (2009) expanded on previous work to delineate seaweed biogeographical Marine Provinces and transition zones in South Africa (Figure 3). Within this framework, South Africa is divided into three main provinces: the Benguela Marine Province (BMP) on the west coast, the Agulhas Marine Province (AMP) on the south coast, and the Indo-West Pacific Marine Province (IWPMP) in the north-eastern part of the country. In addition, two transition zones are recognised: a western transition zone (WTZ) between the BMP and the AMP, and an eastern transition zone (ETZ) between the AMP and IWPMP .

A defining feature of the west coast is that it forms part of a major upwelling region (Bolton, 1996). Although the cold water associated with upwelling contributes to low diversity, Bolton & Stegenga (2002) note that the high variability in temperature and nutrient conditions is likely a more significant driver, as many seaweeds cannot cope with rapid environmental fluctuations. Furthermore, this study suggests that while the east coast is generally less diverse than the south coast, this pattern may partly reflect sampling bias (Bolton & Stegenga, 2002). The south coast flora is relatively well documented, while large stretches of the east coast – particularly in the formerly known Transkei region – remain under-surveyed, indicating that true diversity may be underestimated (Bolton & Stegenga, 2002), and more studies are needed to better understand the seaweed diversity in South Africa.

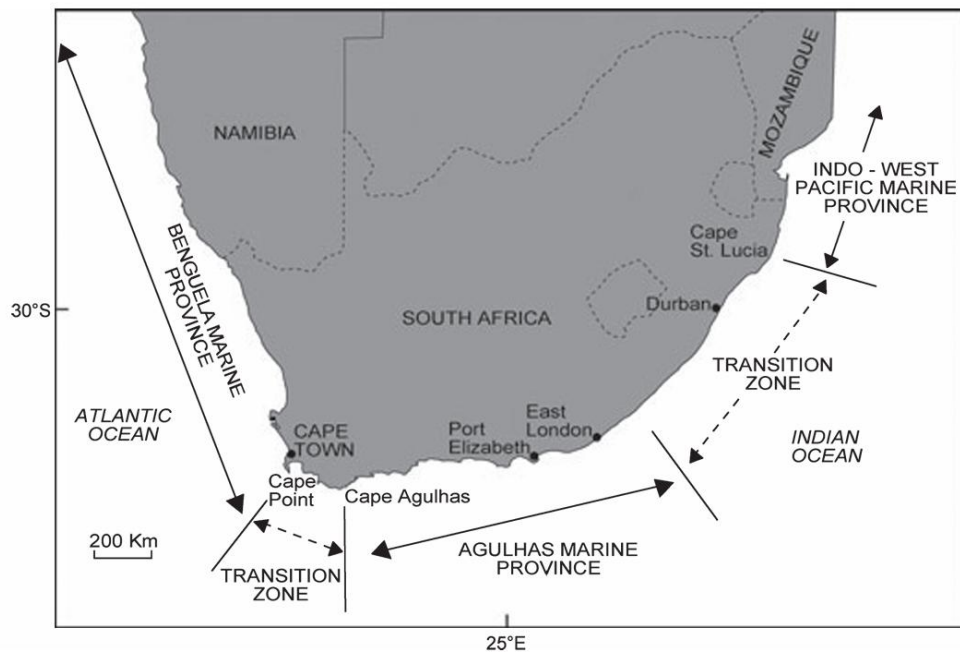


Figure 3. Map taken from Anderson *et al.* (2009) showing the different Marine Bioregions in South Africa

1.3.2. Seaweed diversity in South Africa

The first seaweed formally described from South Africa's coast was *Ecklonia maxima*, originally described as *Fucus maxima* by Osbeck in 1757 (Stegenga *et al.*, 1997; Prew *et al.*, 2024). Descriptions of algae on the South African coast increased significantly around the 1840s (Stegenga *et al.*, 1997). Taxonomic knowledge of South African seaweeds has continued to expand throughout the 20th and 21st century, with 547 recognised species in the 1980s, and nearly 800 species in 1997 (Stegenga *et al.*, 1997). This number increased further to more than 850 by the early 2000s (Bolton & Stegenga, 2002). Current data from Algaebase (Guiry & Guiry, 2025) indicate that approximately 871 seaweed species are now confirmed from South Africa, with a total diversity likely exceeding 900 species (Reddy, M.M., in unpublished data).

Furthermore, South Africa has a high level of endemism, with about 58% of reds, 33% of browns and 28% of greens being restricted to the southern African region (Stegenga *et al.*, 1997). This exceptional diversity has long been recognised, with major algal collections undertaken as early as the 1950s (Bolton & Stegenga, 2002). Three main resources; Stegenga *et al.* (1997), Anderson *et al.* (2016), and De Clerck *et al.* (2005a), each covering one of the coasts of South Africa, are used as a documentation of this diversity.

South Africa has a rich history of seaweed taxonomic research, particularly over the past three decades. Red algae have received the greatest taxonomic attention with numerous genus- and family-level revisions conducted in South Africa. The genera *Gracilaria* and *Gracilariopsis* (family Gracilariaceae) were first revised using morphology alone in 2004 (Iyer *et al.*, 2004), followed by a comprehensive review of the family in southern Africa using the small subunit rDNA and RUBISCO spacer sequences (Iyer *et al.*, 2005). Additional early work includes the description of *Gelidium pteridifolium* (Norris *et al.*, 1987) and a systematic revision leading to the merging of the genera *Gelidiopsis* and *Ceratodictyon* (Norris, 1987). Both of these studies were undertaken prior to widespread adoption of molecular systematics. Subsequent molecular studies built on this foundation (Norris *et al.*, 1987), revising taxa within the order Gelidiales, including *Onikusa* and *Suhria* (Tronchin *et al.*, 2002) (now treated as synonyms of *Gelidium*), *Ptilophora* (Tronchin *et al.*, 2004) and *Beckerella* (Tronchin & Bolton, 2003) (the latter being merged with *Ptilophora*), and *Gelidium*, *Pterocladia*, and *Aphanta* (Tronchin & Freshwater, 2007).

Molecular approaches have further revealed substantial hidden diversity within South African red algae. A molecular study of the *Laurencia* complex resulted in the description of five new species and highlighted an additional six undescribed species (Francis *et al.*, 2017), demonstrating the high amount of seaweed diversity in South Africa that might remain undescribed without the use of molecular tools. Similarly, a morphology-based review of *Plocamium* suggested the presence of eight species within South Africa (Simons, 1964). However, a subsequent study using DNA by Reddy *et al.* (2023a) revealed 14 species in the region, nearly doubling previous diversity estimates.

The first application of DNA-based species delimitation methods to South African taxa was conducted on the Bangiales, uncovering high levels of endemism as well as cryptic diversity (Reddy *et al.*, 2018) – both critical considerations for conservation planning. Continued work on this group led to the description of a new species that was previously overlooked, highlighting the potential of misidentification in the absence of molecular data (Reddy *et al.*, 2020b). This study also could not confirm with DNA two non-native species of *Pyropia* (Reddy *et al.*, 2020b), once again suggesting local species can be overlooked and misidentified as non-native species. Molecular studies on *Callithamnion* further revealed that biogeography can be used to easily identify morphologically similar species in the field (Reddy *et al.*, 2020a).

While the majority of taxonomic work in South Africa have been done on red algae, there are some integrative studies that have been conducted on green algae. For example, a molecular study done on cultivated and wild *Ulva* near seaweed farms revealed five new distribution records for South Africa (Bachoo *et al.*, 2023). This work has recently been expanded through investigating the biodiversity of the genus using a combination of morphological and molecular tools (Roberts, 2025; unpublished).

Despite the extensive taxonomic work undertaken in South Africa, integrative taxonomic studies of brown algae remain limited. This represents a significant opportunity to uncover undescribed and cryptic species, clarify endemism, and improve our understanding of species diversity in the region. Addressing this gap will contribute to essential baseline knowledge of South Africa's marine flora and support future conservation, ecological and applied research.

1.3.3. *Dictyota* in South Africa

Most of the taxonomic research done on the genus *Dictyota* has been conducted in North America, Oceania, Asia, and Europe (Altamirano-Cerecedo *et al.*, 2024, Vieira *et al.* 2025a & 2025b), leaving Africa comparatively understudied and highlighting the need for a modern, molecular-based taxonomic revision of the genus on the continent. In South Africa there is a genus-wide lack of DNA barcodes and at least one undescribed species has been known and documented for a decade (Anderson *et al.*, 2016). This absence of genetic data hampers accurate species identification and limits potential application including cultivation and sustainable exploitation. Below is a literature review of all recorded *Dictyota* species in South Africa. Records were compiled using relevant papers, field guides, and Algaebase (Guiry & Guiry, 2025). All species were recorded along with their type locality, distribution in South Africa, and the GenBank accession numbers of specimens of the species from South Africa (Table 2) (Sayers *et al.*, 2025a).

Table 2. Summary of the *Dictyota* species previously recorded in South Africa, with available South African barcodes. *Rugulopteryx suhrii* and *Canistrocarpus cervicornis* are included in this table as they were previously described as *Dictyota suhrii* and *Dictyota cervicornis*. Species and genera names are in alphabetic order.

Species	Source	Type locality	South African distribution	South African barcodes		
				<i>psbA</i>	<i>rbcL</i>	Cox1
<i>Canistrocarpus cervicornis</i>	De Clerck <i>et al.</i> 2005	Key West, Florida, USA	Mission rocks (KZN) northwards	MW224483	-	-
<i>Dictyota acutiloba</i>	Delva <i>et al.</i> 2023	Oahu, Hawaiian Archipelago	Northern KwaZulu-Natal (Dog Point and Lala Nek)	MW224579, MW224578	-	-
<i>Dictyota bartayresiana</i>	Silva <i>et al.</i> 1996	Antilles, West Indies	Indian Ocean	-	-	-
<i>Dictyota ceylanica</i>	Silva <i>et al.</i> 1996	Sri Lanka	Indian Ocean	-	-	MW223448
<i>Dictyota ciliolata</i>	De Clerck <i>et al.</i> 2005	La Guaira, Venezuela	Mabibi (KZN) northwards	MW224793, MW224792, MW224791, MW224790	-	-
<i>Dictyota dichotoma</i>	Stegenga <i>et al.</i> 1997; Anderson <i>et al.</i> 2016	Walney Island, Lancashire, England	Langebaan (WC) to Natal (EC)	MW224944, MW224943, MW224942, GU255527, GU255514	MW223186	MW223967, MW223920, MW223919, MW223918, MW223917
<i>Dictyota friabilis</i>	De Clerck <i>et al.</i> 2005	Tafaa Point, Tahiti	Northern KwaZulu-Natal	-	-	-
<i>Dictyota hamifera</i>	De Clerck <i>et al.</i> 2002	Tahiti, between Papenu and Huau	Northern KwaZulu-Natal (Sodwana)	MW225072	-	-
<i>Dictyota humifusa</i>	De Clerck <i>et al.</i> 2005	Punta Chengue, Santa Marta, Departamento del Magdalena, Colombia	Isipingo (KZN) northward	MW225107	-	-

<i>Dictyota implexa</i>	Silva <i>et al.</i> 1996	Mediterranean Sea	Indian Ocean (recorded as <i>D. linearis</i>)	-	-	-
<i>Dictyota liturata</i>	De Clerck <i>et al.</i> 2005; Stegenga <i>et al.</i> 1997; Anderson <i>et al.</i> 2016	'Cape of Good Hope', South Africa	South African endemic, Kommetjie (WC) to Umhlali (KZN)	GQ425214	-	-
<i>Dictyota naevosa</i>	De Clerck <i>et al.</i> 2005; Stegenga <i>et al.</i> 1997; Anderson <i>et al.</i> 2016	Algoa Bay, Eastern Cape Province, South Africa	Cape Peninsula (WC) to Sodwana Bay (KZN)	MW225245, MW225244, MW225243, MW225242, JQ061067		MW224127, MW224126, MW224125, JQ061105
<i>Dictyota rigida</i>	De Clerck <i>et al.</i> 2002	Kunduchi, Dar es Salaam, Tanzania	Northern KwaZulu-Natal (Mabibi and Sodwana Bay)	-	-	-
<i>Dictyota sp. 1</i> (referred to as <i>D. sp.7</i> by X)	Anderson <i>et al.</i> 2016	-	False Bay (WC) to Isipingo (KZN)	MW225532, MW225531, MW225529	MW223303, MW223302, MW223301, LN871955, LN871944	MW224260, MW224259, MW224258, MW224257, LN871967
<i>Rugulopteryx suhrii</i>	De Clerck <i>et al.</i> 2005	Algoa Bay, Eastern Cape Province, South Africa	South African endemic, Algoa Bay (EC) to Isipingo (KZN)	-	-	MK516741
<i>Dictyota mertensii</i>	-	Salvador, Brazil	Aliwal Shoal to Sodwana (KZN)	MW225237, MW225236, MW225225	-	-
<i>Dictyota robusta</i>	-	Port Phillip Heads, Victoria, Australia	All collected from Protea Banks (KZN)	MW225604, MW225603, MW225602, MW225601, MW225599	MW223317	MW224301, MW224300, MW224299, MW224298
<i>Dictyota sandvicensis</i>	-	Oahu, Hawaiian Arcipelago	Sodwana (KZN)	MW225337	MW223271	MW224161

<i>Dictyota stolonifera</i>	-	Masachapa, Nicaragua, Pacific Ocean	Dog Point and Mabibi (KZN)	MW225565, MW225566	-	-
-----------------------------	---	-------------------------------------	----------------------------	--------------------	---	---

*Where there were more than 5 sequences for a specific gene of one species, only the first five were included in the table. Unverified samples were not added to the table. Species that have not been formally recorded in South Africa, but for which there are South African sequences available on GenBank is shown in blue. Species that have been moved to different genera are shown in green

The genus *Dictyota* is one of South Africa's understudied and underutilised seaweed genera. Historically, 15 different species of *Dictyota* have been formally recorded from the region (Table 2). The majority of the *Dictyota* diversity has been recorded on the east coast of South Africa, where ten species appear to occur exclusively (Table 2). In contrast, *Dictyota* is almost entirely absent from the west coast, with a single exception: Langebaan, the only locality north of Cape Town where the genus has been recorded (Table 2). Langebaan is known to possess atypical abiotic conditions relative to the exposed cold-temperate west coast and often functions as a climate for species more typical of the south coast (De Gruyter *et al.*, 2001).

Two of the fifteen species recorded have been reassigned to other genera now recognised as *Rugulopteryx suhrii* and *Canistrocarpus cervicornis* (De Clerck *et al.*, 2006). *Dictyota acutiloba* has been collected from Lala Nek and Dog Point in KwaZulu-Natal. This species, however, is morphologically similar to *Canistrocarpus cervicornis* and caution should be taken when assigning a morphological identity. Vieira *et al.* (2021) has barcoded a South African specimen identified as *C. cervicornis*, suggesting this species occurs within South Africa despite having a type locality in the Hawaiian Archipelago.

Three species – *Dictyota ceylanica*, *Dictyota bartayresiana*, and *Dictyota implexa* (recorded as *D. linearis*) – were recorded by Silva (1996) as occurring in South Africa, but no specific sampling locations were documented. Because Silva (1996) sampled broadly within the Indian Ocean as far south as Gqeberha, it is reasonable to infer that these records likely originate from the east coast. However, these records should be treated with scepticism. Of these records, *Dictyota ceylanica* is the only species recollected again and sequenced (Vieira *et al.*, 2021). This sample was sequenced only for the cytochrome c oxidase subunit 3 (cox3) gene, and was morphologically identified as *Dictyota cf. ceylanica*, which also suggests there is some uncertainty to the identity of the species. No other records of *Dictyota bartayresiana* or *Dictyota implexa* exists, causing some scepticism over whether these species do occur on South Africa's coast.

Two species – *Dictyota ciliolata* and *Dictyota rigida* – have been recorded only in the northern-most part of South Africa, being restricted to north of Sodwana. Both have been barcoded, confirming their presence in South Africa. However, *Dictyota rigida*, is morphologically similar to *Rugulopteryx suhrii* (De Clerck, 2003), and caution should be used when assigning identity based on morphology. *Dictyota friabilis* and *Dictyota hamifera* were also both recorded in northern KwaZulu-Natal, however, no South African specimen has been barcoded to date. *Dictyota humifusa* has a slightly broader range from Isipingo (Durban) northwards and has been barcoded for South Africa.

Four species of *Dictyota* exhibit broader distribution ranges across South Africa, suggesting these species have a higher tolerance for colder temperatures, indicating wider ecological niches. These include *Dictyota naevosa*, *Dictyota liturata*, *Dictyota dichotoma* and *Dictyota* sp. 1 (also referred to as *D. 'green lips'*). The former two species both have a type locality in South Africa, in Algoa Bay (Eastern Cape) and the Cape of Good Hope (Western Cape) respectively, and have both been recorded from the Western Cape to northern KwaZulu-Natal. These species have been sequenced, however, currently *Dictyota liturata* has only been sequenced from the east coast despite having a type locality more than 1 000 km away. This discrepancy is potentially problematic as the species' type locality is the Cape of Good Hope in the Western Cape, raising the possibility that east-coast individuals represent a distinct lineage that is morphologically similar but genetically divergent and adapted to different conditions.

The most widely distributed species of *Dictyota* in South Africa is the type species of the genus, *Dictyota dichotoma*. This species has both a narrow and a broad “normal” form in South Africa (Stegenga *et al.*, 1997). Although both forms have been sequenced and are confirmed to be the same species in Europe (Tronholm *et al.*, 2010a), this has not been demonstrated for South African specimens. De Clerck (2003) suggests that only the slender form of *Dictyota* occurs in South Africa, and no normal form of *Dictyota* has been sequenced to confirm its presence in the country. A closer look should be taken to determine whether both forms occur in South Africa.

Finally, one species remains formally undescribed but has been called *Dictyota* ‘green lips’ or *D. sp. 1* (Anderson *et al.*, 2016), by previous researchers. This species looks like *Dictyota dichotoma* but has a green iridescent border. No formal description has been made for this species, despite it being recorded on the south coast seaweed site (Anderson *et al.*, 2016).

Apart from the species that have been formally recorded in South Africa, other records also exist. On GenBank there are four species that have been sequenced from South Africa but not formally recorded (Table 2), namely *D. mertensii*, *D. robusta*, *D. sandvicensis* and *D. stolonifera*. These sequences need to be compared with type sequences to confirm their identity.

2. Rationale

Understanding the diversity of *Dictyota* in South Africa is essential for multiple reasons. As a widespread and ecologically influential genus in tropical and warm-temperate reefs (Tronholm *et al.*, 2008; Bogaert *et al.*, 2020), *Dictyota* contributes to ecosystem functioning, primary production, and habitat structure, and plays key roles in species interactions such as competition, herbivory, and chemical defence (Wanders, 1976; Azzurro *et al.*, 2007; Rasher & Hay, 2010; McCarty & Sotka, 2013; Boisnoir *et al.*, 2019). Accurately documenting the genus is central to understanding patterns of endemism, cryptic diversity, and regional biogeography, all of which inform conservation planning and assessments of marine biodiversity (Bickford *et al.*, 2007; Brodie *et al.*, 2009). A revised and accurate species inventory is therefore crucial for both biodiversity conservation and for interpreting how these species contribute to ecosystem processes. After establishing this foundation, it will also be possible to evaluate the potential application of this genus, including possible contributions to the blue bioeconomy through bioactive metabolites and cultivation potential.

Traditionally, species of *Dictyota* were identified using morphological traits; however, the genus has long proved taxonomically challenging (Tronholm *et al.*, 2010a). Many species display marked polymorphism or pleomorphism, such as the multiple growth forms of *Dictyota dichotoma* (Stegenga *et al.*, 1997). Others appear nearly indistinguishable externally, leading to cryptic species complexes where morphologically similar specimens represent genetically distinct lineages (De Clerck *et al.*, 2001; Tronholm *et al.*, 2010a; Altamirano-Cerecedo *et al.*, 2024). These issues complicate accurate species delimitations, obscure true biogeographic patterns, and limit our ability to assess ecological roles, monitor population change, or detect rare or endemic species.

Molecular tools have made it easier to distinguish between different species (Altamirano-Cerecedo *et al.*, 2024), making it an important tool when resolving species boundaries in

morphologically difficult genera like *Dictyota*. Molecular markers provide objective evidence for distinguishing lineages, uncovering cryptic diversity, and validating morphological identification (e.g. De Clerck, 2003; Tronholm *et al.*, 2010a; Lozano-Orozco *et al.*, 2015). Given the high degree of seaweeds that are morphologically plastid or cryptic, modern taxonomic reviews need to increasingly incorporate integrative approaches that combines morphological and molecular data (Reddy, 2018; Reddy *et al.*, 2023b). This is especially important for genera that may harbour undescribed diversity or regional endemics whose conservation status cannot be evaluated without reliable identification.

The aim of this project is therefore to taxonomically review the genus *Dictyota* in South Africa, while also assessing the distribution of species, thereby contributing to foundational knowledge needed for future conservation and possible application of this genus. The objectives include using an integrative approach to (1) verify historical species records, (2) identify and describe any new species, and (3) update the distribution records of each species found in South Africa. Three molecular markers – *psbA*, *rbcL*, and *cox1* – are commonly used in the systematics of *Dictyota*. In this study, these genes were targeted to reassess species boundaries, verify historical records and identify potentially undescribed taxa of *Dictyota* in South Africa. The molecular data was complemented with morphological data of specimen to get a clearer picture of *Dictyota*, thereby providing baseline knowledge for biodiversity assessments, conservation planning, ecological research, and any future use of the genus in the blue bioeconomy.

3. Materials and methods

3.1. Sample collection and processing

A total of 83 samples of *Dictyota* were collected between 2006-2025 (Table 3). These samples form part of two biological collections, namely the D-list, a comprehensive collection of seaweeds associated to the University of Cape Town, and the C-list, a more recent collection associated with the COMBO project. Samples were collected over approximately 2 000 km of coastline, from Cape Town (Buffel's Bay) to the north-eastern border of South Africa (Banga Nek) (Figure 4). The collections spanned over four of the five different marine provinces of South Africa (Anderson *et al.*, 2009). The west coast was not sampled as *Dictyota* has historically not been collected in the cold-temperate, upwelling-dominated BMP.

Samples from the D-list were historically preserved as (1) a pressed voucher sample deposited in the Bolus Herbarium (BOL), (2), a DNA subsample dried in silica gel, and (3) a morphological subsample for selected taxa stored in a 4% formalin solution buffered with seawater. Preliminary samples from the D-list allowed for the identification of areas and species that needed to be targeted for collection to get a more comprehensive view of the *Dictyota* found in South Africa. Samples collected for the C-list formed part of the COMBO project (Horizon Europe, 2024). Collections took place during low tide, and where possible during a spring low. Most samples were collected either as part of shore collections or while snorkelling between 0 and 5 m depths, with only a few specimens collected while SCUBA diving between 5 and 12 m depths. Voucher specimens were pressed and dried on herbarium paper – these vouchers will be deposited at the Bolus Herbarium (BOL) at the University of Cape Town, South Africa. Molecular subsamples were made by adding a piece of the sample to silica gel and drying it out. Morphological subsamples were made by adding a section of the sample to 4% formalin buffered with seawater. All the South African samples used during this study are recorded in Table 4 and sampling localities can be seen in Figure 4.

When *Dictyota* samples of either collection did not have DNA subsamples for analysis, the pressed specimen was subsampled to use for DNA extractions and amplification, as well as for morphological analysis. Some samples with DNA subsamples had no voucher or morphological (formalin) subsample. These samples, therefore, could only be used for

molecular analysis. Along with these samples, a single specimen from Tristan da Cunha was included in the analysis as the sample resembled the morphology and was given the field ID of *Dictyota liturata* (Stegenga *et al.*, 1997). This was done to ensure material from close to the type locality was sequenced and to determine whether the species truly is endemic to South Africa as it has been previously recorded to be (Stegenga *et al.*, 1997), or whether it occurred more broadly in the Atlantic Ocean.

Table 3. Specimen list of *Dictyota* along the South African coast including new and historic collections.

Voucher ID	Collection site	Province	Coordinates	Depth (m)	Sampling date
C1	Happy wanderers	KwaZulu-Natal	30.3578 °S, 30.71833 °E	0	10/01/2024
C2	Happy wanderers	KwaZulu-Natal	30.3578 °S, 30.71833 °E	0	10/01/2024
C11	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	12/01/2024
C12	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	12/01/2024
C13	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	12/01/2024
C49	Miller's Point	Western-Cape	34.2325 °S, 18.47637 °E	0	02/04/2024
C52	Miller's Point	Western-Cape	34.2325 °S, 18.47637 °E	8	02/04/2024
C194	Miller's Point	Western-Cape	34.2325 °S, 18.47637 °E	0	23/08/2024
C199	Miller's Point	Western-Cape	34.2325 °S, 18.47637 °E	0	23/08/2024
C200	Miller's Point	Western-Cape	34.2325 °S, 18.47637 °E	0	23/08/2024
C201	Buffel's Bay	Western-Cape	34.3206 °S, 18.4615 °E	0	23/08/2024
C202	Buffel's Bay	Western-Cape	34.3206 °S, 18.4615 °E	0	23/08/2024
C203	Buffel's Bay	Western-Cape	34.3206 °S, 18.4615 °E	0	23/08/2024
C206	Buffel's Bay	Western-Cape	34.3206 °S, 18.4615 °E	0	23/08/2024
C207	Buffel's Bay	Western-Cape	34.3206 °S, 18.4615 °E	0	23/08/2024
C219	Strand	Western-Cape	34.1167 °S, 18.82416 °E	0	14/11/2024
C220	Strand	Western-Cape	34.1167 °S, 18.82416 °E	0	14/11/2024
C275	Herold's Bay	Western-Cape	34.0553 °S, 22.38947 °E	0	10/04/2025
C276	Herold's Bay	Western-Cape	34.0553 °S, 22.38947 °E	0	10/04/2025
C277	Herold's Bay	Western-Cape	34.0553 °S, 22.38947 °E	0	10/04/2025
C278	Gericke's Punt, Sedgefield	Western-Cape	34.0362 °S, 22.76611 °E	1	11/04/2025
C279	Summerstrand Gqeberha	Eastern Cape	33.9835 °S, 25.67132 °E	0	13/04/2025
C280	Summerstrand Gqeberha	Eastern Cape	33.9835 °S, 25.67132 °E	0	13/04/2025
C281	Summerstrand Gqeberha	Eastern Cape	33.9835 °S, 25.67132 °E	0	13/04/2025
C282	Summerstrand Gqeberha	Eastern Cape	33.9835 °S, 25.67132 °E	0	13/04/2025
C283	Surfers Point, Jeffrey's Bay	Eastern Cape	34.0267 °S, 24.93111 °E	0	13/04/2025
C285	Surfers Point, Jeffrey's Bay	Eastern Cape	34.0267 °S, 24.93111 °E	0	13/04/2025
C286	Beacon Island, Plettenberg Bay	Western-Cape	34.0599 °S, 23.38038 °E	0	14/04/2025
C287	Beacon Island, Plettenberg Bay	Western-Cape	34.0599 °S, 23.38038 °E	0	14/04/2025
C288	Beacon Island, Plettenberg Bay	Western-Cape	34.0599 °S, 23.38038 °E	0	14/04/2025
C289	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	0	15/04/2025
C290	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	0	15/04/2025
C291	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	0	15/04/2025
C292	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	0	15/04/2025
C293	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	0	15/04/2025
C294	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	0	15/04/2025

C295	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	27/04/2025
C296	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	27/04/2025
C297	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	27/04/2025
C298	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	27/04/2025
C299	Park Rynie	KwaZulu-Natal	30.3133 °S, 30.74361 °E	0	27/04/2025
C301	Ballito	KwaZulu-Natal	29.5017 °S, 31.24083 °E	0	28/04/2025
C302	Ballito	KwaZulu-Natal	29.5017 °S, 31.24083 °E	0	28/04/2025
C304	Ballito	KwaZulu-Natal	29.5017 °S, 31.24083 °E	0	28/04/2025
C305	Ballito	KwaZulu-Natal	29.5017 °S, 31.24083 °E	0	28/04/2025
C310	Port Edward	KwaZulu-Natal	31.0236 °S, 30.24556 °E	0	29/04/2025
C311	Port Edward	KwaZulu-Natal	31.0236 °S, 30.24556 °E	0	29/04/2025
C312	Port Edward	KwaZulu-Natal	31.0236 °S, 30.24556 °E	0	29/04/2025
C313	Port Edward	KwaZulu-Natal	31.0236 °S, 30.24556 °E	0	29/04/2025
C373	Glencairn	Western-Cape	34.1618 °S, 18.4314 °E	0	8/11/2022
C374	Dalebrook, Kalk Bay	Western-Cape	34.124 °S, 18.45295 °E	0	5/08/2024
D1030	Cape Vidal	KwaZulu-Natal	28.1283 °S, 32.55974 °E	-	25/11/2011
D1092	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1093	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1094	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1095	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1096	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1097	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1098	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1099	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	13/04/2012
D1126	Buffel's Bay	Western Cape	34.3206 °S, 18.4615 °E	-	24/08/2012
D1131	Schoenmakerskop	Eastern Cape	34.0417 °S, 25.53897 °E	-	20/09/2012
D1143	Nature's Valley	Western-Cape	34.9888 °S, 23.54746 °E	-	12/12/2012
D1277	Buffel's Bay	Western-Cape	34.3206 °S, 18.4615 °E	-	30/05/2013
D1302	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	11/07/2013
D1312	Hluleka	Eastern Cape	31.8357 °S, 29.29132 °E	-	20/08/2013
D1330	Hluleka	Eastern Cape	31.8357 °S, 29.29132 °E	-	21/08/2013
D1331	Hluleka	Eastern Cape	31.8357 °S, 29.29132 °E	-	21/08/2013
D1343	Hluleka	Eastern Cape	31.8357 °S, 29.29132 °E	-	23/08/2013
D1344	Hluleka	Eastern Cape	31.8357 °S, 29.29132 °E	-	23/08/2013
D1364	Banga Nek	KwaZulu-Natal	27.0098 °S, 32.8644 °E	-	3/10/2013
D1839	Dwesa Point	Eastern Cape	32.2885 °S, 28.86506 °E	-	13/05/2014
D1851	Dwesa Point	Eastern Cape	32.2885 °S, 28.86506 °E	-	13/05/2014
D2180	Glencairn	Western-Cape	34.1618 °S, 18.4314 °E	-	20/04/2014
D2184	Bordjiesrif	Western-Cape	34.3131 °S, 18.46226 °E	-	21/04/2015
D2604	Morgan Bay	Eastern Cape	32.7107 °S, 28.33996 °E	-	5/05/2016
D2712	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	22/06/2016
D2713	Cape St. Francis	Eastern Cape	34.2134 °S, 24.83762 °E	-	22/06/2016
KZN_16_001	Sodwana	KwaZulu-Natal	27.54 °S, 32.67864 °E		08/01/2016
KZN_16_009	Sodwana	KwaZulu-Natal	27.54 °S, 32.67864 °E	0-1	08/01/2016
KZN_16_033	Sodwana	KwaZulu-Natal	27.54 °S, 32.67864 °E	0-1	08/01/2016
KZN_16_116	Raggie's Reef, Sodwana	KwaZulu-Natal	27.54 °S, 32.67864 °E	0-1	11/01/2016
KZN_16_134	Mabibi	KwaZulu-Natal	27.0098 °S, 32.7117 °E	0-1	12/01/2016

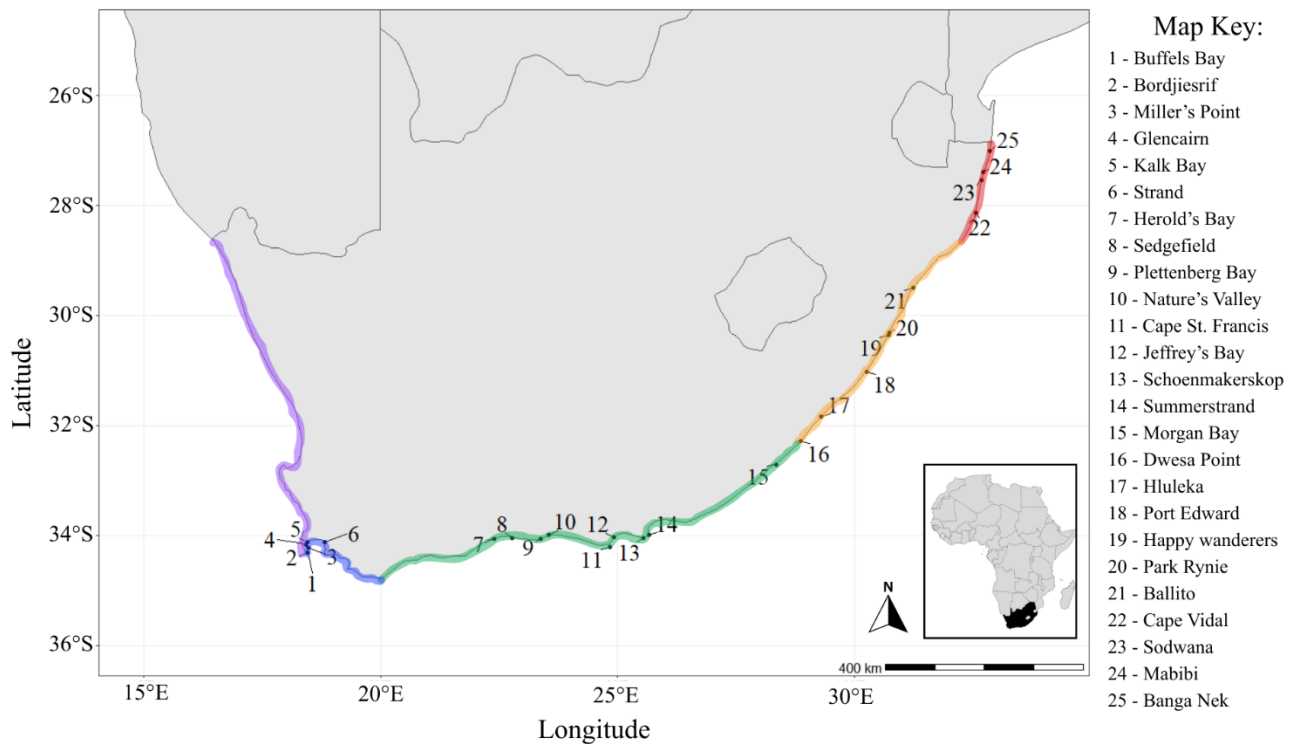


Figure 4. Map of South Africa showing all the sampling localities for this study. The colours show the different marine provinces of Anderson *et al.* (2009); Purple: Benguela Marine Province, Blue: Western Transition Zone, Green: Agulhas Marine Province, Orange: Eastern Transition Zone, Red: Indo-west Pacific Marine Province.

