

Anthony W. D. Larkum · Gary A. Kendrick  
Peter J. Ralph *Editors*

# Seagrasses of Australia

Structure, Ecology and Conservation

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# Preface

In 1989, the *Biology of Seagrasses: Treatise on the Biology of Seagrasses with Special Reference to the Australasian Region* (edited by Anthony W. D. Larkum, Scoresby Shepherd and Arthur McComb) was published at a time when seagrasses were being recognized as keystone benthic species amongst coastal ecosystems. Australia with 40 of the 70+ species around the world and large seagrass beds in both temperate and tropical sites was clearly a central focus of seagrass biology, both in terms of a knowledge base and source for further research into these unique plants. It was early realized that the 70+ species of seagrasses, an incredibly small number of species compared with the several hundred thousand species of flowering plants, have special features which enabled them to enter the marine environment from which their charophyte green algal forebears evolved in the Ordovician Era (some 500 Mya). And this in itself was enough reason to publish a book on Australian seagrasses, which also comprise a major proportion of the world species and have representatives of every seagrass group.

Seagrasses have continued to dominate the world stage in research, and Australia maintains its leading position on this stage, partly because of the prime role that Australian seagrasses hold, but also because of the exceptional quality of Australian seagrass researchers. Thus, there has been an increasing need to revisit the subject of Australian seagrasses over recent years, and we are very grateful to Springer-Verlag for agreeing to publish a new book on this topic.

In 1989, the editors of that volume drew attention to five important aspects of seagrass biology:

1. The economic significance of seagrasses,
2. The importance of physiological studies and microbial interactions,
3. Population studies,
4. The decline of seagrasses and
5. Conservation studies.

Today, these aspects and further realization of the unique features of these plants continue to influence our thinking on the importance of seagrasses both in a world context as well as the unique Australian context. And these themes too are reflected

in the present book, exemplifying the strong research tradition that has passed on to younger researchers in Australia.

Yet, there have been some significant advances in biology that have revolutionized the way we think about seagrasses. These advances have been in the areas of (i) *molecular biology*, (ii) *phylogenetics*, (iii) *global climate change* and (iv) the *blue carbon* aspect of seagrasses. And they have brought about unexpected changes in the way we view seagrasses as well as reinvigorate the original five topics examined in the first edition.

In the area of *molecular biology*, we have seen the ability to carry out a full genome analysis of each species of seagrass. Not just a single assay either, we can now do multiple analyses on a single species. This advance yields extraordinary amounts of information, which, if properly handled, can be used at a number of levels in enhancing our knowledge of seagrasses; however, at this time it must be acknowledged that much of the value lies in the future. Nevertheless, in looking for current examples we can cite taxonomic breakthroughs (Chaps. 1, 5 and 6) specific biochemical pathways in various lineages (Chap. 16) or in understanding the biogeographic range of a seagrass (Chaps. 3, 8 and 9). And in general, this advance has ushered in the era of “*Omics*” which covers everything from the genes and genomes (*genomics*), through *transcriptomics* to *proteomics* and *metabolomics*; this information has filtered through to almost every chapter in this book.

In the area of *phylogenetics*, in conjunction with gene and genomic studies, we have seen sharp changes in our view of seagrass species and their affinities. It has enabled us to understand the evolution of seagrasses, in space and time in a way that was not possible in the first edition (see Chaps. 1 and 5). And in some cases, it will undoubtedly lead to a revision of the accepted species of seagrasses (Chap. 5). Similarly, population genetics, reproduction, dispersal and recruitment and population connectivity have evolved, and our knowledge of both genetic and demographic connectivity has been a focus of research since 2000 (Chaps. 6 and 8).

In the area of *global climate change*, we have seen a vigorous debate emerge in which despite the objections of “climate deniers”, we have seen noticeable shifts in climate in many parts of the world with higher incidence of storms, hurricanes and cyclones. On a world scale, we have seen carbon dioxide levels rise in 2016 to 400 parts per million for the first time in many thousands of years (World Meteorological Organization) and the likelihood that it will continue to rise far into the future. In 2015, 195 countries met in Paris at the Twenty-First Conference of the Parties of the United Nations Framework Convention on Climate Change (UNFCCC) and adopted by consensus on 12 December 2015 the Paris Agreement. This is an agreement within the UNFCCC dealing with greenhouse gases emissions mitigation, adaptation and finance starting in 2020. The agreement went into effect on 4 November 2016 and, despite retraction by the Federal government of the USA in Washington, seems set to have a great influence on future carbon use around the world.

