# CHAPTER 5

# SHIFTING NICHES PROMOTE DIVERSIFICATION ALONG A THERMAL GRADIENT

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# ABSTRACT

The holy grail of ecology is to explain differences in species richness between clades or regions. The diversification rate of clades is a key parameter for understanding such patterns. Here, we use a time calibrated phylogeny in combination with thermal data for the marine brown algal genus *Dictyota* in order to investigate the evolution of niches through time in relation to diversification rates and species diversity patterns. Our results show that species diversification within this genus is positively associated with the ability of clades to shift their thermal niche. This outcome might have implications for the interpretation of large scale marine diversity patterns, however the generality of our findings should be tested in the future.

# INTRODUCTION

Differences in speciation and extinction as well as geographic range changes underlie large-scale biodiversity patterns. Identification of general mechanisms that influence diversification across taxonomic groups and temporal scales, however, has proven a hard nut to crack (e.g. Butlin *et al.*, 2009). Among the many theories to explain the unevenness in biodiversity across large spatial scales, biologists have studied and speculated about a link between species richness and climate for over two centuries (Clarke & Gaston, 2006). This link is most emblematically presented by the latitudinal diversity gradient, a trend of higher biodiversity in the tropics to lower biodiversity towards the poles which has been well characterized for terrestrial (Pianka, 1966; Hillebrand, 2004a; Ricklefs, 2006) as well as marine organisms (Roy *et al.*, 1998; Hillebrand, 2004b). Despite the generality of this trend and a proliferation of different hypotheses, a universally accepted explanation remains elusive (Mittelbach *et al.*, 2007). Differences in diversification rates have featured prominently in several evolutionary explanations. For terrestrial organisms, climate has long been identified as a factor with a pronounced effect on diversification rates. Both rapid shifts (Kozak & Wiens, 2007) as well as conservatism (Kozak & Wiens, 2006) of the climatic niche may interact with rates of diversification. Recently, Kozak & Wiens (2010) demonstrated that rates of ecological niche evolution correlate with diversification rate and these rates are higher in tropical latitudes. The accessibility of global environmental data (Kozak *et al.*, 2008), have created new opportunities for studying species' climatic niches and understanding how past climate changes have shaped extant species diversity. In addition, studies investigating the role of climate on speciation and diversification are receiving renewed attention in the light of anthropogenic climate change (Parmesan & Yohe, 2003; Evans *et al.*, 2009).

Despite covering more than 70% of the earth's surface and hosting a huge diversity of organisms, marine patterns of diversity and the processes underlying these patterns have received considerably less attention compared to terrestrial ecosystems. Moreover some recent studies reveal important contrasts to widely held terrestrial paradigms, which highlight the need to specifically address marine diversification (Tittensor *et al.*, 2010). Accelerated diversification rates for marine organisms have been correlated with large-scale physical restructuring of oceans (Steeman *et al.*, 2009), habitat availability (Williams, 2007; Williams & Duda, 2008) often in combination with increased ecological species interactions (Alfaro *et al.*, 2007; Cowman & Bellwood, 2011) or the acquisition of key innovations(Alfaro *et al.*, 2009; Slater *et al.*, 2010). However, marine studies particularly focusing on the relation between climatic niche evolution and diversification are non-existing.

Temperature has long been regarded a key factor regulating the diversity of organisms and its consistent and dominant role in structuring broad-scale marine diversity patterns was recently endorsed (Tittensor *et al.*, 2010). Seaweeds have featured prominently in studies establishing a crucial role of sea surface temperature in shaping the range and geographical distributions of marine organisms (Pielou, 1977; Van Den Hoek, 1982; Breeman, 1988; Lüning, 1990; Bolton, 1994; Breeman & Pakker, 1994; Santelices & Marquet, 1998; Santelices *et al.*, 2009; Eggert, 2012). Critical temperatures for the completion of the life history were experimentally assessed for many species and correlated well to their respective geographic boundaries (Breeman, 1988). More recently evolutionary studies revealed a strong phylogenetic imprint of temperature and considerable niche conservatism (Breeman *et al.*, 2002; Verbruggen *et al.*, 2009).

Here, we study the evolution of thermal niches through time in relation to diversification rates and species diversity patterns, using the brown macroalga *Dictyota* as model entity.

# MATERIALS AND METHODS

## STUDY TAXON

We use the brown algal genus *Dictyota* as a model taxon for this study. This widespread genus abounds in tropical to cold-temperate seas and is an important constituent of the marine flora in these regions (De Clerck *et al.*, 2006). It has a rich history of phylogenetic studies (De Clerck *et al.*, 2006; Tronholm *et al.*, 2010) with nearly complete global taxon sampling (80-90%), making it a good candidate for this study. A recent study suggested that species' thermal tolerances have influenced biogeographical patterns in the genus (Tronholm *et al.*, 2012), further promoting its suitability as a model to examine the relationship between climate and diversification.

## PHYLOGENY AND DIVERSIFICATION

Testing hypotheses about environmental disparity and diversification requires a time-calibrated phylogeny. We have assembled an 8-locus alignment of 103 *Dictyota* species and 26 outgroup species based on a combination of newly generated and previously published data (De Clerck *et al.*, 2006; Hwang *et al.*, 2009; Tronholm *et al.*, 2010; Tronholm *et al.*, 2012). Phylogenetic trees were inferred using partitioned ML and Bayesian phylogenetic inference, and chronograms were estimated using an auto-correlated clock model with node age constraints derived from a brown algal time-calibrated phylogeny (Silberfeld *et al.*, 2010). We refer to Appendix S1 for details about the construction of the phylogeny and estimation of divergence times. We constructed a consensus tree and selected a random subset of 1,500 chronograms for use in subsequent analyses. Tempo of species diversification was investigated with a three-step procedure (See Appendix S1) taking the consensus tree as the basis for the analyses. The accumulation of lineages over time was first visualized using a lineages-through-time (LTT) plot. We then examined diversity dynamics from the phylogeny using birth–death model of cladogenesis developed by Rabosky (2006) and further elaborated by Morlon *et al.* (2011). The latter are thought to give more realistic estimates of extinction rates while also accommodating for incomplete taxon sampling.

## GEOGRAPHIC AND THERMAL DATA

To estimate the thermal affinities of species, we retrieved geographical coordinates from recently collected specimens for which the identification has been confirmed by DNA sequence information. This resulted in 1,144 unique localities for 103 species. Our sampling represented a good balance between tropical (622) and temperate locations (522) (Figure S2.1). We extracted mean sea surface temperature (SST) data for each of these locations from the marine environmental dataset Bio-ORACLE (Tyberghein *et al.*, 2012). The SST data are summarized in Table S2.1.

## ANALYSIS OF SPECIATION AND BIOGEOGRAPHY

To quantify the relative importance of different modes of diversification, we evaluated all speciation events that gave rise to at least one individual species (see Malay & Paulay, 2009).

Species occurrence records were mapped in ArcGIS and species ranges were visually analyzed. Species were considered allopatric when they had separate ranges. Species ranges that abut were termed parapatric, whereas species ranges that show a certain degree of overlap were called sympatric. The full list of species' geographic distributions relative to each other can be found in Table S2.2.

## THERMAL NICHE EVOLUTION

Patterns of thermal niche evolution were examined with two methods. First, ancestral SST affinities were inferred using a generalized least squares approach implemented in COMPARE (Martins, 2004) and plotted on the chronogram with TreeGradients v1.03 (Verbruggen, 2008). The distribution of thermal affinities was also visualized with a disparity-through-time plot and quantified by calculating a disparity index (MDI = morphological disparity index). Disparity-through-time plots permit a visual exploration of whether for any given time in the phylogeny, environmental differences are more pronounced within subclades or between subclades. The observed disparity for our data was compared with 10,000 simulations under a Brownian motion model of trait evolution (Harmon *et al.*, 2003). The MDI quantifies the overall difference in relative disparity of a clade compared with the expectation under the null model (MDI, Harmon *et al.*, 2003). Analyses were carried out with the 'geiger' package in R (R Development Core Team, 2008; Harmon *et al.*, 2008).

## RELATING DIVERSIFICATION TO THERMAL NICHE EVOLUTION

While the methods above can provide insight in the diversification of the genus as well as the evolution of the thermal niche, they do not relate them. To address the principal goal of examining the influence of thermal niche evolution on the rate of species diversification, we set up two analyses.

First, we optimized a model that relates species' traits to diversification rates in a phylogenetic context to establish whether a relationship exists between rates of diversification and SST affinities in *Dictyota*. This method relates net diversification $\lambda$ to a trait value, in our case SST, as follows:

$$\ln \frac{\lambda}{1 - \lambda} = \beta.\text{SST} + \alpha$$

This model, implemented and published by Paradis (Paradis, 2005), is designed to detect monotonic relationships between the trait value (SST) and the rate of diversification ($\alpha$ and $\beta$ are the model parameters). It was optimized with the yule.cov function in the 'ape' package for R (Paradis *et al.*, 2004). It was compared to the standard Yule model in which the rate of diversification is a constant (and thus unaffected by SST values) with the small sample size-corrected Akaike Information Criterion (AICc). The analysis was performed on the 1,500 posterior trees to take uncertainty in the topology and its time-calibration into account.

Second, we devised a procedure to test the hypothesis that clades with more variable SST affinities show accelerated diversification. This procedure is based on subdividing the tree into major clades and fitting a linear regression model to quantify the association between the rate of thermal

evolution and the rate of diversification of the clades. The clades were defined by slicing the phylogeny using a time-specific threshold. The threshold value (55 Ma) was chosen to postdate the radiation of the genus into its major clades. To avoid conditioning our results on a very specific time in the past, we repeated our analyses on a Bayesian posterior sample of trees and sampled threshold values from a normal distribution around that threshold (standard deviation 4 Ma). Clades containing less than four species were discarded from subsequent analyses because parameter values are unlikely to be inferred accurately.

Net diversification rates of clades were estimated from the clade age and the present species diversity of the clade (method-of-moments estimator) (Magallon & Sanderson, 2001). We will indicate the diversification rate of clade i as $\lambda_i$. The rate of thermal niche evolution was measured as the rate parameter of a Brownian motion model of evolution optimized on the SST affinities of the species in the clade. This parameter is denoted $\sigma_i^2$ for clade i. High $\sigma_i^2$ values indicate faster thermal niche evolution.

As an initial test of concept and to visualize the relationship between $\sigma_i^2$ and $\lambda_i$, we applied this method on the consensus chronogram. Based on the time threshold, the tree was subdivided into independent clades. For each clade, $\sigma_i^2$ and $\lambda_i$ were calculated. The resulting value pairs were plotted, and a linear regression model $\lambda = \beta . \sigma^2 + \alpha$ was fitted to the $(\sigma_i^2, \lambda_i)$ data points. This was then repeated with one hundred random threshold values drawn from the normal distribution.

Subsequently, we conducted the same analysis on the posterior sample of 1,500 time-calibrated trees to evaluate the consistency of the obtained pattern against differences in the topology, node ages and threshold values. We inferred the relationship between $\lambda$ and $\sigma^2$ for each tree individually, storing the slope of the relationship for each of the 1,500 replicates. To verify whether the obtained slopes differ from those expected in the absence of a structural relationship between $\lambda$ and $\sigma^2$, we performed the same analysis on datasets generated under the null model in which diversification does not depend on niche evolution. Therefore, we simulated 1,500 trees under a birth-death model (TreeSim: Stadler, 2011) with the parameters obtained from a randomly drawn *Dictyota* tree from the posterior set. Subsequently we simulated credible SST affinities for the species of the simulated trees using fastBM from the phytools package (Revell, 2011) with the rate parameter estimated from a randomly drawn *Dictyota* tree. For each of the 1,500 simulated datasets, we determined the slope of the relationship between $\lambda$ and $\sigma^2$ as described above. The slopes obtained from the real *Dictyota* data were compared to the slopes from the simulated data using a Wilcoxon signed-rank test.
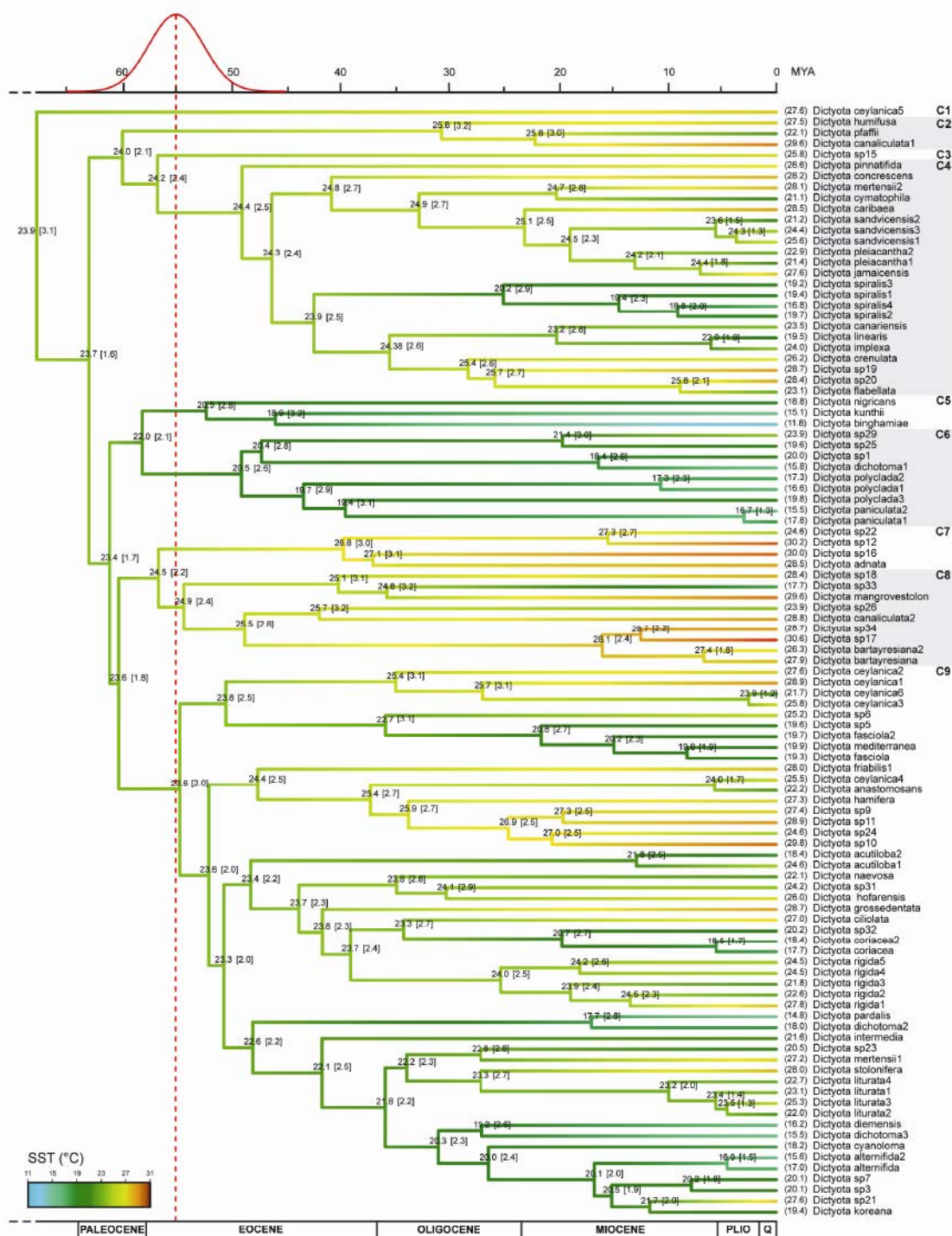
**Figure 1: Inferred evolutionary history of the thermal niche in *Dictyota*,** showing the scattered distribution of species with warmer and colder sea surface temperature affinities across the tree. The estimated ancestral SST affinities are plotted at nodes and visualized on the phylogeny along a color gradient, with blue indicating cold waters over green and yellow colors indicating temperate waters to tropical waters in red. The dashed red line indicates the temporal threshold used to define clades C1-9. This threshold was varied in the analyses according to the normal distribution shown in red at the top of the figure (see text for details).