3.2. Morpho-anatomical analysis

Morphological and anatomical features were measured and used as supporting data for the molecular data. The data was also used to describe new species.

3.2.1. Morphological analysis

The pressed voucher specimens were used for the morphological analysis. Photographs of each sample was taken and uploaded to ImageJ (Rasband, 2018). Measurements were then made for the total height of the sample, as well as length (L), distal width (DW) and proximal width (PW) of ten interdichotomies (Figure 5). Where samples were too small to have 10 interdichotomies, measurements were made for all the available interdichotomies. Notes were also made on the branching pattern and colour of the specimen.

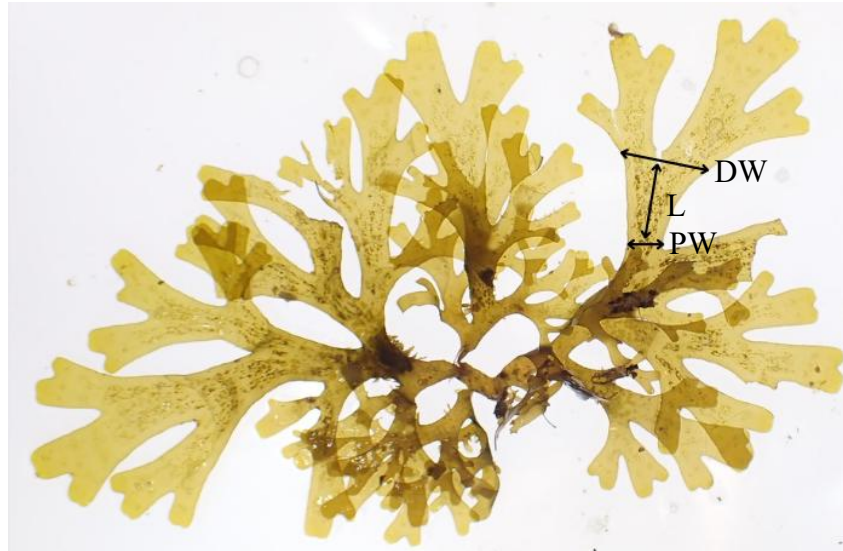


Figure 5. Picture of a *Dictyota* sample, showing the measurement of the interdichotomies.

3.2.2. Anatomical analysis

Formalin samples were analysed using a Leica DM500 light microscope for internal anatomy. Photographs of cells were taken using a Leica Flexacam i5 microscope camera. In the case where no formalin samples were available, dried samples were rehydrated by leaving the sample in artificial seawater for ~1 hour. Both the surface view and transverse sections were observed for the anatomical analysis, with transverse sections being prepared using a sharp scalpel blade (Figure 6). For each specimen 20 measurements were taken for both cortical and medullary cell widths and lengths, and 10 measurements were taken for the cell heights. The shape of apices was noted, and notes were also made on the sporangia, gametangia, and hair tufts or surface proliferations when these were visible.

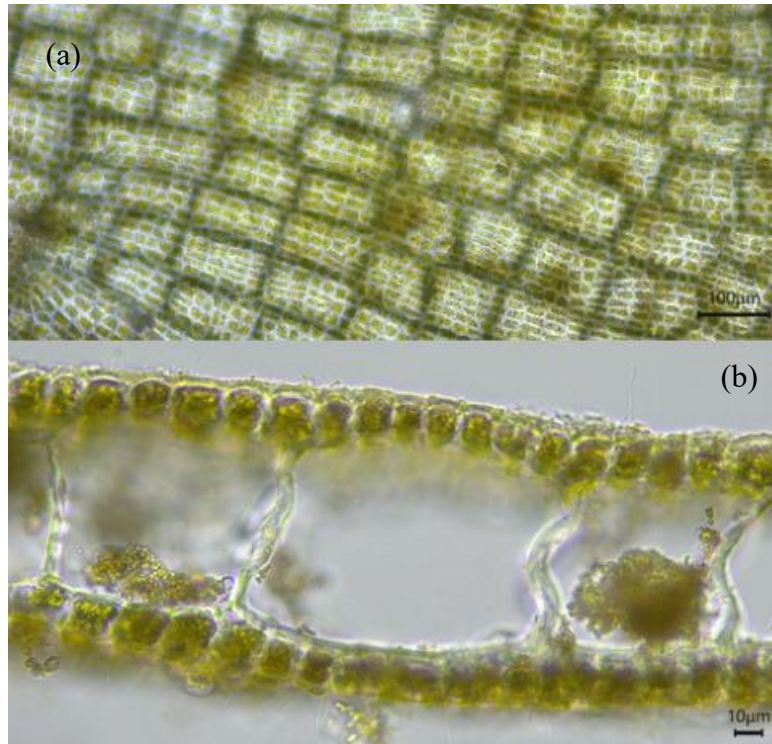


Figure 6. Photograph showing the (a) surface view, and (b) cross section of a *Dictyota* specimen. The medullary cells are the larger cells, and the cortical cells are the smaller cells surrounding the medullary cells in the cross section.

3.3. Phylogenetic analysis

3.3.1. Molecular work

Dictyota samples were subsampled and DNA was extracted using the Qiagen DNAeasy ® Plant Mini kit (Qiagen Inc.) following the manufacturer's instructions with the following adjustments:

- a) 20 µl of Proteinase K was added to the sample before incubation.
- b) Samples were incubated for three hours at 60 °C.
- c) Only 50 µl Buffer AE was used for elution, and this step was not repeated.
- d) For problematic samples, the Buffer AP1 was swapped out for a CTAB buffer, and then the Qiagen DNAeasy ® Plant kit was followed incubation.

Polymerase chain reactions (PCR's) were performed on the extracted DNA using an Applied Biosystems ProFlex PCR System . The plastid-encoded PSII reaction center protein D1 (*psbA*) and RUBISCO LSU (*rbcL*) genes were primarily targeted, with the Cytochrome c

oxidase subunit 1 (cox1 gene) targeted to represent an additional independent genome region. The primers used during PCR amplification was:

- a) **psbA**: *psbAF* (5' ATGACTGCTACTTTAGAAAGACG 3') and *psbAR2* (5' TCATGCATWACTTCCATACCTA 3') (Yoon *et al.*, 2002; Silberfeld *et al.*, 2010; Nelson *et al.*, 2019).
- b) **rbcL**: *DRL2F* (5' TACGTTTAGAAGATATGAGAAT 3') and *DRL2R* (5' WGCCCAATCCATATCRAAGAA 3') (Hwang *et al.*, 2005; Nelson *et al.*, 2019).
- c) **Cox1**: *GazF2* (5' CCAACCAAYAAAGA TATWGGTAC 3') and *GazR2* (5' GGAT GACCAAARAACCAAAA 3') (Lane *et al.*, 2007).

The PCR reaction mixture had a total volume of 25 µl and consisted of 23 µl of a master mix and 2 µl of DNA. The master mix (25 µl) always consisted of 12.5 µl of DreamTaq (Thermo Scientific™), with the quantity of the primers and water being adjusted according to the primer concentration. Primer concentration was changed between 0.2 µM, 0.5 µM and 1µM to optimise for each sample. The PCR thermal profile for the different genes can be seen in Table 5 and 6.

Table 4. Thermal profile for the PCR amplification of genes *cox1* and *rbcL*. Adapted from Delva *et al.* (2024)

	Temperature (°C)	Time	Cycles
Initial denaturation	94	3 min	1
Denaturation	94	45 sec	40
Annealing	40-55	45 sec	
Elongation	72	1 min	
Final elongation	72	6 min	1

Table 5. Thermal profile for the PCR amplification of *psbA* gene. Adapted from Delva *et al.* (2024).

	Temperature (°C)	Time	Cycles
Initial denaturation	94	3 min	1
Denaturation	94	1 min	35
Annealing	40-55	1 min	
Elongation	72	2 min	
Final elongation	72	10 min	1

Once PCRs were run, the PCR products were assessed on a 1% agarose gel to check for fragment size and see whether the PCR was successful. When a product produced a bright band that corresponded with the right base pair length for the gene, the sample was cleaned using ExoSAP-IT Express PCR Product Cleanup (Applied Biosystems™) and sent for sequencing at either LGC genomics or Eurofins. The DNA sequences were then edited using the BioEdit Sequence Alignment Editor version 7.2 (Hall, 1999). To determine a preliminary identification for samples, sequences were put through the Nucleotide BLAST software (Altschul *et al.*, 1990).

For each gene, relevant sequences generated by previous research were downloaded from GenBank (Sayers *et al.*, 2025) and added to the samples generated during this study. AlgaeBase (Guiry & Guiry, 2025) was used to create a list of all the accepted species of *Dictyota* across the globe. The type locality of each species was recorded, and notes were made on whether there were any sequences available on GenBank for each species (Table 7). For the species that had available sequences, these sequences were downloaded. Where possible type specimen or samples collected from or near the type locality of the species were selected and added to the alignment file. All the South African *Dictyota* sequences on GenBank were also downloaded and added to the alignment. A total of 182 *psbA*, 84 *rbcL* and 123 *cox1* were downloaded from GenBank. The sequences used were all recorded with their accession numbers, sample name and sampling location (Supplementary table 1). The sequences for each gene were then aligned in BioEdit version 7.2 (Hall, 1999) using the ClustalX Multiple Alignment clustering program. All sequences generated during this study were uploaded onto GenBank, accession codes of these sequences are available in Supplementary table 2.

Table 6. All accepted species of *Dictyota* with the type locality, whether there are any sequences available for the species, and the accession numbers of sequences from- or close to the type locality.

Species name	Type locality	Barcodes	<i>psbA</i>	<i>rbcL</i>	<i>cox1</i>
<i>Dictyota acutiloba</i> J.Agardh, 1848 C	Oahu, Hawaiian Archipelago	✓	OQ792182	OQ792199	OQ792175
<i>Dictyota adhaerens</i> Noda, 1965 C	Tassha, Sado Island, Japan	x			
<i>Dictyota adnata</i> Zanardini, 1878 C	Kepulauan Kai, Indonesia	x			
<i>Dictyota aegerrima</i> (Allender & Kraft) De Clerck, 2006 C	Far Rocks, Lord Howe Island	x			
<i>Dictyota alternifida</i> J.Agardh, 1894 C	Port Phillip Heads, Victoria	✓	MW224597		
<i>Dictyota bartayresiana</i> J.V.Lamouroux, 1809 C	Antilles, West Indies	✓	GQ425189	MW223149	GQ425129
<i>Dictyota bifurca</i> J.Agardh, 1894 C	Port Denison, Queensland, Australia	x			
<i>Dictyota binghamiae</i> J.Agardh, 1894 C	Santa Barbara, California, USA	✓			
<i>Dictyota canaliculata</i> De Clerck & Coppejans, 1997 C	Patch Reef east of Loloata Island, Port Moresby, Papua New Guinea	✓			
<i>Dictyota canariensis</i> (Grunow) Tronholm, 2013 C	Tenerife, Canary Islands	✓	MW224665	MW223165	
<i>Dictyota caribaea</i> Hörnig & Schnetter, 1992 C	Acuario, Isla de San Andrés, Colombia, Caribbean Sea	✓			
<i>Dictyota ceylanica</i> Kützing, 1859 C	Sri Lanka	✓			
<i>Dictyota chalcicueyecanensis</i> Lozano-Orozco & Senties, 2016 C	Punta Puntillas, Veracruz, México. (18.4655° N, 95.1722° W)	✓	KX819256		KX819253
<i>Dictyota ciliolata</i> Sonder ex Kützing, 1859 C	La Guaira, near Caracas, Venezuela	✓	MF182634	MF182639	
<i>Dictyota concrescens</i> W.R.Taylor, 1945 C	Point Hughes, Cabo San Lazaro, Baja California	x			
<i>Dictyota coriacea</i> (Holmes) I.K.Wang, Hy.S.Kim & W.J.Lee, 2004 C	Enoura, Japan	x			
<i>Dictyota crenulata</i> J.Agardh, 1847 C	San Agustín [Pacific Mexico]	✓	MK516780	GU290253	LN871961
<i>Dictyota cribrosa</i> Setchell & N.L.Gardner, 1930 C	Isla Guadelupe, México	x			
<i>Dictyota crinita</i> (J.Agardh) Hörnig, Schnetter & Prud'homme, 1992 C	Rottnest Is., Western Australia	x			
<i>Dictyota cuneata</i> Dickie, 1874 C	St. Paul Rocks, Atlantic Ocean	x			
<i>Dictyota cyanoloma</i> Tronholm, De Clerck, A.Gómez-Garreta & Rull Lluh, 2010 C	Port de Palamos, Girona, Spain	✓	GU255615	JQ061123	JQ061101
<i>Dictyota cymatophila</i> Tronholm, M.Sanson & Afonso-Carrillo, 2010 C	Punta del Hidalgo (28°35' N, 16°20' W), northern Tenerife, Canary Islands, Spain	✓	MW224891	MW223184	MW223852
<i>Dictyota decumbens</i> (R.W.Ricker) Hörnig, Schnetter & Prud'homme, 1992 C	Green Gorge, Macquarie Island	x			
<i>Dictyota detergenda</i> Kraft, 2009 C	Wsitari Reef, southern Great	x			

	Barrier Reef, Queensland, Australia				
<i>Dictyota dhofarensis</i> (Nizamuddin & A.C.Campbell) De Clerck, 2006 C	No information on type locality	✓			
<i>Dictyota dichotoma</i> (Hudson) J.V.Lamouroux, 1809 C	Walney Island, Lancashire, England	✓	GU265784		
<i>Dictyota diemensis</i> Kützing, 1859 C	George Town, Tasmania, Australia	✓			
<i>Dictyota dimorphosa</i> Ni-Ni-Win & H.Kawai, 2024 C	Reihoku (32°26'50.9"N, 130°01'24.9"E), Amakusa, Kumamoto Prefecture, Japan	✓	LC776669	LC764945	LC765043
<i>Dictyota dolabellana</i> De Paula, Yoneshigue-Valentin & Teixeira, 2008 C	Praia da Penha, Vera Cruz City, Bahia State, Brazil	x			
<i>Dictyota dumosa</i> Børgesen, 1935 C	Back Bay, Bombay, India	x			
<i>Dictyota falklandica</i> Küpper, A.F.Peters, Asensi & De Clerck, 2019 C	"Blue Beach, San Carlos, East Falkland, Falkland Islands"	✓	MK516800	MK516815	MK516760
<i>Dictyota fasciculata</i> Sperk, 1869 C	near Psyrtshki, Caucasus shore of the Black Sea	x			
<i>Dictyota fasciola</i> (Roth) J.V.Lamouroux, 1809 C	No information on type locality	✓			
<i>Dictyota fastigiata</i> Sonder, 1845 C	Western Australia	✓	MW225587		MW127651
<i>Dictyota fenestrata</i> J.Agardh, 1894 C	Port Phillip, Victoria	x			
<i>Dictyota flabellata</i> (Collins) Setchell & N.L.Gardner, 1924 C	La Jolla, California, U.S.A.	✓			
<i>Dictyota flagellifera</i> Kraft, 2009 C	Wistari Reef, southern Great Barrier Reef, Queensland, Australia	x			
<i>Dictyota friabilis</i> Setchell, 1926 C	Tafaa Point, Tahiti	✓	JQ061039	DQ472064	
<i>Dictyota furcellata</i> (C.Agardh) Greville, 1830 C	Shark Bay, Western Australia	x			
<i>Dictyota galapagensis</i> (Farlow) De Clerck, 2006 C	Galapagos Islands	x			
<i>Dictyota grossedentata</i> De Clerck & Coppejans, 1999 C	Holotype locality: Kombe South, Matemwe, Zanzibar, Tanzania	x			
<i>Dictyota guajirae</i> Hörnig, Schnetter & J.M.Over, 1992 C	Riohacha, Dept. Guajira, Colombia, Caribbean Sea	x			
<i>Dictyota guineënsis</i> (Kützing) P.Crouan & H.Crouan, 1878 C	São Tomé, Gulf of Guinea	✓			
<i>Dictyota gunniana</i> (J.Agardh) I.Hörnig, R.Schnetter & Prud'homme, 1992 C	southern Australia, Curdie; Tasmania, Gunn	x			
<i>Dictyota haenyeosa</i> C.W.Vieira, J.C.Kang & M.S.Kim, 2025 C	Ulleungdo, Ulleung County, North Gyeongsang Province, South Korea (37°30'04"N, 130°51'23"E)	✓	PQ616802	PQ616892	PQ616949
<i>Dictyota hamifera</i> Setchell, 1926 C	Tahiti, between Papenu and Huau	✓	OR777557		

<i>Dictyota hauckiana</i> Nizamuddin, 1975 C	Malabar Hill, Bombay, India	x			
<i>Dictyota humifusa</i> Hörnig, Schnetter & Coppejans, 1992 C	Punta Chengué, Santa Marta, Departamento del Magdalena, Colombia	✓	MW225116		
<i>Dictyota implexa</i> (Desfontaines) J.V.Lamouroux, 1809 C	Mediterranean sea	✓	GU255858	MW223234	MW224056
<i>Dictyota intermedia</i> Zanardini, 1874 C	Lord Howe Island, Australia	✓	JQ061047		
<i>Dictyota jamaicensis</i> W.R.Taylor, 1960 C	Don Christofers Cove, Drax Estates, St. Ann Parish, Jamaica	✓			
<i>Dictyota korowai</i> W.A.Nelson, J.E.Sutherland & Ngati Kuri, 2019 C	34°10.52'S, 172°2.84'E, Princes Islands (north side of middle island), Manawatawhi, New Zealand	✓	MK318550	MK318542	
<i>Dictyota kunthii</i> (C.Agardh) Greville, 1830 C	Callao and Huanchaco, Peru	✓	MK516792		MK516754
<i>Dictyota laciniata</i> J.V.Lamouroux, 1809 C	Naples, Italy	x			
<i>Dictyota lata</i> J.V.Lamouroux, 1809 C	"in India orientali"	x			
<i>Dictyota lineolata</i> (C.Agardh) Greville, 1830 C	Circa Venetiam rarissima	x			
<i>Dictyota liturata</i> J.Agardh, 1848 C	Cape of Good Hope, South Africa	✓			
<i>Dictyota major</i> W.R.Taylor, 1945 C	Isla Santa María, Galápagos	x			
<i>Dictyota masonii</i> Setchell & N.L.Gardner, 1930 C	Isla Clarión, Islas Revillagigedo, México	x			
<i>Dictyota mayae</i> Lozano-Orozco & Senties, 2015 C	Puerto Morelos (18°36'22" N, 103°30'05" W), Quintana Roo, Mexican Caribbean	✓	MW225197		
<i>Dictyota mediterranea</i> (Schiffner) G.Furnari, 1997 C	Numerous localities in th	✓	GU255570		MW224113
<i>Dictyota menstrualis</i> (Hoyt) Schnetter, Hörnig & Weber-Peukert, 1987 C	North Carolina, USA	✓	JX312658		
<i>Dictyota mertensii</i> (C.Martius) Kützing, 1859 C	Salvador, Brazil	✓			
<i>Dictyota moniliformis</i> (J.Agardh) Hörnig, Schnetter & Prud'homme, 1992 C	Champion Bay, Western Australia	x			
<i>Dictyota multifida</i> (J.E.Smith) Bory, 1838 C	Yarmouth, England	x			
<i>Dictyota naevosa</i> (Suhr) Montagne, 1840 C	Algoa Bay, Cape Province, South Africa	✓	MW225245		
<i>Dictyota nigrescens</i> Zanardini, 1878 C	[Aru Vokan], Papua New Guinea	x			
<i>Dictyota nigricans</i> J.Agardh, 1882 C	western Australia; Orford, Tasmania	✓			
<i>Dictyota ocellata</i> J.Agardh, 1894 C	Bay of Islands, New Zealand	x			
<i>Dictyota pachyderma</i> Luan Rixiao & Ding Lanping, 2013 C	China, Guangxi, Fangcheng, Bailongwei	x			
<i>Dictyota paniculata</i> J.Agardh, 1841 C	"Hab. ad oras Novae Hollaadiae.	✓	MW225255		MW127659

	(Hb. Agardh et mus. Paris.!); (Agardh 1841: 5)				
<i>Dictyota pedrochei</i> Lozano-Orozco & Senties, 2015 C	Punta Brava, Quintana Roo, Mexican Caribbean	✓	KT445276		
<i>Dictyota phlyctaenodes</i> Montagne, 1852 C	Juan Fernandez Island	✓	MK516798		
<i>Dictyota pinnata</i> (E.Y.Dawson) I.Hörnig, R.Schnetter & Prud'homme, 1993 C	Miramar, Nayarit, Mexico	x			
<i>Dictyota pinnatifida</i> Kützing, 1859 C	Antigua, Leeward Islands	✓	MW225288	MW223257	MW224141
<i>Dictyota plantaginea</i> Lamouroux ex Frauenfeld, 1855 C	Zara, Croatia	x			
<i>Dictyota pleiacantha</i> Tronholm, 2013 C	Holotype locality: Punta del Hidalgo, Tenerife, Canary Islands (28°34'N, 16°20'W)	✓	MW225296	MW223260	
<i>Dictyota polyclada</i> Sonder ex Kützing, 1859 C	Western Australia	✓	MK516805		
<i>Dictyota pontica</i> Sperk, 1869 C	Sukhum-Kale, Caucasus shore of the Black Sea	x			
<i>Dictyota pulchella</i> Hörnig & Schnetter, 1988 C	Punta La Loma, Santa Marta, Colombia, Caribbean Sea	✓			
<i>Dictyota pulvinata</i> Sadeghi, Sohrabipour & De Clerck, 2022 C	Iran: Strait of Hormuz: Larak Island (26 52.891N. 56 24.286E);	x			
<i>Dictyota recumbens</i> Ni-Ni-Win & H.Kawai, 2024 C	Gawt (18°30'13.3"N, 94°15'39.1"E), Thandwe, Rakhine state, Myanmar	✓	LC776658	LC764954	
<i>Dictyota rigida</i> De Clerck & Coppejans, 1999 C	Holotype locality: Kunduchi, Dar es Salaam, Tanzania	✓	GQ425217	MW223266	
<i>Dictyota robusta</i> J.Agardh, 1894 C	Port Phillip Heads, Victoria, Australia	✓	MK516808	MK516814	MK516743
<i>Dictyota rotunda</i> C.Agardh, 1820 C	Mediterranean Sea (African coast)	x			
<i>Dictyota sandvicensis</i> Sonder, 1859 C	[Woahoo] Oahu, Hawaiian Archipelago	✓	GU265783	MW223272	GU290239
<i>Dictyota serrulata</i> J.V.Lamouroux, 1809 C	"in India orientali"	x			
<i>Dictyota spathulata</i> Yamada, 1928 C	in or near Mutsu Bay, Japan	✓	PQ633222	PQ633224	PQ633223
<i>Dictyota spinulosa</i> Hooker f. & Arnott, 1838 C	"Loo-Choo" [Okinawa, Ryukyu Retto, Japan]	✓	MW225537		MW224263
<i>Dictyota spiralis</i> Montagne, 1846 C	Syntype localities: Algeria: near Algiers and near La Calle (El Kala)	✓	GU255607		
<i>Dictyota stolonifera</i> E.Y. Dawson, 1962 C	Masachapa, Nicaragua, Pacific Ocean	✓			
<i>Dictyota sumbisorica</i> C.W.Vieira, J.C.Kang & M.S.Kim, 2025 C	Suryeong Island, Chuja-myeon, Jeju Province, South	✓	PQ616848	PQ616901	PQ616921

	Korea (37°30'04"N, 130°51'23"E)				
<i>Dictyota taewakia</i> C.W.Vieira, J.C.Kang & M.S.Kim, 2025 C	Suryeong Island, Chuja-myeon, Jeju Province, South Korea (37°30'04"N, 130°51'23"E)	✓	PQ616863	PQ616911	PQ616927
<i>Dictyota vieillardii</i> Kützing, 1863 C	New Caledonia	x			
<i>Dictyota vittata</i> Kraft, 2009 C	"Coral Gardens", Heron Island, southern Great Barrier Reef, Queensland, Australia	x			
<i>Dictyota vivesii</i> M.Howe, 1911 C	La Paz, Baja California Sur, México	x			

3.3.2. Phylogenetic analysis

The best model for each gene was assessed using jModeltest2 (2.1.6) run on ACCESS through the CIPRES Science Gateway (Miller *et al.*, 2010). The best model for the *psbA* gene was the GTR+G model, and the best model for both the *rbcL* and *cox1* gene was the TVM+G model. Bayesian phylogenetic analysis was conducted using MrBayes 3.2.7a on ACCESS (Ronquist *et al.*, 2012). Maximum likelihood (ML) phylogenetic analyses were conducted using IQ-TREE (Nguyen *et al.*, 2015) through the IQ-TREE web server 1.6.12. Branch support was assessed using 1 000 ultrafast bootstrap replicates (Hoang *et al.*, 2018). The final trees were visualised and edited in Figtree version 1.4.4 (Rambaut, 2018). Pairwise distances for all three genes were calculated based on the p-distance model using MEGA11: Molecular Evolutionary Genetics Analysis version 11 (Tamura *et al.*, 2021).

For species descriptions, both phylogenetic- and morphological data was used. When selecting a name, the availability of names was determined looking at both AlgaeBase (Guiry & Guiry, 2025) and the International Code of Nomenclature for algae, fungi, and plants: Appendices I-VII (Wiersema *et al.*, 2018).

3.3.3. Haplotype network for *Dictyota dichotoma*

The *cox1* sequences generated for *D. dichotoma* during this study was aligned in BioEdit (Hall, 1999) with all available *cox1* sequences for *D. dichotoma* collected in South Africa, along with sequences from Europe (Scotland, France, Greece, Spain), South America (Argentina), and North Africa (Canary Islands, Madeira), all downloaded from GenBank

(Sayers *et al.*, 2025). A haplotype network was created in PopART (Leigh & Bryant, 2015) using a median-joining network (Bandelt, Forster & Röhl, 1999).

4. Results

4.1. Taxonomic treatment

This study has resulted in a full taxonomic review of *Dictyota* species in South Africa. Using morphological- and phylogenetic data, four new species of *Dictyota* have been described and topotype sequences have been designated for one South African species.

4.1.1. Species descriptions

Dictyota variolata M.B. Geldenhuys et M.M. Reddy *nom. prov.* (Fig 7)

Description:—Plants erect, up to 6 cm high, arising from a single attachment from the holdfast. Growth form erect, branching slightly anistomously dichotomous. Thalli yellowish-green, with short longitudinal bands across the thallus. Some specimens with a distinct yellow margin. Thalli may exhibit bright bluish iridescence *in situ* which disappears once removed from the field. Interdichotomies 4-18 mm long, proximal width 1-8 mm, expanding distally to 1-13 mm. Apices truncate with emarginate apical cells. Thallus distromatic with both medullary cells and cortical cells. Medullary cells 55-148 µm long, 30-86 µm wide and 40-60 µm high; cortical cells 16-63 µm long, 8-25 µm wide and 11-20 µm high.

Reproductive habit consisting of solitary sporangia, scattered along the thallus, in densely fertile specimens, sporangia may occur adjacent to each other. Sporangia broadly ellipsoid to spherical, generally 57-103 µm in diameter.

Type:—SOUTH AFRICA. KwaZulu-Natal: Happy Wanderers (30.3578°S, 30.7183°E), 10 January 2024, M.M. Reddy, C2

Isotype:—SOUTH AFRICA. KwaZulu-Natal: Hluleka, 23 August 2013, D1343

Representative DNA barcodes:—MAD0142 (LN831813, LN871962), KZN2282 (GQ425214, MW223243, MW224083), RA1032 (MW225186, MW224086), JCP058 (KM101060, KY012328), HEC15721 (JQ061063, MW223241, MW224078), Sole1 (GQ425113), HEC15816 (MW223242), JCP073 (MF182640)

Additional material examined—C12 (Park Rynie, 12 January 2024, M.M. Reddy), C299 (Park Rynie, 27 April 2025, M.M. Reddy), D1131 (Scoenmakerskop, 20 September 2012),

D1143 (Nature's Valley, 12 December 2012), D1312 (Hluleka, 20 August 2013), D1331 (Hluleka, 21 August 2013).

Diagnosis:—Characteristic longitudinal spots on the thallus, and a bright blue iridescence *in situ*.

Etymology:—The name *variolata* comes from the Latin word *variola*, which refers to spot-like markings. This name, therefore, means ‘marked with small spots’ and refers to the species’ short longitudinal markings, which have caused it to be misidentified as *D. liturata*.