Now we have seen how a redefinition of the turnover properties of various plant products has led to a re-evaluation of the importance of seagrasses in our environment. This has brought in the new concept of “*Blue Carbon*”; the realization that

carbon deposited in organic form in seagrasses (and salt marshes and mangroves) has a tenfold longer life than that of other plants has increased the respect with which politicians and planners bring to our much threatened seaboard. Much of this work has developed earlier sediment biogeochemistry to address these new policy-driven questions associated with integrating coastal vegetation into greenhouse gas accounting.

Unfortunately, any increased awareness of seagrasses by the public, politicians and planners has been offset by ineluctable desire to build along and out from our beautiful shores and also by the far more insidious but all-pervasive effects of riverine and estuarine pollution and *global climate change*.

*Global warming* in 1989 was viewed by most informed workers in the field as a long way off and something to be mitigated by future tactics. Since those days, it has become apparent to all but a few that climate change is a major, if not the major, problem facing human civilization. One major effect of increased greenhouse gases, especially CO<sub>2</sub>, will be the rise in temperature of the planet. If this can be kept to no more than a 2 °C rise, it would be possible for most plant and animal communities to survive with little harm (Intergovernmental Panel on Climate Change). Indirect effects through increased violent weather events are already becoming apparent. On the good side of the balance, a warming of the seas by 4 °C would not be disastrous for seagrasses as it is likely to be for reef-forming corals, which are likely to be pushed to extinction. Seagrasses could survive. But in addition to warming of the seas, there is also the effect of *ocean acidification (OA)*, a subject that was little talked about in 1989. The effect of OA on seagrasses is not well understood, but the few attempts to factor this phenomenon in have predicted strong effects (see Chap. 21).

Putting all these factors into the balance, the future does not look good for seagrasses. And we need a heightened awareness of the threats to seagrasses if we are to conserve them. We also need a much greater public appreciation of the importance of this source of blue carbon in our national greenhouse gas accounts (Chap. 22).

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**Part I**  
**Biogeography**

# Chapter 1

## Evolution and Biogeography of Seagrasses



Anthony W. D. Larkum, Michelle Waycott and John G. Conran

**Abstract** Seagrasses are an organismal biological group united by their ability to grow in marine environments. As marine flowering plants they have evolved a combined suite of adaptations multiple times enabling the four known lineages containing species of seagrass to survive, and thrive, in the sea. Unlike many other biological groups of plants however, seagrasses are all derived from a single order of flowering plants, the Alismatales. This order, being derived early in the evolution of the monocotyledons, is comprised predominantly of aquatic plants, of all forms—emergent, submerged, freshwater, estuarine and marine. A review of seagrass fossils suggests that new discoveries of seagrass fossils along with confirmation of some earlier finds lead to a clear signal that some seagrass species had a wider distribution in the past compared with today. The discovery of new fossil sites should be encouraged as this will likely produce important valuable information on the evolution of this group. In general the biogeography of seagrasses suggests that these organisms evolved successfully in the Tethys Sea of the Late Cretaceous. However, the modern division into two groups, temperate and tropical tends to suggest that at some point an ecological separation occurred in both the Northern and Southern Hemispheres. There are a disproportionately large number of temperate seagrass species in southern Australia and there is significant endemism shown in *Posidonia*, *Amphibolis* and a unique species of *Halophila* (*H. australis*).

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The use of genetic and genomic techniques has begun to explain these distributions but we can expect a much bigger picture to emerge in the near future.