# RESULTS

Our analyses were aimed at documenting the diversification and thermal evolution of *Dictyota*. Following a brief exploration of some basic results that help introduce the dataset, we will proceed to more detailed analyses that address various details of the relationship between species diversification and thermal niche affinities.

The inferred evolutionary history of sea surface temperature affinities (Figure 1) clearly indicates that evolution along the thermal niche axis has not been homogeneous throughout the genus. While some clades are mainly found in colder water (C5, C6) and others are predominantly tropical (C7, C8), the majority of clades contain a mixture of species from colder and warmer regions. While the ancestral states for the oldest nodes in the tree would suggest that the genus originated in warm-temperate waters, the uncertainty about these estimates is very high (Figure 1). Disparity-through-time plots show that the evolution of SST affinities does not deviate from the expectation under Brownian motion null model (Figure 2; MDI = 0.079, p-value = 0.177).
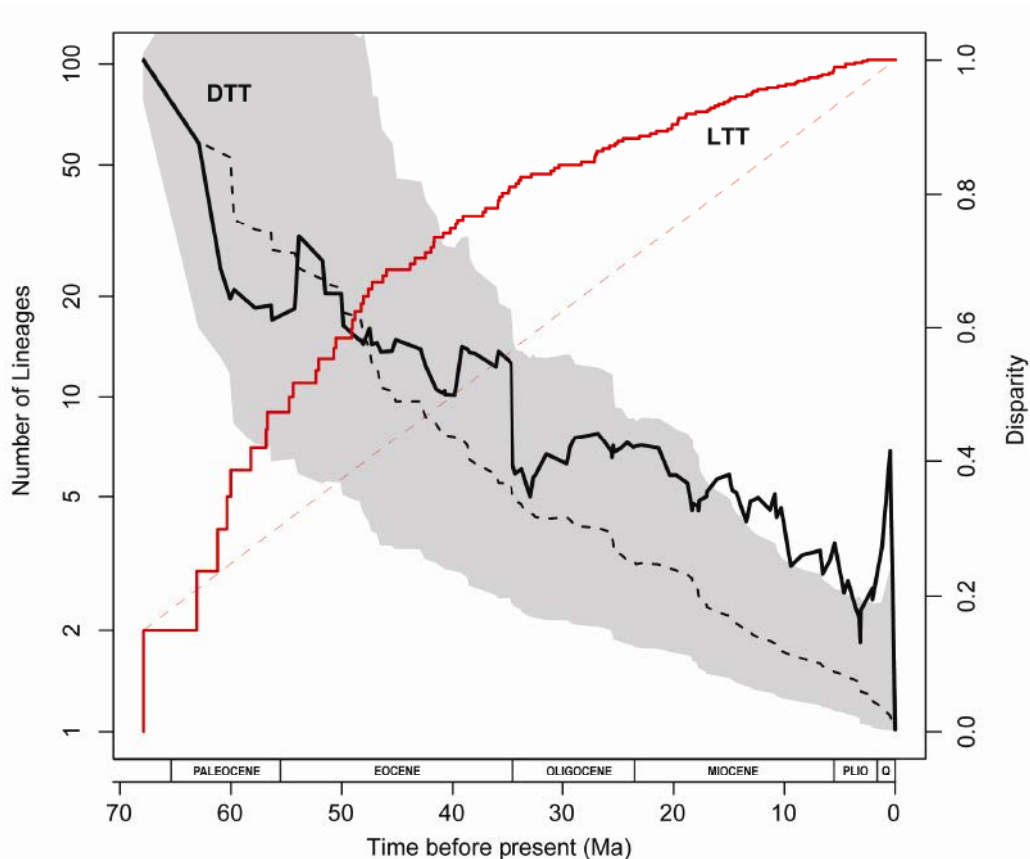


**Figure 2: Lineage- and disparity-through-time plots. The lineage-through-time plot (in red) shows that *Dictyota* shows a period of rapid diversification early on and slower diversification later on. This deviates from the pattern expected under homogeneous diversification (pink ribbon). The disparity-through-time plot (black line) largely lies within the expectation under Brownian motion evolution (gray ribbon), indicating that variation in the thermal niche is not found predominantly within or among clades but is more homogeneously spread across the phylogeny. The grey shaded area indicates the 95% DTT range for the simulated data.**

The phylogenetic tree and a lineages-through-time plot indicate that the genus experienced an early period of rapid diversification in the Paleocene and early Eocene followed by slower diversification in the remainder of the Cenozoic (Figures 1 &2). This visual assessment is confirmed by the fact that diversification models with decreasing rates of diversification better match the data (Table S1.3). A range of analyses indicates that extinction rates have been very low and that extinction is not likely to have played a major role in the diversification dynamics of the group (Tables S1.3 & S1.4).
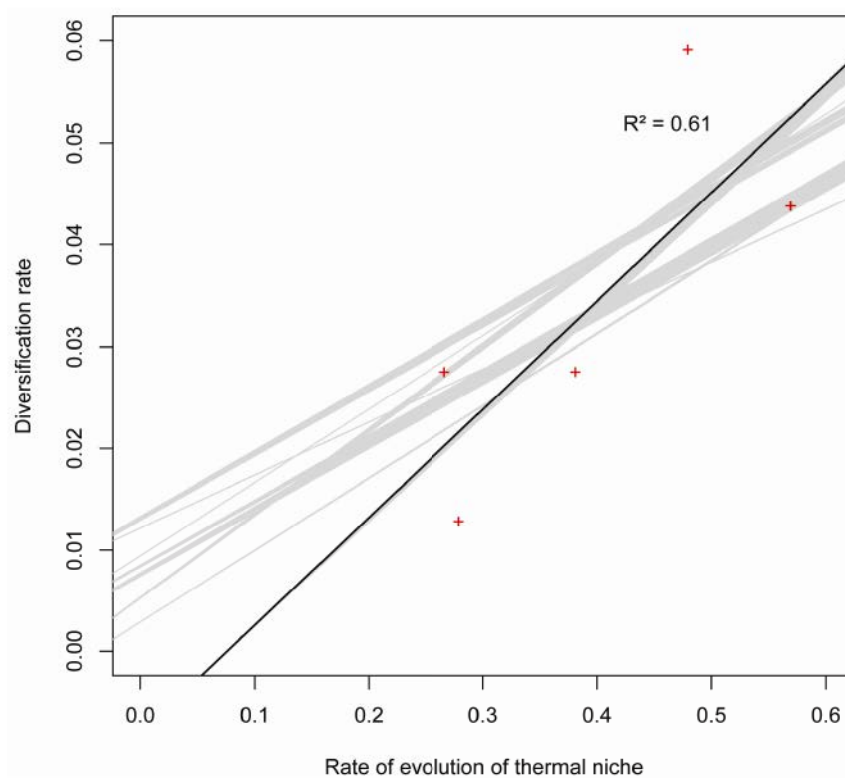


Figure 3: Regression analysis showing the positive relationship between the rate of species diversification and the rate of evolution of the thermal niche among *Dictyota* clades. The black line represents the regression inferred with the temporal threshold set at 55 Ma (red line in Figure 1). Dashed grey lines are regressions based on 100 randomly chosen threshold values from the normal distribution.

A model designed to relate the rate of diversification with species traits shows that the SST affinities of lineages have had very little impact on their diversification rates ($\beta = 0.018 \pm 0.021$), and that this model is not selected over a simple Yule model of diversification ($\Delta$AICc = $-2.05 \pm 0.21$ in favor of simple Yule model). However, analysis aimed at relating diversification to variability in SST affinities did show that clades with variable thermal niches diversify more rapidly (Figure 3). This result is robust to phylogenetic uncertainty and the exact position of the threshold (slope $\beta = 0.06 \pm 0.02$ across trees).Furthermore, this result is not a consequence of an autocorrelation that may exist between the number of species in a clade and the thermal niche diversity of that clade, as indicated by the fact that slopes are, on average, an order of magnitude higher in *Dictyota* than in simulations under the null hypothesis assuming is no association between SST affinities and diversification (Figure 4).
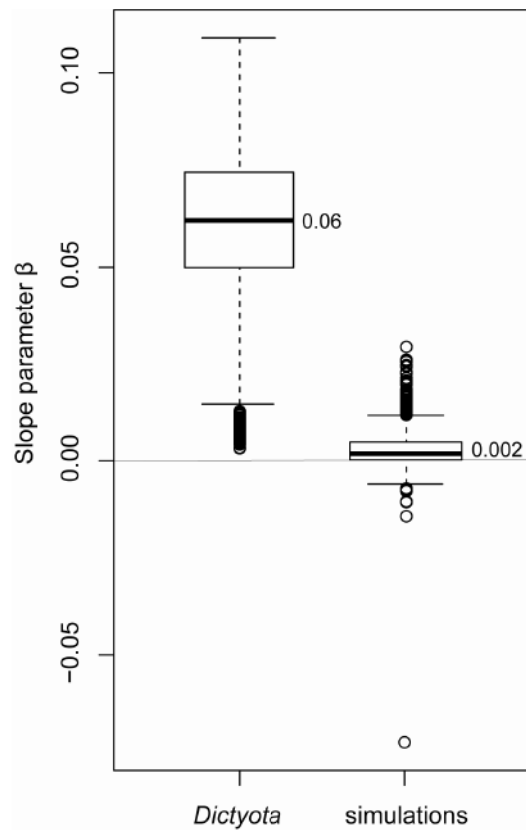
**Figure 4: Comparison of inferred slopes of the rate of diversification as a function of the rate of thermal niche evolution (cf. Figure 3) for our dataset (left boxplot) and the null hypothesis that there is no relationship between diversification and thermal niche evolution (right boxplot). The boxplots represent variation in the topology (sampled from the posterior set of *Dictyota* trees) and the threshold values used to define clades. They show median values (thick line), lower and upper quartiles (box), 5% and 95% percentiles (lines) and outliers (circles).**

The direction of the great majority of thermal niche shifts is from warmer waters to colder waters (Figure S1.3). Among clades that do not have a conserved thermal niche, those that have shifted from warmer to colder waters have higher rates of diversification than those that have moved from colder water into warmer water (Figure S1.3). Among clades with conserved thermal niches, the rate of diversification does not differ between warm-water clades and colder-water clades (Figure S1.4). Interpreting the observed pattern from a geographical perspective demonstrates that the percentage of sister taxa with contiguous, non-overlapping ranges (parapatric species) is higher in clades with higher diversification rates ($R^2$= 0.625, Figure 5a). Similarly, the percentage parapatric species correlates with evolutionary rate of the thermal niche, indicating that these speciation events may follow a latitudinal pattern ($R^2$= 0.857, Figure 5b).
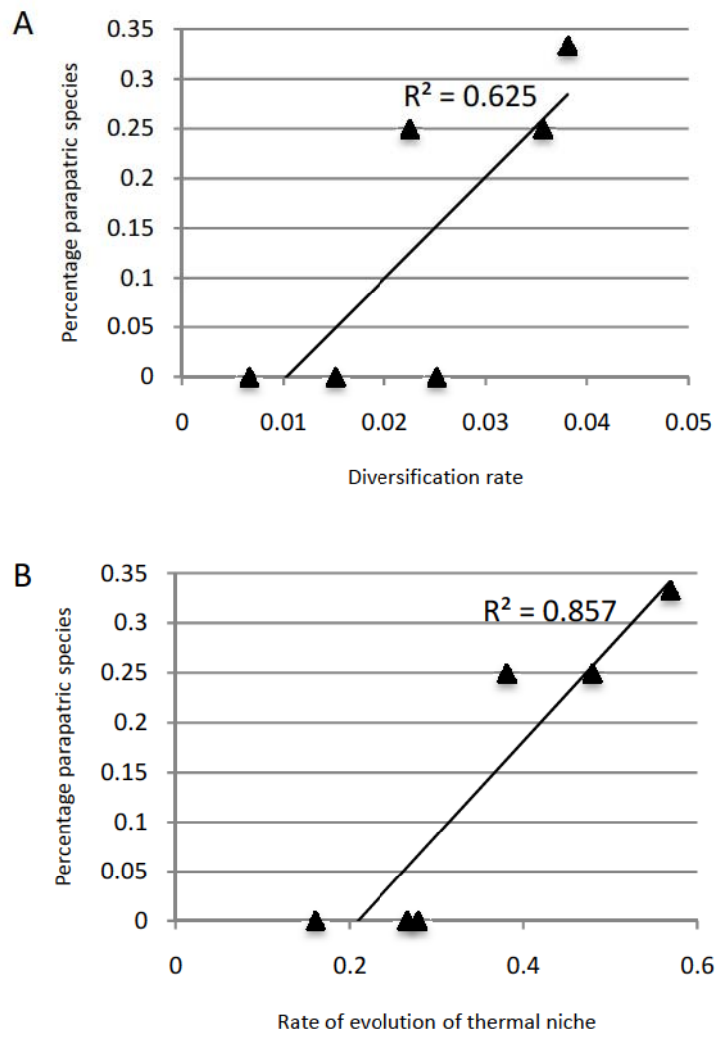
**Figuur 5: Regression analysis showing the positive relationship between the percentage of parapatric species and the rate of species diversification (A) and between the percentage of parapatric species and the rate of evolution of the thermal niche among *Dictyota* clades (B).**

# DISCUSSION

Our results show that species diversification in the marine algal genus *Dictyota* is positively associated with the ability of clades to shift their thermal niche. Despite the seemingly haphazard evolution of the thermal niche and unremarkable diversification dynamics when analyzed separately, the association between both is strong. We demonstrate that this correlation between niche evolution and diversification is robust against topological uncertainty and independent of clade age.

As pointed out by Kozak &Wiens (2010), higher diversification rates are probably caused by higher rates of niche evolution instead of the other way around. A mechanism that can explain increased rates of niche evolution as a consequence of increased diversification is currently unknown. Older, more species rich clades might be expected to spread into more climatic niches by chance alone. However, this possibility is accounted for by evaluating clades comparable of age. In addition to that, the rate of thermal niche evolution within a clade, and not simply the variance in thermal values among species was considered. Indeed, we found no relationship between thermal variance and species richness within a clade.

The evolvability of the niche of a lineage can affect both speciation and extinction rates. In lineages with conserved niches, speciation is more likely to result from vicariance (allopatric) as a result of dispersal limitation than from changes along a niche gradient, which would be a more common speciation mechanism in lineages with higher niche evolvability. This simple model relating the diversification dynamics of a lineage to its niche evolvability is influenced by a number of external elements. An important factor is the steepness and temporal variability of the climatic gradients, in our case the latitudinal gradient in sea surface temperatures. In what follows, we will discuss several aspects of this conceptual model.