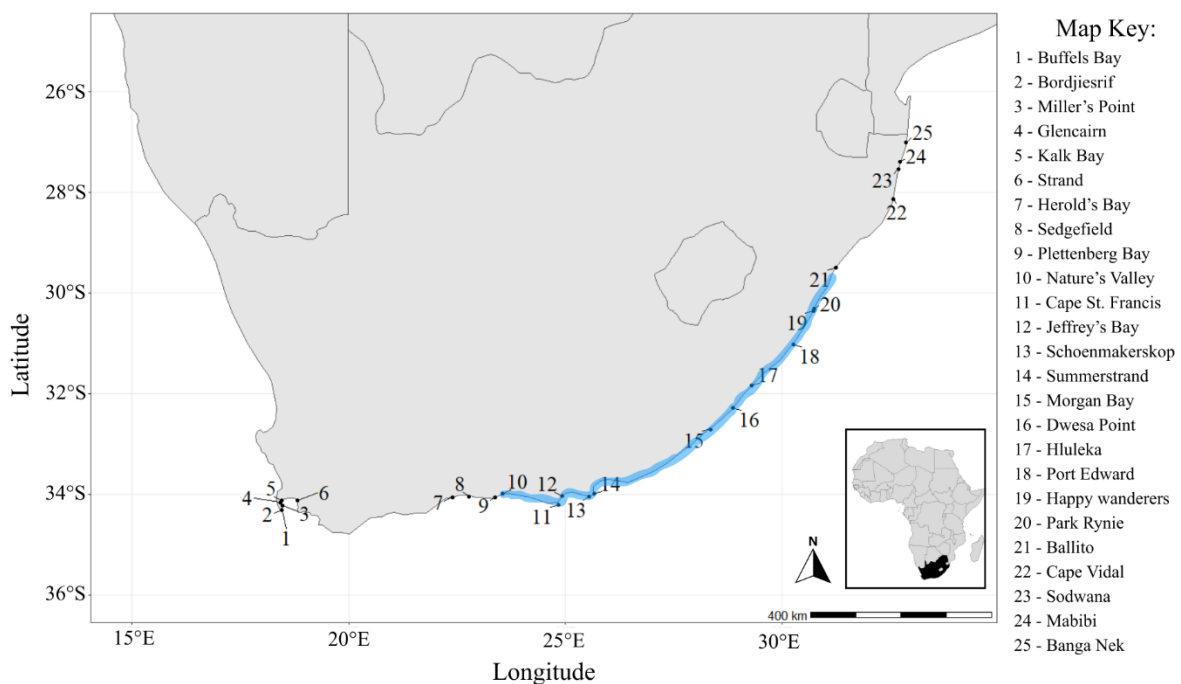


Figure 7. Distribution of *Dictyota variolata* *nom. prov.* in South Africa.

Distribution and habitat:—The species is distributed along the south and east coast of South Africa, from Nature's Valley in the Eastern Cape to The Bluff, Durban in KwaZulu-Natal. DNA results suggest that this species occurs in South Africa, Madagascar, Brazil, Venezuela and Portugal (Madeira).

Remarks:—This species has been previously misidentified as *Dictyota liturata* based on its substantial morphological similarity, particularly the distinct latitudinal bands characteristic of *D. liturata* *bona fide*.

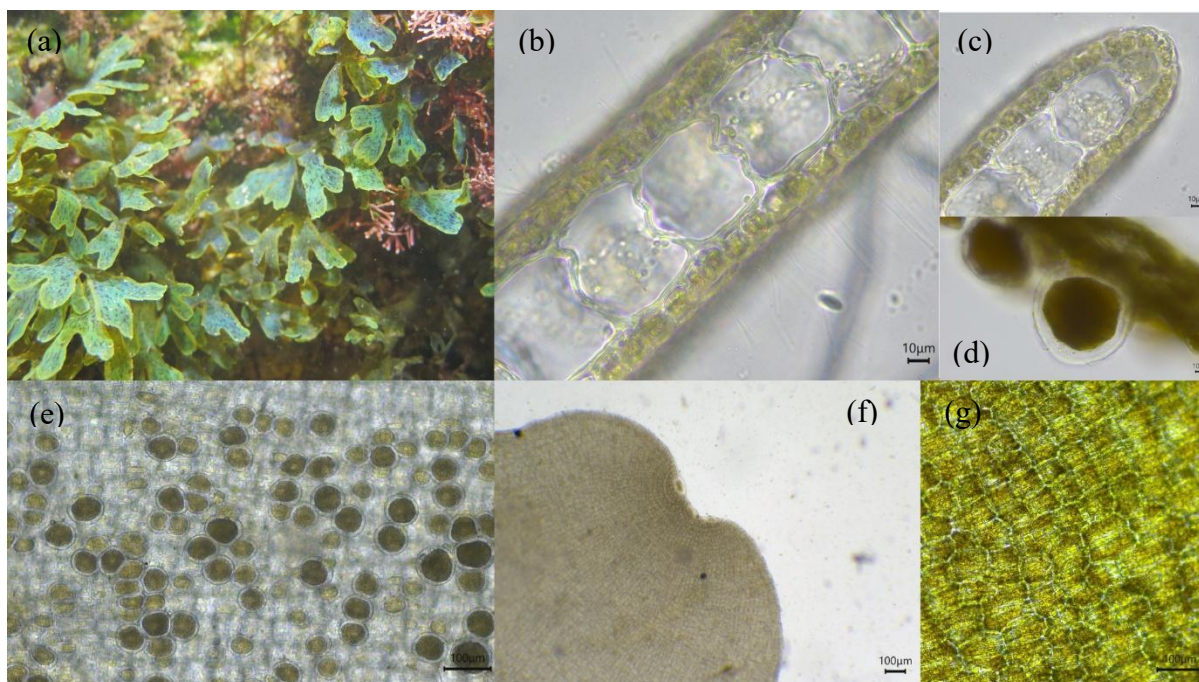


Figure 8. General morphology of *Dictyota variolata* nom. prov. (a) Habit *in situ*. (b-c) Cross-section of the thallus. (d-e) Sporangia. (f) Apical point of the thallus. (g) Surface view of cells.

Dictyota caerulea M.B. Geldenhuys et M.M. Reddy nom. prov. (Fig 8)

Description:—Thalli creeping/repent, green, displaying a striking blue iridescence *in situ*, ranging from dark-blue to purple-blue, iridescence disappears/lost upon emersion. Thalli up to 2 cm high, relatively uniform width throughout, although some branches narrower than others. Branching isotomous, occasionally giving rise to a distinct primary axis. Branching widening distally, terminating in truncate apices. Distromatic thallus typical of *Dictyota*, composed of a single layer of medullary and cortical cells. Medullary cells usually 57-94 µm long, 42-73 µm wide and 38-61 µm high. Cortical cells usually 12-37 µm long, 8-18 µm wide and 15-23 µm high. Sporangia and gametangia not observed.

Type:—SOUTH AFRICA. KwaZulu-Natal: Happy Wanderers (30.3578°S, 30.7183°E), 10 January 2024, M.M. Reddy, C1.

Representative DNA barcodes:—KZN16331 (MW225225), KZN16009 (MW225236), KZN16122 (MW225237)

Diagnosis:—Characteristic dark blue to purple colour *in situ*.

Etymology:— The epithet refers to the distinctly dark blue thallus common in this species, with the name *caerulea* meaning “sky-coloured” or “blue”.

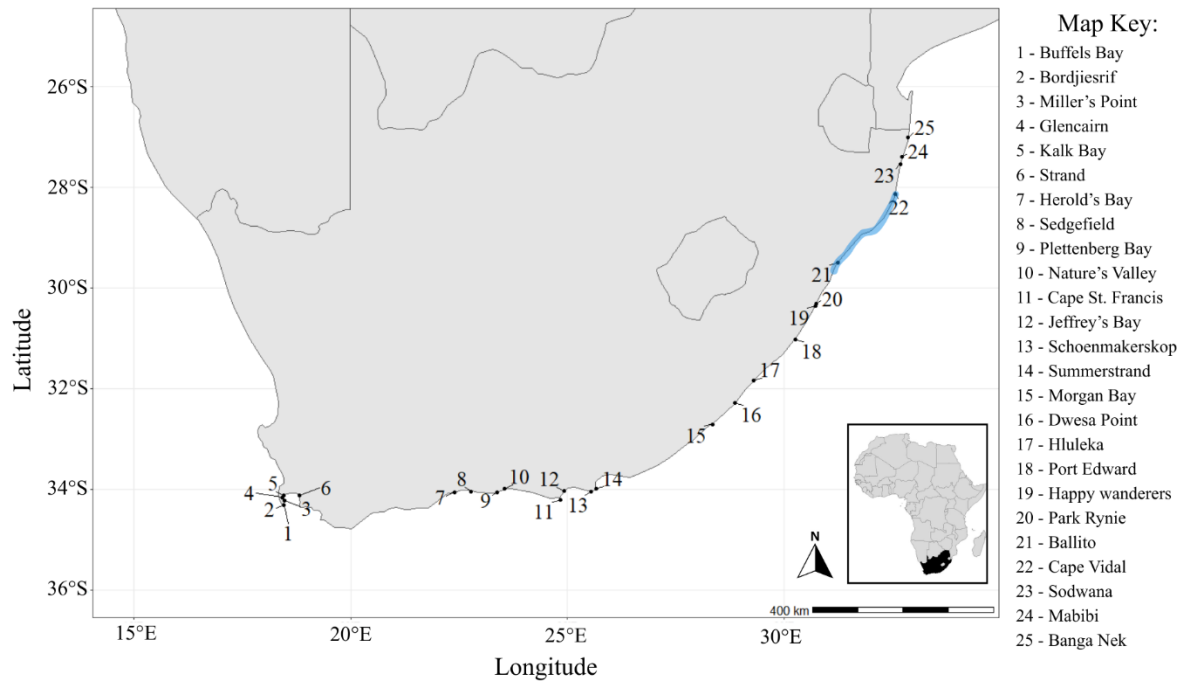


Figure 9. Distribution of *Dictyota caerulea* nom. prov. in South Africa.

Distribution and habitat:—This species has only been recorded on the east coast of South Africa (KwaZulu-Natal), from Happy Wanderers to Sodwana Bay. It may be more widespread and misidentified as either *Dictyota mertensii* or *Dictyota humifusa* due to similar growth forms and blue iridescence. This species appears to be endemic to South Africa but might occur northwards into Mozambique and be misidentified as either *D. mertensii* or *D. humifusa* based on morphology. DNA confirmation is required to confirm its presence outside South Africa.

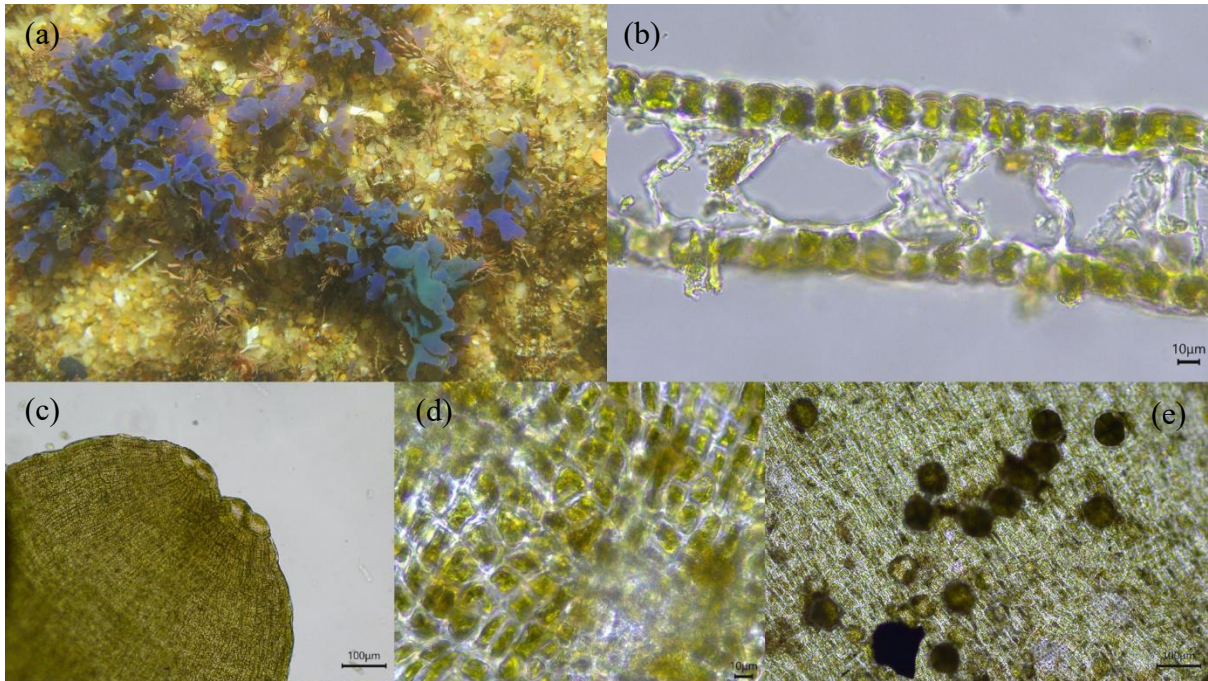


Figure 10. General morphology of *Dictyota caerulea* nom. prov. (a) Habit *in situ*. (b) Cross-section of the thallus. (c) Apical point of the thallus. (d-e) Surface view with (e) showing sporangia.

Dictyota natalensis M.B. Geldenhuys et M.M. Reddy nom. prov. (Fig 9)

Description:—Thalli erect, up to 2 cm high, arising from a single attachment from the holdfast. Branching slightly anistomously dichotomous. Thalli display distinctive colour *in situ*, appearing bright, light blue with a distinct brown marginal band, transverse bands visible across the thallus. Upon preparation of herbarium voucher specimens, colour changes to brown-green with slightly darker edges. Interdichotomies 4-18 mm, proximal width 1-8 mm, expanding distally to 1-13 mm. Apices rounded, with protruding apical cells. Thallus distromatic, with both medullary cells and cortical cells. Medullary cells 55-148 μm long, 30-86 μm wide and 40-60 μm high; cortical cells 16-63 μm long, 8-25 μm wide and 11-20 μm high.

Type:—SOUTH AFRICA. KwaZulu-Natal: Park Rynie (30.3133 °S, 30.7436 °E), 27 April 2025, M.M. Reddy, C296.

Representative DNA barcodes:— KZN16033 (MW225324), KZN16133 (MW225325), RA1018 (MW225326; MW224156), RSAD549 (MW225327), PC0166123 (LN831814), PC0166272 (LN831815)

Diagnosis:—Characteristic blue colour with brown margin *in situ*.

Etymology:— The name *natalensis*, meaning “from Natal”, refers to the historical name of the region KwaZulu-Natal in South Africa. The epithet denotes the species occurrence on the Eastern coast of South Africa, from which it was described.

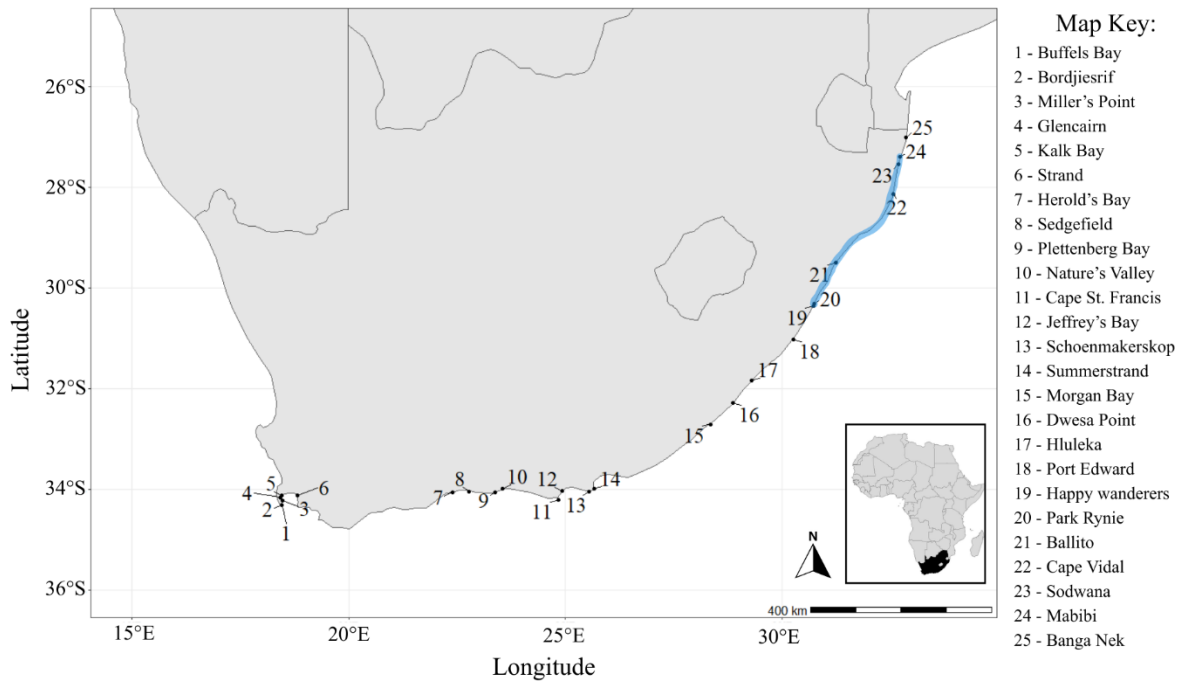


Figure 11. Distribution of *Dictyota natalensis nom. prov.* in South Africa.

Distribution and habitat:—This species occurs from Park Rynie to Mabibi. No samples were collected south of Park Rynie; however, with more extensive sampling, this species may extend further south along the coast. DNA results confirmed this species also occurs in Madagascar. It may occur further north along the east-African shoreline and be misidentified as *D. rigida*; however, DNA analysis would be needed to confirm this.

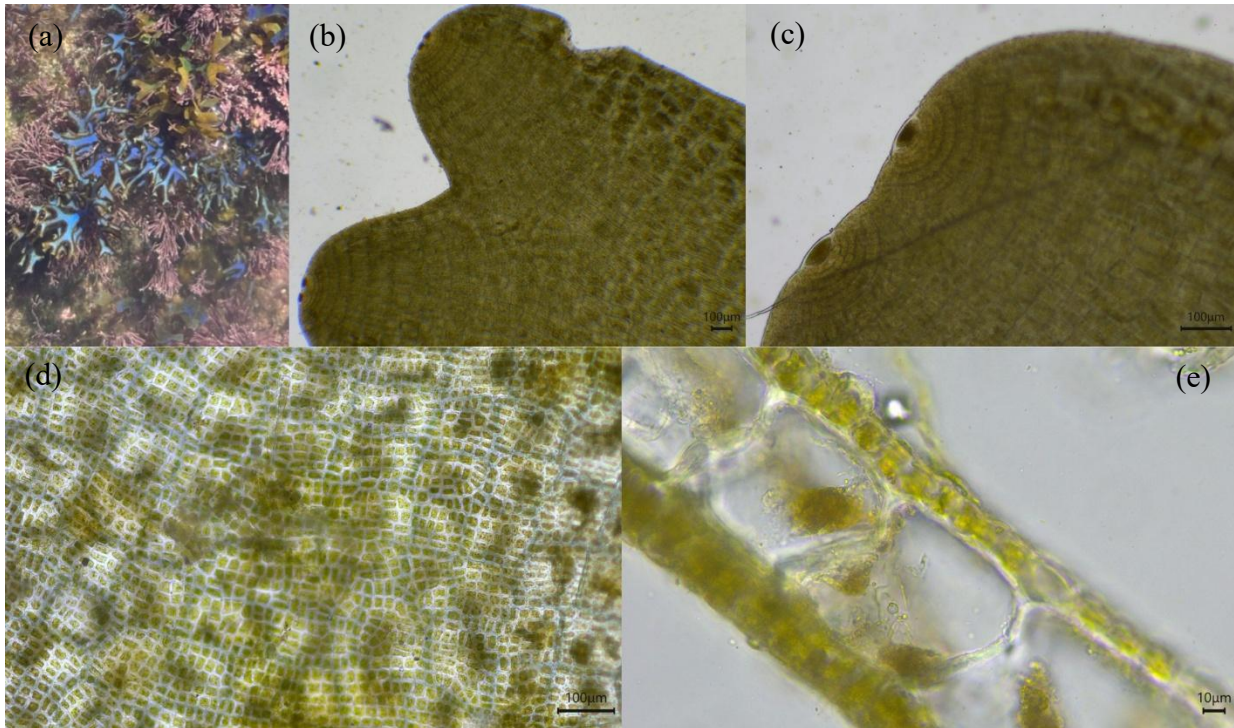


Figure 12. General morphology of *Dictyota natalensis* nom. prov. (a) Habit *in situ*. (b-c) Apical section of the thallus. (d) Surface view of the cells. (e) Cross-section of the thallus.

Dictyota viridilabris M.B. Geldenhuys et M.M. Reddy nom. prov. (Fig 10)

Description:—Plants have an erect growth form that grows up to 5.5 cm tall, with a rhizoidal holdfast. Branching is slightly anistomous dichotomous. This species has an olive-green colour, with distinctive green edges *in situ*. Once the specimen is pressed or dried, the green margins disappear. Apices are rounded. Interdichotomies have a length of 2-10.5 mm, a proximal width of 0.1-4.6 mm and a distal width of 1.2-7.7 mm. Both medullary cells and cortical cells are one cell layer thick. Medullary cells 25-131 μm long, 25-94 μm wide and 27-86 μm high; cortical cells 10-62 μm long, 7-29 μm wide and 10-25 μm high.

Reproductive structures not seen.

Type:—SOUTH AFRICA. Western Cape: Herold's Bay (34.0545 °S, 22.3922 °E), 10 April 2025, M.B. Geldenhuys, C276.

Isotype:—SOUTH AFRICA. Western Cape: Nature's Valley, 15 April 2025 (Isotype, C290)

Representative DNA barcodes:—NU0090952 (OK484652), NU0090950 (OK484650), NU0090949 (OK484649), HEC15817(LN871945, LN871956, LN871968), RAD1344 (MW225531, MW224258), RAD75 (MW225532, MW224260), D206 (MW225529, MW223302), KZN2305 (DQ472066), D186 (MW223301), D207 (MW223303), KZN2308 (LN871955, LN871967), D4032 (MW224257), RAD1348 (MW224259)

Additional material examined:—C275 (Herold’s Bay, 10 April 2025, M.B. Geldenhuys), C278 (Swartvlei, 11 April 2025, M.B. Geldenhuys), C279 (Summerstrand, 13 April 2025, M.B. Geldenhuys), C280 (Summerstrand, 13 April 2025, M.B. Geldenhuys), C284 (Jeffrey’s Bay, 13 April 2025, M.B. Geldenhuys), C287 (Plettenberg Bay, 14 April 2025, M.B. Geldenhuys), C297 (Park Rynie, 27 April 2025, M.M. Reddy), C301 (Ballito, 28 April 2025, M.B. Geldenhuys), C302 (Ballito, 28 April 2025, M.B. Geldenhuys)

Diagnosis:—Characteristic green margin *in situ*.

Etymology:—The specific epithet is derived from the Latin *viridis* (green) and *labrum* (lip) and refers to the informal name historically used by South African phycologists prior to the formal description of this species. The epithet further reflects the distinctive green iridescence along the thallus margins observed *in situ*, which disappears upon removal of the specimen from seawater.

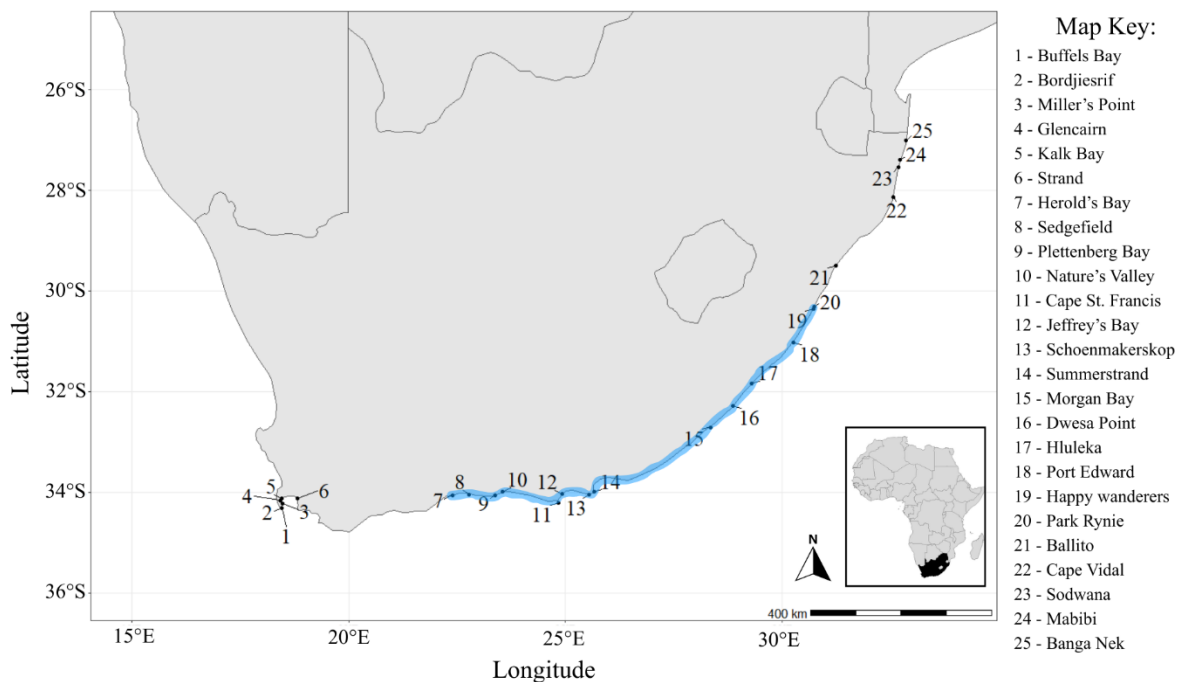


Figure 13. Distribution of *Dictyota virilabris nom. prov.* in South Africa.

Distribution and habitat:—Recorded from Herold’s Bay in the Western Cape to Park Rynie in KwaZulu-Natal.

Remarks:—This species was provisionally described by Anderson, Stegenga & Bolton (2016). Their description was extended here, including additional morphological and molecular information obtained during this study. This species is often found in rockpools under crevices on the south coast.

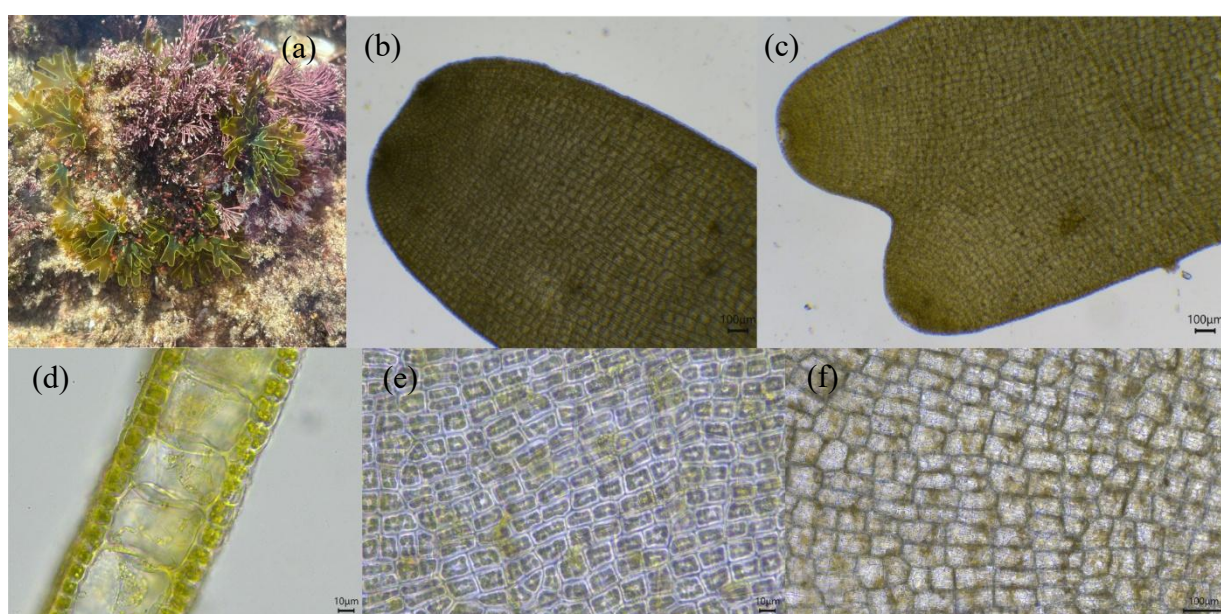


Figure 14. General morphology of *Dictyota vililabris* nom. prov. (a) Habit *in situ*. (b-c) Apical section of the thallus. (d) Cross-section of the thallus. (e) Surface view showing the cortical cells. (f) Surface view showing the medullary cells.

4.1.2. Topotype sequencing

Dictyota liturata J. Agardh 1848: 95

Topotype:—SOUTH AFRICA. Western Cape: Miller’s Point, 2 April 2024 (C52, M.B. Geldenhuys and O.P. Thomas).

Additional material sampled close to type locality:—C219 (Strand, 14 November 2024, M.B. Geldenhuys, M.M. Reddy and C. Roberts), C220 (Strand, 14 November 2024, M.B. Geldenhuys, M.M. Reddy and C. Roberts).

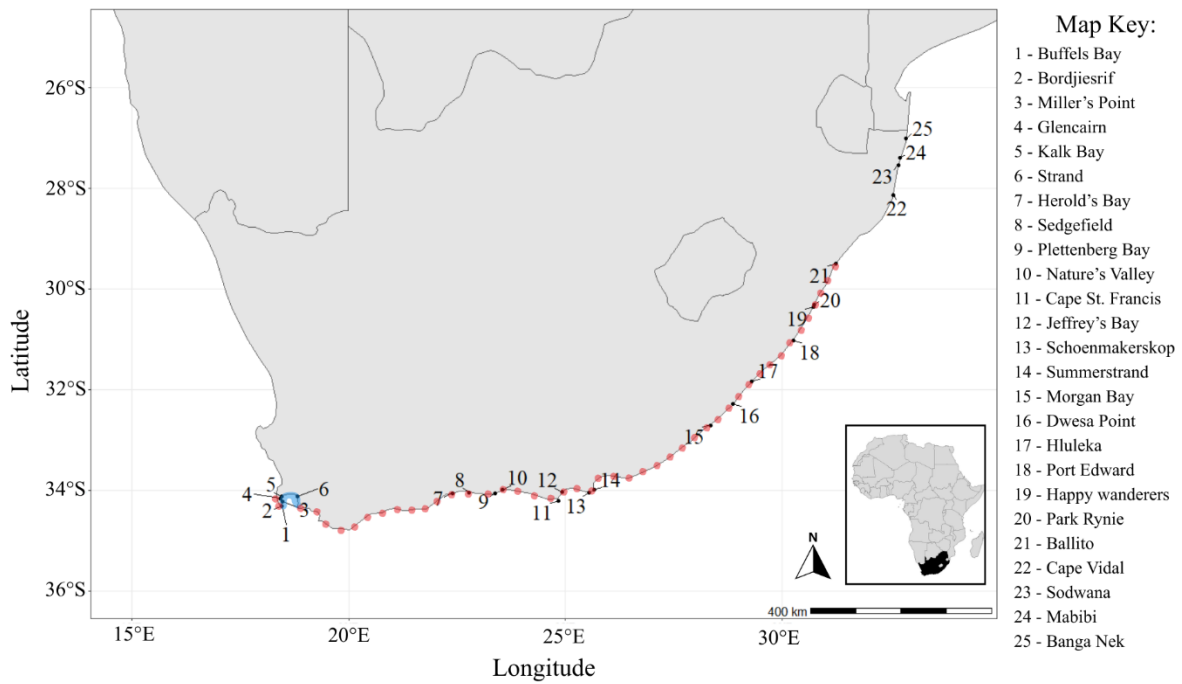


Figure 15. Updated distribution of *Dictyota liturata* in South Africa. Confirmed distribution is shown in blue, while historically recorded distribution is shown with red dots.