## 1.1 Introduction

Among the higher plants, whose ancestors left the sea some four hundred million years ago, the seagrasses are the only group to have returned to a completely submerged marine existence (Arber 1920; Sculthorpe 1967; den Hartog 1970; Larkum and West 1989; Les et al. 1997). Fossil evidence indicates that angiosperms arose in the late Jurassic (Raven and Axelrod 1974) or early Cretaceous Periods (Thomas and Spicer 1984), at around 140 million years ago (Ma) and molecular clock dating also supports an early Cretaceous or Jurassic origin for the angiosperms (Doyle 2012). The limited fossil record for seagrasses indicates their ancestors, which are the basal lineages of the Alismatales (Refer to Table 1.1 for families included in the Alismatales and following the recent classification published by the Angiosperm Phylogeny Group 2016). This group will be referred to as ‘alismatic monocots’ or Alismatales, see discussion in Waycott et al. (2016, Chap. 5), likely evolved more than 100 Ma ago in the Cretaceous Period, modern seagrass families beginning to diverge more than 70 Ma (Anderson and Janssen 2009; Janssen and Bremer 2004; see also Chap. 5). Molecular divergence times across the order Alismatales support these hypotheses that fossil based evidence indicates progenitors to modern seagrasses arose during the mid-Cretaceous (Hertweck et al. 2015; see also Chap. 5). However, the different modern family lineages of seagrasses vary in age and most are considerably younger (Les and Tippery 2013; Waycott et al. 2016, see also Chap. 5). Given such a well-established, long evolutionary history, it is remarkable that although there are several hundred thousand species of angiosperms in existence today there are only some 65 species of seagrasses.

Evidence that there are multiple independently-derived lineages of seagrasses has been well established since the molecular phylogenetic study of Les et al. (1997). The findings of this study, that the alismatic monocots contain within them four, polyphyletic lineages containing seagrasses, provides a framework for the evaluation of the evolution of these groups (e.g. Waycott et al. 2004, 2006, 2014, Chap. 5; Kilminster et al. 2015). The four lineages are (1) the marine Hydrocharitaceae, (2) three families together referred to as the Cymodoceaceae ‘complex’ by Les et al. (1997) including the Cymodoceaceae, Ruppiaceae and Posidoniaceae, (3) the Zosteraceae and (4) a small number of species in the Potamogetonaceae formally in the Zannichelliaceae. The ecological success of these lineages is significant, seagrasses occupying the nearshore, relatively shallow coastal environments on all continents except Antarctica (den Hartog 1970; Short et al. 2007). In addition, seagrasses are crucial to healthy ecosystems of shallow inshore regions of the world (den Hartog 1970; Duarte 2002; Larkum et al. 2006; Orth et al. 2006; Waycott et al. 2006).

**Table 1.1** Current families recognised in the monocotyledonous plant order Alismatales Dumortier (Angiosperm Phylogeny Group 2016). Genera recognised as seagrasses listed next to family recognised in the order, seagrass families and genera are **bold**

Family	'Seagrass' genera	Estimated number of species in family <sup>a</sup>	APG IV family number <sup>b</sup>
Alismataceae (including Limncharitaceae)		88	30
<b>Hydrocharitaceae</b>		116	<b>32</b>
	<i>Enhalus</i>		
	<i>Thalassia</i>		
	<i>Halophila</i>		
Butomaceae		1	31
<b>Cymodoceaceae</b>		16	<b>41</b>
	<i>Cymodocea</i>		
	<i>Thalassodendron</i>		
	<i>Amphibolis</i>		
	<i>Syringodium</i>		
	<i>Halodule</i>		
<b>Ruppiceae</b>	<i>Ruppia</i> <sup>c</sup>	10	<b>40</b>
<b>Posidoniaceae</b>	<i>Posidonia</i>	9	<b>39</b>
<b>Potamogetonaceae</b>		102	
(including Zannichelliaceae)	<i>Lepilaena</i> <sup>c</sup>		<b>38</b>
<b>Zosteraceae</b>		14	<b>37</b>
	<i>Phyllospadix</i>		
	<i>Zostera</i>		
Maundiaceae		1	36
Juncaginaceae		30	35
Scheuchzeriaceae		1	33
Aponogetonaceae		50	34
Araceae		4150	28
Tofieldiaceae		31	29

<sup>a</sup>Following the Angiosperm Phylogeny Website available via <http://www.mobot.org/MOBOT/research/APweb> and organized by P. F. Stevens, from 2001 onwards