The observed diversity pattern in *Dictyota* can be interpreted as an evolutionary response to Cenozoic climatic evolution which established a steep latitudinal temperature gradient. A mechanistic explanation allowing for speciation along such an environmental gradient was offered by Doebeli & Dieckman (2003) who demonstrated that spatial segregation of divergent phenotypes was critically dependent on the steepness of the gradient as well as dispersal capacity (movement). First, compared to the present day, the Early Eocene (55-50 mya) displayed almost no latitudinal SST gradient between subequatorial and subpolar regions (Bijl *et al.*, 2009). Subsequent climatic deterioration established a latitudinal temperature gradient already by the end of the Late Eocene. Secondly, under the model of Doebeli & Dieckman (2003) evolutionary branching and spatial segregation is promoted if movement distances are short. Seaweeds appear to meet this assumption remarkably well, being considered poor dispersers (Kinlan & Gaines, 2003). In other words, local adaptation along a temperature gradient may very well have resulted in higher diversification rates as observed in our data. Clades with higher diversification rates are also characterized by a higher percentage of sister taxa exhibiting contiguous ranges directed along the thermal gradient. The latter forms an indirect source of evidence for a diversification mode which is primarily driven by adaption and subsequent speciation along the thermal gradient. The imprint of extinction toward the diversity pattern is difficult to assess based on phylogenetic evidence only. It has been noted previously that species with more evolvable niches may cope better with changing environmental conditions, decreasing their risk of extinction, while lineages with conserved niches are more likely to suffer extinction (Cooper *et al.*, 2011). By applying analyses which enable to decouple speciation from extinction (e.g. Morlon *et al.*, 2011), extinction rates are consistently estimated very low, regardless of clade (Table S1.4), pointing towards a dominant role for speciation in shaping the observed diversity pattern.

Jablonski et al. (2006) present a model based on genera of fossilized bivalves that is superficially complementary with our findings. The 'out of the tropics model' (OTT model) predicts that taxa preferentially originate in the tropics and expand over time into temperate regions. This is consistent with the directionality of thermal niche evolution of *Dictyota*, whereby the majority of lineages moves from warm to cold waters and not vice versa. However, the OTT model also predicts that diversification should be higher in the tropics, due to higher speciation and lower extinction rates, compared to temperate regions. *Dictyota* lineages constrained to the tropics, however, have consistently lower diversification rates, as do lineages constrained to cold water. Higher diversification rates are observed in those lineages which speciate along a thermal gradient, manifesting itself in high mid-latitudinal diversity.

In addition to the argumentation above linking the ability of lineages to shift niches to their evolutionary success (measured as the rate of diversification), an alternative but not necessarily exclusive scenario is also worth considering. In the marine realm, changes in ocean currents through time are thought to affect connectivity across large geographic scales (Veron, 1995; Paulay & Meyer, 2002; Thiel & Haye, 2006). In periods of low connectivity, population sizes are small and speciation rates increase due to peripatric and allopatric isolation. These isolated populations can evolve more rapidly through genetic drift, creating the potential for rapid thermal niche evolution. Furthermore, if such isolated populations were scattered along various points of the latitudinal thermal gradient, they would be subject to selection for different thermal niche optima, which would also increase their rate of thermal evolution. Similar mechanisms can also affect terrestrial species if climatic cycles lead to speciation by subdividing widespread species into isolated populations. It has to be noted that in both these scenarios, the rate of speciation does not cause increased niche evolution. Instead, an external factor (a selection regime caused by a thermal gradient) impacts simultaneously on rates of speciation and rates of niche evolution, leading to an association between both.

Kozak & Wiens (2010) previously showed a similar association between rates of climatic niche evolution and diversification in plethodontid salamanders. Our study shows that similar mechanisms also affect marine biota. The primary difference between our study and that of Kozak & Wiens (2010) is that the latter analyzed evolution of the multi-dimensional climatic niche whereas we have focused on evolution along the thermal dimension of the niche. Plethodontid salamanders diversify more rapidly in the tropics, where they also have higher rates of niche evolution, for example along the elevational gradient. So, whereas for plethodontids shifts between climatic regimes occur more rapidly in tropical regions where the thermal climate is relatively stable, we find higher diversification in lineages that do vary broadly in their thermal affinities. Differentiation along elevational gradients as found in tropical terrestrial animals is comparable to a latitudinal temperature gradient for algae. A second difference with the study of Kozak & Wiens is that whereas they find rapid niche shifting, our results clearly show that niche evolution is concentrated in a small subset of the branches of the tree, followed by diversification in the newly invaded thermal region. A mere 6% of the branches are responsible for 55% of all thermal niche evolution in the genus. This means that there are a few major niche shifts and other than that thermal evolution is fairly slow and gradual. Almost all of the fast branches move from warmer to colder (one exception) and about half of the fast branches are internal, i.e. they represent an ancestral lineage invading colder water and subsequently diversifying there.

It is intriguing that lineages shown to have a positive association between the rates of niche evolution and diversification also feature a marked decrease in the diversification rate over time. Decreasing diversification has often been interpreted as evidence of diversity-dependent processes (Phillimore & Price, 2008; Rabosky, 2009) acting on speciation-extinction dynamics. Assuming that there are diversity-dependent limits on diversification, the positive association could indicate that niche shifts permits clades to escape from these limits by invading new areas. In the case of

*Dictyota*, we do not consider this possibility very likely for two reasons. First, the ecological literature suggests that seaweed communities are not saturated and that introduced seaweeds are more likely to establish in naturally more diverse habitats (Mineur *et al.*, 2008). Second, the fact that most niche shifts occur from warmer to colder habitats, coincident with the expansion of temperate habitat on both sides of the narrowing tropical belt during the Cenozoic, suggests that clades that have spawned cold-adapted lineages have been able to invade this new habitat, adding to their diversification potential, while clades with more restricted niches have not benefited from this opportunity.

Our results also have implications for the interpretation of latitudinal diversity patterns. The higher overall diversity in the tropics has been attributed to a number of potential causes. In our dataset, we find no evidence for higher diversification in tropics based on the model relating SST to diversification rates. The same result also falsifies other hypotheses such as a relationship between diversification to energy availability, surface areas (tropical provinces are larger, on average), or the time to diversify (tropics have been around for longer). Interestingly, seaweeds display a bimodal latitudinal diversity pattern, with warm-temperate regions being more species-rich than the tropics (Bolton, 1994; Kerswell, 2006; Santelices *et al.*, 2009). Based on a study of global patterns of generic diversity, Kerswell (2006) concluded that richness patterns of seaweeds are shaped by ocean currents through dispersal. Large ocean gyres, travelling poleward along western ocean boundaries and back towards the tropics along the eastern edges, would result in the greatest algal richness in western ocean regions and depauperate tropical floras in the east. Our results counter that explanation because even though *Dictyota* is present in the tropics as well as the rich temperate regions, it is clearly not a consequence of currents extending it into temperate waters. Our results clearly show that the species occurring at mid-latitudes are temperate-water specialists that are endemic in these regions, and they are not mid-latitude extensions of essentially tropical species. In fact, our results prove that any explanation based only on mechanisms working in an ecological timescale cannot explain the patterns of diversity. It is only using an evolutionary approach that one can discover how temperate water has been colonized from the tropics through niche shifts.

# CONCLUSION

The question of what determines rates of diversification is a key problem for both ecologists and evolutionary biologists. We show that for the marine algal genus *Dictyota*, species diversification is positively associated with the ability of clades to shift their thermal niche. This study is the first to present a pattern for marine species in which higher niche evolution leads to higher rates of diversification. Although this is very intriguing, other studies are necessary to investigate the universality of this pattern.

## AUTHOR CONTRIBUTIONS

LT, HV and ODC conceived and designed the study. LT carried out the analyses and wrote the manuscript. HV and ODC assisted LT in writing the final version. CD assembled biological information.

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# APPENDIX

## S1: PHYLOGENY AND DIVERSIFICATION

Species phylogenies were inferred from a multi-gene alignment (*rbc*L, *psa*A, *psb*A, *nad*1, *cox*1, *cox*3, 18S and 26S) of 129 species, using Bayesian inference (BI) and maximum likelihood (ML). The genera Canistrocarpus, Dilophus, Padina, Rugulopteryx, Scoresbyella and Dictyopteris were used as outgroup.

1. Model Selection

Using the Bayesian information criterion (BIC), a suitable partition strategy and suitable models of sequence evolution were selected. The guide tree used during the entire procedure was obtained by maximum-likelihood (ML) analysis of the unpartitioned concatenated alignment with PhyML, using a JC + $\Gamma 8$ model (Guindon & Gascuel, 2003). Twelve alternative partitioning strategies were evaluated (table S1.1). All subsequent likelihood optimizations and BIC calculations were carried out with Treefinder (Jobb et al., 2004). The preferential model of sequence evolution and partitioning strategy was a GTR + $\Gamma 4$ for which all protein coding genes were partitioned in three codon positions and nuclear genes were separated (table S1.2).

**Table S1.1: Partitioning strategies**

| Strategy | Partitions | Details |
|---|---|---|
| 1 | 1 | All data |
| 2 | 8 | Partitioned by gene |
| 3 | 3 | Mitochondrial genes + Chloroplast genes + Nuclear genes |
| 4 | 2 | Protein coding genes + Nuclear genes |
| **5** | **20** | **Protein coding genes (separate codon positions per gene) + Nuclear genes (separated)** |
| 6 | 19 | Protein coding genes (separate codon positions per gene) + Nuclear genes |
| 7 | 5 | Protein coding genes (separate codon positions) + Nuclear genes (separated) |
| 8 | 4 | Protein coding genes (codon positions 1 & 2 + codon position 3) + Nuclear genes (separated) |
| 9 | 4 | Protein coding genes (separate codon positions) + Nuclear genes |
| 10 | 3 | Protein coding genes (codon positions 1 & 2 + codon position 3) + Nuclear genes |
| 11 | 14 | Protein coding genes (codon positions 1 & 2 + codon position 3, per gene) + Nuclear genes (separated) |
| 12 | 13 | Protein coding genes (codon positions 1 & 2 + codon position 3, per gene) + Nuclear genes |

**Table S1.2: Results top ten**

| PMTstrategy | substmodel | RAStype | likelihood | parameters | AIC | AICc | BIC |
|---|---|---|---|---|---|---|---|
| **5** | **GTR** | **G4** | **-105745.73** | **456** | **212403.5** | **212453.2** | **215635.1** |
| 5 | GTR | IG4 | -105745.73 | 476 | 212443.5 | 212497.8 | 215816.8 |
| 6 | GTR | G4 | -105900.63 | 446 | 212693.3 | 212740.8 | 215854 |
| 11 | GTR | G4 | -106171.06 | 396 | 213134.1 | 213171.4 | 215940.5 |
| 6 | GTR | IG4 | -105900.63 | 465 | 212731.3 | 212783 | 216026.6 |
| 11 | GTR | IG4 | -106171.06 | 410 | 213162.1 | 213202.1 | 216067.7 |
| 12 | GTR | G4 | -106325.95 | 386 | 213423.9 | 213459.3 | 216159.4 |
| 12 | GTR | IG4 | -106325.95 | 399 | 213449.9 | 213487.7 | 216277.5 |
| 7 | GTR | G4 | -107217.39 | 306 | 215046.8 | 215068.8 | 217215.3 |
| 7 | GTR | IG4 | -107217.39 | 311 | 215056.8 | 215079.5 | 217260.8 |

## 2. Phylogenetic analysis

ML analyses were performed using RAxML v. 7.2.8 (Stamatakis, 2006). Statistical support for individual nodes was assessed via bootstrapping with 1,000 replicates. BI was conducted with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). Six parallel runs, each consisting of four incrementally heated chains, were run for 30 to 40 million generations, sampling every 2,500 generations. Convergence of log-likelihoods and parameter values were evaluated in Tracer v1.5 (Rambaut & Drummond, 2007). After discarding an appropriate burn-in, we built a consensus tree based on the runs achieving the highest converged likelihoods. The complete BI analysis was then repeated using this consensus tree as a user defined starting tree. The final resulting maximum clade credibility tree is shown in figure S1.2. All analyses were run on the Simon Stevin Computation Cluster at Ghent University, Belgium.

## 3. Divergence-Time Analysis

Chronograms were estimated using PhyloBayes (Lartillot & Philippe, 2004). We randomly sampled 1,500 trees from the MrBayes posterior set and used a log normal clock model to estimate divergence times. The root of the tree was constrained in geological time based on a brown algal time-calibrated phylogeny (Silberfeld et al., 2010). We applied a gamma root height prior set at 110 Ma (95%: 98 – 134).
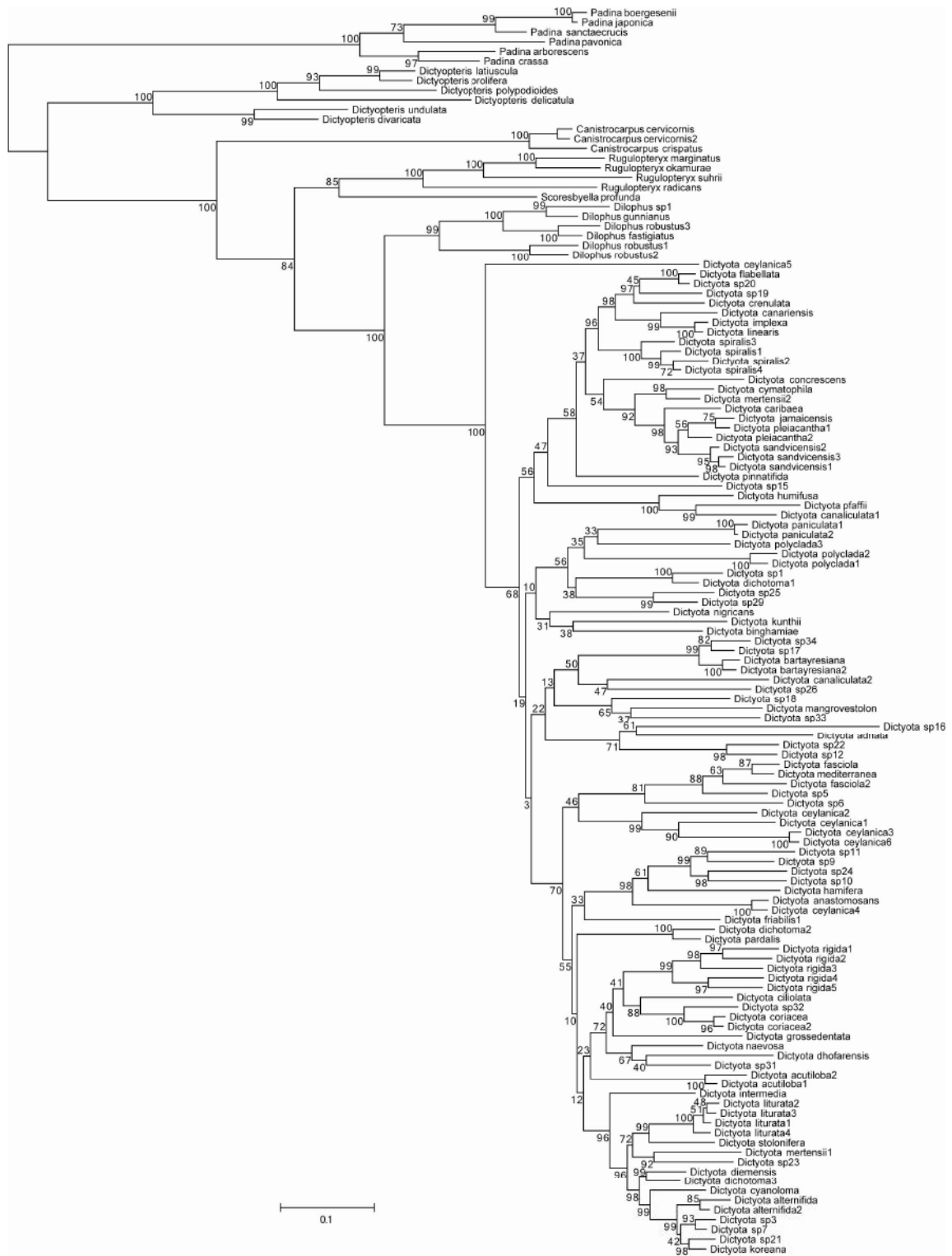
**Figure S1.1: Maximum likelihood phylogeny based on the combined dataset of eight genes. Numbers at nodes indicate ML bootstrap proportions (as percentages).**
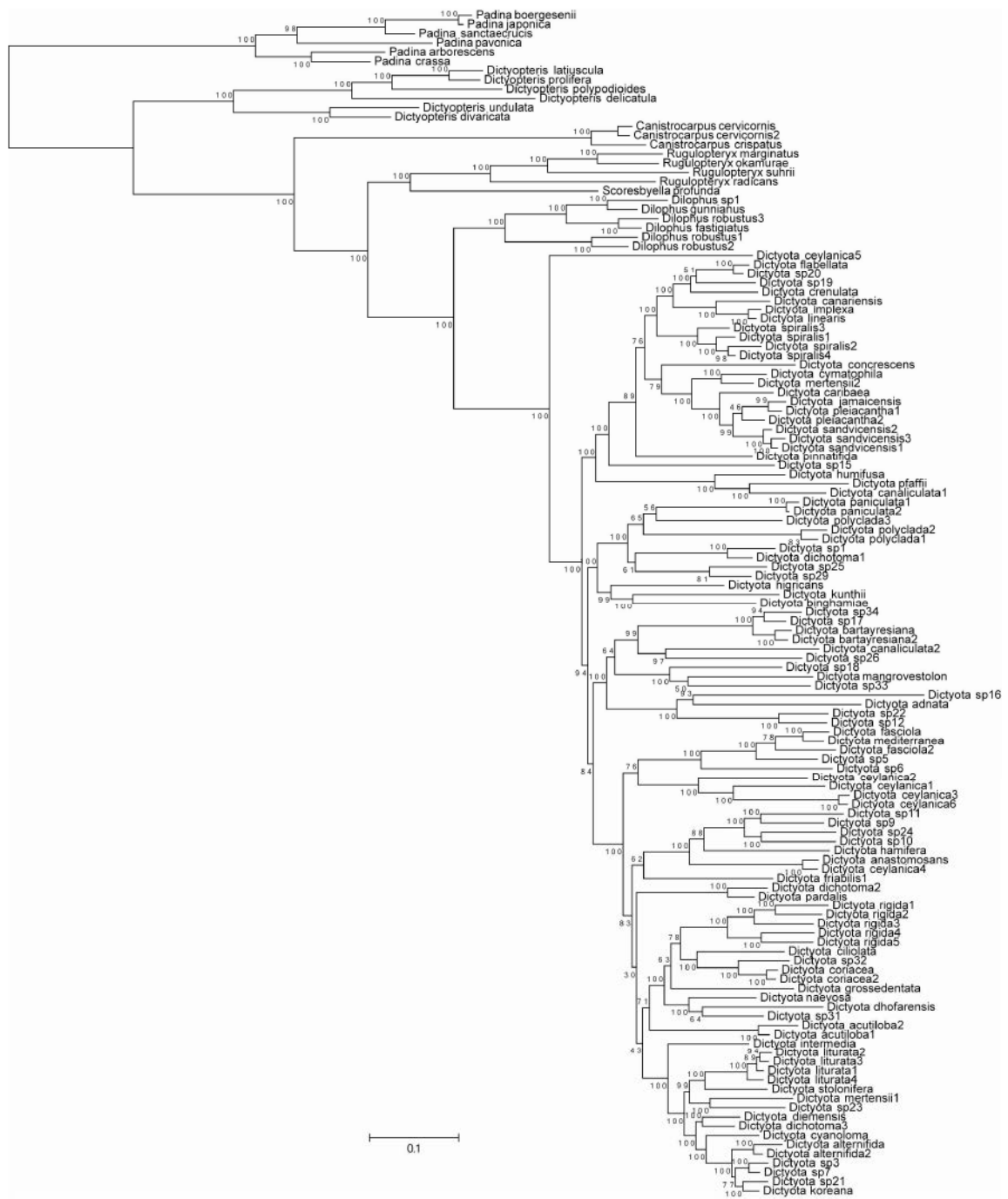
**Figure S1.2:** Bayesian consensus phylogeny based on the combined dataset of eight genes. Numbers at nodes indicate BI posterior probabilities (as percentages).