4.2. Morphology of South African *Dictyota*

4.2.1. Gross morphology of samples

The morphology and anatomy of South African *Dictyota* species were summarised in Table 8, using data collected during this study and from various field guides for the region (Stegenga *et al.*, 1997; De Clerck *et al.*, 2005; Anderson *et al.*, 2016). Where measurements obtained in this study differed from those in the guides, values from this study were used, with previous measurements provided in brackets. No data for *D. ciliolata* or *D. humifusa* were collected during this study; however, because these species are noted previously, they were included in Table 8. Species excluded from the table were DNA-confirmed taxa for which no morphological data were available ("*D. robusta*", *D. stolonifera*, *D. hamifera*, *D. sp. 24*, *D. sp. 9*, *D. sandivensis*, *D. sp. 45*) and species recorded historically in South Africa but lacking DNA-confirmed records (*D. bartayresiana*, *D. ceylanica*, *D. friabilis*, and *D. implexa*).

Table 7. Morphological traits of South African *Dictyota* species. The table includes information from South African previous records as well as newly generated data. Columns highlighted in green depict newly described species.

		<i>D. ciliolata</i>	<i>D. dichotoma</i>	<i>D. virilabris</i> nom. prov.	<i>D. humifusa</i>	<i>D. caerulea</i> nom. prov.	<i>D. liturata</i>	<i>D. variolata</i> nom. prov.	<i>D. naevosa</i>	<i>D. rigida</i>	<i>D. natalensis</i> nom. prov.
Size (cm)		Up to 8cm	5.5-17 (up to 6cm)	1.3-5.5 (up to 2.5cm)	Up to 6cm	1.61	2.9-5.1 (8-25)	3.2-5.6	3.5-21.3 (up to 35cm)	0.9-3	2.1
Habit		Erect	Erect	Erect	Procumbent to repent	Repent	Erect	Erect	Erect	Erect	Erect
Branching		Dichotomous	Dichotomous	Dichotomous/ sub-dichotomous	Dichotomous	Dichotomous	Appears alternate	Slightly anistomous dichotomous	Sub-dichotomous	Dichotomous	Anistomous dichotomous
Apices shape		Rounded	Rounded	Acute to rounded	Rounded to truncate	Truncate	Rounded to truncate	Truncate	Rounded	Rounded	Rounded
Dentation		Margins dentate, teeth directed towards apices	Smooth	Smooth	Smooth	Smooth	Smooth	smooth	Smooth	Smooth	Smooth
Surface hairs		Hair tufts common		Hair tufts present	Hair tufts common		Hair tufts common		Hair tufts present		
Colour		Medium brown	Mid-brown to yellow brown	Olive brown	Pale yellowish-brown	Blue-green	Yellow-green to brown with longitudinal bands	Yellowish-green	Pale brown to yellowish-brown	Olive brown	Bright blue with dark, brown-green edges
Iridescence		Slight iridescence, often with transverse bands		Green iridescent margins	Bright blue	Dark blue to purple		Bright blue	Blue	Iridescence that can range from orange to blue	Blue
Interdichotomies	Length (mm)	11-14	2.8-31.2	2-10.5	3.2-3.6	1.9-4.1	3.8-15.1 (7-15)	3.9-17.5	3.3-43.2 (24-48)	2.2-11.2	3-5.4
	Proximal width (mm)	5.5-7	2.7-6.1	0.1-4.6	1.2-2.7	1.3-2.5	1.2-5.7 (4-6.5)	1.1-7.6	1.8-10.7 (6-11)	0.1-3.7	0.6-3.7
	Distal width (mm)		0.7-12	1.2-7.7		2.3-5.4	1.7-11.5	0.4-12.6	2.2-19.2	2.4-7.7	1.3-3.2

Cortical cells	length (µm)	42-45	17-66	10-62	38-42	12-37	13.6-62.3 (14-48)	12.5-62.5	15-63 (22-23)	15-51	16-40
	width (µm)	19-20	6-21	7-29	19-20	8-18	7.5-57.8 (10-22)	7.5-25	8-31 (14-16)	7.5-29	13-20
	height (µm)	23-25	12-27 (10-13)	10-25 (about 15)	13-14	15-23	13.6-27.5 (13-18)	7.5-22.5	13-32 (23-26)	12-27.5	14-23
Medullary cells	length (µm)	216-242	53-190	25-131	82-94	57-94	51.3-170 (60-130)	55-150	53-179 (112-120)	69-349	106-165
	width (µm)	118-132	17-98	25-94	46-49	42-73	40-100 (34-79)	30-86	46-110 (68-71)	41-133	44-121
	height (µm)	180-205	32-84 (75-80)	27-86 (40-90)	35-41	38-61	44.3-75.7 (88-136)	40-90	51-129 (130-160)	49-109	51-78
Sporangia	Width (µm)	95-110			75-108		47-97.5 (110-135)	30-103			
Distribution within South Africa		Mabibi northwards	False Bay to the Eastern Cape (Langebaan and False Bay to KwaZulu-Natal)	Herold's Bay to Park Rynie (False Bay to Isipingo)	Isipingo northwards	Isipingo to Sodwana Bay	False Bay (Kommetjie to Umhlali)	Nature's Valley to Happy wanderers	Nature's Valley to Dwesa (False Bay to Mission rocks)	Port Edward to Sodwana	Park Rynie to Mabibi
Reference		De Clerck <i>et al.</i> (2005)	Current study; Stegenga <i>et al.</i> (1997); Anderson <i>et al.</i> (2016)	Current study; Anderson <i>et al.</i> (2016)	De Clerck <i>et al.</i> (2005)	Current study	Current study; Stegenga <i>et al.</i> (1997); De Clerck <i>et al.</i> (2005a); Anderson <i>et al.</i> (2016)	Current study	Current study; Stegenga <i>et al.</i> (1997); De Clerck <i>et al.</i> (2005a); Anderson <i>et al.</i> (2016)	Current study	Current study

4.2.2. Key for the South African *Dictyota*

- 1a. Thallus procumbent and/or repent..... 2
- 1b. Thallus erect..... 3
- 2a. Thallus repent with dichotomous branching, truncate apices and colour *in situ* dark blue..... *D. variolata*
- 2b. Thallus procumbent to repent with dichotomous branching, rounded to truncate apices and colour a yellowish-brown with a bright blue iridescence..... *D. humifusa*
- 3a. Branching appears alternate..... 4
- 3b. Branching is dichotomous or sub-dichotomous..... 5
- 4a. Species occur on the east coast of South Africa, has a bright blue iridescence and longitudinally arranged spots..... *D. caurulea nom. prov.*
- 4b. Species occurs in the Western Cape, has no iridescence and longitudinal bands.....*D. liturata*
- 5a. Apices acute to rounded, and has a distinct green margin *in situ*.....*D. virilabris*
- 5b. Apices rounded.....6
- 6a. Margins smooth.....7
- 6b. Margins dentate with teeth directed towards the apices.....*D. ciliolata*
- 7a. Colour a shade of brown/green with no distinct margins.....8
- 7b. Colour a bright blue with a distinct margin and transverse bands across the thallus.....*D. natalensis*
- 8a. Specimen between 3 and 22 cm tall.....9
- 8b. Specimen \leq 3 cm, olive-brown with an orange iridescence *in situ*.....*D. rigida*
- 9a. Plants robust, branching sub-dichotomous, pale to yellowish brown colour with blue iridescence, hair tufts present.....*D. naevosa*
- 9b. Branching dichotomous, yellow-brown iridescence with no or slight green iridescence.....*D. dichotoma*

4.3 Phylogenetics data

A total of 61, 81 and 26 sequences were generated for the *psbA*, *rbcL* and *cox1* genes, respectively. Average sequence lengths were approximately 935 for *psbA*, and around 630 for *rbcL* and *cox1*. Of the 96 *Dictyota* species currently confirmed on AlgaeBase (Table 7), almost half (43%) remain with no available barcode data. Furthermore, only two fifths of the species have DNA barcodes from regions close to their type localities. For the markers used in this study, ~40% of accepted *Dictyota* species have *psbA* barcodes close to the type locality, whereas only ~20% have *rbcL* and *cox1* barcodes close to the type locality. The plastid *psbA* gene is by far the most widely used for *Dictyota* (Table 7), with 2 152 *psbA*, 845 *rbcL* and 996 *cox1* sequences available on GenBank (Sayers *et al.*, 2025).

4.3.1. Species diversity and distribution in South Africa

Bayesian and maximum-likelihood analyses produced relatively congruent topologies for all three genes, with minor differences occurring only in poorly supported nodes (PP < 0.75, BP < 65%; Figure 11-13). The Bayesian inference phylogenies are presented, with Bayesian posterior probabilities (PP) and maximum-likelihood bootstrap percentages (BP) indicated at moderate ($0.75 \leq \text{PP} < 0.85$; $65\% \leq \text{BP} < 75\%$) and well supported ($0.85 \leq \text{PP}$; $75\% \leq \text{BP}$) clades (Figure 11-13). Based on the phylogeny, *Dictyota* from South Africa were resolved in eight different clades (A-H) and appeared to group in 18 distinct species – the phylogeny of *Dictyota* in South Africa (Figures 1-3) is discussed below. Species occurring in South Africa is indicated on the phylogenies.

Dictyota robusta specimens collected in Australia, *D. fasciola* specimens from Australia and *D. robusta* specimens previously collected from Protea Banks on the southeast coast of South Africa (forms part of the ETZ, Figure 4), formed a well-supported clade for *psbA* and *rbcL* (PP = 1, BP = 100%). Both *D. robusta* and *D. fasciola* have type localities in Australia (Table 7). The South African samples were more distantly related to *D. robusta* (*rbcL*: 6.16% distance; *cox*: >10% distance) and instead formed sister to *D. fasciola* (*psbA*: 1.8% distance; *rbcL*: 2.4% distance; *cox*: >5% distance).

The second clade included two species; *D. dichotoma* and an undescribed species from South Africa identified as *Dictyota* sp. 45. All three genes supported that specimens collected from

South Africa represented *D. dichotoma*, as it formed a well-supported group with sequences from Tristan da Cunha, France, England (Type locality - LC776643, *psbA*), Greece and Portugal (*psbA*, *rbcL* and *cox1*: PP = 1, BP = 100%). Both the normal form (D1126) and the intricate form (C49) was present in this clade. The sister species to the true *D. dichotoma* was the undescribed South African species (*psbA*: 4.1-4.4%). For the *cox1* gene, *D. sp. 45* was not the sister species, but an internal clade of *D. dichotoma*.

Another clade was well supported for *psbA* (PP = 0.97, BP = 93%) and *cox1* (PP = 0.93, BP = not supported), and moderately supported for *rbcL* (PP = 0.86BP = 73%), and contained two South African species. *Dictyota humifusa* from South Africa (MW225107) clustered with *D. humifusa* from Colombia (MW225112), the type locality. However, this relationship was only supported by *psbA* (1.95% distance, PP = 0.97, BP = 100%) as there were no sequences available for *rbcL* and *cox1* genes. *Dictyota sandvicensis* from South Africa clustered strongly with specimens from the type locality in Hawaii, USA and was supported by all three genes (*psbA*: <1% distance, PP = 1, BP = 100%; *rbcL*: <1% distance, PP = 1, BP = 100%; *cox1*: 2% distance, PP = 1, BP = 100%). *Dictyota sandvicensis* appeared to be the sister species of *D. pleiakantha* from Spain, whereas *D. humifusa* appeared to be the sister species of *Dictyota canaliculata* from the Philippines. Other specimens within this clade were collected from the America's (Mexico, USA, Panama), the Caribbean (Cuba, Jamaica, the Dominican Republic), and Atlantic islands (Bermuda, Canary Islands), as well as two species (*Dictyota implexa*, *Dictyota pulchella*) collected from France.

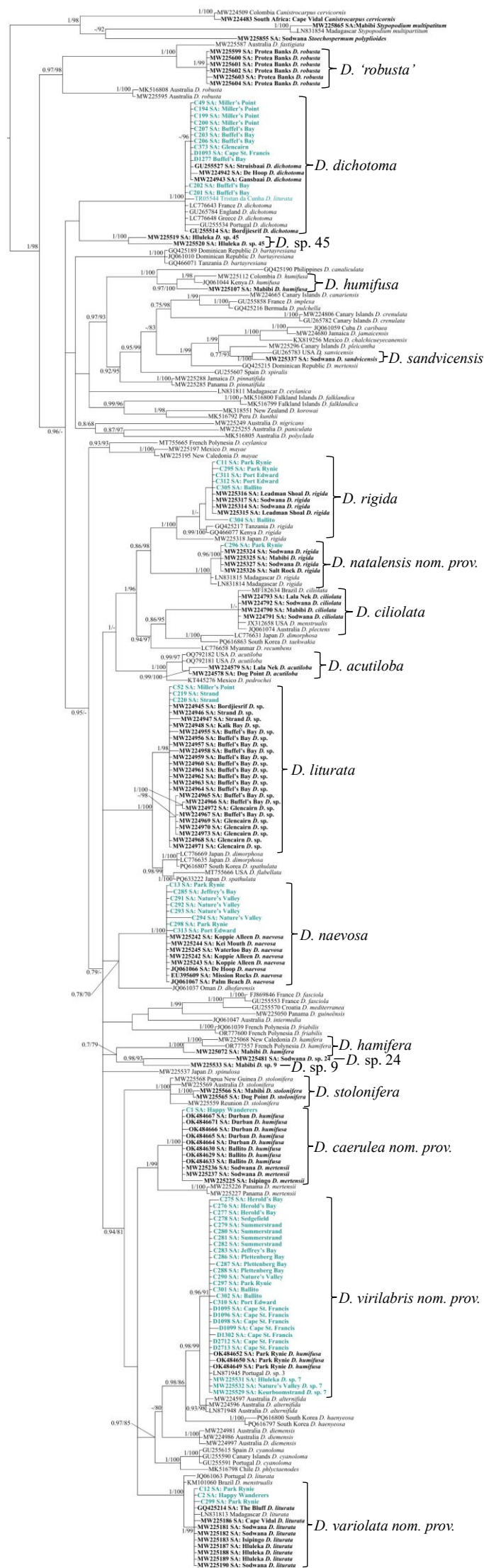


Figure 16. Phylogenetic tree of *Dictyota* species inferred from Bayesian- and Maximum likelihood analyses of *psbA* sequences. The tree was rooted with *Canistrocarpus cervicornis*, *Stypopodium multipartitum*, and *Stoechospermum polypodioides* (Family Dictyotaceae). Tip labels show the accession number, sampling country, and originally recorded species name. Brackets indicated clades supported by the data and are annotated with the accepted species names. Specimen sampled in South Africa are indicated in bold, and sequences generated during this study is indicated in blue, together with their associated sample code and sampling location. Bayesian posterior probabilities are shown at nodes when ≥ 0.75 , and maximum likelihood bootstrap percentages are shown when $\geq 65\%$.

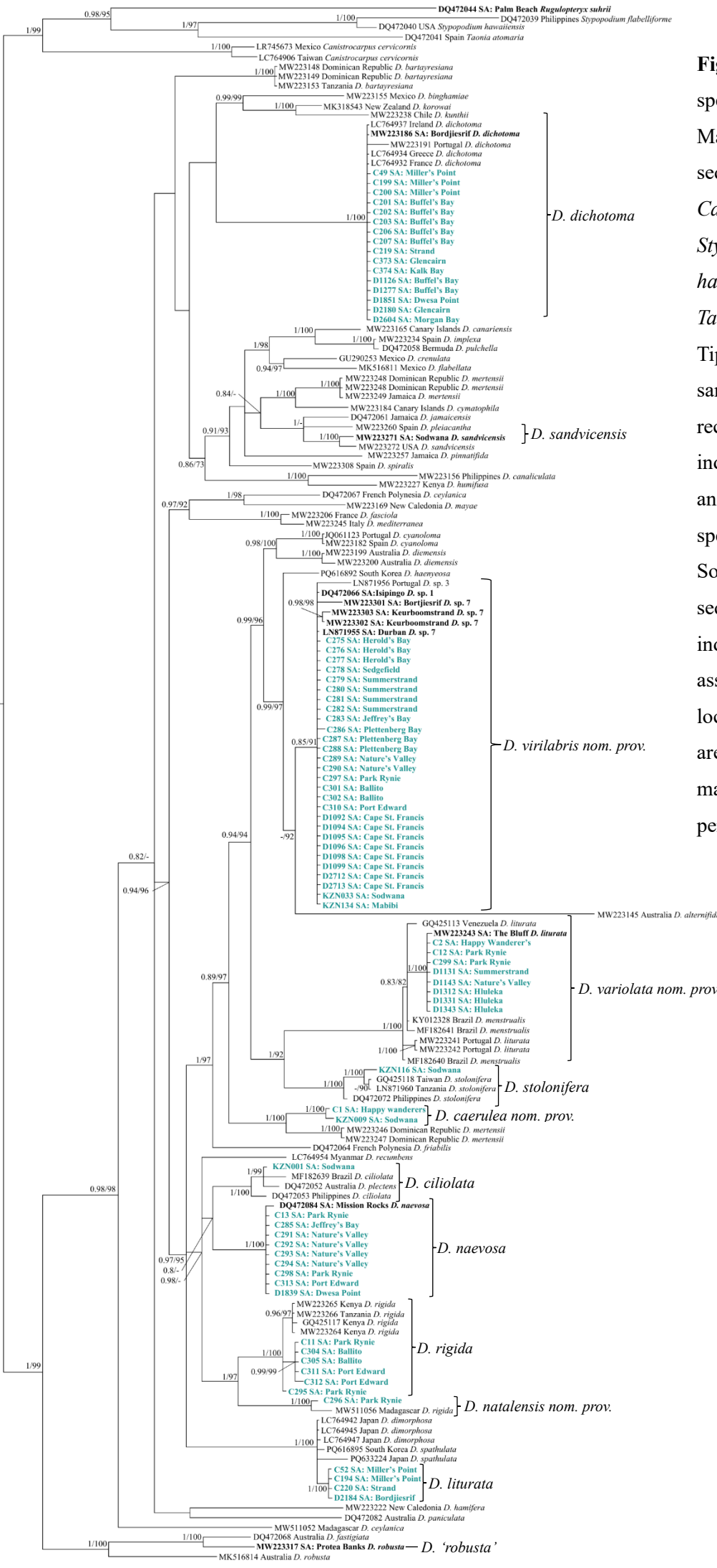


Figure 17. Phylogenetic tree of *Dictyota* species inferred from Bayesian- and Maximum likelihood analyses of *rbcL* sequences. The tree was rooted with *Canistrocarpus cervicornis*, *Styopodium flabelliforme*, *Styopodium hawaiiensis*, *Rugulopteryx suhrii*, and *Taonia atomaria* (Family Dictyotaceae). Tip labels show the accession number, sampling country, and originally recorded species name. Brackets indicated clades supported by the data and are annotated with the accepted species names. Specimen sampled in South Africa are indicated in bold, and sequences generated during this study is indicated in blue, together with their associated sample code and sampling location. Bayesian posterior probabilities are shown at nodes when ≥ 0.8 , and maximum likelihood bootstrap percentages are shown when $\geq 65\%$.

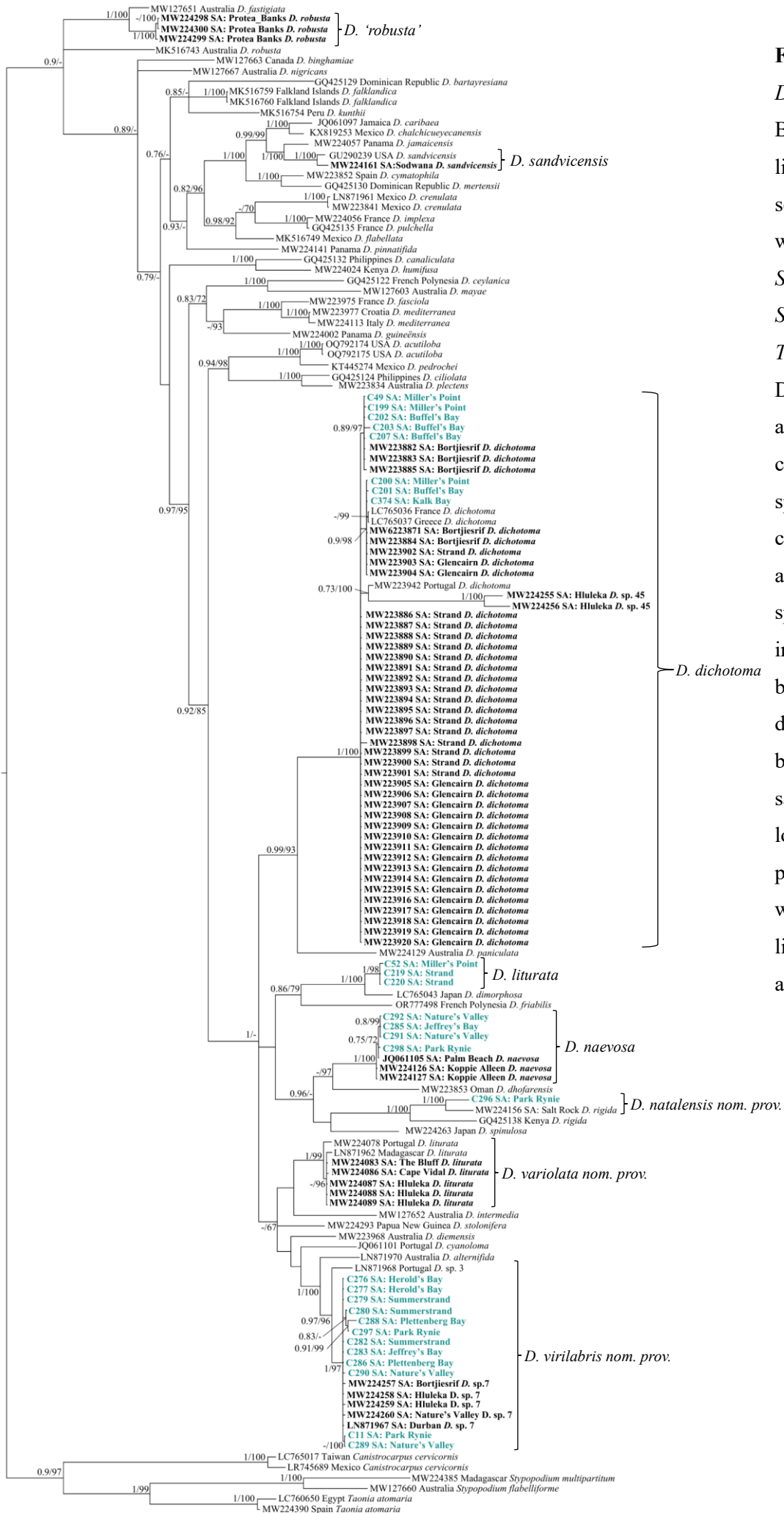


Figure 18. Phylogenetic tree of *Dictyota* species inferred from Bayesian- and Maximum likelihood analyses of cox1 sequences. The tree was rooted with *Canistrocarpus cervicornis*, *Stypopodium multipartitum*, *Stypopodium flabelliforme*, and *Taonia atomaria* (Family Dictyotaceae). Tip labels show the accession number, sampling country, and originally recorded species name. Brackets indicated clades supported by the data and are annotated with the accepted species names. Specimen sampled in South Africa are indicated in bold, and sequences generated during this study is indicated in blue, together with their associated sample code and sampling location. Bayesian posterior probabilities are shown at nodes when ≥ 0.8 , and maximum likelihood bootstrap percentages are shown when $\geq 65\%$.

Dictyota rigida formed a well-supported clade (*psbA*: PP = 0.86, BP = 98%; *rbcL*: PP = 1, BP = 97%; *cox1*: PP = 1, BP = 100%) containing two distinct species. South African *D. rigida* clustered closely with specimens from the type locality (Tanzania; *psbA*: <1% distance, PP = 1, BP = 100%; *rbcL*: <1% distance, PP = 1, BP = no support). Several additional South African specimens identified as *D. rigida*, were more distantly related and instead formed the sister species to *D. rigida* (*psbA*: 3.28% distance, *rbcL*: 3.2% distance; *cox1*: >10% distance). For the *rbcL* and *psbA* genes, the *D. rigida* and *D. natalensis nom. prov.* occurred in a clade with *D. ciliolata* collected in South Africa and *D. ciliolata* collected from the type locality, with *D. ciliolata* from South Africa and the type locality grouping together (*psbA*: <1% distance, PP = 1, BP: no support; *rbcL*: <1% distance, PP = 1, BP = 99%). The *psbA* also includes *D. acutiloba* collected from South Africa that formed an internal species clade with *D. acutiloba* from the type locality on the Hawaiian Archipelago (<1% distance, PP = 0.99, BP = 97%).

For both the *cox1* and *rbcL* genes, *D. naevosa* fell in the same clade as *D. rigida*; however, in the *psbA* phylogeny it formed its own distinct clade (PP = 0.78, BP = 70%), with *D. dhofaerensis*. Specimens collected during this study identified morphologically as *D. naevosa*, clustered closely with *D. naevosa* previously collected in South Africa for all three genes forming a well-supported clade (PP = 1, BP = 100%). For both *cox1* and *psbA* datasets, results further indicate that the sister species of the *D. naevosa*, which is a South African endemic, is *D. dhofaerensis* from Oman (*psbA*: 2.8-3.5%; *cox1*: 12.5%). This was moderately supported (*psbA*: PP = 0.78, BP = 70%; *cox1*: PP = not supported; BP = 97%).

For sample C52, this is the first time that morphology and DNA have been used together to designate barcodes from the type locality of *D. liturata*. The sequence generated from sample C52 is therefore topotype material for *D. liturata*, and formed a well-supported clade with C219, C220, and numerous additional GenBank sequences previously identified as *Dictyota* sp. (*psbA* and *cox1*: PP = 1, BP = 98%, *rbcL*: PP = 1, BP = 100%). The *Dictyota liturata* samples form part of a larger well-supported clade (*psbA*, *rbcL* and *cox1*: PP = 1, BP = 100%) which also included specimens from Asia (Japan, South Korea) and America (Pacific coast) identified as *D. spathulata*, *D. dimorphosa* or *D. flabellata*. This taxon forms the sister species to South African *D. liturata*.

Previously collected *D. hamifera* from South Africa formed a well-supported clade with a sample from French Polynesia for the *psbA* phylogeny (OR777557; type locality Tahiti;

1.21% distance, PP = 1, BP = 100%). These samples were found in a larger moderately supported clade (*psbA*: PP = not supported, BP = 79%) in which two distinct (3.42% distance), undescribed species (*Dictyota* sp. 9 MW22553, *Dictyota* sp. 24 MW225481) were also present. All three of these South African samples were collected from northern KwaZulu-Natal and form a clade with specimens from French Polynesia and New Caledonia.

Dictyota stolonifera formed a well-supported clade with *D. stolonifera* from Reunion, Australia, Taiwan, Tanzania, and Papua New Guinea (*psbA* and *rbcL*: <1% distance, PP = 1, BP = 100%). Specimen C1 represented a new species that clusters with previously collected South African samples misidentified as either *D. mertensii* or *D. humifusa* (*psbA*: PP = 1, BP = 100%). The sample KZN009 clustered with this specimen for the *rbcL* phylogeny (PP = 1, BP = 100%). This species is distinct from *D. humifusa* from the type (Colombia) and *D. mertensii* from close to the type locality (Panama; type locality: Brazil) and is the sister species to *D. mertensii* (*psbA*: 1.99%, PP = 1, BP = 99%, *rbcL*: 2.8-3.3%, PP = 1, BP = 100%). *Dictyota virilabris* nom. prov. is the sister species of *D. alternifida* from Australia (*rbcL*: >2%, PP = no support, BP = 92%; *cox1*: >5%, PP = 0.97, BP = 96%). In the *psbA* phylogeny, the new species formed a distinct group separate from *D. alternifida* (PP = 0.98, BP = 99%), although, the genetic distance between them was <1%. This species was also closely related to *D. haenyeosa* from South Korea, *D. diemensis* from Australia, *D. cyanoloma* from Spain, Portugal and the Canary Islands, *D. phlyctaenodes* from Chile, and a specimen from Papua New Guinea (*psbA*: PP = 0.97, BP = 85%, *rbcL*: PP = 0.99, BP = 96%).

A third newly described species, *D. variolata* nom. prov., has historically been misidentified as *D. liturata* but is genetically distinct from the newly generated topotype material (*psbA*: >2%; *rbcL*: >8%; *cox1*: >10%). This new species formed a well-supported clade with specimen collected from Brazil (type locality: North Carolina, USA) identified as *D. menstrualis* (*psbA*: <1% distance; *rbcL*: <1%), as well as specimens identified as *D. liturata* from Madagascar, Portugal, and Venezuela (*psbA* and *rbcL*: PP = 1, BP = 100%; *cox1*: PP = 1, BP = 99%).

4.3.2. Biogeography notes

The majority of *Dictyota* species were found on the east coast of South Africa, occurring predominantly in the AMP and the ETZ (Figure 4, Table 8). *Dictyota ciliolata* occurred

exclusively in the IWPMP from Mabibi northwards, while *D. naevosa* occurred exclusively in the AMP between Nature's Valley and Dwesa. *Dictyota liturata* exclusively occurred in the WTZ within False Bay despite being historically recorded to occur throughout the south coast (AMP).

Two species occurred over three provinces, with *D. humifusa* and *D. caerulea nom. prov.* occurring in the IWPMP, the ETZ and the AMP. These species are recorded from Durban (Isipingo) northwards. *Dictyota dichotoma* occurred in two marine provinces, the WTZ and the AMP, being confirmed from False Bay to Morgan Bay. *Dictyota virilabris nom. prov.* and *D. variolata nom. prov.* both occurred in the AMP and the ETZ. The former has been confirmed between Herold's Bay and Park Rynie, and the latter between Nature's Valley and Happy Wanderers. Similarly, *D. rigida* and *D. natalensis nom. prov.* occurred over two marine provinces – the ETZ and the IWPMP – with *D. rigida* being confirmed from Port Edward to Sodwana and *D. natalensis nom. prov.* being confirmed from Park Rynie to Mabibi.

4.3.3. Haplotype network for *Dictyota dichotoma*

The haplotype network for *D. dichotoma* revealed 11 different haplotypes arranged in a stellar pattern (Figure 14). The central haplotype (H5), as well as three other haplotypes (H6, H7, H8) consisted exclusively of South African samples. H7 and H8 differed from H5, and from each other by two substitutions of the *cox1* gene. H6 differed from H5 by three substitutions. H9 differed from H5 by three substitutions, and was the most geographically widespread haplotype, including specimens from South Africa, France, Greece, Spain, and Scotland. H10 consists of one sample from Scotland and differs from H9 by one substitution, while H11 consisted exclusively of specimens from Argentina and differed from H9 by one substitution. H4, H3 and H2 all consisted of exclusively Canary Island specimen. H4 and H3 differed from H5 by three substitutions and H2 differed from H3 by one substitution. H1 consisted of specimens exclusively from Madeira and differed from H3 by one substitution.