<sup>b</sup>The numerical designation given to each family in the orders identified by APG IV (Angiosperm Phylogeny Group 2016)

<sup>c</sup>Not always treated as seagrasses although species are tolerant of salinities ranging from brackish to marine to hypersaline salinities

Despite a long evolutionary history, there is a distinct lack of speciation amongst seagrasses, which appears inconsistent with their apparent widespread success (Les et al. 1997; Waycott et al. 2016, Chap. 5). Indeed, the majority of significant diversity in the group occurs among genera (Waycott et al. 2006). Given the poor fossil record and the lack of species diversity within genera it is likely that

seagrasses have suffered major extinctions throughout their evolutionary history. Indeed, evidence for this may be seen in the relationship seagrasses have with Sirenia (i.e. dugong and manatee) where, as the major food source (see Chap. 19) their histories have been interlinked. Turtles feed on seagrass leaves alone, whereas Sirenia often feed on leaves and below ground structures. And the evolution of Sirenia seems to have depended on the presence of seagrasses (Domning 1981, 2001; Fitzgerald et al. 2013; Chap. 19). However, it is likely that we will not know much more about the factors involved with speciation in these unusual flowering plants until we know more about the processes of speciation in general (Lockhart et al. 2015) and the genetic variability present within and among seagrass species in particular (see Chaps. 5, 6 and 8).

In this chapter we will discuss:

1. The current evidence of seagrass evolution based on the fossil record;
2. A summary of the current knowledge on the biogeography of seagrasses; and
3. The distribution of Australian seagrass communities.

## 1.2 Fossils and Seagrasses

One consequence of seagrasses being polyphyletic across a long evolutionary history and among multiple alismatid lineages is that identifying seagrass fossils can be problematic. In particular, the determination of fossils as being seagrasses, when found in aquatic fossil deposits when no reproductive structures are detected is a significant limitation (Iles et al. 2015). Here we present a summary of the fossil evidence known for the overall order that seagrasses occur in, the Alismatales and summarise what is known about seagrasses from among the evidence known to date. For reference, the work of Les and Tippery (2013) and Iles et al. (2015) in addition to Les et al. (1997) and Waycott et al. (2006) and the summary presented in Chap. 6 (viz. Waycott et al. 2016) provide details for the wider (and non seagrass) taxonomic groups being discussed. We have adopted here, with respect to higher order taxonomy, the Angiosperm Phylogeny Group IV classification, which provides a listing of all families and orders of the Angiosperms following the latest synthesis (Angiosperm Phylogeny Group 2016).

### 1.2.1 Fossil Record of the Alismatales

The fossil record of Alismatales has been summarised recently by Stockey (2006), Friis et al. (2000, 2004, 2011), Smith (2013), Conran et al. (2015a) and Iles et al. (2015). There are fossils known from most of the families in the order, but the majority of the reliable records are for freshwater members of this order of monocotyledons. Because of the morphological and anatomical similarities, particularly in leaf blade form, between the marine members of Cymodoceaceae,

Hydrocharitaceae, Posidoniaceae and Zosteraceae (Stockey 2006; van der Ham et al. 2007; Benzecry and Brack-Hanes 2008; Smith 2013) they are generally just treated as ‘seagrasses’ even though they represent several lineages of the Alismatales with convergent exaptation to a submerged aquatic habit (Les et al. 1997; Ross et al. 2015). This is particularly problematic for fossils, where reproductive material is rarely preserved, making their accurate generic, or even family placement extremely difficult in most cases. For reference, go to Chap. 5 (Waycott et al. 2016) to review relationships in the monocotyledon order Alismatales.

### 1.2.2 *Alismataceae*

Fossils with similarities to Alismataceae (including Limnocharitaceae) occur from the Late Cretaceous onward (Stockey 2006; Smith 2013), including the genera *Cardstonia* M.G. Riley & Stockey, *Haemanthophyllum* Budantzev and *Heleophyton* D.M. Erwin & Stockey (Erwin and Stockey 1989; Golovneva 1987; Riley and Stockey 2004). These fossils show strong similarities to living Alismataceae, but some also share characters with Aponogetonaceae and Butomaceae and the earliest reliable fossils are late Eocene Alismataceae fruits from the Isle of Wight (Collinson 1983; Hooker et al. 2009) and Northern Hemisphere Oligo–Miocene fossil fruits of the extant genus *Caldesia* Parl. (reviewed in Haggard and Tiffney 1997) and Miocene fruits resembling *Limnophyton* Miquel (Haggard and Tiffney 1997). There are Miocene *Alisma* fossils known from Germany (Mai 2000), but the precise identity of these requires confirmation (Iles et al. 2015).