4. Diversification analyses

Step 1:

A lineage through time plot was developed with the 'APE' package in R (Paradis et al., 2004).

Step2:

We used LASER (Rabosky, 2006) to detect temporal variation in diversification rates on the consensus Dictyota phylogeny. We evaluated the fit of the temporal pattern of lineage diversification in Dictyota to a set of rate-constant and rate-variable models:

1. Pure birth model (Yule)
2. Birth-death model
3. Density-dependent model (exponential)
4. Density-dependent model (linear)
5. Yule-2-rate model
6. Yule-3-rate model

The Akaike Information Criterion (AIC) is used for to select among the different models of diversification. The model with the lowest AIC is taken to be the model that best approximates the data. Results are shown in Table S1.3.

Step 3:

In addition to step two, we also made use of a recently published method (Morlon et al., 2011) to estimate diversity dynamics from phylogenies. Morlon presented an approach that provides estimates of present-day diversification rates and how these rates vary across lineages. The Dictyota phylogeny was subdivided in clades similar as in figure 1. All nine models were fit each of these clades. Results are shown in Table S1.4.

Table S1.3: Results of fitting rate-constant and rate-variable birth–death models to the empirical *Dictyota* consensus tree (Rabosky, 2006). The best scoring rate-constant model (pink) is a pure birth model. We notice an extinction fraction of 0 (green) when fitting a birth-death model. The best model overall is a yule-3-rate model (blue) with diversification shifts at 33.8 and 3 million years ago. (Legend: np = number of parameters; r1,r2,r3 = net diversification rates; st1,st2 = shift times; a = extinction fraction; $x_p$ = parameter from the ddx model; k = parameter from the DDL model)

| model | np | type | lnL | AIC | $r_1$ | $r_2$ | $r_3$ | $st_1$ | $st_2$ | a | $x_p$ | k |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| pure birth | 1 | constant | -73.04 | 148.07 | 0.033 | — | — | — | — | — | — | — |
| birth–death | 2 | constant | -73.04 | 150.07 | 0.033 | — | — | — | — | 0.000 | — | — |
| density-dependent (DDX) | 2 | variable | -56.06 | 116.11 | 0.519 | — | — | — | — | — | 0.702 | — |
| density-dependent (DDL) | 2 | variable | -56.37 | 116.74 | 0.080 | — | — | — | — | — | — | 116.65 |
| yule2rates | 3 | variable | -57.27 | 120.54 | 0.075 | 0.023 | — | 33.79 | — | — | — | — |
| yule3rates | 5 | variable | -52.90 | 115.80 | 0.075 | 0.026 | 0.003 | 33.79 | 2.96 | — | — | — |

Table S1.4: A survey of 9 models of diversification (Morlon *et al.*, 2011) clearly indicates that speciation-only models are the most appropriate for all major clades in Fig 1 (based on the AICc values tabulated here, best-scoring models indicated in blue). When models with variable birth rates were preferred (clades 4,5,8,9), parameter estimates indicated decreasing birth rates through time as also suggested by the results in Table S1.3 above.

| model category | model | clade 2 | clade 4 | clade 5 | clade 6 | clade 7 | clade 8 | clade 9 |
|---|---|---|---|---|---|---|---|---|
| speciation only | B constant | 23.28 | 179.76 | 24.69 | 75.37 | 32.16 | 76.84 | 433.37 |
| | B variable E | 29.66 | 177.90 | 27.15 | 75.75 | 35.03 | 75.50 | 414.50 |
| | B variable L | 28.84 | 177.69 | 23.71 | 76.32 | 34.44 | 76.37 | 416.11 |
| | BD constant | 29.95 | 181.96 | 31.36 | 77.96 | 36.36 | 79.43 | 435.45 |
| | B variable E, D constant | 49.66 | 180.21 | 44.70 | 77.32 | 42.03 | 77.46 | 416.49 |
| speciation and extinction | B variable L, D constant | 48.84 | 179.64 | 44.66 | 77.04 | 41.42 | 76.48 | 414.86 |
| | B constant, D variable E | 49.95 | 184.28 | 51.36 | 80.95 | 43.36 | 82.42 | 437.57 |
| | B constant, D variable L | 49.92 | 180.34 | 44.64 | 79.90 | 41.78 | 81.30 | 420.03 |
| | B variable E, D variable E | | 182.65 | | 80.80 | 56.03 | 80.90 | 417.83 |

**Figure S1.3: Diversification as a function of the direction of thermal evolution (TE). The majority of movements are from warmer water into colder water (more points on left side of graph). Rates of diversification are clearly higher in clades shifting their niches from warmer to colder habitats, as indicated by the downward trend in the purple points. This trend is not obvious in clades with more conserved niches (orange points) or clades with intermediate levels of niche evolution (black points). The direction of the thermal niche shift was quantified by subtracting the average SST of contemporary species in the clade from the estimated SST at the ancestral node of the clade in question (dSST). While this metric does not capture the full complexity of niche evolution in the clade, it is a good approximation of the global direction of thermal niche evolution.**
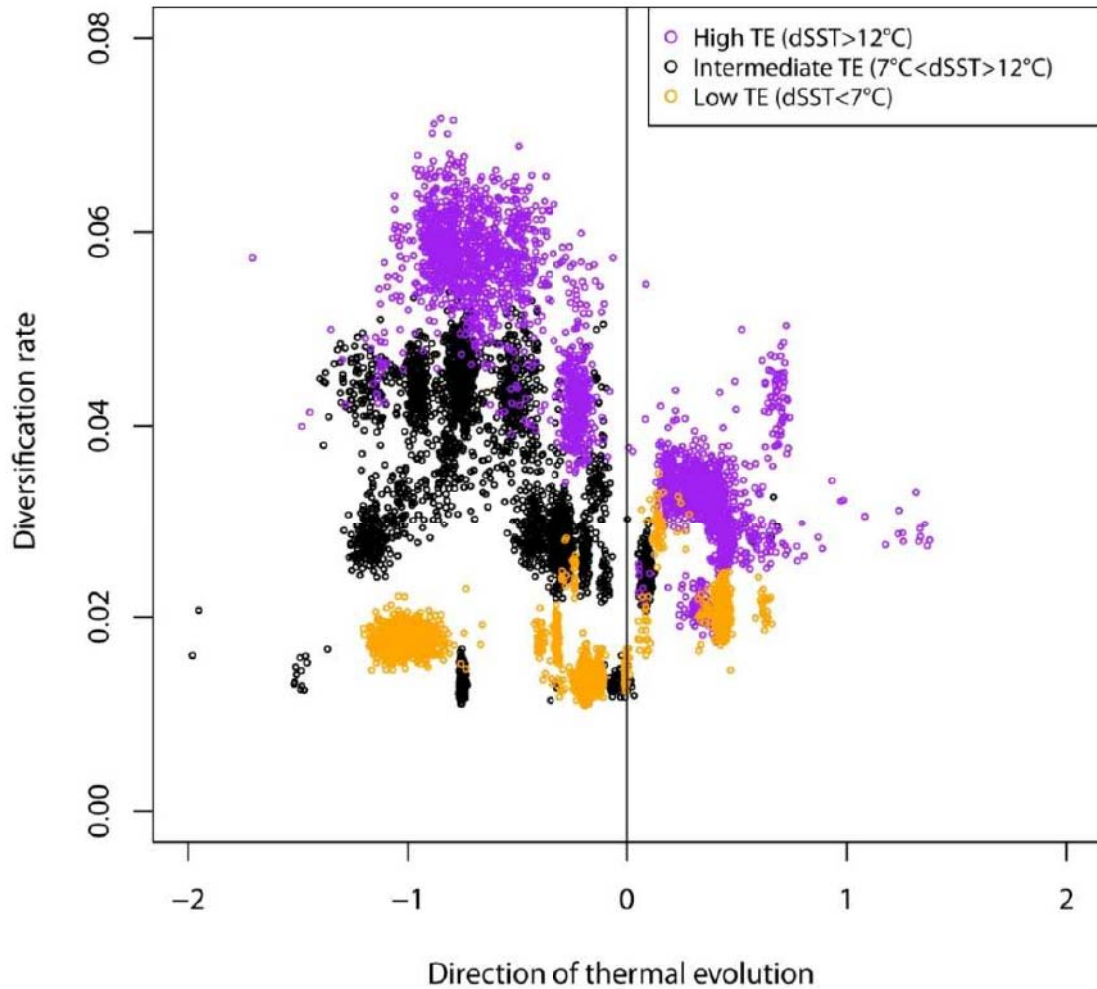
**Figure S1.4: There is no clear trend relating the rate of diversification of clades with conservative niches to the thermal niche of those clades. The regression line $y = -2.3 \ 10^{-4} x + 2.23 \ 10^{-2}$ has an adjusted $R^2$ of 0.057. Conservative clades are defined as above, i.e. its species differ by less than 7°C in average SST.**
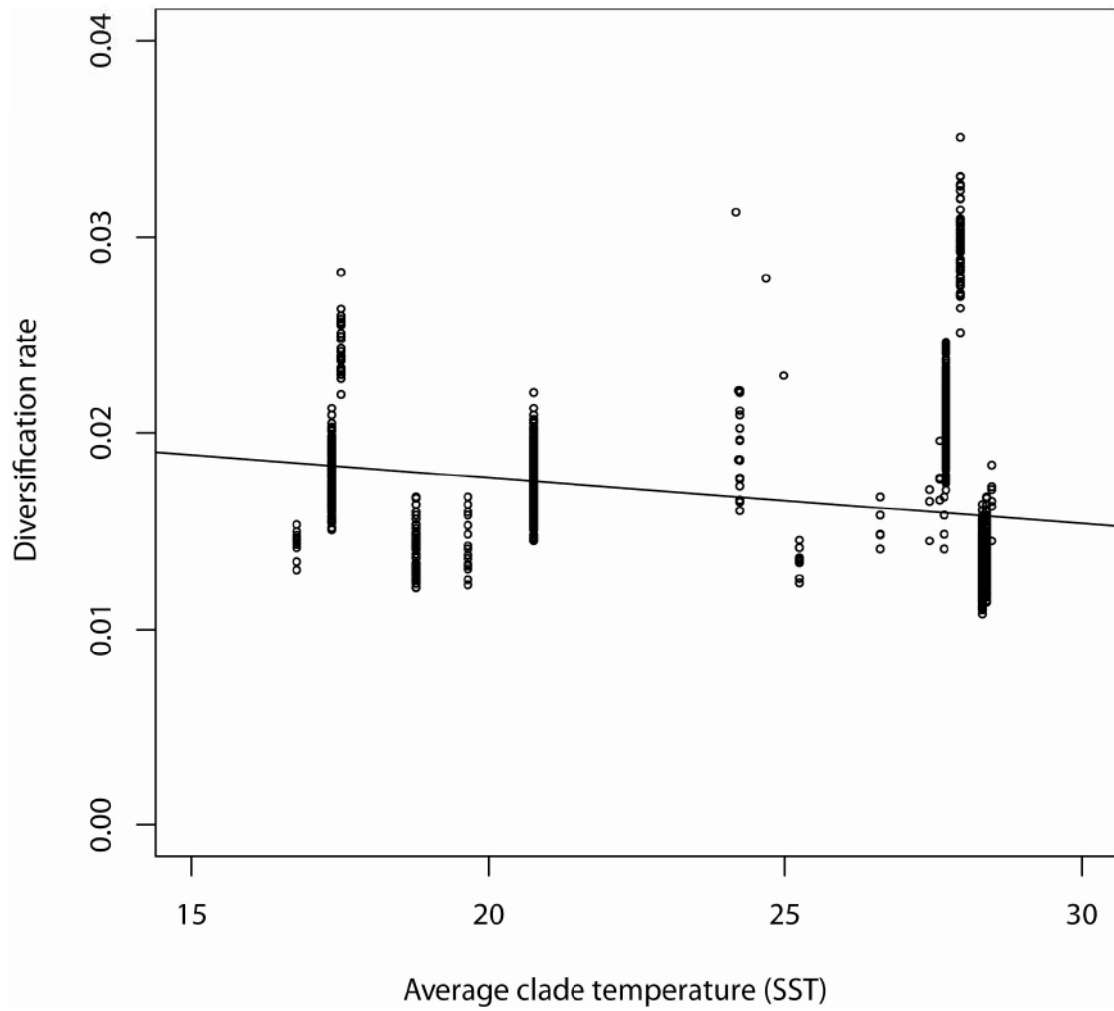
Figure S1.5. Data availability matrix. Graphical representation of the concatenated alignment, showing the availability of sequence data. The color of column and row headers indicate the amount of data available for that column or row. Green indicates high data availability, red indicates low data availability, and yellow/orange represents intermediate data availability.