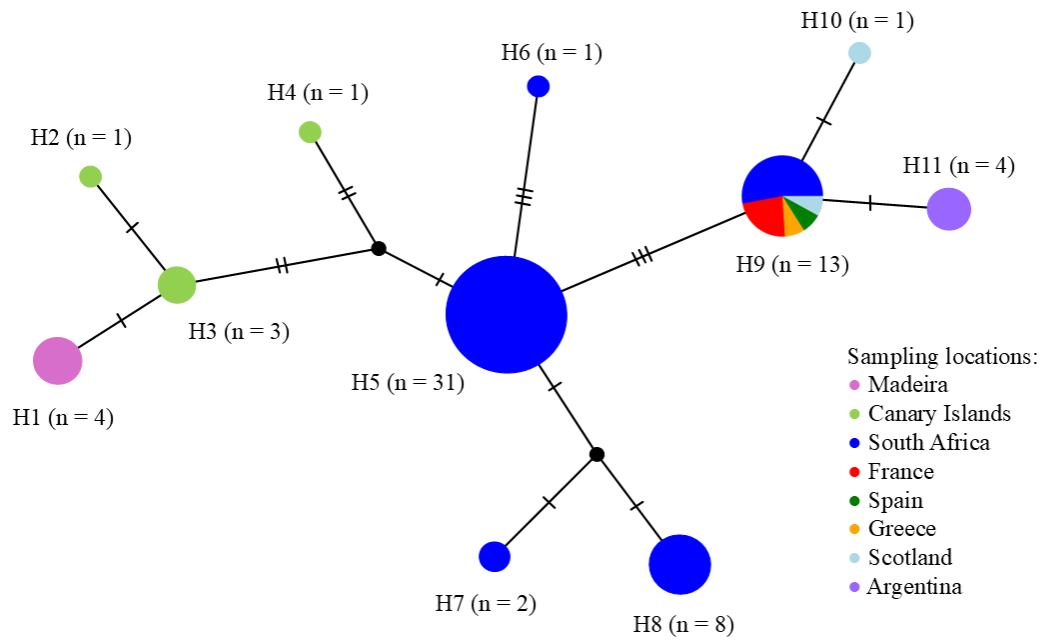


Figure 19. Median-joining haplotype network for *Dictyota dichotoma* using the *cox1* gene. The number of hatch marks indicate the number of mutations between haplotypes.

5. Discussion

This study revised the species diversity and distribution of *Dictyota* in South Africa using three genetic markers, complemented by morphological data. A total of 83 specimens collected over a decade were used, covering ~2 000 km of coastline, and stretching over four marine provinces. Four species are described. In addition, this study reports another four genetically distinct entities that may represent additional species, a new distribution record for South Africa and another for Tristan da Cunha, and clarifies the distribution ranges for all *Dictyota* species found within South Africa. The study also contributed greatly to the number of barcodes available for each gene, especially *rbcL*, for which there were only seven South African barcodes prior to this study.

5.1. Biodiversity assessment

Prior to this study, 13 species of *Dictyota* were formally recorded in South Africa (Table 2). This study, along with previous genetic studies, have failed to confirm the presence of four of these species, *D. bartayresiana*, *D. ceylanica*, *D. friabilis*, and *D. implexa*, in South Africa. All four of these species have morphologies similar to South African species (see morphological notes), suggesting these species might not occur in South Africa, or have disappeared in previous year. The following species, however, have been confirmed in South Africa with molecular data; *D. acutiloba*, *D. ciliolata*, *D. dichotoma*, , *D. liturata*, *D. naevosa*, *D. hamifera*, *D. humifusa*, and *D. rigida*.

This study described the species referred to as *Dictyota* sp. 1 which has previously been recorded in South Africa but was never described (described here as *D. virilabris nom. prov.*). In addition, this study revealed a further seven new species, three of which are described here: *D. variolata nom. prov.*, *D. caerulea nom. prov.*, and *D. natalensis nom. prov.*; and a new distribution recorded, *D. stolonifera*. The species *D. sandvicensis* is also confirmed in South Africa, however, this species has been reported to occur in the country according to AlgaeBase (Guiry & Guiry, 2025), and therefore does not constitute as a new distribution record. Nevertheless, it is acknowledged here as a recent addition to the South Africa Flora. The updated South African species list now contains 14 described species and 4 undescribed species. All species are clearly defined, having both highly supported branches and low

genetic divergence between specimens of the same species. These findings highlight the importance of conducting taxonomic reviews in understudied areas that incorporate molecular data, as there are still considerable amounts of diversity to be discovered and described.

Although falling outside of the scope of this study, it is interesting to note that both *Canistrocarpus cervicornis* and *Rugulopteryx suhrii*, which were initially described as *Dictyota* species, have been confirmed to occur within South Africa using molecular data. This study therefore shows that the Dictyoteae species diversity in South Africa comprises twenty species. This is comparable to Japan, which has eighteen species (Vieira *et al.*, 2025), despite Japan having a coastline roughly ten times longer than South Africa's (Hydrographic and Oceanographic Department of the Japan Coast Guard, 2017; Claassens *et al.* 2022). This agrees with the idea that South Africa has a rich seaweed diversity (Bolton & Stegenga, 2002).

5.2. Misapplied names

5.2.1. Misapplied names of morphologically similar species

This study revealed numerous instances of the misapplication of *Dictyota* species names, which once again highlights the need for molecular taxonomic revisions globally. Among the eight novel species, half matched with existing GenBank sequences that have been identified as previously described species, suggesting there has been a misapplication of species names. This illustrates how a misidentification can occur and a sequence with a misapplied name is uploaded to databases like GenBank, which can lead to further misapplications of the name when the sequences are simply used for barcode identification and not phylogenetic studies. An example of this can be seen with the newly described *Dictyota variolata* *nom. prov.*, which was historically misidentified as either *D. liturata* or *D. menstrualis*, and uploaded on GenBank, leading to further misidentifications (this is further discussed in the next section).

Specimens from Protea Banks represent an undescribed species more closely related to *D. fasciola* from the type locality than *D. robusta* from the type locality, suggesting that these specimens have been misidentified as *D. robusta* and represents a new species. This species remains undescribed as there were no morphological data available for analysis during this

study. This is the first recorded deepwater species of *Dictyota* in South Africa, occurring at ~40 m depth. This species has not been recorded from anywhere other than this one site, and appear to be absent from intertidal floras. This highlights the need to do deepwater surveys in South Africa. Most of our current knowledge on South African seaweed diversity is based on coastal and intertidal collections, with only one study specifically targeting a deepwater site (Anderson & Stegenga, 1989). Species of *Dictyota* have been recorded to occur at deeper sites in other places of the world (Searles & Schneider, 1987), suggesting that there might be undiscovered diversity hidden in South Africa's deeper marine sites. Furthermore, species of other genera have been described from Protea banks (Tronchin *et al.*, 2004), suggesting that a targeted deepwater survey may uncover more than just undescribed species of *Dictyota*. This also illustrates how novel, local diversity is often overlooked due to a morphological resemblance to a more cosmopolitan species. Similarly, Nelson *et al.* (2019) found that a local undescribed species from New Zealand was often given the name *D. intermedia*, described from Australia.

Another misapplication of a South African endemic is the application of the name *D. rigida* to the distinct, newly described species *D. natalensis nom. prov.* This species had a similar branching pattern to *D. rigida* (De Clerck *et al.*, 2002), making it easy to misidentify the species in the field, but once taking a closer look, it was found that it differed in other morphological aspects (see morphological notes). Similarly, the distinct blue colour of *D. caerulea nom. prov.* could be mistaken for the blue iridescence seen in both *D. mertensii*, *D. humifusa* (Littler & Littler, 2000), and in some specimens of *D. rigida* on the South African coast. This shows how important DNA data can be, as in both of these cases the molecular data was the first clue to uncovering a new species, and was what prompted a closer look at the morphology – allowing for the description of these species. Studies on other genera have shown similar results, with *Pyropia meridionalis* being overlooked and only described after the use of molecular data (Reddy *et al.*, 2020b), suggesting South Africa might harbour a rich diversity of seaweeds that remain undiscovered without the use of DNA data.

5.2.2. Other possible misapplications

This study also reports the different species names being assigned to phylogenetically similar sequences downloaded from GenBank. This includes the specimens identified as *D. spathulata*, *D. dimorphosa*, and *D. flabellata*. These samples are not from South Africa and

are outside the scope of this study. This case will therefore not be discussed further, however, this data suggests that researchers from Asia and USA need to review the taxonomy of *Dictyota* using an integrative approach to determine to which of these three species the specimens belong to.

A note should be made on *D. humifusa* recorded in South Africa. Although the results suggest this species is present in South Africa, caution should be taken. This relationship is only supported for one molecular marker, *psbA*, which is a conserved marker (Vieira *et al.*, 2025), and since no *D. humifusa* was collected during this study, no morphological comparisons could be made either. This suggests additional research is required to clarify the relationship between *D. humifusa* from South Africa and Colombia, and to determine whether this has been a misapplication of the name. This research can include additional, less conservative genetic markers as well as morphological data to confirm whether the South African specimens are indeed *D. humifusa* or a new, undescribed species.

5.2.3. The importance of type and topotype material

The final misapplication of a species name is that of both *D. liturata* and *D. menstrualis*. One of the clades found in South Africa include specimens identified as *D. liturata* from South Africa, Madagascar and Portugal, and specimens identified as *D. menstrualis* from Brazil. It is important to note that none of these samples were collected from the type localities of these species. When considering the specimens identified as *D. liturata*, the South African samples were all collected from the south coast to the east coast of South Africa in what would be considered the transition zone between the AMP and the IWPMP (Anderson *et al.*, 2009). The type locality, on the other hand, is the Cape of Good Hope in the Western Cape. This locality falls in the transition zone between the AMP and the BMP. Since specimens are distinct from the *D. liturata* collected in the type locality of the species (C52), we can conclude that this is not *D. liturata* specimen and that it has been a misapplication of the name.

Furthermore, Tronholm *et al.* (2013) has shown that *D. menstrualis* collected from the type locality in North Carolina, USA, is not distinct from *D. ciliolata* collected from the type locality in Venezuela. This would suggest that the two species should be synonymised and that the older name should be adopted, which is *D. ciliolata* (Guiry & Guiry, 2025). When looking at the *D. menstrualis* collected from Brazil, however, these specimens do not group

with the *D. ciliolata* from Venezuela suggesting it is a distinct species. These specimens, however, cannot be assigned the species name *D. menstrualis* since the name should be synonymised with *D. ciliolata*, suggesting that this species should be described as a new species. In summary, *D. menstrualis* from the type locality is conspecific with *D. ciliolata*, *D. menstrualis* from Brazil is a distinct species that groups up with misidentified *D. liturata* samples that are distinct from *D. liturata* from the type locality. This taxon is therefore described as *D. variolata* *nom. prov.*

5.3. Distribution ranges and biogeography

The molecular data generated during this study provides reliable species occurrence and distribution records. Historical distribution records (Table 2) tended to be more widespread than the DNA confirmed records generated here with old records suggesting numerous species distributed over multiple biogeographic regions, whereas here it is shown that most species were confined to one or two biogeographic regions. *Dictyota ciliolata* represented the only species previously recorded in South Africa for which the distribution within South Africa has been extended, with confirmed records from Sodwana. Previously, it was thought to occur exclusively from Mabibi northwards, indicating a broader presence in KwaZulu-Natal. The molecular data also revealed for South Africa, most of the diversity of *Dictyota* occurred on the east coast, with diversity decreasing as you moved west. No *Dictyota* has been collected and sequenced from the west coast of South Africa. This suggests that the species does not occur on this coast, which is supported by the fact that no *Dictyota* has been found in Namibia (Kreiner *et al.* 2019a; 2019b; 2019c), which falls in the same marine province (Benguela Province - (Spalding *et al.*, 2007)).

The presence of both *D. stolonifera* and *D. sandvicensis* in South Africa was confirmed solely on previously generated DNA data from Vieira *et al.* (2021). However, this is the first formal recognition of the former species in South Africa. Both species occurred exclusively in the IWPMP (Anderson *et al.* 2009), suggesting the two species are more tropical or warm water adapted species. This in turn suggests that these species might occur more north on the African coastline, extending into Mozambique, however, this has yet to be confirmed. A further five species had similar distribution ranges: *D. ciliolata*, *D. acutiloba* and three undescribed species (species 9, 24 and 45). These species are in different clades, suggesting these species simply have similar thermal tolerances.

All the described species mentioned above are found around the globe. *Dictyota stolonifera* has previously been reported from Madagascar and Japan (Steen *et al.*, 2015), as well as the Philippines (De Clerck *et al.*, 2006). This indicates the species occurs throughout the tropical Indian Ocean and extends into the Pacific. *Dictyota sandvicensis* is known from its type locality in Hawaii (De Clerck *et al.*, 2006), as well as New Zealand (Nelson *et al.*, 2019). This is, therefore the first record of the species, supported by molecular data, outside of the Pacific Ocean. A more widespread species, *D. ciliolata*, is known to occur in pantropical to warm-temperate ecosystems in Asia, the Red Sea, America, the Caribbean, Australia, Indonesia, and on the east coast of Africa (Tronholm *et al.*, 2013). Its presence in the northeastern part of South Africa is unsurprising as it has been reported from Tanzania and from Kenya (Tronholm *et al.*, 2013). However, the absence of confirmed records from Mozambique is strange, suggesting that there is likely a gap in sampling effort in this region. *Dictyota acutiloba* is another widespread species, known from Australia, New Caledonia, Hawaii, Japan, the Persian Gulf, the Mediterranean and the Red Sea (Delva *et al.*, 2024). It has not been found further north on the African coast, however, this might once again be due to a lack of sampling effort.

Dictyota hamifera is presumed to display a slightly broader thermal tolerance, spanning two Marine Provinces (IWPMP and ETZ), and occurring throughout the east coast of South Africa, however, molecular data has only confirmed its presence in Mabibi, in the IWPMP. This species has a type locality in Tahiti, but has been recorded worldwide, in the Pacific, Indian, and Atlantic Oceans (Ni-Ni-Win *et al.*, 2024; Guiry & Guiry, 2025). *Dictyota humifusa* is found in both the IWPMP and the ETZ. Both species are widely distributed species (Ni-Ni-Win *et al.*, 2024; Vieira *et al.*, 2025), inhabiting warm-water environments in both the Southern and Northern hemispheres (Guiry & Guiry, 2025). This suggests that both species likely occur further north along the African coastline.

Three species are found predominantly in the transition area between the IWPMP and the AMP. These are *D. caerulea nom. prov.*, *D. rigida* and *D. natalensis nom. prov.* Currently, the newly described species are exclusively known from the east coast of South Africa, however, more extensive sampling of the Eastern Cape, KwaZulu-Natal and Mozambique might reveal a wider distribution range. *Dictyota rigida* has been recorded from the type locality in Tanzania, as well as Madagascar and the Caribbean, however, Steen *et al.* (2015) suggests that this species probably consist of a few morphologically similar and genetically distinct taxa, each with a very restricted distribution. This study, however, does show that *D. rigida*

from South Africa groups with that of Tanzania, indicating that the species likely occurs along the entire southeast African coast.

The newly described *D. variolata nom. prov.* has a wide distribution along South Africa's south and east coasts. This species exhibits a warm-temperate affinity, occurring within the ETZ and the warm-temperate AMP. A note should be made on sample KZN2282. This sample was previously collected and has been given the sampling location of St. James, Cape Town on GenBank, falling within the cold-temperate WTZ. This sample was the only sample within the *D. variolata nom. prov.* that had been collected so far west on the South African coast. A closer look was taken at the sample, as the collection location appeared unusual for this species and the sample name (starting with KZN) suggested it was collected in the KwaZulu-Natal province. Metadata on the Meise herbarium website suggests the sample was collected at the Bluff (Treasure Beach), Durban (Meise Botanic Garden, n.d.), thereby confirming the species has a more warm-temperate affinity.

Dictyota virilabris nom. prov. and the endemic *D. naevosa* are largely restricted to the Agulhas Marine Province, suggesting they are unlikely to occur in tropical waters. Within South Africa, both species have been reported to have wider distribution ranges, however, these records are not confirmed with molecular data. Although *Dictyota naevosa* has been reported from several regions outside of South Africa (Guiry & Guiry, 2025), none of these records have been confirmed with DNA data. It is likely that these represent misapplications of the name *D. naevosa*. For instance, in Australia *D. diemensis*, a morphologically similar species, is thought to occur on the eastern side of Australia's coast whereas *D. naevosa* records are from the western coast (Board of Botanic Gardens and State Herbarium: Adelaide, 2025b). Although there are slight morphological differences in size and colour (Board of Botanic Gardens and State Herbarium: Adelaide, 2025b), these traits might simply reflect local adaptations of the same species to different coastal conditions. It is likely that *D. diemensis* specimens has been misidentified as *D. naevosa* in Australia, which would support the view that *D. naevosa* is endemic to South Africa. Future research should, however, focus on barcoding Australia specimens currently identified as *D. naevosa* to determine with certainty whether the species is truly present there. As there is no molecular data currently supporting these distribution records, *D. naevosa* is currently still accepted to be endemic.

Dictyota liturata is one of two species found in the warm-temperate transition zone between the Agulhas Marine Province and the Benguela Marine province. It's confirmed range is

confined to the False Bay region, from Strand to Cape Point, representing less than 100 km of coastline. This makes *D. liturata* one of the most narrowly distributed *Dictyota* species in South Africa. The data generated during this study further supports the historical belief that it is a South African endemic (Stegenga *et al.*, 1997). All the specimens that have been collected outside of South Africa and identified as *D. liturata* (from Portugal, Madagascar and Tristan da Cunha) have been resolved within *D. variolata nom. prov.* This supports the view that *D. liturata* has an exceptionally limited distribution of less than 100 km.

The west coast of South Africa forms a distinct Marine Province from Cape Point northwards (Anderson *et al.*, 2009). This coastline is characterised by the Benguela Upwelling System, which generates highly variable and predominantly cold seawater conditions in comparison to the rest of the Western Cape (Bolton & Stegenga, 2002). Such variability suggests that *D. liturata* is unlikely to expand into this region, as it is adapted to the more stable, warm-temperate conditions of False Bay. This raises concerns about the future persistence of the species and highlights it as a priority for conservation.

Under global climate change, sea surface temperatures are expected to increase in the future (Müller *et al.*, 2009). However, regional patterns do not always follow global trends and a study done by Rouault *et al.* (2010) indicates that the west and south coasts of South African experienced significant cooling between 1982 and 2009. This was linked to changes in wind patterns and intensified upwelling (Rouault *et al.*, 2010). If this trend continues, both the BMP and the WTZ may shift towards an increasingly cold-temperate regime. For *D. liturata*, which has a restricted warm-temperate distribution, this scenario could prove to be fatal as an expansion into colder waters may not be physiologically possible. The combination of geographic confinement and potential regional cooling could therefore put *D. liturata* at risk of extinction.

Dictyota dichotoma is another interesting species within South Africa. It has previously been proposed that *D. dichotoma* is an invasive species in South Africa (Steen *et al.*, 2019). However, the results in this study challenges this view. The haplotype network shows that South African species form five different haplotypes. This suggests that the species has been present in South Africa for a considerable evolutionary time, long enough to accumulate intraspecific divergence. Moreover, the South African haplotypes occupy central positions in the network. North African haplotypes (from Madeira and the Canary Islands), appear to have evolved from H5, a haplotype found exclusively in South Africa. A South American

haplotype and a Scottish haplotype appear to have originated from H9, which includes both European and South African specimens. This suggests that South Africa acts as a genetic source rather than having evolved from a European ancestor. Further support come from the observation that the sister species of *D. dichotoma* is an undescribed South African species (*D. sp. 45*). The presence of a sister species within the same region strongly implies that *D. dichotoma* has had a long evolutionary history in South Africa. This all suggests that it is unlikely that this species is invasive. Instead, these results suggest that *D. dichotoma* may have dispersed to other regions after originating within southern Africa. Alternatively, the region could have acted as ancient refugia through the ice ages. Further studies should be done to confirm this hypotheses, using more appropriate population level markers, for example microsatellites (Krueger-Hadfield *et al.*, 2017). It should also be noted, that although this falls outside of the scope of this study, this work documents the first confirmed records of *D. dichotoma* in Tristan da Cunha.

A note should be made regarding the undescribed *D. sp. 45*. This species appears to be divergent from *D. dichotoma* based on *psbA*, but not *cox1*. Both markers are relatively conserved, which may indicate that *cox1* is failing to capture underlying genetic diversity in this group, once again highlighting the importance of using multiple markers. However, additional research is required to confirm this interpretation. Future studies should prioritise resampling this species and conducting detailed morphological analyses. This will help determine whether the species is in fact a distinct species, as it is treated in this study, or whether it reflects a locally adapted population of *D. dichotoma* occurring in the slightly warmer waters of Hluleka (ETZ compared to the WTZ and AMP of other *D. dichotoma* samples).

The overall diversity of *Dictyota* in South Africa is concentrated along the southeastern and eastern coastline of South Africa. This finding differs from the findings of Bolton & Stegenga (2002), who used only morphological identification of specimens and reported that the species diversity of seaweeds in South Africa is generally more diverse on the south coast than the east coast. This once again suggests that DNA provides more accurate biodiversity estimates. However, they did note that this finding might have been influenced by a sampling bias, particularly with sampling gaps on the east coast region (Bolton & Stegenga, 2002). In the present study, a number of specimens used from the East Cape and KwaZulu-Natal were sourced from previous collections and not collected during this study. Despite this limited sampling effort, most of the new species discovered was reported from this area, highlighting

substantial undocumented *Dictyota* diversity. This suggests that more extensive and targeted sampling of the eastern coastline could reveal additional, undiscovered species. It should also be noted that the contribution of historically collected material greatly enhanced this current study, as it increased the study area by nearly 500 km, and allowed for the analysis of species found in the IWPMP, which starts in the northernmost part of South Africa. This highlights the importance of creating species repositories that can be used in the future for taxonomic revisions, monitoring under global climate change, and biodiscovery research (Reddy, *et al.*, 2021).

Interestingly, *Dictyota* has the highest diversity in the warmer areas of South Africa. This pattern indicates the genus has a warm-temperate or tropical centre of diversity. This interpretation aligns with the findings of Vieira *et al.* (2021), who shows that the diversity of Dictyotales peaks in the Central Indo-Pacific, where 186 species and 14 genera are recorded. These patterns therefore support the view that *Dictyota* has its highest diversity in warm-temperate or tropical waters, and that the Central Indo-Pacific likely also represents the centre of diversity for the genus.

5.4. Morphological notes

The morphological analysis of specimens clearly demonstrates that species-level identification in *Dictyota* is challenging when based on morphology alone. A number of characters exhibit considerable overlap between species, reducing their reliability for discrimination. This might in part be due to the morphological plasticity that is known to be a characteristic of *Dictyota* species. All species had a single layer of both medullary- and cortical cells characteristic of the genus.

One of the distinguishing features was the thallus size of specimens. In South Africa, *Dictyota dichotoma* and *D. naevosa* appears to be the only two species capable of exceeding 10 cm in length. However, this interpretation should be made cautiously. Most, although not all, of the specimens in this study were collected during the same season (summer to early autumn, ~70%), and previous research has demonstrated that some species undergo substantial seasonal size reduction or may even disappear from the visible flora during certain periods (Steen *et al.*, 2019). This suggests that size alone should not be used when identifying species of *Dictyota* in South Africa.

It's also important to note that reproductive structures were largely absent from the specimens examined. This may likewise be a consequence of non-seasonal sampling. These findings collectively highlight the importance of future research incorporating year-round, seasonal sampling, where the same sites are surveyed and sampled across all seasons. This would provide a more comprehensive understanding of morphological variation and reproduction phenology across species.

A key distinguishing feature among species in South Africa was the presence and colour of *in situ* iridescence. *Dictyota dichotoma*, *D. ciliolata* and *D. liturata* are characterised by little to no iridescence. *Dictyota virilabris nom. prov.* has a distinct green iridescent margin, distinguishing it from other *Dictyota* species. In contrast, numerous South African species are characterised by a blue iridescent, although the specific shade and intensity differ somewhat between the species.

Dictyota caerulea nom. prov. displays a dark blue to purple iridescence which might be the reason why this species has been misidentified as *D. humifusa* and *D. mertensii*. The species can, however, be distinguished from *D. mertensii* by its repent growth habit and truncate apices, whereas *D. mertensii* typically exhibits an erect habit and largely rounded apices (Littler & Littler, 2000). *Dictyota humifusa* appears to be significantly larger than *D. caerulea nom. prov.*, although, as previously mentioned, size can be variable and seasonally dependent. These challenges underscore the importance of molecular data for accurately distinguishing *D. caerulea nom. prov.* from morphologically similar species in the field.

The newly described species *D. variolata nom. prov.* can be distinguished from *D. liturata* by its bright blue iridescence. While both species exhibit spots on the thallus, the pattern differs, with *D. liturata* displaying longer streaks and *D. variolata nom. prov.* having a more spotted appearance. The primary distinction between these two species, however, is biogeographical rather than morphological. *Dictyota variolata nom. prov.* occurs on the east coast of the country whereas *D. liturata* occurs in False Bay, making their biogeographic affinities a key distinguishing factor. This mirrors findings by (Reddy *et al.*, 2020a) where *Callithamnion africanum* was described using an integrative approach that included distributional data and highlights the importance of integrated taxonomy using multiple markers (morphological, molecular and biogeographical).

Dictyota rigida and *D. natalensis nom. prov.* share a broadly similar branching pattern, however, they differ significantly in regard to colour and iridescence. *Dictyota rigida* is

characterised by an olive-brown thallus with blue or orange iridescence, whereas *D. natalensis nom. prov.* exhibits a bright blue thallus with a brown-green margin and obvious blue iridescence. *Dictyota naevosa* is the most easily recognised species in South Africa, being clearly distinct from other species. It is a robust plant, with sub-dichotomous branching, a pale to yellowish brown colour and a slight blue to turquoise iridescence *in situ*, making it readily identifiable in the field.

It is important to address the morphology of species from the South African that have not yet been confirmed using DNA, as records of these four taxa might be the results of misapplied names. *Dictyota friabilis*, previously recorded in South Africa (De Clerck *et al.*, 2005a), is characterised by a bluish iridescence and the presence of small non-iridescence spots. These features resemble the morphology of the newly described *D. variolata nom. prov.*, which could have resulted in the misapplication of the name *D. friabilis*. The two species, are however different in several diagnostic features, allowing us to describe the new species based on morphology and DNA results. The apices of *D. friabilis* are rounded to obtuse (De Clerck *et al.*, 2005a), where *D. variolata nom. prov.* exhibits distinctly truncate apices. They also differ in their growth habit, with *D. variolata nom. prov.* is an erect species, while *D. friabilis* having a completely procumbent growth form (De Clerck *et al.*, 2005a).

Dictyota linearis was recorded from South Africa by Silva (1996). However, this name has since been synonymised with *D. implexa* (Tronholm *et al.*, 2010b), which explains why *D. implexa* is recognised in South Africa. The basionym of *Dictyota linearis* is *Zonaria linearis*, a name now considered synonymous with *Dictyota dichotoma var. intricata* (Guiry & Guiry, 2025). This suggests that *D. dichotoma var. intricata* is morphologically similar to *D. implexa*. It is therefore possible that the specimens identified by Silva (1996) were actually *D. dichotoma var. intricata*, representing a historical misapplication of the name rather than the presence of *D. linearis sensu stricto*, and therefore *D. implexa*, in South Africa.

Both *D. bartayresiana* and *D. ceylanica* were also recorded on the east coast of South Africa by Silva (1996). The former is characterised by an erect thallus and dark olive-brown colour with iridescent blue and green transverse bands (Littler & Littler, 2000). It is therefore possible that the name *D. bartayresiana* might have been misapplied to specimens now described as *D. natalensis nom. prov.*, which also displays transverse bands, a blue iridescence and a similar branching pattern to *D. bartayresiana*. *Dictyota natalensis nom.*

prov. additionally has a brownish colour once removed from the field, further contributing to the confusion.

Dictyota ceylanica likewise has transverse bands *in situ*, along with a blue to yellowish iridescence (De Clerck, 2003), suggesting a similar morphology to *D. natalensis nom. prov.* However, this species has also been regarded as a synonym of *Dictyota dichotoma var. intricata*, implying a close affinity to the intricate form of the type species. Together, these lines of evidence indicate the South African records of *D. ceylanica* may also represent misidentifications. Given the uncertainties, a cautious approach is warranted. These four species should only be recognised on the South African *Dictyota* species list once their presence has been confirmed using molecular methods.

The morphology of *Dictyota* species has long been considered problematic, with few reliable characters available for morphological identification (Hwang *et al.*, 2005; Tronholm *et al.*, 2010b). The results of this study further support this conclusion, with a substantial overlap seen in morphological features across species, particularly in respect to cell dimensions (Table 8). These findings illustrate the limitations of using morphology alone and highlight the need for an integrative approach using molecular data, as well as ecological, biogeographical or chemical data.

5.5. Notes on the molecular data

This study highlights the importance of incorporating genetic data when reviewing the taxonomy of morphologically challenging species. The four newly described species exhibit morphologies similar to previously recognised taxa, making it easy to overlook them when using exclusively traditional identification methods. In all cases, DNA data provided the first indication that these might represent new species, prompting a closer morphological examination that confirmed their distinctness. It is therefore important to recognise the limitations of traditional morphology-based methods for species identification when working with *Dictyota*, and crucial to build up a DNA reference library so that future identification can be easily carried out using barcoding and molecular systematics. This will enable researchers to detect undescribed species in understudied regions, ultimately improving the global taxonomy of the genus.

A significant research gap is present with regards to the group *Dictyota*, with a lack of type specimen sequences available on GenBank. Robust taxonomic revision using DNA data ideally requires sequences from the type specimen, however, as type material is often difficult to amplify or is not available for DNA barcoding, it becomes essential for taxonomists to confidently identify topotype material that can be used to barcode (Tautz *et al.*, 2003), thereby providing sequences that can be used for molecular systematics. This highlights the importance of the research presented here, as it provides the first confirmed topotype sequence for *D. liturata*, enabling its distinction from the east coast species *D. variolata nom. prov.*

It is important to reflect on the molecular markers employed during this study. The marker *psbA* is the most widely used marker for *Dictyota* and has also been previously proposed to be the choice marker for the genus (Vieira *et al.*, 2025). However, *psbA* is a relatively conserved marker (Vieira *et al.*, 2025), and in some cases does not provide sufficient resolution within *Dictyota*. This is evident in the case of *D. virilabris nom. prov.*, where *psbA* failed to distinguish between the species and *D. alternifida*. Such examples highlight the importance of using multiple molecular markers when conducting taxonomic assessments, as markers might differ in their ability to capture recent divergence.

Despite the crucial role of DNA data in modern-day taxonomy, molecular evidence alone cannot entirely replace morphological analysis (DeSalle, 2006). The distinct morphological differences between *D. virilabris nom. prov.* and *D. alternifida* (Board of Botanic Gardens and State Herbarium: Adelaide, 2025a) clearly also indicated that they represent separate species, reinforcing the value of an integrated approach that combines morphology and molecular data.

5.6. Broader implications of these findings

This study provides foundational knowledge on the diversity, morphology and distribution of *Dictyota* species in South Africa. Beyond the taxonomic contributions, the study has broader implications for both the conservation and application of species in the blue bioeconomy. Of the eighteen species now recognised from South Africa, half appear to be endemic; *D. natalensis*, *D. liturata*, *D. virilabris nom. prov.*, *D. natalensis nom. prov.*, *D. caerulea nom. prov.*, *D. sp. 9*, *D. sp. 24*, *D. sp. 45* and the undescribed species previously misidentified as *D.*

stolonifera. This high level of endemism suggests that considerable unexplored diversity remains within the region, presenting potential opportunities for future commercial applications.