| TAXA | 18S | 26S | cox1 | cox3 | nad1 | psaA | psbA | rbcL |
|---|---|---|---|---|---|---|---|---|
| Canistrocarpus cervicornis | | GenBank: XX<br>strain: D192<br>length: 1197 nt | GenBank: XX<br>strain: GWS025739<br>length: 657 nt | | GenBank: GQ425184<br>strain: D192<br>length: 729 nt | GenBank: XX<br>strain: HV711<br>length: 1436 nt | GenBank: XX<br>strain: NR26-20-07<br>length: 969 nt | GenBank: XX<br>strain: DAP031<br>length: 1341 nt |
| Canistrocarpus cervicornis2 | | | GenBank: XX<br>strain: GWS024405<br>length: 660 nt | | | | | |
| Canistrocarpus crispatus | | GenBank: GQ425150<br>strain: HV721<br>length: 1182 nt | GenBank: GQ425137<br>strain: ODC1444<br>length: 610 nt | GenBank: GQ425146<br>strain: ODC1444<br>length: 648 nt | GenBank: GQ425176<br>strain: ODC1444<br>length: 734 nt | GenBank: XX<br>strain: HV721<br>length: 1433 nt | GenBank: XX<br>strain: NR11a-01-12<br>length: 959 nt | GenBank:<br>GQ425119<br>strain: HV721<br>length: 1298 nt |
| Dictyopteris delicatula | | | | | | GenBank: EU579898<br>strain: LBC37<br>length: 1438 nt | GenBank: XX<br>strain: XX<br>length: 813 nt | GenBank:<br>EU579943<br>strain: Bit.LBC82<br>length: 1096 nt |
| Dictyopteris divaricata | GenBank: AB087112<br>strain: XX<br>length: 1806 nt | | | | | GenBank: AY422600<br>strain: IK44<br>length: 1532 nt | GenBank: AY430343<br>strain: Lee.WJ10<br>length: 870 nt | GenBank:<br>AY422676<br>strain: Lee.IK44<br>length: 1293 nt |
| Dictyopteris latiuscula | | | | | | GenBank: AY422601<br>strain: IK52<br>length: 1532 nt | GenBank: AY430349<br>strain: Lee.WJ11<br>length: 870 nt | GenBank:<br>AY422677<br>strain: Lee.IK52<br>length: 1293 nt |
| Dictyopteris polypodioides | GenBank: AB095293<br>strain: XX<br>length: 1805 nt | GenBank: DQ472097<br>strain: ODC1031<br>length: 1108 nt | GenBank: EU681404<br>strain: Sil.FRA0513<br>length: 639 nt | GenBank: EU681445<br>strain: Sil.FRA0533<br>length: 654 nt | | GenBank: EU579899<br>strain: LBC38<br>length: 1488 nt | GenBank: EU681639<br>strain: Sil.FRA0513<br>length: 845 nt | GenBank:<br>EU579932<br>strain: Bit.LBC71<br>length: 1272 nt |
| Dictyopteris prolifera | GenBank: AB087114<br>strain: XX<br>length: 1810 nt | | | | | GenBank: AY422602<br>strain: IK50<br>length: 1532 nt | GenBank: AY430346<br>strain: Lee.WJ15<br>length: 870 nt | GenBank:<br>AY422678<br>strain: Lee.IK50<br>length: 1293 nt |
| Dictyopteris undulata | GenBank: AB087115<br>strain: XX<br>length: 1806 nt | | | | | GenBank: AY528446<br>strain: IK55<br>length: 1519 nt | GenBank: AY430353<br>strain: Lee.WJ14<br>length: 870 nt | GenBank:<br>AY430333<br>strain: Lee.WJ12<br>length: 1293 nt |
| Dictyota acutiloba1 | | GenBank: DQ472111<br>strain: ODC888<br>length: 1176 nt | GenBank: GU290238<br>strain: ODC888<br>length: 605 nt | | GenBank: XX<br>strain: JAP047<br>length: 744 nt | GenBank: XX<br>strain: ODC888<br>length: 1424 nt | GenBank: XX<br>strain: LT0379<br>length: 969 nt | GenBank:<br>DQ472056<br>strain: ODC888<br>length: 1162 nt |

| Species | | | | | | | |
|---|---|---|---|---|---|---|---|
| Dictyota acutiloba2 | GenBank: XX<br>strain: LT0324<br>length: 1130 nt | | | GenBank: XX<br>strain: LT0316<br>length: 744 nt | GenBank: XX<br>strain: LT0316<br>length: 1485 nt | GenBank: XX<br>strain: LT0316<br>length: 969 nt | GenBank: XX<br>strain: LT0316<br>length: 1060 nt |
| Dictyota adnata | GenBank: GQ425154<br>strain: ODC1485<br>length: 1062 nt | GenBank: XX<br>strain: ODC1485<br>length: 583 nt | GenBank: XX<br>strain: ODC1485<br>length: 654 nt | GenBank: GQ425178<br>strain: ODC1485<br>length: 714 nt | | GenBank: XX<br>strain: SD712204<br>length: 882 nt | GenBank:<br>GQ425106<br>strain: SD712204<br>length: 1234 nt |
| Dictyota alternifida | GenBank: XX<br>strain: LT0051<br>length: 580 nt | GenBank: XX<br>strain: LT0051<br>length: 494 nt | GenBank: XX<br>strain: LT0051<br>length: 652 nt | GenBank: XX<br>strain: LT0052<br>length: 738 nt | GenBank: AY422586<br>strain: NS1<br>length: 1532 nt | GenBank: XX<br>strain: LT0052<br>length: 967 nt | GenBank:<br>AY422662<br>strain: XX<br>length: 1427 nt |
| Dictyota alternifida2 | | | | | | GenBank: XX<br>strain: HV2341<br>length: 967 nt | |
| Dictyota anastomosans | GenBank: XX<br>strain: HV1949<br>length: 1103 nt | | GenBank: XX<br>strain: HV1949<br>length: 654 nt | GenBank: XX<br>strain: HV1949<br>length: 744 nt | | GenBank: XX<br>strain: HV1949<br>length: 969 nt | GenBank: XX<br>strain: HV1949<br>length: 1229 nt |
| Dictyota bartayresiana | GenBank: GQ425153<br>strain: DR7<br>length: 1106 nt | GenBank: GQ425129<br>strain: DR7<br>length: 617 nt | GenBank: XX<br>strain: ODC1513<br>length: 648 nt | GenBank: GQ425183<br>strain: ODC1513<br>length: 738 nt | | GenBank: XX<br>strain: D1701<br>length: 969 nt | GenBank:<br>GQ425107<br>strain: ODC1588<br>length: 1280 nt |
| Dictyota bartayresiana2 | | GenBank: XX<br>strain: NVT133<br>length: 608 nt | | | | GenBank: XX<br>strain: JAP028<br>length: 961 nt | |
| Dictyota binghamiae | GenBank: XX<br>strain: Lane<br>length: 1183 nt | GenBank: FJ409139<br>strain: XX<br>length: 657 nt | | | | GenBank: XX<br>strain: HV1542<br>length: 871 nt | GenBank: XX<br>strain: HV1801<br>length: 1129 nt |
| Dictyota canaliculata1 | GenBank: GQ425167<br>strain: SD712709<br>length: 1105 nt | GenBank: GQ425132<br>strain: ODC1477<br>length: 639 nt | GenBank: XX<br>strain: ODC1477<br>length: 654 nt | GenBank: GQ425177<br>strain: ODC1477<br>length: 733 nt | | GenBank: GQ425190<br>strain: ODC1477<br>length: 824 nt | GenBank:<br>GQ425108<br>strain: SD712709<br>length: 1284 nt |
| Dictyota canaliculata2 | GenBank: DQ472117<br>strain: HV678<br>length: 1175 nt | GenBank: XX<br>strain: SD712656<br>length: 617 nt | GenBank: XX<br>strain: SD712656<br>length: 648 nt | GenBank: XX<br>strain: SD712656<br>length: 738 nt | GenBank: XX<br>strain: HV678<br>length: 880 nt | GenBank: XX<br>strain: D1552<br>length: 969 nt | GenBank:<br>DQ472062<br>strain: HV678<br>length: 1300 nt |
| Dictyota canariensis | GenBank: XX<br>strain: D504<br>length: 987 nt | GenBank: XX<br>strain: D319<br>length: 632 nt | GenBank: XX<br>strain: D319<br>length: 654 nt | GenBank: XX<br>strain: D319<br>length: 735 nt | | GenBank: XX<br>strain: D1559<br>length: 969 nt | GenBank: XX<br>strain: D504<br>length: 1276 nt |
| Dictyota caribaea | GenBank: DQ472116<br>strain: HV926<br>length: 1162 nt | GenBank: XX<br>strain: HV926<br>length: 633 nt | GenBank: XX<br>strain: HV926<br>length: 653 nt | GenBank: XX<br>strain: HV926<br>length: 738 nt | | GenBank: XX<br>strain: D630<br>length: 805 nt | GenBank:<br>DQ472061<br>strain: HV926<br>length: 1079 nt |
| Dictyota ceylanica1 | GenBank: GQ425152<br>strain: HV214a<br>length: 1173 nt | GenBank: GQ425122<br>strain: HV214a<br>length: 621 nt | | GenBank: GQ425175<br>strain: ODC1442<br>length: 709 nt | | GenBank: XX<br>strain: NR15-05-03<br>length: 969 nt | GenBank:<br>DQ472067<br>strain: HV214a<br>length: 1328 nt |
| Dictyota ceylanica2 | GenBank: XX | GenBank: XX | GenBank: XX | GenBank: XX | | GenBank: XX | GenBank: XX |

Note: This page contains a single large table rotated 90°. Species names appear as row labels (colored cells). The table is transcribed below with species as rows and the sequence/marker data as columns. Each data cell gives GenBank accession, strain, and sequence length.

| Species | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Dictyota ceylanica3** | GenBank: XX strain: TZ0713 length: 1280 nt | strain: D629 length: 875 nt | | strain: RC153 length: 733 nt | strain: D629 length: 538 nt | strain: RC153 length: 609 nt | strain: D629 length: 1061 nt |
| | strain: D629 length: 576 nt | | | | | | |
| **Dictyota ceylanica4** | GenBank: XX strain: ODC1624 length: 1281 nt | GenBank: XX strain: HV1891 length: 969 nt | | GenBank: XX strain: TZ0713 length: 731 nt | GenBank: XX strain: FG31.5.9.2.13 length: 583 nt | GenBank: XX strain: TZ0713 length: 636 nt | GenBank: XX strain: SD712460 length: 1031 nt |
| | | | | | | GenBank: XX strain: MAD0143 length: 608 nt | |
| **Dictyota ceylanica5** | GenBank: XX strain: ODC1662 length: 1256 nt | GenBank: XX strain: CMX219 length: 964 nt | GenBank: XX strain: ODC1662 length: 1470 nt | GenBank: XX strain: TZ0173 length: 744 nt | GenBank: XX strain: TZ0173 length: 654 nt | GenBank: XX strain: TZ0173 length: 604 nt | GenBank: XX strain: HV713 length: 1181 nt |
| **Dictyota ceylanica6** | | | | | | GenBank: XX strain: GWS023931 length: 657 nt | |
| **Dictyota ciliolata** | GenBank: GQ425109 strain: D191 length: 1317 nt | GenBank: XX strain: RD90067 length: 969 nt | GenBank: XX strain: TC2 length: 1484 nt | GenBank: GQ425173 strain: D191 length: 744 nt | | GenBank: GQ425124 strain: HV632 length: 626 nt | GenBank: XX strain: HV723 length: 1183 nt |
| **Dictyota concrescens** | | GenBank: XX strain: CFMX318 length: 964 nt | | | | | |
| **Dictyota coriacea** | GenBank: DQ472054 strain: CSUF003 length: 1223 nt | GenBank: XX strain: HV1810 length: 867 nt | | GenBank: GU290251 strain: CSUF003 length: 735 nt | | GenBank: GU290234 strain: CSUF003 length: 621 nt | GenBank: DQ472109 strain: CSUF003 length: 1168 nt |
| **Dictyota coriacea2** | GenBank: AY422651 strain: WI length: 1427 nt | GenBank: XX strain: HV1940 length: 969 nt | GenBank: AY748318 strain: JALee11 length: 1566 nt | | GenBank: XX strain: HV1940 length: 654 nt | GenBank: HQ990529 strain: GWS018356 length: 654 nt | |
| **Dictyota crenulata** | GenBank: GU290253 strain: HV1074 length: 1280 nt | GenBank: XX strain: CMX393 length: 969 nt | GenBank: XX strain: MX0208 length: 1466 nt | GenBank: GU290252 strain: HV1074 length: 733 nt | GenBank: XX strain: MX0208 length: 643 nt | GenBank: XX strain: MX0208 length: 590 nt | GenBank: GU290231 strain: HV1074 length: 1006 nt |
| **Dictyota cyanoloma** | GenBank: XX strain: D544 length: 1284 nt | GenBank: XX strain: D1567 length: 969 nt | GenBank: XX strain: D502 length: 1486 nt | GenBank: XX strain: D544 length: 734 nt | GenBank: XX strain: D544 length: 654 nt | GenBank: XX strain: GWS016003 length: 660 nt | GenBank: XX strain: D502 length: 1020 nt |
| **Dictyota cymatophila** | GenBank: GQ425111 strain: D397 length: 1136 nt | GenBank: XX strain: D696 length: 842 nt | GenBank: XX strain: D403 length: 1460 nt | GenBank: GQ425179 strain: D403 length: 738 nt | GenBank: XX strain: D306 length: 643 nt | GenBank: GQ425128 strain: D406 length: 622 nt | GenBank: GQ425162 strain: D397 length: 1023 nt |
| **Dictyota dhofarensis** | GenBank: XX strain: DHO0163 length: 782 nt | GenBank: XX strain: DHO0163 length: 752 nt | | GenBank: XX strain: DHO0163 length: 738 nt | | GenBank: XX strain: DHO0163 length: 603 nt | GenBank: DQ472127 strain: DHO0163 length: 1180 nt |
| **Dictyota dichotoma1** | GenBank: AY527200 strain: IK81 length: 1428 nt | GenBank: XX strain: RSAD204 length: 969 nt | GenBank: AY528450 strain: IK81 length: 1519 nt | GenBank: AY500368 strain: Genbank length: 744 nt | GenBank: AY500368 strain: Genbank length: 654 nt | GenBank: XX strain: F5244 length: 642 nt | GenBank: GQ425155 strain: D190 length: 1192 nt |

| Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Dictyota dichotoma2 | GenBank: AF350227 strain: 1CH length: 1776 nt | | GenBank: XX strain: HV1890 length: 600 nt | GenBank: XX strain: HV1890 length: 591 nt | GenBank: XX strain: HV1890 length: 733 nt | GenBank: AY748316 strain: JALee05 length: 1566 nt | GenBank: XX strain: HV1941 length: 969 nt | GenBank: AY422669 strain: IK14 length: 1427 nt |
| Dictyota dichotoma3 | | GenBank: XX strain: HV2252 length: 1132 nt | GenBank: XX strain: GWS015099 length: 660 nt | GenBank: XX strain: LT0172 length: 654 nt | GenBank: XX strain: LT0103 length: 733 nt | GenBank: XX strain: LT0103 length: 1062 nt | GenBank: XX strain: LT0172 length: 969 nt | GenBank: XX strain: LT0172 length: 1170 nt |
| Dictyota diemensis | | GenBank: XX strain: LT0108 length: 989 nt | GenBank: HM891273 strain: GWS015568 length: 657 nt | GenBank: XX strain: LT0108 length: 645 nt | GenBank: XX strain: HV2368 length: 733 nt | GenBank: XX strain: HV2368 length: 1476 nt | GenBank: XX strain: HV2350 length: 969 nt | GenBank: XX strain: HV2368 length: 1216 nt |
| Dictyota fasciola | | GenBank: GQ425166 strain: ODC1057 length: 1143 nt | GenBank: GQ425133 strain: ODC1065 length: 639 nt | GenBank: GQ425143 strain: ODC1065 length: 654 nt | GenBank: GQ425172 strain: ODC1065 length: 737 nt | GenBank: XX strain: ODC1065 length: 1486 nt | GenBank: XX strain: D1565 length: 969 nt | GenBank: GQ425110 strain: ODC1065 length: 1291 nt |
| Dictyota fasciola2 | | | | | | | GenBank: XX strain: ODC2027 length: 962 nt | |
| Dictyota flabellata | | GenBank: XX strain: HV1562 length: 1106 nt | GenBank: XX strain: HV1654 length: 604 nt | | GenBank: XX strain: HV1564 length: 744 nt | GenBank: XX strain: HV1655 length: 1475 nt | GenBank: XX strain: HV1560 length: 873 nt | GenBank: XX strain: TACO16 length: 1191 nt |
| Dictyota friabilis1 | | GenBank: DQ472120 strain: ODC898 length: 1177 nt | GenBank: GU290237 strain: DML67250 length: 533 nt | GenBank: GU290244 strain: ODC898 length: 652 nt | GenBank: GU290249 strain: ODC898 length: 738 nt | GenBank: XX strain: ODC898 length: 1428 nt | GenBank: XX strain: ODC898 length: 866 nt | GenBank: DQ472064 strain: HV153 length: 1328 nt |
| Dictyota grossedentata | | GenBank: XX strain: TZ0490 length: 853 nt | GenBank: XX strain: TZ0490 length: 639 nt | GenBank: XX strain: TZ0490 length: 615 nt | GenBank: XX strain: TZ0490 length: 737 nt | | GenBank: XX strain: C29-1-23 length: 969 nt | GenBank: XX strain: TZ0490 length: 1304 nt |
| Dictyota hamifera | | GenBank: DQ472110 strain: HV222 length: 1181 nt | GenBank: GQ425123 strain: HV222 length: 616 nt | GenBank: GQ425141 strain: HV222 length: 654 nt | GenBank: GQ425169 strain: HV222 length: 701 nt | | GenBank: XX strain: FS887 length: 958 nt | GenBank: GQ425112 strain: DML67438 length: 1266 nt |
| Dictyota humifusa | | GenBank: XX strain: SD712066 length: 1025 nt | GenBank: XX strain: ODC1659 length: 642 nt | GenBank: XX strain: SD712066 length: 597 nt | GenBank: XX strain: ODC1659 length: 701 nt | GenBank: XX strain: MX0198 length: 1472 nt | GenBank: XX strain: CFR858 length: 969 nt | GenBank: XX strain: SD712066 length: 1293 nt |
| Dictyota implexa | | GenBank: GQ425163 strain: ODC1238 length: 1179 nt | GenBank: GQ425135 strain: FS271 length: 642 nt | GenBank: GQ425140 strain: LLGO249 length: 654 nt | GenBank: GQ425168 strain: LLGO300 length: 738 nt | GenBank: XX strain: LLGO249 length: 790 nt | GenBank: XX strain: ODC2157 length: 962 nt | GenBank: GQ425116 strain: Kooistra1 length: 1330 nt |
| Dictyota intermedia | | | GenBank: XX strain: GWS022767 length: 657 nt | GenBank: XX strain: LT0063 length: 570 nt | GenBank: XX strain: TC1 length: 725 nt | GenBank: XX strain: LT0063 length: 1471 nt | GenBank: XX strain: LT0063 length: 969 nt | GenBank: DQ472086 strain: TC1 length: 1207 nt |
| Dictyota jamaicensis | | | GenBank: XX strain: DR27 length: 633 nt | | GenBank: XX strain: DR27 length: 738 nt | | GenBank: XX strain: FS881 length: 954 nt | |
| Dictyota koreana | GenBank: AB090387 | GenBank: HV1978 | | GenBank: XX | GenBank: XX | GenBank: AY422591 | GenBank: XX | GenBank: AY422665 |

| Species | strain: SZKIZ067 length: 1812 nt | strain: HV1978 length: 1125 nt | GenBank: GU290237 | strain: HV1894 654 nt | strain: HV1894 733 nt | strain: IK23 1532 nt | strain: SGAD0909027 969 nt | strain: IK21 1427 nt |
|---|---|---|---|---|---|---|---|---|
| Dictyota kunthii | | GenBank: GU290231 strain: D104 length: 1172 nt | strain: D102 length: 598 nt | GenBank: GU290245 strain: D102 length: 620 nt | GenBank: GU290250 strain: D102 length: 738 nt | GenBank: XX strain: D102 length: 1427 nt | GenBank: EU395618 strain: D102 length: 766 nt | GenBank: DQ472057 strain: D102 length: 1253 nt |
| Dictyota linearis | | GenBank: XX strain: ODC1254 length: 1179 nt | GenBank: XX strain: FS335 length: 633 nt | GenBank: XX strain: ODC1254 length: 654 nt | GenBank: XX strain: D391 length: 738 nt | GenBank: XX strain: ODC1254 length: 1460 nt | GenBank: XX strain: ODC2026 length: 962 nt | GenBank: XX strain: ODC1254 length: 1266 nt |
| Dictyota liturata1 | | GenBank: XX strain: HEC15721 length: 604 nt | GenBank: XX strain: HEC15816 length: 607 nt | | GenBank: GQ425174 strain: HEC15721 length: 736 nt | GenBank: XX strain: HEC15721 length: 1452 nt | GenBank: XX strain: FS892 length: 964 nt | GenBank: XX strain: HEC15721 length: 1212 nt |
| Dictyota liturata2 | | GenBank: GQ425159 strain: KZN2282 length: 1185 nt | GenBank: XX strain: MAD0142 length: 605 nt | | | | GenBank: XX strain: FG31.5.9.2.7 length: 969 nt | GenBank: XX strain: KZN2282 length: 1265 nt |
| Dictyota liturata3 | | | GenBank: XX strain: HV2768 length: 608 nt | | | | GenBank: XX strain: JH88425 length: 955 nt | GenBank: GQ425113 strain: Sole1 length: 1313 nt |
| Dictyota liturata4 | | | GenBank: XX strain: GWS023781 length: 657 nt | | | | | |
| Dictyota mangrovestolon | | GenBank: XX strain: ODC1486 length: 976 nt | GenBank: XX strain: ODC1486 length: 632 nt | GenBank: XX strain: ODC1486 length: 643 nt | GenBank: XX strain: ODC1486 length: 744 nt | | GenBank: XX strain: ODC1486 length: 860 nt | GenBank: XX strain: ODC1486 length: 1225 nt |
| Dictyota mediterranea | | GenBank: GU290233 strain: SGAD1116 length: 1178 nt | GenBank: XX strain: LLGO313 length: 612 nt | GenBank: XX strain: LLGO224 length: 646 nt | GenBank: XX strain: LLGO313 length: 744 nt | | GenBank: XX strain: ODC2066 length: 962 nt | GenBank: GU290254 strain: D595 length: 1247 nt |
| Dictyota mertensii1 | | GenBank: XX strain: HV924 length: 666 nt | GenBank: XX strain: DR30 length: 590 nt | | GenBank: XX strain: HV924 length: 719 nt | GenBank: XX strain: D628 length: 1447 nt | GenBank: XX strain: HV924 length: 879 nt | GenBank: DQ472060 strain: HV924 length: 1318 nt |
| Dictyota mertensii2 | | GenBank: GQ425158 strain: HV911 length: 1178 nt | GenBank: GQ425130 strain: DR31 length: 607 nt | GenBank: XX strain: HV911 length: 587 nt | GenBank: GQ425180 strain: DR31 length: 724 nt | GenBank: XX strain: HV911 length: 1483 nt | GenBank: GQ425215 strain: DR31 length: 834 nt | GenBank: GQ425114 strain: DR32 length: 1096 nt |
| Dictyota naevosa | | GenBank: DQ472108 strain: KZNb2345 length: 595 nt | GenBank: XX strain: KZNb2345 length: 600 nt | GenBank: XX strain: KZNb2345 length: 560 nt | GenBank: XX strain: KZNb2345 length: 726 nt | GenBank: XX strain: D659 length: 1386 nt | GenBank: XX strain: RSAD482 length: 969 nt | GenBank: DQ472084 strain: KZN2241 length: 1199 nt |
| Dictyota nigricans | | GenBank: XX strain: HV2583 length: 1073 nt | GenBank: XX strain: D92 length: 600 nt | | GenBank: XX strain: D92 length: 729 nt | | GenBank: XX strain: HV2583 length: 969 nt | GenBank: DQ472077 strain: D92 length: 1328 nt |
| Dictyota paniculata1 | | GenBank: XX strain: LT0366 | GenBank: XX strain: GWS024729 | GenBank: XX strain: D97 | GenBank: XX strain: D97 | | GenBank: XX strain: LT0354 | GenBank: DQ472082 strain: D97 |

| Species | length: 1044 nt | length: 660 nt | length: 654 nt | length: 735 nt | | length: 969 nt | length: 752 nt |
|---|---|---|---|---|---|---|---|
| Dictyota paniculata2 | | GenBank: XX strain: GWS016687 length: 660 nt | | | | GenBank: XX strain: HV2331 length: 969 nt | |
| Dictyota pardalis | | | | | GenBank: AY422596 strain: IK26N length: 1532 nt | GenBank: AY422633 strain: IK26 length: 765 nt | GenBank: AY422671 strain: IK26 length: 1427 nt |
| Dictyota pfaffii | GenBank: XX strain: HEC15779 length: 596 nt | GenBank: XX strain: D361 length: 596 nt | GenBank: XX strain: D361 length: 642 nt | GenBank: XX strain: D361 length: 705 nt | GenBank: XX strain: D361 length: 1234 nt | GenBank: XX strain: FS933 length: 937 nt | GenBank: XX strain: D285 length: 1237 nt |
| Dictyota pinnatifida | GenBank: GQ425157 strain: CLO31302 length: 1171 nt | GenBank: GQ425126 strain: HV902 length: 611 nt | GenBank: GQ425142 strain: HV932 length: 619 nt | GenBank: GQ425171 strain: HV932 length: 744 nt | GenBank: XX strain: HV932 length: 876 nt | GenBank: XX strain: DR4 length: 868 nt | GenBank: GQ425115 strain: Sole3 length: 1317 nt |
| Dictyota pleiacantha1 | GenBank: XX strain: D193 length: 1192 nt | GenBank: XX strain: D404 length: 617 nt | | GenBank: XX strain: D404 length: 738 nt | GenBank: XX strain: D310 length: 870 nt | GenBank: XX strain: D1560 length: 969 nt | GenBank: XX strain: D324 length: 1200 nt |
| Dictyota pleiacantha2 | | | | | | GenBank: XX strain: WNC2009-090 length: 571 nt | |
| Dictyota polyclada1 | GenBank: XX strain: FG79607 length: 1129 nt | | GenBank: XX strain: KD88618 length: 643 nt | GenBank: XX strain: FG79607 length: 744 nt | GenBank: XX strain: HV2282 length: 1463 nt | GenBank: XX strain: HV2282 length: 969 nt | GenBank: DQ472050 strain: GWS0139 length: 1202 nt |
| Dictyota polyclada2 | GenBank: XX strain: LT0317 length: 1122 nt | | GenBank: XX strain: LT0317 length: 561 nt | GenBank: XX strain: LT0317 length: 731 nt | | GenBank: XX strain: LT0317 length: 969 nt | |
| Dictyota polyclada3 | GenBank: XX strain: HV2404 length: 1028 nt | GenBank: XX strain: HV2404 length: 592 nt | GenBank: XX strain: HV2404 length: 583 nt | GenBank: XX strain: HV2404 length: 739 nt | | GenBank: XX strain: HV2404 length: 818 nt | GenBank: XX strain: HV2404 length: 1227 nt |
| Dictyota rigida1 | GenBank: XX strain: ODC1623 length: 1112 nt | GenBank: GQ425138 strain: ODC1657 length: 605 nt | GenBank: XX strain: ODC1623 length: 653 nt | GenBank: GQ425181 strain: ODC1657 length: 721 nt | | GenBank: XX strain: ODC1623 length: 871 nt | GenBank: GQ425117 strain: ODC1623 length: 1280 nt |
| Dictyota rigida2 | | | GenBank: XX strain: HV1948 length: 654 nt | GenBank: XX strain: HV1948 length: 721 nt | | GenBank: XX strain: HV1948 length: 969 nt | |
| Dictyota rigida3 | GenBank: XX strain: HV2556 length: 554 nt | GenBank: XX strain: HV2572 length: 608 nt | GenBank: XX strain: HV2572 length: 654 nt | GenBank: XX strain: HV2556 length: 701 nt | | GenBank: XX strain: HV2556 length: 968 nt | GenBank: XX strain: HV2572 length: 1217 nt |
| Dictyota rigida4 | | GenBank: XX strain: MAD2157 length: 598 nt | | | | GenBank: XX strain: RSAD549 length: 969 nt | |
| Dictyota rigida5 | GenBank: GQ425164 strain: TCn6 | GenBank: XX strain: TCn6 | GenBank: XX strain: TCn6 | GenBank: XX strain: TCn6 | | | GenBank: XX strain: TCn6 |

| Species | length: 1175 nt | length: 479 nt | length: 643 nt | length: 737 nt | | | length: 1189 nt |
|---|---|---|---|---|---|---|---|
| Dictyota sandvicensis1 | GenBank: DQ472118 / strain: ODC896 / length: 1058 nt | GenBank: GU290239 / strain: ODC896 / length: 604 nt | | GenBank: GU290248 / strain: ODC896 / length: 724 nt | GenBank: XX / strain: ODC896 / length: 1454 nt | GenBank: XX / strain: ODC896 / length: 867 nt | GenBank: DQ472063 / strain: ODC896 / length: 1320 nt |
| Dictyota sandvicensis2 | GenBank: XX / strain: KD88671 / length: 1123 nt | GenBank: XX / strain: GWS023922 / length: 657 nt | | GenBank: XX / strain: KD88671 / length: 726 nt | | GenBank: XX / strain: KD88671 / length: 969 nt | GenBank: XX / strain: KD88671 / length: 1217 nt |
| Dictyota sandvicensis3 | GenBank: XX / strain: HV1095 / length: 1180 nt | GenBank: XX / strain: HV1095 / length: 440 nt | | | | | GenBank: XX / strain: HV1095 / length: 1094 nt |
| Dictyota sp1 | GenBank: XX / strain: D323 / length: 568 nt | GenBank: XX / strain: D328 / length: 614 nt | GenBank: XX / strain: D328 / length: 647 nt | GenBank: XX / strain: D323 / length: 744 nt | GenBank: XX / strain: D328 / length: 1308 nt | GenBank: XX / strain: D328 / length: 873 nt | GenBank: XX / strain: D328 / length: 1219 nt |
| Dictyota sp10 | | GenBank: XX / strain: SD712275 / length: 605 nt | GenBank: XX / strain: SD712275 / length: 644 nt | GenBank: XX / strain: SD712275 / length: 710 nt | | GenBank: XX / strain: SD712275 / length: 860 nt | GenBank: XX / strain: SD712275 / length: 1084 nt |
| Dictyota sp11 | GenBank: XX / strain: TZ0327 / length: 750 nt | GenBank: XX / strain: TZ0327 / length: 614 nt | GenBank: XX / strain: TZ0327 / length: 641 nt | GenBank: XX / strain: TZ0327 / length: 744 nt | | GenBank: XX / strain: NR02-10-04 / length: 969 nt | GenBank: XX / strain: TZ0327 / length: 1261 nt |
| Dictyota sp12 | GenBank: XX / strain: SD712079 / length: 988 nt | | GenBank: XX / strain: SD712079 / length: 453 nt | GenBank: XX / strain: SD712079 / length: 738 nt | | GenBank: XX / strain: SD712079 / length: 826 nt | GenBank: XX / strain: SD712079 / length: 1136 nt |
| Dictyota sp15 | GenBank: XX / strain: CLO12603 / length: 556 nt | GenBank: XX / strain: CLO12603 / length: 608 nt | GenBank: XX / strain: SGAD1051 / length: 647 nt | GenBank: XX / strain: DML68137 / length: 741 nt | | GenBank: XX / strain: DML67430 / length: 873 nt | GenBank: XX / strain: DML67430 / length: 1289 nt |
| Dictyota sp16 | GenBank: XX / strain: SD712520 / length: 1088 nt | GenBank: XX / strain: SD712641 / length: 597 nt | GenBank: XX / strain: SD712520 / length: 595 nt | GenBank: XX / strain: SD712641 / length: 735 nt | | GenBank: XX / strain: NR07-25-12 / length: 960 nt | GenBank: XX / strain: SD712520 / length: 1136 nt |
| Dictyota sp17 | GenBank: XX / strain: SD712436 / length: 988 nt | GenBank: XX / strain: SD712436 / length: 599 nt | | GenBank: XX / strain: SD712436 / length: 743 nt | | GenBank: XX / strain: SD712436 / length: 847 nt | |
| Dictyota sp18 | GenBank: XX / strain: D745 / length: 1099 nt | GenBank: XX / strain: D745 / length: 589 nt | GenBank: XX / strain: D745 / length: 642 nt | GenBank: XX / strain: D745 / length: 736 nt | | GenBank: XX / strain: D745 / length: 766 nt | GenBank: XX / strain: D745 / length: 1179 nt |
| Dictyota sp19 | GenBank: XX / strain: MX0335 / length: 1076 nt | GenBank: XX / strain: MX0335 / length: 586 nt | GenBank: XX / strain: MX0335 / length: 643 nt | GenBank: XX / strain: MX0335 / length: 737 nt | | GenBank: XX / strain: CFCR844 / length: 969 nt | GenBank: XX / strain: MX0335 / length: 1227 nt |
| Dictyota sp20 | GenBank: XX / strain: HV1590 / length: 842 nt | GenBank: XX / strain: HV1590 / length: 622 nt | | GenBank: XX / strain: HV1590 / length: 738 nt | GenBank: XX / strain: MX0334 / length: 1439 nt | GenBank: XX / strain: CRNI565 / length: 969 nt | GenBank: XX / strain: HV1590 / length: 1216 nt |
| Dictyota sp21 | GenBank: XX / strain: MX0360 / length: 552 nt | GenBank: XX / strain: MX0360 / length: 606 nt | GenBank: XX / strain: MX0360 / length: 654 nt | GenBank: XX / strain: MX0360 / length: 645 nt | | GenBank: XX / strain: CFMX389 / length: 969 nt | GenBank: XX / strain: MX0360 / length: 1132 nt |
| Dictyota sp22 | GenBank: XX | GenBank: XX | GenBank: XX | GenBank: XX | | GenBank: XX | GenBank: XX |

| Species | Col1 | Col2 | Col3 | Col4 | Col5 | Col6 |
|---|---|---|---|---|---|---|
| | strain: D1694 length: 1127 nt | strain: D1694 length: 451 nt | strain: D1694 length: 649 nt | strain: D1694 length: 739 nt | strain: HV2568 length: 967 nt | strain: D1694 length: 748 nt |
| Dictyota sp23 | GenBank: XX strain: LTO430 length: 556 nt | | | GenBank: XX strain: LTO430 length: 709 nt | GenBank: XX strain: LTO430 length: 969 nt | GenBank: XX strain: LTO430 length: 1221 nt |
| Dictyota sp24 | GenBank: XX strain: JH88416 length: 534 nt | GenBank: XX strain: JH88416 length: 591 nt | GenBank: XX strain: JH88416 length: 654 nt | GenBank: XX strain: JH88416 length: 724 nt | GenBank: XX strain: JH88416 length: 671 nt | GenBank: XX strain: JH88416 length: 679 nt |
| Dictyota sp25 | GenBank: XX strain: LTO347 length: 1003 nt | | GenBank: XX strain: LTO347 length: 649 nt | | GenBank: XX strain: LTO411 length: 969 nt | GenBank: XX strain: LTO347 length: 1222 nt |
| Dictyota sp26 | GenBank: XX strain: KD88202 length: 1093 nt | GenBank: XX strain: KD88202 length: 609 nt | GenBank: XX strain: KD88202 length: 554 nt | | GenBank: XX strain: KD88202 length: 937 nt | GenBank: XX strain: KD88202 length: 789 nt |
| Dictyota sp29 | | | | | GenBank: XX strain: WNC2009-133 length: 950 nt | |
| Dictyota sp3 | GenBank: XX strain: D321 length: 569 nt | GenBank: XX strain: FS562 length: 608 nt | GenBank: XX strain: HEC15817 length: 654 nt | GenBank: XX strain: HEC15817 length: 733 nt | GenBank: XX strain: D505 length: 873 nt | GenBank: XX strain: HEC15817 length: 1168 nt |
| Dictyota sp31 | | GenBank: XX strain: MAD2178 length: 590 nt | | | | |
| Dictyota sp32 | | GenBank: XX strain: GWS018563 length: 660 nt | | | | |
| Dictyota sp33 | | GenBank: XX strain: GWS016917 length: 660 nt | | | | |
| Dictyota sp34 | | GenBank: XX strain: GWS025859 length: 657 nt | | | | |
| Dictyota sp5 | GenBank: XX strain: HEC15763 length: 605 nt | | GenBank: XX strain: HEC15763 length: 653 nt | GenBank: XX strain: HEC15763 length: 737 nt | GenBank: XX strain: HEC15763 length: 853 nt | GenBank: XX strain: HEC15763 length: 1227 nt |
| Dictyota sp6 | | | | | GenBank: XX strain: FS958 length: 954 nt | |
| Dictyota sp7 | GenBank: DQ472121 strain: KZN2308 length: 1055 nt | GenBank: XX strain: D186 length: 616 nt | GenBank: XX strain: D186 length: 641 nt | GenBank: XX strain: KZN2308 length: 729 nt | GenBank: XX strain: KZN2308 length: 871 nt | GenBank: DQ472066 strain: KZN2308 length: 1338 nt |
| Dictyota sp9 | GenBank: XX strain: ODC1552 length: 565 nt | GenBank: XX strain: ODC1552 length: 537 nt | GenBank: XX strain: ODC1552 length: 654 nt | GenBank: XX strain: ODC1552 length: 715 nt | GenBank: XX strain: ODC1552 length: 873 nt | GenBank: XX strain: ODC1552 length: 1066 nt |

| Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Dictyota spiralis1 | GenBank: AB090392, strain: XX, length: 1810 nt | GenBank: GQ425161, strain: ODC1225, length: 1180 nt | GenBank: XX, strain: ODC1029, length: 632 nt | GenBank: XX, strain: ODC1225, length: 654 nt | GenBank: XX, strain: ODC1225, length: 744 nt | | GenBank: XX, strain: FS486, length: 857 nt | GenBank: DQ472074, strain: ODC1029, length: 1344 nt |
| Dictyota spiralis2 | | GenBank: XX, strain: D290, length: 203 nt | GenBank: XX, strain: FS302, length: 633 nt | | | | GenBank: XX, strain: ODC2116, length: 962 nt | GenBank: XX, strain: D290, length: 939 nt |
| Dictyota spiralis3 | | GenBank: XX, strain: ODC1056, length: 1029 nt | GenBank: XX, strain: FS231, length: 633 nt | GenBank: XX, strain: HEC15815, length: 643 nt | GenBank: XX, strain: HEC15815, length: 694 nt | GenBank: XX, strain: HEC15815, length: 657 nt | GenBank: XX, strain: ODC2031, length: 962 nt | GenBank: XX, strain: HEC15815, length: 1234 nt |
| Dictyota spiralis4 | | | GenBank: GU290235, strain: ODC1071, length: 633 nt | GenBank: XX, strain: ODC1071, length: 637 nt | GenBank: XX, strain: ODC1071, length: 733 nt | | | |
| Dictyota stolonifera | | GenBank: GQ425160, strain: TZ0488, length: 841 nt | GenBank: GQ425139, strain: TZ0488, length: 598 nt | GenBank: XX, strain: TZ0488, length: 637 nt | GenBank: GQ425182, strain: TZ0488, length: 740 nt | GenBank: XX, strain: TZ0377, length: 887 nt | GenBank: XX, strain: RD88740, length: 969 nt | GenBank: GQ425118, strain: D264, length: 1267 nt |
| Dilophus fastigiatus | | GenBank: DQ472123, strain: D96, length: 1171 nt | GenBank: XX, strain: KD15-5-09-01-07, length: 590 nt | | GenBank: GQ425170, strain: D96, length: 744 nt | GenBank: XX, strain: D96, length: 1440 nt | GenBank: XX, strain: LT0443, length: 969 nt | GenBank: DQ472068, strain: D96, length: 1196 nt |
| Dilophus gunnianus | | GenBank: XX, strain: D1537, length: 1130 nt | GenBank: HM891296, strain: GWS016245, length: 657 nt | | GenBank: XX, strain: D744, length: 744 nt | | GenBank: XX, strain: D1537, length: 955 nt | GenBank: XX, strain: D744, length: 1231 nt |
| Dilophus robustus1 | | GenBank: XX, strain: HV2604, length: 681 nt | | | | GenBank: XX, strain: HV2497, length: 1371 nt | GenBank: XX, strain: HV2604, length: 969 nt | GenBank: XX, strain: HV2604, length: 1205 nt |
| Dilophus robustus2 | | GenBank: XX, strain: D1702, length: 1129 nt | GenBank: XX, strain: D1702, length: 448 nt | GenBank: XX, strain: D1702, length: 654 nt | GenBank: XX, strain: D1702, length: 269 nt | | GenBank: XX, strain: D1702, length: 969 nt | GenBank: XX, strain: D1702, length: 1215 nt |
| Dilophus robustus3 | | GenBank: XX, strain: ODC1110, length: 1179 nt | GenBank: XX, strain: ODC1108, length: 590 nt | | | GenBank: XX, strain: ODC1100, length: 1465 nt | GenBank: XX, strain: ODC1119, length: 882 nt | GenBank: XX, strain: ODC1120, length: 1153 nt |
| Dilophus sp1 | | | | | | | GenBank: XX, strain: LT0215, length: 685 nt | |
| Padina arborescens | | GenBank: EU579996, strain: Bit.LBC135, length: 314 nt | | GenBank: AB358939, strain: Win2, length: 654 nt | | GenBank: AY430316, strain: IK65, length: 1519 nt | GenBank: AY430357, strain: Lee.IK65, length: 870 nt | GenBank: AB358904, strain: Win2, length: 1238 nt |
| Padina boergesenii | | GenBank: DQ472093, strain: ODC890, length: 978 nt | | | | | | GenBank: DQ472037, strain: ODC890, length: 1183 nt |
| Padina crassa | GenBank: AB095297, strain: XX, length: 1801 nt | | | GenBank: AB358943, strain: Win1, length: 654 nt | | GenBank: AY430318, strain: IK70, length: 1519 nt | GenBank: AY430361, strain: Lee.WJ21, length: 870 nt | |

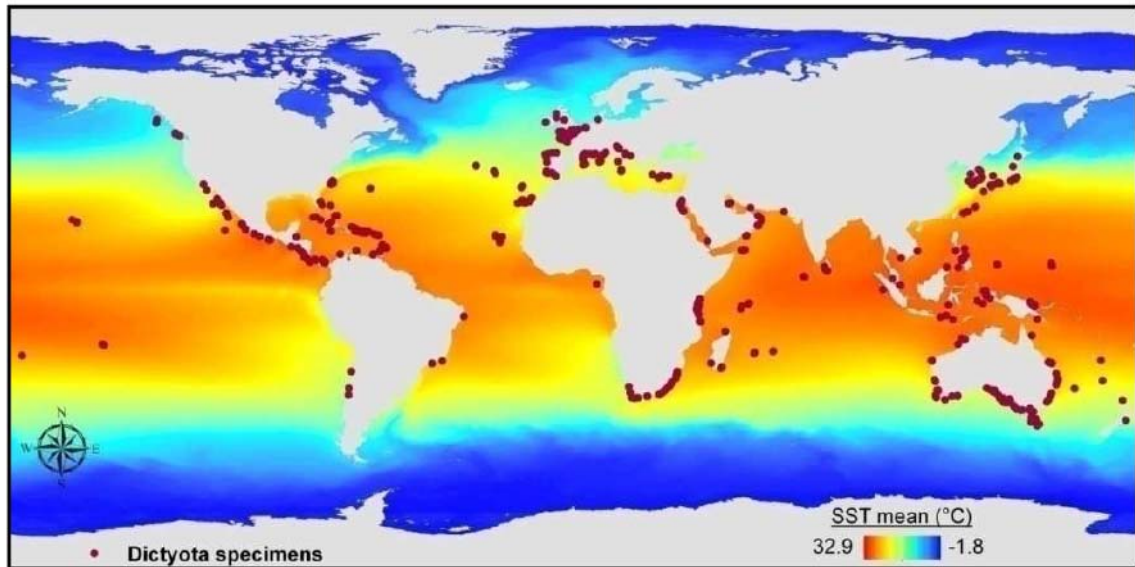| Species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Padina japonica | GenBank: AB095298, strain: XX, length: 1802 nt | | | GenBank: AB358942, strain: Win4, length: 654 nt | | GenBank: AY430319, strain: IK71, length: 1519 nt | GenBank: AY430360, strain: Lee.IK71, length: 870 nt | GenBank: AB358910, strain: Win4, length: 1238 nt |
| Padina pavonica | GenBank: EU580000, strain: Bit.LBC139, length: 386 nt | | | GenBank: EU681454, strain: Sil.FRA0509, length: 654 nt | GenBank: EU681498, strain: Sil.FRA0509, length: 713 nt | GenBank: EU579919, strain: LBC58, length: 1463 nt | GenBank: EU681649, strain: Sil.FRA0509, length: 845 nt | GenBank: EU579961, strain: Bit.LBC100, length: 1194 nt |
| Padina sanctaecrucis | GenBank: DQ472092, strain: CL030305, length: 783 nt | | | GenBank: AB489969, strain: Win3, length: 654 nt | | | | GenBank: DQ472036, strain: CL030305, length: 885 nt |
| Rugulopteryx marginatus | GenBank: DQ472098, strain: GWS0111, length: 1176 nt | | GenBank: XX, strain: GWS023125, length: 657 nt | GenBank: XX, strain: LT0291, length: 647 nt | GenBank: XX, strain: HV2153, length: 744 nt | | GenBank: XX, strain: HV2153, length: 969 nt | |
| Rugulopteryx okamurae | GenBank: AB090388, strain: XX8, length: 1806 nt | GenBank: GQ425149, strain: D194, length: 1124 nt | GenBank: HQ990525, strain: GWS018267, length: 651 nt | GenBank: XX, strain: HV1958, length: 654 nt | GenBank: GQ425185, strain: FS280, length: 744 nt | GenBank: AY422598, strain: IK43, length: 1532 nt | GenBank: XX, strain: FS328, length: 846 nt | GenBank: AY422675, strain: WI7, length: 1407 nt |
| Rugulopteryx radicans | | GenBank: DQ472100, strain: D98, length: 599 nt | GenBank: XX, strain: D98, length: 419 nt | | GenBank: XX, strain: D98, length: 728 nt | | GenBank: XX, strain: HV2449, length: 969 nt | GenBank: DQ472045, strain: D98, length: 1178 nt |
| Rugulopteryx suhrii | | GenBank: DQ472099, strain: KZNb2315, length: 1174 nt | GenBank: XX, strain: KZNb2315, length: 617 nt | | GenBank: Dic35, strain: KZNb2315, length: 740 nt | | GenBank: EU395617, strain: KZNb2346, length: 766 nt | GenBank: DQ472044, strain: KZNb2315, length: 1304 nt |
| Scoresbyella profunda | | GenBank: XX, strain: HV2553, length: 1119 nt | GenBank: GQ425121, strain: DIC44, length: 607 nt | GenBank: GQ425148, strain: DIC44, length: 518 nt | | | GenBank: XX, strain: HV2570, length: 969 nt | GenBank: XX, strain: HV2553, length: 1230 nt |