The newly discovered species may provide novel chemical diversity with potential future applications. No *Dictyota* species are currently commercially exploited on a large scale (Bogaert *et al.*, 2020), however, preliminary research has shown that the secondary metabolites produced by this genus has great potential to produce high-value products like anti-inflammatory, anti-viral and antibiotic pharmaceutical products. This could be particularly significant for South Africa, as such discoveries may contribute to socio-economic development through job creation and the expansion of commercially valuable products.

The COMBO project is currently investigating the potential use of South African seaweeds in the blue bioeconomy, including chemical analyses of some of the samples used in this study. One example highlighting the potential of South African *Dictyota* is the newly described species *D. variolata nom. prov.* While no current research have yet been published for South African material, previous research on Brazilian specimens identified as *D. menstrualis*, now shown in this study to belong to *D. variolata nom. prov.*, has demonstrated that the species produces compounds with anti-viral, anti-inflammatory and anti-tumour effects (Gomes *et al.*, 2015; Cirne-Santos *et al.*, 2019; do Nascimento Ávila *et al.*, 2019). Ongoing chemical research within the COMBO project aims to further investigate the bioactive potential of this species and its possible application within the blue bioeconomy.

At present, only a small number of seaweed species are exploited on a commercial scale in South Africa (Anderson *et al.*, 1987), indicating substantial untapped potential within the sector. The seaweeds currently exploited are also mostly used for low-value products like animal feed, plant-growth enhancers and food products (Anderson *et al.*, 1987). These findings highlight the opportunity for growth within the aquaculture industry and underscore the importance of viewing marine resources in terms of their potential for sustainable use in the blue bioeconomy (Reddy *et al.*, 2021).

However, these findings also indicate the need for conservation. As species begin to be considered for their economic potential, it becomes essential to ensure their use is accompanied by effective conservation strategies. Unlike kelp, which can become highly

dominant in South African ecosystems (Blamey & Bolton, 2018, Prew *et al.* 2024), *Dictyota* species do not typically form such extensive populations within South Africa. In the present study, the only time *Dictyota* was found to be dominant in an ecosystem was when it occurred in tidal pools (e.g. *Dictyota dichotoma* in Miller's Point and Buffel's Bay, Western Cape). This is especially relevant in the case of *D. liturata*. As noted, this species has a highly restricted geographic range making it particularly vulnerable to the impacts of future climate change. Its limited distribution heightens the risk of extinction, emphasising the need for targeted conservation efforts to ensure its long-term persistence.

Sustainable exploitation will require management frameworks that balance utilisation with long-term conservation, ensuring that these species remain viable in the future. At present, the harvesting of *Dictyota* species occurs on a small scale, with thalli collected from natural populations (Bogaert *et al.*, 2020). However, if commercial-scale exploitation were to develop, it would become essential to shift toward cultivation rather than relying on wild stocks in order to prevent overexploitation of natural populations.

5.7. Future research

The present research represents an important first step in revising the taxonomy of South African *Dictyota*, but substantial work remains to be done. This project has generated novel insights into the taxonomy, diversity, and biogeography of *Dictyota* species. Vieira *et al.* (2025) suggests that all three the markers used in this study are relatively conserved. Although they are effective in resolving phylogenetic relationships within *Dictyota*, the use of more variable markers may reveal additional undescribed species. Future studies should therefore explore the application of less conserved molecular markers to improve resolution and enhance species discovery. Although the methods and markers were sufficient for the scope of this research, future research could also incorporate species delimitation methods in perplexing cases (Reddy *et al.*, 2018), for example, the relationship between *D. virilabris nom. prov.* and *D. alternifida*.

Furthermore, the discovery of four previously undescribed species indicates the need for a more comprehensive taxonomic revision of the genus. Achieving this will require a more extensive and systematic sampling effort. This should include both the east coast, which has historically received less sampling effort despite harbouring considerable diversity (Bolton &

Stegenga, 2002), as well as subtidal and deepwater sites like Protea Banks. Despite the progress this study has made, it is important to acknowledge the gaps that persist due to limited sampling. Most of the collections were conducted in False Bay, along the south coast, and in the southern KwaZulu-Natal region. In contrast, and most of the samples collected from northern KwaZulu-Natal and the Eastern Cape formed part of more general historical collections and not targeted sampling efforts. This allowed for the molecular analysis of samples, but since no morphological subsamples was available for analysis, no species descriptions of these specimens could be made. Targeted and expanded sampling in these regions will allow for the collection of morphological material and the description of species leading to a more complete understanding of the genus' distribution and diversity.

Apart from more extensive sampling within South Africa, the biogeography results suggest that numerous species found on the east coast of South Africa have tropical affinities. This suggests that they may occur further north in the IWPMP, suggesting its occurrence in Mozambique. A full taxonomic review, similar to this one, should be applied to Mozambique, where extensive sampling should be done along the whole coast. This could potentially improve the knowledge of the species present in South Africa, as it appears to be the southern limit of some species (e.g. *D. natalensis nom. prov.*). Additionally, this research could uncover more undescribed species, further increasing the knowledge we have on the global diversity of *Dictyota*.

Another avenue of future research could include the integration of DNA and morphological data with chemistry. The chemistry of specimens of the genus might give us hints as to where species are found. For example, research currently being done has shown that specimens sampled on the east coast of South Africa that has been identified as *D. liturata* has the same chemical profile as *D. menstrualis* from Brazil (pers. com. Olivier Thomas). This finding supports the taxonomic treatment that these two species are one, now described as *D. variolata nom. prov.* Chemistry can therefore give biogeographical clues to where species occur. Ongoing research suggests that C12 (a specimen of *D. variolata nom. prov.*) has the same chemical profile as a specimen from Australia (Blount *et al.*, 1982), suggesting the new species might also occur in Australia.

6. Conclusion

This study makes a substantial contribution to the taxonomy of *Dictyota* and underscores the importance of revising seaweed taxonomy in understudied regions. By integrating molecular and morphological data, this work updates the South African species list from 13 recorded species to 18 species, revised the distribution ranges of these taxa, and provided evidence that *D. dichotoma* may not be invasive in South Africa. Future research should build on these findings by expanding geographic and seasonal sampling, incorporating deepwater habitats, and including reproductive material to further refine species boundaries and improve the resolution of taxonomic classifications. Global taxonomic research of the genus should focus on reviewing species in understudied regions, as well as barcoding type specimen or allocating and barcoding topotype material, therefore increasing the confidence we have in the taxonomic conclusions made from molecular data.

7. References

- Abdelfattah, H.M.E., Hussein, H.A., Teleb, S.S., El-Demerdash, M.M. & George, N.M. 2024. Chemotaxonomy compared to morphological and anatomical taxonomy of five Hibiscus species. *Journal of Plant Research*. 137(6):967–984. DOI: 10.1007/s10265-024-01566-9.
- Altamirano-Cerecedo, M. del C., López-Fuerte, F.O., López-Vivas, J.M., Serviere-Zaragoza, E. & León-Cisneros, K. 2024. Review of Taxonomic Knowledge of Dictyota (Phaeophyceae; Dictyotales); Two Centuries after its Description. DOI: 10.20944/preprints202404.0841.v1.
- Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. 1990. Basic local alignment search tool. *Journal of Molecular Biology*. 215(3):403–410. DOI: 10.1016/S0022-2836(05)80360-2.
- Anderson, R.J. & Stegenga, H. 1989. Subtidal Algal Communities at Bird Island, Eastern Cape, South Africa. *Botanica Marina*. 32: 299-311.
- Anderson, R.J., Bolton, J.J. & Stegenga, H. 2009. Using the biogeographical distribution and diversity of seaweed species to test the efficacy of marine protected areas in the warm-temperate Agulhas Marine Province, South Africa. *Diversity and Distributions*. 15(6):1017–1027. DOI: 10.1111/j.1472-4642.2009.00614.x.
- Anderson, R.J., Stegenga, H. & Bolton, J.J. 2016. *Seaweeds of the South African South Coast*. Available: <http://southafrseaweeds.uct.ac.za/> [2025, November 28].
- Aragay, J., Vitales, D., Gómez Garreta, A., Ribera Siguan, M.A., Steen, F., De Clerck, O., Garnatje, T. & Rull Lluch, J. 2016. Phenological and molecular studies on the introduced seaweed *Dictyota cyanoloma* (Dictyotales, Phaeophyceae) along the Mediterranean coast of the Iberian Peninsula. *Mediterranean Marine Science*. 17(3):766–776. DOI: 10.12681/mms.1872.
- Assis, J., Castilho Coelho, N., Alberto, F., Valero, M., Raimondi, P., Reed, D. & Alvares Serrão, E. 2013. High and Distinct Range-Edge Genetic Diversity despite Local Bottlenecks. *PLoS ONE*. 8(7). DOI: 10.1371/journal.pone.0068646.
- Azzurro, E., Fanelli, E., Mostarda, E., Catra, M. & Andaloro, F. 2007. Resource partitioning among early colonizing *Siganus luridus* and native herbivorous fish in the Mediterranean: An integrated study based on gut-content analysis and stable isotope signatures. *Journal of the*

- Marine Biological Association of the United Kingdom*. 87(4):991–998. DOI: 10.1017/S0025315407056342.
- Bachoo, T., Bolton, J.J., Macey, B.M., Kandjengo, L. & Reddy, M.M. 2023. Resolving the identity of commercially cultivated *Ulva* (Ulveae, Chlorophyta) in integrated seaweed-abalone aquaculture farms in South Africa. *Journal of Phycology*. 59(6):1272–1283. DOI: 10.1111/jpy.13391.
- Bandelt, H., Forster, P. & Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*. 16(1):37–48.
- Bengtson, S., Sallstedt, T., Belivanova, V. & Whitehouse, M. 2017. Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae. *PLoS Biology*. 15(3). DOI: 10.1371/journal.pbio.2000735.
- Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. & Das, I. 2007. Cryptic species as a window on diversity and conservation. *Trends in ecology & evolution*. 22(3): 148-155. DOI: 10.1016/j.tree.2006.11.004.
- Blamey, L.K. & Bolton, J.J. 2018. The economic value of South African kelp forests and temperate reefs: Past, present and future. *Journal of Marine Systems*. 188:172–181. DOI: 10.1016/j.jmarsys.2017.06.003.
- Blount, J.F., Dunlop, R.W., Erickson, K.L. & Wells, R.J. 1982. Two Diterpenes with New Carbocyclic Ring Systems from an Australian Collection of the Brown Alga *Dictyota dichotoma*. *Australian Journal of Chemistry*. 35(1): 145-163. DOI: 10.1071/CH9820145.
- Board of Botanic Gardens and State Herbarium: Adelaide. 2025. *Dictyota alternifida* J.Agardh, in (ed.), *Flora SA*. Available: <https://flora.sa.gov.au/taxon/60034-dictyota-alternifida?view=list&tab=1> [2025, December 05].
- Board of Botanic Gardens and State Herbarium: Adelaide. 2025b. *Dictyota diemensis* Kutz., in (ed.), *Flora SA*. Available: <https://flora.sa.gov.au/taxon/60056-dictyota-diemensis> [2025, December 04].
- Bogaert, K.A., Arun, A., Coelho, S.M. & De Clerck, O. 2013. Brown algae as a model for plant organogenesis. *Methods in Molecular Biology*. 959:97–125. DOI: 10.1007/978-1-62703-221-6_6.

- Bogaert, K.A., Delva, S. & De Clerck, O. 2020. Concise review of the genus *Dictyota* JV Lamouroux. *Journal of Applied Phycology*. 32(2): 1521-1543. DOI: 10.1007/s10811-020-02121-4.
- Boisnoir, A., Pascal, P.Y., Cordonnier, S. & Lemée, R. 2019. Spatio-temporal dynamics and biotic substrate preferences of benthic dinoflagellates in the Lesser Antilles, Caribbean sea. *Harmful Algae*. 81:18–29. DOI: 10.1016/j.hal.2018.11.012.
- Bolton, J.J. 1996. Patterns of species diversity and endemism in comparable temperate brown algal floras. *Hydrobiologia*. 326(1): 173-178.
- Bolton, J.J. 2010. The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgoland marine research*. 64(4): 263-279 DOI: 10.1007/s10152-010-0211-6.
- Bolton, J.J. 2016. What is aquatic botany?- And why algae are plants: The importance of non-taxonomic terms for groups of organisms. *Aquatic Botany*. 132:1–4. DOI: 10.1016/j.aquabot.2016.02.006.
- Bolton, J.J. 2020. The problem of naming commercial seaweeds. *Journal of Applied Phycology*. 32(2):751–758. DOI: 10.1007/s10811-019-01928-0.
- Bolton, J.J. & Stegenga, H. 2002. Seaweed species diversity in South Africa. *South African Journal of Marine Science*. 24:9–18.
- Bolton, J.J., Anderson, R.J., Smit, A.J. & Rothman, M.D. 2012. South African Kelp Moving Eastwards: The Discovery of *Ecklonia Maxima* (Osbeck) Papenfuss at De Hoop Nature Reserve on the South Coast of South Africa. *African Journal of Marine Science*. 34(1):147–151. DOI: 10.2989/1814232X.2012.675125.
- Breeman, A.M. 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence*. *Helgolander Meeresunters*. 42:199–241.
- Brodie, J., Andersen, R.A., Kawachi, M. & Millar, A.J.K. 2009. Endangered algal species and how to protect them. *Phycologia*. 48(5): 423-438. DOI: 10.2216/09-21.1.
- Brodie, J., Wilbraham, J., Maggs, C.A., Baldock, L., Bunker, F., Mieszkowska, N., Scanlan, C., Tittley, I., Wilkinson, M. & Yesson, C. 2023. Red List for British seaweeds: evaluating the

- IUCN methodology for non-standard marine organisms. *Biodiversity and Conservation*. 32(12):3825–3843. DOI: 10.1007/s10531-023-02649-0.
- Carrión-Cortez, J.A., Zárate, P. & Seminoff, J.A. 2010. Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. *Journal of the Marine Biological Association of the United Kingdom*. 90(5):1005–1013. DOI: 10.1017/S0025315410000226.
- CBOL Plant Working Group. 2009. A DNA barcode for land plants. *PNAS*. 106(31):12794–12797. DOI: 10.1073/pnas.0905845106.
- Chakrabarty, P., Warren, M., Page, L.M. & Baldwin, C.C. 2013. GenSeq: An updated nomenclature and ranking for genetic sequences from type and non-type sources. *ZooKeys*. 346:29–41. DOI: 10.3897/zookeys.346.5753.
- Chan, C.X., Ho, C.L. & Phang, S.M. 2006. Trends in seaweed research. *Trends in Plant Science*. 11(4): 165-166. DOI: 10.1016/j.tplants.2006.02.003.
- Chapman, V.J. & Chapman, D.J. 1980. Occurrence, distribution and historical perspective. In *Seaweeds and their uses*. 3rd ed. Springer Netherlands.
- Chase, M.W., Salamin, N., Wilkinson, M., Dunwell, J.M., Kesanakurthi, R.P., Haidar, N. & Savolainen, V. 2005. Land plants and DNA barcodes: Short-term and long-term goals. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 360(1462):1889–1895. DOI: 10.1098/rstb.2005.1720.
- Cheminée, A., Pastor, J., Bianchimani, O., Thiriet, P., Sala, E., Cottalorda, J.M., Dominici, J.M., Lejeune, P., & Francour, P. 2017. Juvenile fish assemblages in temperate rocky reefs are shaped by the presence of macro-Algae canopy and its three-dimensional structure. *Scientific Reports*. 7(1). DOI: 10.1038/s41598-017-15291-y.
- Chen, J., Li, H., Zhao, Z., Xia, X., Li, B., Zhang, J. & Yan, X. 2018. Diterpenes from the marine algae of the genus *Dictyota*. *Marine Drugs*. 16(5): 159. DOI: 10.3390/md16050159.
- Choi, S.W., Graf, L., Choi, J.W., Jo, J., Boo, G.H., Kawai, H., Choi, C.G., Xiao, S., Knoll, A.H., Andersen, R.A. & Yoon, H.S. 2024. Ordovician origin and subsequent diversification of the brown algae. *Current Biology*. 34(4):740-754.e4. DOI: 10.1016/j.cub.2023.12.069.
- Cirne-Santos, C., Barros, C., Gomes, M., Gomes, R., Cavalcanti, D., Obando, J., Ramos, C., Villaça, R. Teixeira, V. & Paixão I. 2019. *In vitro* antiviral activity against Zika virus from a

natural product of the Brazilian brown seaweed *Dictyota menstrualis*. *Natural Product Communications*. 14(7).

Claassens, L., de Villiers, N.M. & Waltham, N.J. 2022. How developed is the South African coast? Baseline extent of South Africa's coastal and estuarine infrastructure. *Ocean and Coastal Management*. 222. DOI: 10.1016/j.ocecoaman.2022.106112.

Coleman, M.A., Reddy, M., Nimbs, M.J., Marshall, A., Al-Ghassani, S.A., Bolton, J.J., Jupp, B.P., De Clerck, O., Leliaert, F., Champion, C., Pearson, G.A., Serrão, E.A., Madeira, P. & Wernberg, T. 2022. Loss of a globally unique kelp forest from Oman. *Scientific Reports*. 12(1). DOI: 10.1038/s41598-022-08264-3.

Collins, R.A. & Cruickshank, R.H. 2013. The seven deadly sins of DNA barcoding. *Molecular Ecology Resources*. 13(6):969–975. DOI: 10.1111/1755-0998.12046.

Corrales, M.B., Gavio, B., Beltrán-Rozo, T., D'hondt, S., Dueñas, L.F. & De Clerck, O. 2025. Molecular phylogeny and genetic diversity of three dentate species of the genus *Dictyota* (Dictyotales, Phaeophyceae) from the Caribbean Sea, with emphasis on the Colombian Islands and Saint Kitts. *Botanica Marina*. DOI: 10.1515/bot-2025-0046.

Corrigan, S., Cottier-Cook, E.J., Lim, P.-E. & Brodie, J. 2025. *The state of the world's seaweeds*. London: Natural History Museum.

De Clerck, O. de. 2003. *The genus Dictyota (Dictyotales, Phaeophyta) in the Indian Ocean*. National Botanic Garden.

De Clerck, O. & Coppejans, E. 1999. Two new species of *Dictyota* (Dictyotales, Phaeophyta) from the Indo-Malayan region. *Phycologia*. 38(3):184–194. DOI: 10.2216/i0031-8884-38-3-184.1.

De Clerck, O., De Vos, P., Gillis, M. & Coppejans, E. 2001. Molecular Systematics in the Genus *Dictyota* (Dictyotales, Phaeophyta): A First Attempt Based on Restriction Patterns of the Internal Transcribed Spacer 1 of the rDNA (ARDRA-ITS1). *Systematics and Geography of Plants*. 71: 25-35.

De Clerck, O., Engledow, H.R., Bolton, J.J., Anderson, R.J. & Coppejans, E. 2002. Twenty marine benthic algae new to South Africa, with emphasis on the flora of Kwazulu-Natal. *Botanica Marina*. 45(5):413–431. DOI: 10.1515/BOT.2002.042.

- De Clerck, O., Bolton, J.J., Anderson, R.J. & Coppejans, E. 2005a. *Guide to the seaweeds of KwaZulu-Natal*. V. 33. Flanders Marine Institute (VLIZ)/Flemish Community/National Botanic Garden of Belgium: Meise: Scripta Botanica Belgica.
- De Clerck, O., Gavio, B., Fredericq, S., Bárbara, I. & Coppejans, E. 2005b. Systematics of *Grateloupia filicina* (Halymeniaceae, Rhodophyta), based on rbcL sequence analyses and morphological evidence, including the reinstatement of *G. minima* and the description of *G. capensis* sp. nov. *Journal of Phycology*. 41(2):391–410. DOI: 10.1111/j.1529-8817.2005.04189.x.
- De Clerck, O., Leliaert, F., Verbruggen, H., Lane, C.E., De Paula, J.C., Payo, D.A. & Coppejans, E. 2006. A revised classification of the Dictyoteae (Dictyotales, Phaeophyceae) based on rbcL and 26S ribosomal DNA sequence analyses. *Journal of Phycology*. 42(6):1271–1288. DOI: 10.1111/j.1529-8817.2006.00279.x.
- De Clerck, O., Guiry, M.D., Leliaert, F., Samyn, Y. & Verbruggen, H. 2013. Algal taxonomy: a road to nowhere? *Journal of Phycology*. 49(2):215–225. DOI: 10.1111/jpy.12020.
- Delva, S., de la Hoz, C.F., Bafort, Q., D'hondt, S., Shabaka, S., Hamdy Rashedy, S., Sherwood, A.R., Guy-Haim, T., Israel, A. & De Clerck, O. 2024. Tracing the introduction of *Dictyota acutiloba* (Dictyotales, Phaeophyceae) in the Mediterranean Sea, with a reassessment of its geographic distribution. *European Journal of Phycology*. 59(1):38–50. DOI: 10.1080/09670262.2023.2214184.
- DeSalle, R. 2006. Species discovery versus species identification in DNA barcoding efforts: response to Rubinoff. *Conservation Biology*. 20(5): 1545–1547. DOI: 10.1111/j.1523-1739.2006.00543.x.
- De Gruyter, W., Berlin, , York, N., Schils, T., De Clerck, O., Leliaert, F., Bolton, J.J. & Coppejans, E. 2001. The Change in Macroalgal Assemblages through the Saldanha Bay/Langebaan Lagoon Ecosystem (South Africa). *Botanica Marina*. 44: 295–305.
- De Reviere, B., Rousseau, F. & Draisma, S.G.A. 2007. Classification of the Phaeophyceae from past to present and current challenges. *The systematics association special volume series*. 267–284.
- Diaz-Pulido, G. & McCook, L. 2008. Macroalgae (Seaweeds). In *The State of the Great Barrier Reef On-line*. Townsville: Great Barrier Reef Marine Park Authority. Available:

http://www.gbrmpa.gov.au/corp_site/info_services/publications/sotr/downloads/SORR_Macroalgae.pdf [2025, November 26].

- do Nascimento Ávila, F., da Silva Souza, L.G., de Macedo Carneiro, P.B., Santos, F.A., Sasahara, G.L., Marinho Filho, J.D.B., Araújo, A.J., Barros, A.B., Monteiro, N.D.K.V., Silveira, E.R. and Pessoa, O.D.L., 2019. Anti-inflammatory diterpenoids from the Brazilian alga *Dictyota menstrualis*. *Algal Research*. 44:101695.
- Duarte, C.M., Middelburg, J.J. & Caraco, N. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*. 2(1): 1-8.
- Duarte, C.M., Gattuso, J.P., Hancke, K., Gundersen, H., Filbee-Dexter, K., Pedersen, M.F., Middelburg, J.J., Burrows, M.T., Krunhansl, K.A., Wernberg, T., Moore, P., Pessarrodona, A., Ørberg, S.B., Pinto, I.S., Assis, J., Queirós, A.M., Smale, D.A, Bekkby, T., Serrão, E.A. & Krause-Jensen, D. 2022. Global estimates of the extent and production of macroalgal forests. *Global Ecology and Biogeography*. 31(7):1422–1439. DOI: 10.1111/geb.13515.
- Duggins, D.O., Simenstad, C.A. & Estes, J.A. 1989. Magnification of Secondary Production by Kelp Detritus in Coastal Marine Ecosystems. *Science*. 245(4914):170–173.
- Dunne, A., Coker, D.J., Kattan, A., Tietbohl, M.D., Ellis, J.I., Jones, B. & Berumen, M. 2023. Importance of coastal vegetated habitats for tropical marine fishes in the Red Sea. *Marine Biology*. 170(7). DOI: 10.1007/s00227-023-04234-z.
- Eger, A.M., Marzinelli, E.M., Beas-Luna, R., Blain, C.O., Blamey, L.K., Byrnes, J.E.K., Carnell, P.E., Choi, C.G., Hessing-Lewis, M., Kim, K.Y., Kumagai, N.H., Lorda, J., Moore, P., Nakamura, Y., Pérez-Matus, A., Pontier, O., Smale, D., Steinberg, P.D. & Vergés, A. 2023. The value of ecosystem services in global marine kelp forests. *Nature Communications*. 14(1). DOI: 10.1038/s41467-023-37385-0.
- El Gamal, A.A. 2010. Biological importance of marine algae. *Saudi pharmaceutical journal*. 18(1): 1-25. DOI: 10.1016/j.jsps.2009.12.001.
- Erickson, D.L., Spouge, J., Resch, A., Weigt, L.A. & Kress, W.J. 2008. DNA barcoding in land plants: developing standards to quantify and maximize success. *Taxon*. 57(4): 1304-1316. DOI: 10.1002/tax.574020.
- Fairbrothers, D.E., Mabry, T.J., Scogin, R.L. & Turner, B.L. 1975. The bases of Angiosperm phylogeny: Chemotaxonomy. *Annals of the Missouri Botanical Garden*. 62(3): 765–800.

- Filbee-Dexter, K., Wernberg, T., Grace, S.P., Thormar, J., Fredriksen, S., Narvaez, C.N., Feehan, C.J. & Norderhaug, K.M. 2020. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Scientific Reports*. 10(1). DOI: 10.1038/s41598-020-70273-x.
- Filbee-Dexter, K., Pessarrodona, A., Pedersen, M.F., Wernberg, T., Duarte, C.M., Assis, J., Bekkby, T., Burrows, M.T., Carlson, D.F., Gattuso, J.P. and Gundersen, H., 2024. Carbon export from seaweed forests to deep ocean sinks. *Nature Geoscience*. 17(6): 552-559.
- Francis, C., Bolton, J.J., Mattio, L., Mandiwana-Neudani, T.G. & Anderson, R.J. 2017. Molecular systematics reveals increased diversity within the South African *Laurencia* complex (Rhodomelaceae, Rhodophyta). *Journal of Phycology*. 53(4):804–819. DOI: 10.1111/jpy.12543.
- Fraser, C.I. 2012. Is bull-kelp kelp? The role of common names in science. *New Zealand Journal of Marine and Freshwater Research*. 46(2): 279-284. DOI: 10.1080/00288330.2011.621130.
- Freshwater, D.W. & Rueness, J. 1994. Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on rbcL nucleotide sequence analysis. *Phycologia*. 33(3): 187-194.
- Lozano-Orozco, J.G. , Senties, A., De Clerck, O., M. Dreckmann, K. & Díaz-Larrea, J. 2015. Two New Species of the Genus *Dictyota* (Phaeophyceae: Dictyotales) from the Mexican Caribbean. *American Journal of Plant Sciences*. 06(15):2492–2501. DOI: 10.4236/ajps.2015.615251.
- Gauna, M.C., Cáceres, E.J. & Parodi, E.R. 2013. Temporal variations of vegetative features, sex ratios and reproductive phenology in a *Dictyota dichotoma* (Dictyotales, Phaeophyceae) population of Argentina. *Helgoland Marine Research*. 67(4):721–732. DOI: 10.1007/s10152-013-0357-0.
- Goff, L.J., Liddle, L., Silva, P.C., Voytek, M. & Coleman, A.W. 1992. Tracing species invasion in *Codium*, a siphonous green alga, using molecular tools. *American Journal of Botany*. 79(11): 1279-1285
- Gomes, D.L., Telles, C.B.S., Costa, M.S.S.P., Almeida-Lima, J., Costa, L.S., Keesen, T.S.L. & Rocha, H.A.O. 2015. Methanolic extracts from brown seaweeds *Dictyota cilliolata* and

- Dictyota menstrualis* induce apoptosis in human cervical adenocarcinoma HeLa cells. *Molecules*. 20(4):6573–6591. DOI: 10.3390/molecules20046573.
- Guiry, M.D. 2024. How many species of algae are there? A reprise. Four kingdoms, 14 phyla, 63 classes and still growing. *Journal of Phycology*. 60(2):214–228. DOI: 10.1111/jpy.13431.
- Guiry, M.D. & Guiry, G.M. 2025. *AlgaeBase*. National University of Ireland. Available: <https://www.algaebase.org> [Accessed 18 November 2025].
- Griffiths, C.L., Robinson, T.B., Lange, L. & Mead, A. 2010. Marine Biodiversity in South Africa: An Evaluation of Current States of Knowledge. *PLoS ONE*. 5(8): e12008.
- Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic acids symposium series*. 41:95–98.
- Hanley, M.E., Firth, L.B. & Foggo, A. 2024. Victim of changes? Marine macroalgae in a changing world. *Annals of Botany*. 133(1): 1-16. DOI: 10.1093/aob/mcad185.
- Hardt, I.H., Fenical, W., Cronin, G. & Hay, M.E. 1996. Acutilols, potent herbivore feeding deterrents from the tropical brown alga, *Dictyota acutiloba*. *Phytochemistry*. 43(1): 7173.
- Hebert, P.D.N. & Gregory, T.R. 2005. The promise of DNA barcoding for taxonomy. *Systematic biology*. 54(5): 852-859. DOI: 10.1080/10635150500354886.
- Hebert, P.D.N., Cywinska, A., Ball, S.L. & DeWaard, J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences*. 270(1512):313–321. DOI: 10.1098/rspb.2002.2218.
- Herren, L.W., Walters, L.J. & Beach, K.S. 2006. Fragment generation, survival, and attachment of *Dictyota* spp. at Conch Reef in the Florida Keys, USA. *Coral Reefs*. 25(2):287–295. DOI: 10.1007/s00338-006-0096-7.
- Hickerson, M.J., Meyer, C.P. & Moritz, C. 2006. DNA barcoding will often fail to discover new animal species over broad parameter space. *Systematic Biology*. 55(5):729–739. DOI: 10.1080/10635150600969898.
- Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. 2018. UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution*. 35(2):518–522. DOI: 10.1093/molbev/msx281.

- Hofmann, L.C., Nettleton, J.C., Neefus, C.D. & Mathieson, A.C. 2010. Cryptic diversity of *Ulva* (Ulvales, Chlorophyta) in the great bay Estuarine system (Atlantic USA): Introduced and indigenous distromatic species. *European Journal of Phycology*. 45(3):230–239. DOI: 10.1080/09670261003746201.
- Horizon Europe. 2024. *COMBO*. Available: <https://combo.biomarep.org/> [2025, November 27].
- Hörnig, I., Schnetter, R., Prud'homme van Reine, W.F., Coppejans, E., Achenbach-Wege, K. & Over, J.M. 1992. The genus *Dictyota* in the North Atlantic. I. A new generic concept and new species. *Nova Hedwigia*. 54:4562.
- Hughey, J.R., Silva, P.C. & Hommersand, M.H. 2002. ITS1 sequences of type specimens of *Gigartina* and *Sarcothalia* and their significance for the classification of South African Gigartinaceae (Gigartinales, Rhodophyta). *European Journal of Phycology*. 37(2):209–216. DOI: 10.1017/S0967026202003633.
- Hwang, I.K., Kim, H.S. & Lee, W.J. 2005. Polymorphism in the brown alga *Dictyota dichotoma* (Dictyotales, Phaeophyceae) from Korea. *Marine Biology*. 147(4):999–1015. DOI: 10.1007/s00227-005-1623-8.
- Hydrographic and Oceanographic Department of the Japan Coast Guard. 2017. *Exploring the sea brochure*. Available: https://www1.kaiho.mlit.go.jp/eng/brochure_Jan2017_E.pdf?utm_source=chatgpt.com [2025, December 03].
- IUCN. 2025. *IUCN Red List of Threatened Species*.
- Iyer, R., De Clerck, O., Bolton, J.J., Coyne, V.E. & Sym, S.D. 2004. Morphological and taxonomic studies of *Gracilaria* and *Gracilariopsis* species (Gracilariales, Rhodophyta) from South Africa. *South African Journal of Botany*. 70(4):521–539. DOI: 10.1016/S0254-6299(15)30192-7.
- Iyer, R., Tronchin, E.M., Bolton, J.J. & Coyne, V.E. 2005. Molecular systematics of the Gracilariaceae (Gracilariales, Rhodophyta) with emphasis on southern Africa. *Journal of Phycology*. 41(3):672–684. DOI: 10.1111/j.1529-8817.2005.00088.x.
- James, N.C. & Whitfield, A.K. 2023. The role of macroalgae as nursery areas for fish species within coastal seascapes. *Cambridge Prisms: Coastal Futures*. 1. DOI: 10.1017/cft.2022.3.