# S2: GEOGRAPHIC AND THERMAL DATA



**Figure S2.1: Overview *Dictyota* sampling records. The background is represents a mean sea surface temperature layer derived from Bio-ORACLE (Tyberghein *et al.*, 2012).**

**Table S2.1: Overview *Dictyota* species: amount of samples, amount of unique localities, mean sea surface temperature, standard error of mean sea surface temperature.**

| Taxa | # samples | # unique localities | mean SST | mean SST Standard Error | Taxa | # samples | # unique localities | mean SST | mean SST Standard Error |
|---|---|---|---|---|---|---|---|---|---|
| Dictyota acutiloba1 | 35 | 24 | 24.55 | 0.44 | Dictyota naevosa | 17 | 13 | 22.06 | 0.76 |
| Dictyota acutiloba2 | 6 | 3 | 18.37 | 0.17 | Dictyota nigricans | 12 | 12 | 18.84 | 0.56 |
| Dictyota adnata | 24 | 18 | 28.48 | 0.39 | Dictyota paniculata1 | 9 | 8 | 17.77 | 0.47 |
| Dictyota alternifida | 16 | 13 | 16.98 | 0.48 | Dictyota paniculata2 | 5 | 3 | 15.46 | 0.21 |
| Dictyota alternifida2 | 2 | 2 | 15.62 | 0.25 | Dictyota pardalis | 2 | 1 | 14.80 | 0.00 |
| Dictyota anastomosans | 1 | 1 | 22.18 | 0.00 | Dictyota pfaffii | 24 | 16 | 22.11 | 0.40 |
| Dictyota bartayresiana | 106 | 72 | 27.94 | 0.13 | Dictyota pinnatifida | 12 | 9 | 26.61 | 0.71 |
| Dictyota bartayresiana2 | 12 | 4 | 26.31 | 1.04 | Dictyota pleiacantha1 | 13 | 7 | 21.42 | 0.53 |
| Dictyota binghamiae | 15 | 10 | 11.75 | 1.00 | Dictyota pleiacantha2 | 2 | 2 | 22.85 | 0.19 |
| Dictyota canaliculata1 | 3 | 3 | 29.55 | 0.42 | Dictyota polyclada1 | 11 | 10 | 16.55 | 0.36 |
| Dictyota canaliculata2 | 14 | 12 | 28.83 | 0.37 | Dictyota polyclada2 | 2 | 2 | 17.28 | 1.26 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Dictyota canariensis | 25 | 11 | 23.47 | 0.44 | Dictyota polyclada3 | 5 | 4 | 19.75 | 1.03 |
| Dictyota caribaea | 6 | 6 | 28.46 | 0.24 | Dictyota rigida1 | 14 | 9 | 27.83 | 0.12 |
| Dictyota ceylanica1 | 4 | 3 | 28.85 | 0.32 | Dictyota rigida2 | 2 | 2 | 22.58 | 0.41 |
| Dictyota ceylanica2 | 2 | 1 | 27.55 | 0.00 | Dictyota rigida3 | 4 | 3 | 21.78 | 1.66 |
| Dictyota ceylanica3 | 5 | 3 | 25.83 | 0.93 | Dictyota rigida4 | 6 | 6 | 24.51 | 0.16 |
| Dictyota ceylanica4 | 10 | 8 | 25.53 | 1.07 | Dictyota rigida5 | 1 | 1 | 24.49 | 0.00 |
| Dictyota ceylanica5 | 31 | 24 | 27.55 | 0.39 | Dictyota sandvicensis1 | 4 | 4 | 25.62 | 0.13 |
| Dictyota ceylanica6 | 4 | 3 | 21.71 | 0.00 | Dictyota sandvicensis2 | 11 | 6 | 21.19 | 0.52 |
| Dictyota ciliolata | 147 | 91 | 26.97 | 0.27 | Dictyota sandvicensis3 | 1 | 1 | 24.43 | 0.00 |
| Dictyota concrescens | 1 | 1 | 28.24 | 0.00 | Dictyota sp1 | 8 | 5 | 19.97 | 0.45 |
| Dictyota coriacea | 4 | 2 | 17.66 | 0.10 | Dictyota sp10 | 1 | 1 | 29.78 | 0.00 |
| Dictyota coriacea2 | 16 | 13 | 18.44 | 0.62 | Dictyota sp11 | 4 | 4 | 28.88 | 0.39 |
| Dictyota crenulata | 16 | 15 | 26.20 | 0.95 | Dictyota sp12 | 1 | 1 | 30.21 | 0.00 |
| Dictyota cyanoloma | 92 | 21 | 18.21 | 0.48 | Dictyota sp15 | 4 | 4 | 25.83 | 1.00 |
| Dictyota cymatophila | 11 | 7 | 21.11 | 0.14 | Dictyota sp16 | 3 | 3 | 30.03 | 0.42 |
| Dictyota dhofarensis | 4 | 4 | 25.97 | 0.02 | Dictyota sp17 | 1 | 1 | 30.63 | 0.00 |
| Dictyota dichotoma1 | 789 | 107 | 15.82 | 0.32 | Dictyota sp18 | 1 | 1 | 28.37 | 0.00 |
| Dictyota dichotoma2 | 23 | 15 | 18.00 | 0.78 | Dictyota sp19 | 17 | 16 | 28.71 | 0.19 |
| Dictyota dichotoma3 | 10 | 5 | 15.47 | 0.16 | Dictyota sp20 | 40 | 24 | 28.39 | 0.31 |
| Dictyota diemensis | 37 | 22 | 16.20 | 0.26 | Dictyota sp21 | 2 | 1 | 27.56 | 0.00 |
| Dictyota fasciola | 38 | 19 | 19.30 | 0.50 | Dictyota sp22 | 3 | 2 | 24.60 | 4.09 |
| Dictyota fasciola2 | 2 | 2 | 19.73 | 0.68 | Dictyota sp23 | 3 | 1 | 20.51 | 0.00 |
| Dictyota flabellata | 21 | 9 | 23.12 | 0.84 | Dictyota sp24 | 1 | 1 | 24.62 | 0.00 |
| Dictyota friabilis1 | 90 | 65 | 27.95 | 0.21 | Dictyota sp25 | 5 | 3 | 19.57 | 0.60 |
| Dictyota grossedentata | 21 | 15 | 28.72 | 0.18 | Dictyota sp26 | 1 | 1 | 23.86 | 0.00 |
| Dictyota hamifera | 20 | 14 | 27.32 | 0.54 | Dictyota sp29 | 9 | 6 | 23.93 | 0.25 |
| Dictyota humifusa | 69 | 54 | 27.49 | 0.23 | Dictyota sp3 | 8 | 4 | 20.11 | 0.97 |
| Dictyota implexa | 75 | 55 | 24.03 | 0.61 | Dictyota sp31 | 1 | 1 | 24.22 | 0.00 |
| Dictyota intermedia | 59 | 31 | 21.58 | 0.22 | Dictyota sp32 | 1 | 1 | 20.22 | 0.00 |
| Dictyota jamaicensis | 28 | 25 | 27.60 | 0.29 | Dictyota sp33 | 1 | 1 | 17.67 | 0.00 |
| Dictyota koreana | 17 | 14 | 19.40 | 0.72 | Dictyota sp34 | 2 | 1 | 28.69 | 0.00 |
| Dictyota kunthii | 7 | 4 | 15.12 | 0.56 | Dictyota sp5 | 2 | 2 | 19.63 | 0.70 |
| Dictyota linearis | 21 | 10 | 19.54 | 0.58 | Dictyota sp6 | 2 | 2 | 25.20 | 1.16 |
| Dictyota liturata1 | 16 | 9 | 23.11 | 0.62 | Dictyota sp7 | 6 | 5 | 20.06 | 1.11 |
| Dictyota liturata2 | 21 | 14 | 22.04 | 0.94 | Dictyota sp9 | 1 | 1 | 27.43 | 0.00 |
| Dictyota liturata3 | 4 | 2 | 25.29 | 1.61 | Dictyota spiralis1 | 31 | 21 | 19.38 | 0.35 |
| Dictyota liturata4 | 3 | 3 | 22.70 | 1.03 | Dictyota spiralis2 | 8 | 6 | 19.74 | 0.74 |
| Dictyota mangrovestolon | 1 | 1 | 29.61 | 0.00 | Dictyota spiralis3 | 22 | 11 | 19.17 | 0.81 |
| Dictyota mediterranea | 27 | 12 | 19.94 | 0.30 | Dictyota spiralis4 | 1 | 1 | 16.83 | 0.00 |
| Dictyota mertensii1 | 13 | 9 | 27.21 | 0.54 | Dictyota stolonifera | 37 | 24 | 27.95 | 0.39 |
| Dictyota mertensii2 | 4 | 3 | 28.10 | 0.25 | | | | | |

**Table S2.1: List species' geographic distributions relative to each other.**

| Clade | X | Y | Speciation |
|---|---|---|---|
| C2 | canaliculata1 | pfaffii | allopatric |
| C2 | humifusa | canaliculata1, pfaffii | sympatric |
| C4 | flabellata | sp20 | parapatric |
| C4 | sp19 | sp20, flabellata | sympatric |
| C4 | crenulata | sp19, sp20, flabellata | sympatric |
| C4 | implexa | linearis | sympatric |
| C4 | canariensis | linearis, implexa | sympatric |
| C4 | spiralis2 | spiralis4 | sympatric |
| C4 | spiralis1 | spiralis4, spiralis2 | sympatric |
| C4 | spiralis3 | spiralis4, spiralis2, spiralis1 | sympatric |
| C4 | jamaicensis | pleiacantha1 | parapatric |
| C4 | pleiacantha2 | pleiacantha1, jamaicensis | parapatric |
| C4 | sandvicensis1 | sandvicensis3 | allopatric |
| C4 | sandvicensis2 | sandvicensis3, sandvicensis1 | allopatric |
| C4 | caribaea | pleiacantha1, pleiacantha2, jamaicensis, sandvicensis3, sandvicensis1, sandvicensis2 | sympatric |
| C4 | cymatophila | mertensii2 | allopatric |
| C4 | concrescens | pleiacantha1, pleiacantha2, jamaicensis, sandvicensis3, sandvicensis1, sandvicensis2, caribaea, cymatophila, mertensii2 | allopatric |
| C4 | pinnatifida | rest of clade C4 | sympatric |
| C5 | kunthii | binghamiae | allopatric |
| C5 | nigricans | binghamiae, kunthii | allopatric |
| C6 | paniculata1 | paniculata2 | sympatric |
| C6 | polyclada3 | paniculata2, paniculata1 | parapatric |
| C6 | polyclada1 | polyclada2 | sympatric |
| C6 | sp1 | dichotoma1 | sympatric |
| C6 | sp29 | sp25 | allopatric |
| C7 | sp22 | sp12 | allopatric |
| C7 | sp16 | adnata | sympatric |
| C8 | bartayresiana | bartayresiana2 | parapatric |
| C8 | sp17 | sp34 | sympatric |
| C8 | canaliculata2 | sp26 | allopatric |
| C8 | mangrovestolon | sp33 | allopatric |
| C8 | sp18 | sp33, mangrovestolon | sympatric |
| C9 | koreana | sp21 | allopatric |
| C9 | sp3 | sp7 | parapatric |
| C9 | alternifida | alternifida2 | sympatric |
| C9 | cyanoloma | alternifida, alternifida2, sp3, sp7, sp21, koreana | sympatric |
| C9 | diemensis | dichotoma3 | sympatric |
| C9 | liturata2 | liturata3 | allopatric |
| C9 | liturata1 | liturata3, liturata2 | allopatric |
| C9 | liturata4 | liturata1, liturata2, liturata3 | allopatric |
| C9 | stolonifera | liturata1, liturata2, liturata3, liturata4 | parapatric |
| C9 | sp23 | mertensii1 | allopatric |
| C9 | intermedia | alternifida, alternifida2, sp3, sp7, sp21, koreana, liturata1, liturata2, liturata3, liturata4, mertensii1, sp23, stolonifera, diemensis, dichotoma3, cyanoloma | parapatric |
| C9 | dichotoma2 | pardalis | sympatric |
| C9 | rigida1 | rigida2 | allopatric |
| C9 | rigida3 | rigida1,2 | allopatric |
| C9 | rigida4 | rigida5 | allopatric |
| C9 | coriacea | coriacea2 | allopatric |
| C9 | sp32 | coriacea, coriacea2 | sympatric |
| C9 | ciliolata | sp32, coriacea, coriacea2 | sympatric |
| C9 | grossedentata | rigida1, rigida2, rigida3, rigida4, rigida5, ciliolata, sp32, coriacea, coriacea2 | sympatric |
| C9 | dhofarensis | sp31 | allopatric |
| C9 | naevosa | sp31, dhofarensis | allopatric |
| C9 | acutiloba1 | acutiloba2 | parapatric |

| C9 | sp10 | sp24 | parapatric |
|---|---|---|---|
| C9 | sp11 | sp9 | sympatric |
| C9 | hamifera | sp9, sp10, sp11, sp24 | sympatric |
| C9 | anastomosans | ceylanica4 | parapatric |
| C9 | friabilis1 | ceylanica4, hamifera, anastomosans, sp9, sp10, sp11, sp24 | sympatric |
| C9 | fasciola | mediterranea | sympatric |
| C9 | fasciola2 | mediterranea, fasciola | sympatric |
| C9 | sp5 | mediterranea, fasciola, fasciola2 | sympatric |
| C9 | sp6 | mediterranea, fasciola, fasciola2, sp5 | parapatric |
| C9 | ceylanica3 | ceylanica6 | allopatric |
| C9 | ceylanica1 | ceylanica3, ceylanica6 | sympatric |
| C9 | ceylanica2 | ceylanica1, ceylanica3, ceylanica6 | allopatric |

# APPENDIX REFERENCES

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