- Johannesson, K., Johansson, D., Larsson, K.H., Huenchuñir, C.J., Perus, J., Forslund, H., Kautsky, L. & Pereyra, R.T. 2011. Frequent clonality in fucoids (*Fucus radicans* and *Fucus vesiculosus*; Fucales, Phaeophyceae) in the Baltic sea. *Journal of Phycology*. 47(5):990–998. DOI: 10.1111/j.1529-8817.2011.01032.x.
- Kim, S., Choi, S.K., Van, S., Kim, S.T., Kang, Y.H. & Park, S.R. 2022. Geographic Differentiation of Morphological Characteristics in the Brown Seaweed *Sargassum thunbergii* along the Korean Coast: A Response to Local Environmental Conditions. *Journal of Marine Science and Engineering*. 10(4). DOI: 10.3390/jmse10040549.
- Kreiner, A., Bolton, J., Branch, G., Lima, F., Reddy, M., Serrão, E. & Thomas, M. 2019a. Report: coastal biodiversity surveys—survey 1. *Namibia: Subdivision Environment, National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources*, 51.
- Kreiner, A., Reddy, M., Seabra, R. & Thomas, M. 2019b. Report: coastal biodiversity surveys—survey 2. *Namibia: Subdivision Environment, National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources*, 51.
- Kreiner, A., Branch, G., Ferreira, L., Reddy, M., Serrão, E. & Thomas, M. 2019c. Report: coastal biodiversity surveys—survey 3. *Namibia: Subdivision Environment, National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources*, 51.
- Kress, W.J. & Erickson, D.L. 2012. DNA Barcodes: Methods and Protocols. In *DNA Barcodes Methods and Protocols*. V. 858. W.J. Kress & D.L. Erickson, Eds. New York, NY, USA: Springer Science+Business Media. 3–8. DOI: 10.1002/tax.574020.
- Krieger, E.C., Taise, A., Nelson, W.A., Grand, J., Le Ru, E., Davy, S.K. & Cornwall, C.E. 2023. Tolerance of coralline algae to ocean warming and marine heatwaves. *PLOS Climate*. 2(1). DOI: 10.1371/journal.pclm.0000092.
- Krueger-Hadfield, S.A., Kollars, N.M., Strand, A.E., Byers, J.E., Shainker, S.J., Terada, R., Greig, T.W., Hammann, M., Murray, D.C., Weinberger, F. and Sotka, E.E., 2017. Genetic identification of source and likely vector of a widespread marine invader. *Ecology and evolution*. 7(12): 4432-4447.
- Ktari, L., Ali, I.-B., Redjem, B., Langar, H. & El Bour, M. 2010. Antifouling activity and chemical investigation of the brown alga *Dictyota fasciola* (Dictyotales) from Tunisian coast. *Cahiers de biologie marine*. 51(2): 109.

- Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R. & Beach, K.S. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*. 323:107–117.
- Lamouroux, J.V.F. 1809. Exposition des caractères du genre *Dictyota*, et tableau des espèces qu'il referme. *Journal de Botanique (Desvaux)*. 2:38-44.
- Lane, C.E., Lindstrom, S.C. & Saunders, G.W. 2007. A molecular assessment of northeast Pacific *Alaria* species (Laminariales, Phaeophyceae) with reference to the utility of DNA barcoding. *Molecular Phylogenetics and Evolution*. 44(2): 634–648. DOI: 10.1016/j.ympev.2007.03.016.
- Leal, C. V., Bispo, A., Takaki, M., Freire, V.F., Reddy, M.M., Thompson, F.L., Hajdu, E., Thomas, O.P. & Berlinck, R.G.S. 2025. Sponge taxonomy in the -omics era: resolving Haplosclerida polytomies with phylogenetics and metabolomics. *Biochemical Systematics and Ecology*. 120. DOI: 10.1016/j.bse.2025.104971.
- Leigh, J.W. & Bryant, D. 2015. PopART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution*. 6(9):1110–1116.
- Leliaert, F., Verbruggen, H., Vanormelingen, P., Steen, F., López-Bautista, J.M., Zuccarello, G.C. & De Clerck, O. 2014. DNA-based species delimitation in algae. *European Journal of Phycology*. 49(2): 179–196. DOI: 10.1080/09670262.2014.904524.
- Littler, D.S. & Littler, M.M. 2000. *Caribbean Reef Plants: An identification guide for the reef plants of the Caribbean, Bahamas, Florida and the Gulf of Mexico*. Washington DC: Offshore Graphics.
- Mac Monagail, M., Cornish, L., Morrison, L., Araújo, R. & Critchley, A.T. 2017. Sustainable harvesting of wild seaweed resources. *European Journal of Phycology*. 52(4) :371–390. DOI: 10.1080/09670262.2017.1365273.
- McCarty, A.T. & Sotka, E.E. 2013. Geographic variation in feeding preference of a generalist herbivore: The importance of seaweed chemical defenses. *Oecologia*. 172(4): 1071–1083. DOI: 10.1007/s00442-012-2559-6.
- McCauley, L.A.R. & Wehr, J.D. 2007. Taxonomic reappraisal of the freshwater brown algae, *Bodanella*, *Ectocarpus*, *Heribaudiella*, and *Pleurocladia* (Phaeophyceae) on the basis of rbcL sequences and morphological characters. *Phycologia*. 46(4):429–439.

- Meise Botanic Garden. *Specimen: BR5010122471379V*. Available:
<https://www.botanicalcollections.be/specimen/BR5010122471379V> [2025, December 19].
- Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *2010 Gateway Computing Environments Workshop (GCE)*. IEEE. 1–8. DOI: 10.1109/GCE.2010.5676129.
- Mols-Mortensen, A., Neefus, C.D., Nielsen, R., Gunnarsson, K., Egilsdóttir, S., Pedersen, P.M. & Brodie, J. 2012. New insights into the biodiversity and generic relationships of foliose Bangiales (Rhodophyta) in Iceland and the faroe Islands. *European Journal of Phycology*. 47(2): 146–159. DOI: 10.1080/09670262.2012.666678.
- Müller, R., Laepple, T., Bartsch, I. & Wiencke, C. 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Botanica Marina*. 52(6) :617–638. DOI: 10.1515/BOT.2009.080.
- Nelson, W.A., Sutherland, J.E., Ringham, S. & Murupaenga, H. 2019. *Dictyota korowai* sp. nov. (Dictyotales, Phaeophyceae) from Manawatāwhi/Three Kings Islands, northern New Zealand, previously confused with *Dictyota intermedia*. *Phycologia*. 58(4) :433–442. DOI: 10.1080/00318884.2019.1625256.
- Ng, B.F., Ng, W.L., Lum, W.M., Yeap, S.K. & Yong, Y.S. 2024. Feasibility of Biomarker-Based Taxonomic Classification: A Case Study of the Marine Red Alga *Laurencia snackeyi* (Weber Bosse) M. Masuda. *Phycology*. 4(3): 363–369. DOI: 10.3390/phycolgy4030019.
- Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. 2015. IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Molecular Biology and Evolution*. 32(1): 268–274. DOI: 10.1093/molbev/msu300.
- Ni-Ni-Win, Hanyuda, T., Kato, A., Shimabukuro, H., Uchimura, M., Kawai, H. & Tokeshi, M. 2021. Global diversity and geographic distributions of *Padina* species (Dictyotales, Phaeophyceae): new insights based on molecular and morphological analyses. *Journal of Phycology*. 57: 454–72. DOI: 10.1111/jpy.13076-19-202.
- Ni-Ni-Win, Hanyuda, T., Mya-Kyawt-Wai, Mardiansyah, Putri, L.S.E., Geraldino, P.J.L. & Kawai, H. 2024. Two new species of *Dictyota* (Dictyotales, Phaeophyceae), *D. dimorphosa* sp. nov. and *D. recumbens* sp. nov., based on morphological and molecular investigations. *Phycologia*. 63(3): 290–302. DOI: 10.1080/00318884.2024.2335606.

- Nizamuddin, M. & Campbell, A.C. 1995. *Glossophorella*, a new genus of the family Dictyotaceae and its ecology from the coast of the sultanate of Oman. *Pakistan Journal of Botany*. 27(2): 257–262.
- Norris, R.E. 1987. The systematic position of *Gelidiopsis* and *Ceratodictyon* (Gigartinales, Rhodophyceae), genera new to South Africa. *South African Journal of Botany*. 53(3):239–246. DOI: 10.1016/S0254-6299(16)31436-3.
- Norris, R.E., Hommersand, M.H. & Fredericq, S. 1987. *Gelidium pteridifolium* (Rhodophyceae), a new species from Natal and the eastern Cape. *South African Journal of Botany*. 53(5):375–380. DOI: 10.1016/S0254-6299(16)31400-4.
- Paabo, S. 1989. Ancient DNA: extraction, characterization, molecular cloning, and enzymatic amplification. *Proceedings of the National Academy of Sciences*. 86(6): 1939-1943.
- Palinska, K.A. & Surosz, W. 2014. Taxonomy of cyanobacteria: a contribution to consensus approach. *Hydrobiologia*. 740(1): 1–11. DOI: 10.1007/s10750-014-1971-9.
- Pardo-Vargas, A., Oliveira, I.D.B., Stephens, P.R.S., Cirne-Santos, C.C., Paixão, I.C.N.D.P., Ramos, F.A., Jiménez, C., Rodríguez, J., Resende, J.A.L.C., Texeira, V.L. & Castellanos, L. 2014. Dolabelladienols A-C, new diterpenes isolated from Brazilian brown alga *Dictyota pfaffii*. *Marine Drugs*. 12(7): 4247–4259. DOI: 10.3390/md12074247.
- Peltomaa, E., Asikainen, H., Blomster, J., Pakkanen, H., Rigaud, C., Salmi, P. & Taipale, S. 2023. Phytoplankton group identification with chemotaxonomic biomarkers: In combination they do better. *Phytochemistry*. 209. DOI: 10.1016/j.phytochem.2023.113624.
- Pereira, L. 2018. Seaweeds as source of bioactive substances and skin care therapy—cosmeceuticals, algototherapy, and thalassotherapy. *Cosmetics*. 5(4): 68. DOI: 10.3390/cosmetics5040068.
- Pfaff, M.C., Hart-Davis, M., Smith, M.E. & Veitch, J. 2022. A new model-based coastal retention index (CORE) identifies bays as hotspots of retention, biological production and cumulative anthropogenic pressures. *Estuarine, Coastal and Shelf Science*. 273. DOI: 10.1016/j.ecss.2022.107909.
- Phillips, J.A., Clayton, M.N., Maier, I., Boland, W. & Müller, D.G. 1990. Sexual reproduction in *Dictyota diemensis* (Dictyotales, Phaeophyta). *Phycologia*. 29(3): 367–379.

- Pongparadon, S., Zuccarello, G.C. & Prathep, A. 2017. High morpho-anatomical variability in *Halimeda macroloba* (Bryopsidales, Chlorophyta) in Thai waters. *Phycological Research*. 65(2): 136–145. DOI: 10.1111/pre.12172.
- Porebski, S., Bailey, L.G. & Baum, B.R. 1997. Modification of a CTAB DNA Extraction Protocol for Plants Containing High Polysaccharide and Polyphenol Components. *Plant Molecular Biology Reporter*. 15(1): 8–15.
- Porse, H. & Rudolph, B. 2017. The seaweed hydrocolloid industry: 2016 updates, requirements, and outlook. *Journal of applied phycology*. 29(5): 2187–2200. DOI: 10.1007/s10811-017-1144-0.
- Prew, Z.S., Reddy, M.M., Mehta, A., Dyer, D.C. & Smit, A.J. 2024. The African seaforest: a review. *Botanica Marina*. 67(5): 425-442. DOI: 10.1515/bot-2023-0060.
- Rambaut, A. 2009. FigTree v. 1.4.4. *Institute of Evolutionary Biology, University of Edinburgh*.
- Rashband, W. 2018. ImageJ. *National Institute of Health, Bethesda, Maryland, USA*.
- Rasher, D.B. & Hay, M.E. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings of the National Academy of Sciences of the United States of America*. 107(21): 9683–9688. DOI: 10.1073/pnas.0912095107.
- Ratnasingham, S. & Hebert, P.D.N. 2007. BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes*. 7(3): 355–364. DOI: 10.1111/j.1471-8286.2007.01678.x.
- Reddy, M.M. 2018. Taxonomy and Systematics of the Bangiales (Rhodophyta) in South Africa using an Integrative Approach. PhD thesis. University of Cape Town.
- Reddy, M.M., Clerck, O. De, Leliaert, F., Anderson, R.J. & Bolton, J.J. 2018. A rosette by any other name: species diversity in the Bangiales (Rhodophyta) along the South African coast. *European Journal of Phycology*. 53(1): 67–82. DOI: 10.1080/09670262.2017.1376256.
- Reddy, M.M., Stegenga, H., Anderson, R.J. & Bolton, J.J. 2020a. An updated species inventory of *Callithamnion* sensu lato Rhodophyta, Callithamniaceae in South Africa with the description of *Callithamnion africanum* sp. nov. *Phytotaxa*. 461(3): 138–154. DOI: 10.11646/phytotaxa.461.3.1.

- Reddy, M.M., De Clerck, O., Leliaert, F., Anderson, R.J. & Bolton, J.J. 2020b. An appraisal of the genus *Pyropia* (Bangiales, Rhodophyta) from southern Africa based on a multi-gene phylogeny, morphology and ecology, including the description of *Pyropia meridionalis* sp. nov. *South African Journal of Botany*. 131: 18–32. DOI: 10.1016/j.sajb.2019.12.027.
- Reddy, M.M., du Plessis, J., Roodt-Wilding, R., Anderson, R.J. & Bolton, J.J. 2023a. The reinstatement of *Plocamium robertiae* (Rhodophyta, Plocamiales) and an updated species inventory of the genus in South Africa. *Phycologia*. 62(2): 194–202. DOI: 10.1080/00318884.2023.2174342.
- Reddy, M., Van Schalkwyk, J., Bolton, J.J., Anderson, R.J. & Roodt-Wilding, R. 2023b. A taxonomically informed DNA reference library to facilitate future biodiversity assessments and monitoring: a case study using seaweeds along a tropical-temperate transition zone. *bioRxiv*. 2023-09. DOI: 10.1101/2023.09.14.557690.
- Reddy, M.M., Jennings, L. & Thomas, O.P., 2021. Marine biodiscovery in a changing world. In *Progress in the Chemistry of Organic Natural Products*. 116: 1-36. Cham: Springer International Publishing.
- Reddy, M.M., Madeira, P., Assis, J., Bolton, J.J., Rothman, M.D., Anderson, R.J., Kandjengo, L., Kreiner, A., Coleman, M.A., Wernberg, T., De Clerck, O., Leliaert, F., Bandeira, S., Ada, A.M., Neiva, J., Pearson, G.A. & Serrão, E.A. 2024. Cryptic diversity of southern African kelp. *Scientific Reports*. 14: 11071. DOI: 10.1038/s41598-024-61336-4.
- Robba, L., Russell, S.J., Barker, G.L. & Brodie, J. 2006. Assessing the use of the mitochondrial *cox1* marker for use in DNA barcoding of red algae (Rhodophyta). *American Journal of Botany*. 93(8): 1101–1108. DOI: 10.3732/ajb.93.8.1101.
- Roberts, C.H. 2025. Biodiversity assessment of *Ulva* sensu lato (Ulvaceae, Chlorophyta) from the southern Benguela Marine Province, using morpho-anatomical and molecular methods. Masters of Science. University of Cape Town.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. & Huelsenbeck, J. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*. 61(3): 539-542.

- Rothman, M.D., Anderson, R.J., Kandjengo, L. & Bolton, J.J. 2020. Trends in seaweed resource use and aquaculture in South Africa and Namibia over the last 30 years. *Botanica Marina*. 63(4): 315-325. DOI: 10.1515/bot-2019-0074.
- Rouault, M., Pohl, B. & Penven, P. 2010. Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science*. 32(2): 237–246.
- Round, F.E. 1981. *The ecology of algae*. Cambridge: Cambridge University Press .
- Rousseau, F., Leclerc, M.-C., De Reviere, B. & De, B. 1997. Molecular phylogeny of European Fucales (Phaeophyceae) based on partial large-subunit rDNA sequence comparisons. *Phycologia*. 36(6): 438-446.
- Rousseau, F., Burrowes, R., Peters, A.F., Kuhlenkamp, R. & De Reviere, B. 2001. A comprehensive phylogeny of the Phaeophyceae based on nrDNA sequences resolves the earliest divergences. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie*. 324(4): 305-319.
- Rushdi, M.I., Abdel-Rahman, I.A.M., Attia, E.Z., Saber, H., Saber, A.A., Bringmann, G. & Abdelmohsen, U.R. 2022. The biodiversity of the genus Dictyota: Phytochemical and pharmacological natural products perspectives. *Molecules*. 27(3): 672. DOI: 10.3390/molecules27030672.
- Saunders, G.W. 2005. Applying DNA barcoding to red macroalgae: A preliminary appraisal holds promise for future applications. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 360(1462): 1879–1888. DOI: 10.1098/rstb.2005.1719.
- Saunders, G.W. & McDevit, D.C. 2013. DNA barcoding unmasks overlooked diversity improving knowledge on the composition and origins of the Churchill algal flora. *BMC Ecology*. 13. DOI: 10.1186/1472-6785-13-9.
- Sayers, E.W., Beck, J., Bolton, E.E., Brister, J.R., Chan, J., Connor, R., Feldgarden, M., Fine, A.M., Funk, K., Hoffman, J., Kannan, S., Kelly, C., Klimke, W., Kim, S., Lathrop, S., Marchler-Bauer, A., Murphy, T.D., O’Sullivan, C., Schmierer, E., Skripchenko, Y., Stine, A., Thibaud-Nissen, F., Wang, J., Ye, J., Zellers, E., Schneider, V.A. & Pruitt, K.M. 2025. Database resources of the National Center for Biotechnology Information in 2025. *Nucleic Acids Research*. 53(D1):D20–D29. DOI: 10.1093/nar/gkaf979.

- Searles, R.B. & Schneider, C.W. 1987. Observations on the deep-water flora of Bermuda. *Hydrobiologia*. 151/152:261–266.
- Siemer, B.L., Stam, W.T., Olsen, J.L. & Pedersen, P.M. 1998. Phylogenetic relationships of the brown algal orders Ectocarpales, Chordariales, Dictyosiphonales, and Tilopteridales (Phaeophyceae) based on RUBISCO large subunit and spacer sequences. *Journal of Phycology*. 34(6): 1038–1048. DOI: 10.1046/j.1529-8817.1998.341038.x.
- Silberfeld, T., Leigh, J.W., Verbruggen, H., Cruaud, C., de Reviers, B. & Rousseau, F. 2010. A multi-locus time-calibrated phylogeny of the brown algae (Heterokonta, Ochrophyta, Phaeophyceae): Investigating the evolutionary nature of the “brown algal crown radiation”. *Molecular Phylogenetics and Evolution*. 56(2): 659–674. DOI: 10.1016/j.ympev.2010.04.020.
- Siless, G.E., García, M., Pérez, M., Blustein, G. & Palermo, J.A. 2018. Large-scale purification of pachydictyol A from the brown alga *Dictyota dichotoma* obtained from algal wash and evaluation of its antifouling activity against the freshwater mollusk *Limnoperna fortunei*. *Journal of Applied Phycology*. 30(1): 629–636. DOI: 10.1007/s10811-017-1261-9.
- Silva, P.C. 1961. The International Phycological Society. *Phycologia*. 1(1):1–3. DOI: 10.2216/i0031-8884-1-1-1.1.
- Silva, P.C. 1996. *Catalogue of the benthic marine algae of the Indian Ocean*. Berkeley : University of California Press.
- Simas, D.L.R., Kaiser, C.R., Gestinari, L.M., Duarte, H.M., de Paula, J.C. & Soares, A.R. 2014. Diterpenes from the brown seaweed *Dictyota caribaea* (Dictyotaceae, Phaeophyceae): The ecological and taxonomic significance. *Biochemical Systematics and Ecology*. 52: 33–37. DOI: 10.1016/j.bse.2013.11.001.
- Simons, R.H. 1964. Species of *Plocamium* on the South African Coast. *Bothalia*. 8(2): 183–193. DOI: 10.4102/abc.v8i2.1630.
- Smit, A.J., Roberts, M., Anderson, R.J., Dufois, F., Dudley, S.F.J., Bornman, T.G., Olbers, J. & Bolton, J.J. 2013. A coastal seawater temperature dataset for biogeographical studies: Large biases between in situ and remotely-sensed data sets around the coast of South Africa. *PLoS ONE*. 8(12). DOI: 10.1371/journal.pone.0081944.

- Song, X., Yao, J., Roleda, M.Y., Liang, Y., Xu, R., Lin, Y., Gonzaga, S.M.C., Du, Y. & Duan, D. 2025. Genetic Diversity and Connectivity of Reef-Building *Halimeda macroloba* in the Indo-Pacific Region. *Plants*. 14(10). DOI: 10.3390/plants14101497.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*. 57(7).
- Stache-Crain, B., Muller, D.G. & Goff, L.J. 1997. Molecular systematics of *Ectocarpus* and *Kuckuckia* (Ectocarpales, Phaeophyceae) inferred from phylogenetic analysis of nuclear- and plastid-encoded DNA sequences. *Journal of Phycology*. 33: 152–168.
- Steen, F., Vieira, C., Leliaert, F., Payri, E.C. & De Clerck, O. 2015. Biogeographic affinities of Dictyotales from Madagascar: A phylogenetic approach. *Cryptogamie, Algologie*. 36(2):129–141. DOI: 10.7872/crya.v36.iss2.2015.129.
- Steen, F., Marc, V., D'hondt, S., Vieira, C. & Clerck, O. De. 2019. Population structure and geographically structured reproductive strategies of the haplodiplontic seaweed *Dictyota dichotoma*. *BioRxiv*. 595587. DOI: 10.1101/595587.
- Stengena, H., Bolton, J.J. & Anderson, R.J. 1997. *Seaweeds of the South African West Coast*. A.V. Hall ed. Contributions from the Bolus Herbarium 18.
- Steinhagen, S., Kramár, L. & Toth, G.B. 2022. The unheeded existence of the tubular greens: molecular analyses reveal the distribution of a new *Ulva* species (Ulvophyceae, Chlorophyta), *Ulva capillata* sp. nov. in the Atlantic-Baltic Sea transect. *Journal of Applied Phycology*. 35(1): 509-522. DOI: 10.1007/s10811-022-02886-w.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental conservation*. 29(4): 436-459. DOI: 10.1017/S0376892902000322.
- Stirk, W.A., Reinecke, D.L. & Van Staden, J. 2007. Seasonal variation in antifungal, antibacterial and acetylcholinesterase activity in seven South African seaweeds. *Journal of Applied Phycology*. 19(3): 271–276. DOI: 10.1007/s10811-006-9134-7.
- Van Der Strate, H.J., Boele-Bos, S.A., Olsen, J.L., Van De Zande, L. & Stam, W.T. 2002. Phylogeographic studies in the tropical seaweed *Cladophoropsis membranacea* (Chlorophyta,

- Ulvophyceae) reveal a cryptic species complex. *Journal of Phycology*. 38(3): 572–582. DOI: 10.1046/j.1529-8817.2002.01170.x.
- Subbotin, S.A., Waeyenberge, L. & Moens, M. 2013. Molecular systematics. In *Plant nematology*. 41–58.
- Tamura, K., Stecher, G. & Kumar, S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution*. 38: 3022–3027.
- Tang, Q., Pang, K., Yuan, X. & Xiao, S. 2020. A one-billion-year-old multicellular chlorophyte. *Nature Ecology and Evolution*. 4(4): 543–549. DOI: 10.1038/s41559-020-1122-9.
- Tautz, D., Arctander, P., Minelli, A., Thomas, R.H. & Vogler, A.P. 2003. A plea for DNA taxonomy. *Opinion TRENDS in Ecology and Evolution*. 18(2): 70
- Teixeira, V.L. & Kelecom, A. 1988. A chemotaxonomic study of the diterpenes from marine brown algae of the genus *Dictyota*. *The Science of the Total Environment*. 75: 271–283.
- Tronchin, E.M. & Bolton, ; D W Freshwater; J J. 2003. A re-evaluation of the genera *Beckerella* and *Ptilophora* (Gelidiales, Rhodophyta) based on molecular and morphological data. *Phycologia*. 42(1): 80-89.
- Tronchin, E.M. & Freshwater, D.W. 2007. Four Gelidiales (Rhodophyta) new to southern Africa, *Aphanta pachyrrhiza* gen. et sp. nov., *Gelidium profundum* sp. nov., *Pterocradiella caerulescens* and *P. psammophila* sp. nov. *Phycologia*. 46(3): 325–348. DOI: 10.2216/06-73.1.
- Tronchin, E.M., Freshwater, D.W., Bolton, J.J. & Anderson, R.J. 2002. A Reassessment and Reclassification of Species in the Genera *Onikusas Akatsuka* and *Suhria J. Agardh ex Endlicher* (Gelidiales, Rhodophyta) Based on Molecular and Morphological Data. *Botanica Marina*. 45:548–558.
- Tronchin, E.M., De Clerck, O., Freshwater, D.W., Bolton, J.J. & Anderson, R.J. 2004. *Ptilophora leliaertii* and *Ptilophora coppejansii*, two new species of Gelidiales (Rhodophyta) from South Africa. *European Journal of Phycology*. 39(4): 395–410. DOI: 10.1080/09670260410001721491.
- Tronholm, A., Sansón, M., Afonso-Carrillo, J. & De Clerck, O. 2008. Distinctive morphological features, life-cycle phases and seasonal variations in subtropical populations of *Dictyota*

- dichotoma* (Dictyotales, Phaeophyceae). *Botanica Marina*. 51(2): 132–144. DOI: 10.1515/BOT.2008.017.
- Tronholm, A., Sansón, M., Afonso-Carrillo, J., Verbruggen, H. & De Clerck, O. 2010a. Niche partitioning and the coexistence of two Cryptic *Dictyota* (dictyotales, phaeophyceae) species from the Canary Islands. *Journal of Phycology*. 46(6): 1075–1087. DOI: 10.1111/j.1529-8817.2010.00912.x.
- Tronholm, A., Steen, F., Tyberghein, L., Leliaert, F., Verbruggen, H., Antonia Ribera Siguan, M. & De Clerck, O. 2010b. Species delimitation, taxonomy, and biogeography of *Dictyota* in Europe (dictyotales, phaeophyceae). *Journal of Phycology*. 46(6): 1301–1321. DOI: 10.1111/j.1529-8817.2010.00908.x.
- Tronholm, A., Afonso-Carrillo, J., Sansón, M., Leliaert, F., Fernández-García, C. & De Clerck, O. 2013. Taxonomy of the *Dictyota ciliolata-crenulata* complex (Dictyotales, Phaeophyceae). *Phycologia*. 52(2): 171–181. DOI: 10.2216/12-005.1.
- Tschaikner, A., Ingolić, E. & Gärtner, G. 2007. Observations in a new isolate of *Coelastrella terrestris* (Reisigl) Hegewald & Hanagata (Chlorophyta, Scenedesmaceae) from alpine soil. *PHYTON Annales rei botanicae*, 23, 1845-1858.
- Vieira, C., Steen, F., D'hondt, S., Bafort, Q., Tyberghein, L., Fernandez-García, C., Wysor, B., Tronholm, A., Mattio, L., Payri, C., Kawai, H., Saunders, G., Leliaert, F., Verbruggen, H. & De Clerck, O. 2021. Global biogeography and diversification of a group of brown seaweeds (Phaeophyceae) driven by clade-specific evolutionary processes. *Journal of Biogeography*. 48(4): 703–715. DOI: 10.1111/jbi.14047.
- Vieira, C., Akita, S., Suzuki, M., Terada, R., Hanyuda, T., Shimada, S., Uwai, S. & Kawai, H. 2025a. A taxonomic sudoku: Resolving the long-standing puzzle of Japanese Dictyoteae (Dictyotales, Phaeophyceae) with new records and biogeographic insights. *Journal of Phycology*. 61(5): 1457-1485. DOI: 10.1111/jpy.70084.
- Vieira, C., Kang, J.C., Daudinet, M., Akita, S. & Kim, M.S. 2025b. Critical taxonomic revision of Korean Dictyoteae describing three new species and honoring Haenyeo culture. *Journal of Phycology*. 61(2): 353–378. DOI: 10.1111/jpy.70010.

- Wanders, J.B.W. 1976. The role of benthic algae in the shallow reef of Curaçao (Netherlands antilles) II: Primary productivity of the *Sargassum* beds on the north-east coast submarine plateau. *Aquatic Botany*. 2: 327–335. DOI: 10.1016/0304-3770(76)90030-9.
- Wehr, J.D. 2015. Brown Algae. In *Freshwater Algae of North America: Ecology and Classification*. Elsevier Inc. 851–871. DOI: 10.1016/B978-0-12-385876-4.00019-0.
- Wiersema, J.H., Turland, N.J., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Morno, A.M., Prado, J., Price, M.J. & Smith, G.F. 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017: Appendices*. Available: <https://naturalhistory2.si.edu/botany/codes-proposals/> [2025, December 02].
- Williams, J.L. 1904. Studies in the Dictyotaceae. II. The Cytology of the Gametophyte Generation. *Annals of Botany*. 18: 183–204. Available: <https://about.jstor.org/terms>.
- Yang, M.Y. & Kim, M.S. 2023. Deep genetic divergences and geographic distribution of the red algal genus *Caulacanthus* (Gigartinales). *Frontiers in Marine Science*. 10. DOI: 10.3389/fmars.2023.1087507.
- Yoon, H.S., Hackett, J.D., Pinto, G. & Bhattacharya, D. 2002. The single, ancient origin of chromist plastids. *Proceedings of the National Academy of Sciences*. 99(24): 15507–15512. DOI: 10.1073/pnas.242379899.
- Zardi, G.I., Nicastro, K.R., Canovas, F., Costa, J.F., Serrão, E.A. & Pearson, G.A. 2011. Adaptive traits are maintained on steep selective gradients despite gene flow and hybridization in the intertidal zone. *PLoS ONE*. 6(6). DOI: 10.1371/journal.pone.0019402.

8. Supplementary material

Supplementary Table 1. Samples used in phylogenetic analysis, with accession numbers and sampling locations

Species	Sample	psbA	rbcL	cox1	Sampling location
<i>Dictyota acutiloba</i>	KZN16241	MW224578			South Africa: Kwazulu-Natal, Dog Point
<i>Dictyota acutiloba</i>	KZN16276	MW224579			South Africa: Kwazulu-Natal, Lala Nek
<i>Dictyota acutiloba</i>	ARS00117	OQ792181		OQ792174	USA: Hawaii, Oahu
<i>Dictyota acutiloba</i>	ARS08250	OQ792182	OQ792199	OQ792175	USA: Hawaii, Oahu
<i>Dictyota alternifida</i>	LT0051	LN871948		LN871970	Australia
<i>Dictyota alternifida</i>	LT0052	MW224596	MW223145		Australia: New South Wales, Newcastle
<i>Dictyota alternifida</i>	LT0197	MW224597			Australia: Victoria, Bellarine Peninsula, Point Lonsdale, Glaneuse Reef
<i>Dictyota bartayresiana</i>	DR17	JQ061010	MW223148		Dominican Republic: Catalina Island
<i>Dictyota bartayresiana</i>	DR7	GQ425189	MW223149	GQ425129	Dominican Republic: Punta Cana, Playa Bavaro
<i>Dictyota bartayresiana</i>	TZ0802c	GQ466071	MW223153		Tanzania: Zanzibar, Chwaka
<i>Dictyota binghamiae</i>	GWS035729			MW127663	Canada: British Columbia, Bolkus Islands(Kelp bed to NE), Gwaii Haanas
<i>Dictyota binghamiae</i>	HV1802		MW223155		Mexico: Baja California, Kennedy Camp
<i>Dictyota canaliculata</i>	ODC1477	GQ425190	MW223156	GQ425132	Philippines
<i>Dictyota canariensis</i>	D1559	MW224665			Spain: Canary Islands, Tenerife, Playa de El Socorro
<i>Dictyota canariensis</i>	D504		MW223165		Canary Islands, Tenerife, Buenavista, Playa de Las Arenas
<i>Dictyota caribaea</i>	RC175	JQ061059			Cuba: Santa Cruz del Sur
<i>Dictyota caribaea</i>	HV926			JQ061097	Jamaica: St. Ann Parish, St. Ann's Bay, Drax Hall
<i>Dictyota ceylanica</i>	HV214a	MT755665	DQ472067	GQ425122	Tahiti: Faaa
<i>Dictyota ceylanica</i>	MADA18ALG072		MW511052		Madagascar: Antsiranana Bay, Petite passe
<i>Dictyota ceylanica</i>	PC0166718	LN831811			Madagascar
<i>Dictyota chalcicueyecanensis</i>	POK100	KX819256		KX819253	Mexico: Punta Puntillas, Veracruz
<i>Dictyota ciliolata</i>	JCP026	MF182634	MF182639		Brazil
<i>Dictyota ciliolata</i>	HV632		DQ472053	GQ425124	Phillipines: SE Olango Island
<i>Dictyota ciliolata</i>	KZN16135	MW224790			South Africa: Kwazulu-Natal, Mabibi

<i>Dictyota ciliolata</i>	KZN16175	MW224791			Sodwana Jesser point KZN
<i>Dictyota ciliolata</i>	KZN16176	MW224792			South Africa: Sodwana Bay, 9-Mile Reef
<i>Dictyota ciliolata</i>	KZN16274	MW224793			South Africa: Kwazulu-Natal, Lala Nek
<i>Dictyota crenulata</i>	HV1074	GU265782	GU290253		Mexico: Baja California Sur, Cabo San Lucas, Playa Santa Maria
<i>Dictyota crenulata</i>	MX0208			LN871961	Mexico
<i>Dictyota crenulata</i>	MX0300	MW224806		MW223841	Mexico: Colima, Manzanillo, Juluapan
<i>Dictyota cyanoloma</i>	D544	GU255591	JQ061123	JQ061101	Portugal: Algarve, Portimao, Praia da Rocha
<i>Dictyota cyanoloma</i>	D502	GU255590	MW223182		Spain: Canary Islands, Gran Canaria, Arinaga, Zoco del Negro
<i>Dictyota cyanoloma</i>	D746	GU255615			Spain: Girona, Puerto de Palamos
<i>Dictyota cymatophila</i>	D306		MW223184		Spain: Canary Islands, Tenerife, Punta del Hidalgo
<i>Dictyota cymatophila</i>	ODC2386			MW223852	Spain: Canary Islands, Tenerife, Punta del Hidalgo
<i>Dictyota dhofarensis</i>	DHO0163	JQ061037		MW223853	Oman: Dhofar, Mirbat
<i>Dictyota dichotoma</i>	ODC1689	GU265784			United Kingdom: England, Barrow-in-furness, Walney Island
<i>Dictyota dichotoma</i>	KU-184	LC776643	LC764932	LC765036	France: Roscoff
<i>Dictyota dichotoma</i>	KU-5307	LC776648	LC764934	LC765037	Greece: Lesbos Is.
<i>Dictyota dichotoma</i>	HEC15759	GU255534	MW223191	MW223942	Portugal: Madeira, Porto Santos
<i>Dictyota dichotoma</i>	D185	GU255514	MW223186	MW223871	South Africa: Western Cape Province, Cape Peninsula, Bortjesrif
<i>Dictyota dichotoma</i>	D4029			MW223882	South Africa: Western Cape Province, Cape Peninsula, Bortjesrif
<i>Dictyota dichotoma</i>	D4030			MW223883	South Africa: Western Cape Province, Cape Peninsula, Bortjesrif
<i>Dictyota dichotoma</i>	D4031			MW223884	South Africa: Western Cape Province, Cape Peninsula, Bortjesrif
<i>Dictyota dichotoma</i>	D4033			MW223885	South Africa: Western Cape Province, Cape Peninsula, Bortjesrif
<i>Dictyota dichotoma</i>	D4043			MW223886	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4044			MW223887	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4045			MW223888	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4046			MW223889	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4047			MW223890	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4048			MW223891	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4049			MW223892	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4050			MW223893	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4051			MW223894	South Africa: Western Cape Province, False Bay, Strand

<i>Dictyota dichotoma</i>	D4052			MW223895	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4053			MW223896	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4054			MW223897	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4055			MW223898	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4056			MW223899	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4058			MW223900	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4059			MW223901	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4060			MW223902	South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota dichotoma</i>	D4079			MW223903	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4080			MW223904	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4081			MW223905	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4082			MW223906	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4083			MW223907	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4084			MW223908	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4085			MW223909	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4086			MW223910	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4087			MW223911	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4088			MW223912	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4089			MW223913	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4090			MW223914	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4091			MW223915	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4092			MW223916	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4093			MW223917	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4094			MW223918	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4095			MW223919	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D4096			MW223920	South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota dichotoma</i>	D656	GU255527			South Africa: Western Cape Province, Struisbaai
<i>Dictyota dichotoma</i>	RA950	MW224942			South Africa: Western Cape Province, De Hoop, Noetsie
<i>Dictyota dichotoma</i>	RSAD204	MW224943			South Africa: Western Cape Province, Gansbaai, Romansbaai
<i>Dictyota dichotoma</i>	KU-22497		LC764937		Ireland: Howth

<i>Dictyota diemensis</i>	HV2368	MW224981	MW223199	MW223968	Australia: South Australia, Robe
<i>Dictyota diemensis</i>	LT0184	MW224986			Victoria: Flinders
<i>Dictyota diemensis</i>	LT0290	MW224997	MW223200		South Australia: Port Noarlunga
<i>Dictyota dimorphosa</i>	Rei-Dic4	LC776669	LC764945	LC765043	Japan:Kumamoto, Amakusa, Reihoku
<i>Dictyota dimorphosa</i>	Tsu-Dic3	LC776631	LC764942		Japan:Kumamoto, Amakusa, Tsuji Is.
<i>Dictyota dimorphosa</i>	Ush-Dic5	LC776635	LC764947		Japan:Kumamoto, Amakusa, Ushibuka
<i>Dictyota falklandica</i>	F1718201	MK516800		MK516760	Falkland Islands (Islas Malvinas): East Falkland, San Carlos, Blue Beach
<i>Dictyota falklandica</i>	F1720301	MK516799		MK516759	Falkland Islands (Islas Malvinas): East Falkland, San Carlos, Blue Beach
<i>Dictyota fasciola</i>	FS1630			MW223975	France: Languedoc-Roussillon, Cote Vermeille, Banyuls-sur-mer
<i>Dictyota fasciola</i>	ODC1057	FJ869846			France: Languedoc-Roussillon, Banyuls, Cap du Troc
<i>Dictyota fasciola</i>	ODC1064	GU255553	MW223206		France: Languedoc-Roussillon, Cote Vermeille, CerbFre, Cap Peyferite
<i>Dictyota fasciola</i>	LLGO313			MW223977	Croatia: Split
<i>Dictyota fastigiata</i>	D96_Goldberg		DQ472068		Woody Island, Esperance Bay, South Australia
<i>Dictyota fastigiata</i>	GWS024841			MW127651	Australia: Western Australia, Cape Leeuwin Lighthouse
<i>Dictyota fastigiata</i>	LT0463	MW225587			Australia: Western Australia, Port Denison, Leander Reef
<i>Dictyota flabellata</i>	HV1654			MK516749	Mexico: Baja California Sur, Santa Rosalia
<i>Dictyota flabellata</i>	TACOX16		MK516811		Mexico: Baja California Sur, El Sauzoso
<i>Dictyota flabellata</i>	UC1918252	MT755666			San Diego, California,
<i>Dictyota friabilis</i>	HV153	JQ061039	DQ472064		French Polynesia: Tahiti, Arue
<i>Dictyota friabilis</i>	PF927	OR777600		OR777498	French Polynesia: Tuamotu Islands, Rangiroa
<i>Dictyota guineënsis</i>	BW01812	MW225050		MW224002	Panama: Bocas del Toro, Isla Colon, Swan key
<i>Dictyota haenyeosa</i>	JNU0611	PQ616797	PQ616892		South Korea: Jeju, Seogwipo City, Marado
<i>Dictyota haenyeosa</i>	JNU1100	PQ616800			South Korea: North Gyeongsang, Ulleung County, Ulleung Island
<i>Dictyota hamifera</i>	PF679	OR777557			French Polynesia: Society Islands, Tahiti
<i>Dictyota hamifera</i>	IRD4384	MW225068	MW223222		New Caledonia: North Province, Ile Yande,Lagon Nord
<i>Dictyota hamifera</i>	KZN16254	MW225072			South Africa: Kwazulu-Natal, Mabibi
<i>Dictyota humifusa</i>	SVCAR184	MW225112			Santa Marta: Chengue bay
<i>Dictyota humifusa</i>	ODC1659	JQ061044	MW223227	MW224024	Kenya: Gazi, Chale Island
<i>Dictyota humifusa</i>	KZN16303	MW225107			Mabibi, KZN
<i>Dictyota humifusa</i>	NU0090956	OK484667			South Africa

<i>Dictyota humifusa</i>	NU0090955	OK484666			South Africa
<i>Dictyota humifusa</i>	NU0090954	OK484665			South Africa
<i>Dictyota humifusa</i>	NU0090953	OK484664			South Africa
<i>Dictyota humifusa</i>	NU0090979	OK484630			South Africa
<i>Dictyota humifusa</i>	NU0090978	OK484629			South Africa
<i>Dictyota humifusa</i>	NU0090982	OK484633			South Africa
<i>Dictyota humifusa</i>	NU0090952	OK484652			South Africa
<i>Dictyota humifusa</i>	NU0090950	OK484650			South Africa
<i>Dictyota humifusa</i>	NU0090949	OK484649			South Africa
<i>Dictyota implexa</i>	FS338	GU255858			France: Provence, Cassis, Cap Canaille
<i>Dictyota implexa</i>	THAU2			MW224056	France: Languedoc-Roussillon, Lagune de Thau, Meze
<i>Dictyota implexa</i>	ODC1252b		MW223234		Spain: Cataluna, Gerona, Palam
<i>Dictyota intermedia</i>	GWS022794			MW127652	Australia: New South Wales, Lord Howe I., Neds Beach
<i>Dictyota intermedia</i>	GWS1020	JQ061047			Australia: New South Wales, Lord Howe Island
<i>Dictyota jamaicensis</i>	HV926	MW224680	DQ472061		Drax Hall, East of St. Ann's Bay, St. Ann Parish, Jamaica
<i>Dictyota jamaicensis</i>	BW01746			MW224057	Panama: Bocas del Toro, Tervi Bight
<i>Dictyota korowai</i>	ASN643	MK318551	MK318543		New Zealand: Three Kings Islands/Manawatawhi, South East Bay
<i>Dictyota kunthii</i>	D104		MW223238		Chile: Maitencillo
<i>Dictyota kunthii</i>	D2590	MK516792		MK516754	Peru: San Lorenzo Island
<i>Dictyota liturata</i>	MAD0142	LN831813		LN871962	Madagascar
<i>Dictyota liturata</i>	HEC15721	JQ061063	MW223241	MW224078	Portugal: Madeira Island, Rais Magos
<i>Dictyota liturata</i>	KZN2282	GQ425214	MW223243	MW224083	South Africa
<i>Dictyota liturata</i>	RA1032	MW225186		MW224086	South Africa: Kwazulu-Natal, Cape Vidal
<i>Dictyota liturata</i>	Sole1		GQ425113		Venezuela: Isla De Margarita, Porlamar, Playa El Agua
<i>Dictyota cf. liturata</i>	KZN16116	MW225181			South Africa: Kwazulu-Natal, Raggie's Reef
<i>Dictyota cf. liturata</i>	KZN16149	MW225182			South Africa: Sodwana Bay, Seven-Mile Reef
<i>Dictyota cf. liturata</i>	KZN16337	MW225183			South Africa: Kwazulu-Natal, Durban, Isipingo
<i>Dictyota cf. liturata</i>	RAD1312	MW225187		MW224087	South Africa: Hluleka, Transkei
<i>Dictyota cf. liturata</i>	RAD1331	MW225188		MW224088	South Africa: Hluleka, Transkei
<i>Dictyota cf. liturata</i>	RAD1343	MW225189		MW224089	South Africa: Hluleka, north end

<i>Dictyota cf. liturata</i>	RSAD590	MW225190			South Africa: Sodwana Bay, Seven Mile Reef
<i>Dictyota cf. liturata</i>	HEC15816		MW223242		Portugal: Madeira, Porto da Cruz
<i>Dictyota mayae</i>	GWS023172			MW127603	Australia: New South Wales, Lord Howe I. Neds Beach
<i>Dictyota mayae</i>	Jorge5916	MW225197			Mexico: Quintana Roo, Puerto Morelos
<i>Dictyota mayae</i>	IRD4360	MW225195	MW223169		New Caledonia: South Province, Laregnere, Lagon sud ouest
<i>Dictyota mediterranea</i>	LLGO313	GU255570			Croatia: Korcula Island, Kneza
<i>Dictyota mediterranea</i>	SGAD1256		MW223245	MW224113	Italy: Sicily, Capo di Milazzo
<i>Dictyota menstrualis</i>	JCP058	KM101060	KY012328		Brazil
<i>Dictyota menstrualis</i>	Searles.1	JX312658			North Carolina: Beaufort: Radio Island
<i>Dictyota menstrualis</i>	JCP073		MF182640		Brazil
<i>Dictyota menstrualis</i>	JCP1079		MF182641		Brazil
<i>Dictyota mertensii</i>	DR31	GQ425215	MW223248		Punta Cana: Playa Bavaro
<i>Dictyota mertensii</i>	KZN16009	MW225236			Sodwana Jesser point KZN
<i>Dictyota mertensii</i>	KZN16122	MW225237			Raggie's reef KZN
<i>Dictyota mertensii</i>	KZN16331	MW225225			Isipingo, KZN
<i>Dictyota mertensii</i>	BW01770	MW225226			Panama: Bocas del Toro, Isla Bastimentos, E of Wild Cane Cay
<i>Dictyota mertensii</i>	BW01771	MW225227			Panama: Bocas del Toro, Isla Bastimentos, E of Wild Cane Cay
<i>Dictyota mertensii</i>	DR31			GQ425130	Dominican Republic
<i>Dictyota cf. mertensii</i>	DR29		MW223246		Dominican Republic: Punta Cana, Playa Bavaro
<i>Dictyota cf. mertensii</i>	DR30		MW223247		Dominican Republic: Punta Cana, Playa Bavaro
<i>Dictyota cf. mertensii</i>	HV911		MW223249		Jamaica: St. Ann Parish, Priory
<i>Dictyota naevosa</i>	D659	JQ061066			Western Cape Province: De Hoop Nature Reserve
<i>Dictyota naevosa</i>	KZN2241	EU395609	DQ472084		South Africa: Mission Rocks, Kwazulu-Natal
<i>Dictyota naevosa</i>	KZNB2345	JQ061067		JQ061105	Kwazulu-Natal: Palm Beach
<i>Dictyota naevosa</i>	RA2164	MW225242		MW224126	Western Cape Province: Koppie Alleen
<i>Dictyota naevosa</i>	RA2176	MW225243		MW224127	Western Cape Province: Koppie Alleen
<i>Dictyota naevosa</i>	RAD699	MW225244			South Africa: Eastern Cape Province, Kei Mouth
<i>Dictyota naevosa</i>	RSAD482	MW225245			South Africa: Eastern Cape Province, Waterloo Bay
<i>Dictyota nigricans</i>	GWS024382			MW127667	Australia: Western Australia, Little Beach
<i>Dictyota nigricans</i>	LT0456	MW225249			Australia: Western Australia, Port Denison, Leander Reef

<i>Dictyota paniculata</i>	D97_Goldberg		DQ472082		Frederick Island, Esperance Bay, South Australia
<i>Dictyota paniculata</i>	LT0366	MW225255		MW224129	Australia: Western Australia, Hopetoun, Flathead Point
<i>Dictyota pedrochei</i>	UAMIZ:1234	KT445276		KT445274	Punta Brava, Quintana Roo, Mexico
<i>Dictyota pinnatifida</i>	HV932	MW225288	MW223257		Jamaica: St. Ann Parish, Priory, Chris Cove
<i>Dictyota pinnatifida</i>	BW07092	MW225285		MW224141	Panama: Bocas del Toro, Isla Colon, Mimbi Timbi
<i>Dictyota plectens</i>	GWS001029	JQ061074	DQ472052	MW223834	Australia: New South Wales, Lord Howe Island, Neds Beach
<i>Dictyota pleiacantha</i>	D324		MW223260		Spain: Canary Islands, Tenerife, Buenavista, Playa de Las Arenas
<i>Dictyota pleiacantha</i>	ODC2361	MW225296			Spain: Canary Islands, Tenerife, Punta del Hidalgo
<i>Dictyota phlyctaenodes</i>	JF0272	MK516798			Chile: Region de Valparaiso, Juan Fernandez Archipelago, El Palillo
<i>Dictyota polyclada</i>	HV2282	MK516805			Australia: Victoria, Flinders
<i>Dictyota pulchella</i>	CL030101	GQ425216	DQ472058		East side of airport causeway, St. George, Bermuda
<i>Dictyota pulchella</i>	FS271			GQ425135	France: Provence, Carry-le-Rouet, Sausset les Pins
<i>Dictyota recumbens</i>	Kya-Dic3	LC776658	LC764954		Myanmar: Ayeyarwady, Patheingyi, Kyaukse, Kyaukse
<i>Dictyota rigida</i>	ODC1657	GQ466077	MW223265	GQ425138	Kenya: Mombasa, McKenzie Point
<i>Dictyota rigida</i>	KZN16011	MW225314			South Africa: Sodwana Bay, Jessor Point
<i>Dictyota rigida</i>	TZ0731C	GQ425217	MW223266		Tanzania: Zanzibar, Matemwe
<i>Dictyota rigida</i>	PC0166272	LN831815			Madagascar
<i>Dictyota rigida</i>	PC0166123	LN831814			Madagascar
<i>Dictyota rigida</i>	MADA18AL		MW511056		Madagascar: Antsiranana Bay, Petite passe Orangea
<i>Dictyota rigida</i>	ODC1623		GQ425117		Kenya: Mombasa, McKenzie Point
<i>Dictyota cf. rigida</i>	KZN16033	MW225324			South Africa: Sodwana Bay, Jessor Point
<i>Dictyota cf. rigida</i>	KZN16103	MW225315			South Africa: Kwazulu-Natal, Leadsman Shoal
<i>Dictyota cf. rigida</i>	KZN16109	MW225316			South Africa: Kwazulu-Natal, Leadsman Shoal
<i>Dictyota cf. rigida</i>	KZN16133	MW225325			South Africa: Kwazulu-Natal, Mabibi
<i>Dictyota cf. rigida</i>	KZN16177	MW225317			South Africa: Sodwana Bay, 9-Mile Reef
<i>Dictyota cf. rigida</i>	HV1948	MW225318			Japan: Shikoku, Kochi Prefecture, Tosakure
<i>Dictyota cf. rigida</i>	RA1018	MW225326		MW224156	South Africa: Kwazulu-Natal, Salt Rock
<i>Dictyota cf. rigida</i>	RSAD549	MW225327			South Africa: Sodwana, Jessor Point
<i>Dictyota cf. rigida</i>	ODC1553		MW223264		Kenya: Tiwi
<i>Dictyota robusta</i>	D1702	MK516808	MK516814	MK516743	Western Australia: Yallingup, Canal Rocks

<i>Dictyota robusta</i>	HV2495	MW225595			Western Australia: Recherche Archipelago
<i>Dictyota robusta</i>	KZN2203b	MW225599			Kwazulu-Natal: Protea Banks: Northern Pinnacle
<i>Dictyota robusta</i>	ODC1100	MW225600		MW224298	Kwazulu-Natal: Protea Banks: Southern Pinnacle
<i>Dictyota robusta</i>	ODC1108	MW225601		MW224299	Kwazulu-Natal: Protea Banks: Southern Pinnacle
<i>Dictyota robusta</i>	ODC1110	MW225602			Kwazulu-Natal: Protea Banks: Southern Pinnacle
<i>Dictyota robusta</i>	ODC1119	MW225603		MW224300	Kwazulu-Natal: Protea Banks: Southern Pinnacle
<i>Dictyota robusta</i>	ODC1120	MW225604	MW223317		Kwazulu-Natal: Protea Banks: Southern Pinnacle
<i>Dictyota sandvicensis</i>	KD88671	MW225337	MW223271	MW224161	South Africa: Sodwana Bay, Jesser Point
<i>Dictyota sandvicensis</i>	ODC889	GU265783	MW223272	GU290239	USA: Hawaii, Oahu, Honolulu, Ala Moana
<i>Dictyota spathulata</i>	NAT01	PQ633222	PQ633224		Japan: Aomori Prefecture, Mutsu Bay, Natsudomari
<i>Dictyota spathulata</i>	JNU0111	PQ616807	PQ616895		South Korea: Jeju, Chuja-myeon, South of Chuja
<i>Dictyota spinulosa</i>	OKI080	MW225537		MW224263	Japan: Teniya, Okinawa Island
<i>Dictyota spiralis</i>	ODC1225	GU255607	MW223308		Spain: Cataluna, Girona, Palamos, Cala Corbs
<i>Dictyota stolonifera</i>	RD88740	MW225569			Australia: Queensland, Heron Island
<i>Dictyota stolonifera</i>	PNGMAD3710	MW225568		MW224293	Papua New Guinea: Rasch Passage
<i>Dictyota stolonifera</i>	ARV667	MW225559			Reunoin: grand tombant
<i>Dictyota stolonifera</i>	KZN16228	MW225565			South Africa: Kwazulu-Natal, Dog Point
<i>Dictyota stolonifera</i>	KZN16252	MW225566			South Africa: Mabibi
<i>Dictyota stolonifera</i>	D264		GQ425118		Taiwan
<i>Dictyota stolonifera</i>			LN871960		Tanzania
<i>Dictyota stolonifera</i>			DQ472072		Philippines: Dancalan, N of Bulusan, SW Luzon
<i>Dictyota taekwakia</i>	JNU0444	PQ616863			South Korea: Jeju, Chuja-myeon, Suryeong Island
<i>Dictyota sp.</i>	D4028	MW224945			South Africa: Western Cape Province, Cape Peninsula, Bortjiesrif
<i>Dictyota sp.</i>	D4034	MW224946			South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota sp.</i>	D4037	MW224947			South Africa: Western Cape Province, False Bay, Strand
<i>Dictyota sp.</i>	D4061	MW224948			South Africa: Western Cape Province, Kalk Bay
<i>Dictyota sp.</i>	RA006	MW224955			South Africa: Western Cape Province, Cape Peninsula, Buffel's Bay
<i>Dictyota sp.</i>	RA007	MW224956			South Africa: Western Cape Province, Cape Peninsula, Buffel's Bay
<i>Dictyota sp.</i>	RA008	MW224957			South Africa: Western Cape Province, Cape Peninsula, Buffel's Bay

<i>Dictyota sp.</i>	RA010	MW224958			South Africa: Western Cape Province, Cape Peninsula, Buffel's Bay
<i>Dictyota sp.</i>	RA011	MW224959			South Africa: Western Cape Province, Cape Peninsula, Buffel's Bay
<i>Dictyota sp.</i>	RA012	MW224960			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA013	MW224961			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA014	MW224962			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA015	MW224963			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA016	MW224964			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA017	MW224965			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA018	MW224966			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA019	MW224967			South Africa: Western Cape Province, Cape Peninsula, Buffels Bay
<i>Dictyota sp.</i>	RA020	MW224968			South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota sp.</i>	RA021	MW224969			South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota sp.</i>	RA022	MW224970			South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota sp.</i>	RA023	MW224971			South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota sp.</i>	RA024	MW224972			South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota sp.</i>	RA025	MW224973			South Africa: Western Cape Province, False Bay, Glencairn
<i>Dictyota sp. 1</i>	KZN2305		DQ472066		South Africa: Isipingo, Kwazulu-Natal
<i>Dictyota sp. 3</i>	HEC15817	LN871945	LN871956	LN871968	Portugal
<i>Dictyota sp. 7</i>	D186		MW223301		South Africa: Western Cape Province, Bortjiesrif
<i>Dictyota sp. 7</i>	D206	MW225529	MW223302		South Africa: Western Cape Province, Plettenberg Bay, Keurboomstrand
<i>Dictyota sp. 7</i>	D207		MW223303		South Africa: Western Cape Province, Plettenberg Bay, Keurboomstrand
<i>Dictyota sp. 7</i>	D4032			MW224257	South Africa: Western Cape Province, Cape Peninsula, Borjesrif
<i>Dictyota sp. 7</i>	KZN2308		LN871955	LN871967	South Africa: eManzimtoti, Durban
<i>Dictyota sp. 7</i>	RAD1344	MW225531		MW224258	South Africa: Hluleka, north end
<i>Dictyota sp. 7</i>	RAD1348			MW224259	South Africa: Hluleka, north end
<i>Dictyota sp. 7</i>	RAD75	MW225532		MW224260	South Africa: Western Cape Peninsula, Nature's Valley
<i>Dictyota sp. 9</i>	KZN16253	MW225533			South Africa: Kwazulu-Natal, Mabibi
<i>Dictyota sp. 24</i>	KZN16154	MW225481			South Africa: Sodwana Bay, Seven-Mile Reef
<i>Dictyota sp. 45</i>	RAD1330	MW225519		MW224255	South Africa: Hluleka, Transkei
<i>Dictyota sp. 45</i>	RAD1342	MW225520		MW224256	South Africa: Hluleka, north end

<i>Canistrocarpus cervicornis</i>	SVCAR211	MW224509			Colombia
<i>Canistrocarpus cervicornis</i>	FEZA3768		LR745673	LR745689	Mexico:Tamaulipas, Punta Piedra
<i>Canistrocarpus cervicornis</i>	RA1030	MW224483			South Africa: Kwazulu-Natal, Cape Vidal
<i>Canistrocarpus cervicornis</i>	KU-3584		LC764906	LC765017	Taiwan: Kenting
<i>Stoechospermum polyplioides</i>	KZN16145	MW225855			South Africa: Sodwana Bay, Seven-Mile Reef
<i>Stypopodium flabelliforme</i>	HV661		DQ472039		Philippines: NW side of Cabilao Island
<i>Stypopodium flabelliforme</i>	GWS023782			MW127660	Australia: New South Wales, Split Rock, Lord Howe
<i>Stypopodium hawaiiensis</i>	ODC900		DQ472040		Hawaii: Lanikai, Oahu
<i>Stypopodium multipartitum</i>	KZN16255	MW225865			South Africa: Kwazulu-Natal, Mabibi
<i>Stypopodium multipartitum</i>	PC0166346	LN831854			Madagascar
<i>Stypopodium multipartitum</i>	MAD0379			MW224385	Madagascar: Anosy, Pointe d'Ambero
<i>Taonia atomaria</i>	HV887		DQ472041		Spain: Cap Creus
<i>Taonia atomaria</i>	no ID			LC760650	Egypt
<i>Taonia atomaria</i>	ODC2203			MW224390	Spain: Canary Islands, Tenerife, Punta del Hidalgo

Supplementary Table 2. Accession numbers of samples analysed during this study.

Sample ID	Accession number		
	<i>rbcL</i>	<i>psbA</i>	<i>cox1</i>
C1	PX802761	PX852446	-
C2	PX802762	PX852447	-
C11	PX802763	PX852448	PX852421
C12	PX802764	PX852449	-
C13	PX802765	PX852450	-
C49	PX802766	PX852451	PX852422
C52	PX802767	PX852452	PX852418
C194	PX802768	PX852453	-
C199	PX802769	PX852454	PX852424
C200	PX802770	PX852455	PX852425
C201	PX802771	PX852456	PX852426
C202	PX802772	PX852457	PX852427
C203	PX802773	PX852458	PX852419
C206	PX802774	PX852459	-
C207	PX802775	PX852460	PX852428
C219	PX802776	PX852461	PX852429
C220	PX802777	PX852462	PX852430
C275	PX802778	PX852463	-
C276	PX802779	PX852464	PX852431
C277	PX802780	PX852465	PX852432
C278	PX802781	PX852466	-
C279	PX802782	PX852467	PX852433
C280	PX802783	PX852468	PX852434
C281	PX802784	PX852469	-
C282	PX802785	PX852470	PX852435
C283	PX802786	PX852471	PX852436
C285	PX802787	PX852472	PX852437
C286	PX802788	PX852473	PX852438
C287	PX802789	PX852474	-
C288	PX802790	PX852475	PX852420
C289	PX802791	PX852476	PX852439
C290	PX802792	PX852477	PX852440
C291	PX802793	PX852478	PX852441
C292	PX802794	PX852479	-
C293	PX802795	PX852480	-
C294	PX802796	PX852481	-
C295	PX802797	PX852482	-
C296	PX802798	PX852483	PX852442
C297	PX802799	PX852484	PX852443

C298	PX802800	PX852485	PX852444
C299	PX802801	PX852486	-
C301	PX802802	PX852487	-
C302	PX802803	PX852488	-
C304	PX802804	PX852489	-
C305	PX802805	PX852490	-
C310	PX802806	PX852491	-
C311	PX802807	PX852492	-
C312	PX802808	PX852493	-
C313	PX802809	PX852494	-
C373	PX802810	PX852495	-
C374	PX802811	PX852496	PX852445
D1092	PX802812	-	-
D1094	PX802813	-	-
D1095	PX802814	PX852497	-
D1096	PX802815	PX852498	-
D1098	PX802816	PX852499	-
D1099	PX802817	PX852500	-
D1126	PX802818	-	-
D1131	PX802819	-	-
D1143	PX802820	-	-
D1277	PX802821	PX852501	-
D1302	-	PX852502	-
D1312	PX802822	-	-
D1331	PX802823	-	-
D1343	PX802824	-	-
D1839	PX802825	-	-
D1851	PX802826	-	-
D2180	PX802827	-	-
D2184	PX802828	-	-
D2604	PX802829	-	-
D2712	PX802830	PX852503	-
D2713	PX802831	PX852504	-
KZN_16_001	PX802832	-	-
KZN_16_009	PX802833	-	-
KZN_16_033	PX802834	-	-
KZN_16_116	PX802835	-	-
KZN_16_134	PX802836	-	-
TR05544	-	PX852505	-