### 1.2.3 *Aponogetonaceae*

Several fossil leaves have been considered to have affinity with Aponogetonaceae, but alternative assignments to other alismatid families are often possible (Smith 2013). The pollen of Aponogetonaceae is distinctive and is known from Late Cretaceous and early Cenozoic sediments from North America and Greenland (Grímsson et al. 2014), with three species referred to different pollen subtypes within *Aponogeton* L.f.

### 1.2.4 *Hydrocharitaceae*

Seeds assigned to the extant genus *Stratiotes* L. genera first appear in the late Palaeocene of England (Sille et al. 2006; Stockey 2006; Smith 2013). Additional Eocene to Miocene fossils have also been assigned to modern genera, but most of these require further study (Smith 2013; Iles et al. 2015).



### 1.2.5 *Potamogetonaceae–Cymodoceaceae* (Incl. *Ruppia*ceae)

These worldwide families of submerged to floating aquatic macrophytes have similar, characteristic endocarps that have been found in Cretaceous to Pliocene marshy, lacustrine or estuarine fossil deposits mainly across the Northern Hemisphere, but with some recent Southern Hemisphere discoveries (Collinson 1983; Zhao et al. 2004; Gandolfo et al. 2009; Smith 2013; Iles et al. 2015). However, despite being regarded traditionally as closely related to each other, *Potamogeton* L. (Potamogetonaceae) and *Ruppia* L. (Cymodoceaceae) are only distantly related, *Ruppia* belonging instead to a diverse clade that includes the seagrass families Cymodoceaceae, Posidoniaceae and Zosteraceae (Les et al. 1997; Iles et al. 2015). As a result, although numerous genera have been created for fossil *Potamogeton*- and *Ruppia*-like fruits, their relationships require re-evaluation in the light of these revised family relationships.

Pole (1993) suggested that some long-tailed, short-beaked fruits found in the Miocene Lake Manuherikia fossil deposit represented possible Poaceae, interpreting their elongated tail-like structures as awns. However, re-examination of these fossils showed that the fruits actually represent the first Neogene record of *Ruppia*-like macrofossils for New Zealand (Conran et al. 2015a). *Potamogeton* and *Ruppia* are both dispersed over long-distances by water birds (Green et al. 2002), so it is not surprising that they were present in the paleo-Lake Manuherikia, as diverse water birds were abundant there in the middle Miocene (Worthy et al. 2007, 2008). There are also Pliocene-aged fruits described by Oliver (1928) as achenes of *Clematis obovata* W.R.B. Oliver (Ranunculaceae), which more closely resemble long-stalked *Ruppia* endocarps (Conran, unpubl. obs.) and these are the subject of ongoing research.

The endocarps at Lake Manuherikia occur in close association with abundant (>60%) *Sparganiaceapollenites* Potonié pollen from several species. This is similar to the Paleogene South American sediments studied by Gandolfo et al. (2009) where *S. barungensis* Harris pollen was recorded in association with fossil *Baibiancarpus* Gandolfo et al. fruits (Potamogetonaceae). That study noted considerable morphological variation in the *S. barungensis* pollen, suggesting that it may represent a range of possible taxa, including Typhaceae/Sparganiaceae, Potamogetonaceae and *Ruppia* (Gandolfo et al. 2009). *Ruppia* pollen does not preserve well in sediments or transport easily, its presence in sediments is generally taken to indicate a local source (Ashworth and Markgraf 1989). Potamogetonaceae pollen is listed as present in New Zealand from the early Miocene onwards (Mildenhall 1980; Conran et al. 2015b), but it is unclear on what these pre-Quaternary records were based.

Machin (1971) suggested that there were similarities of the fossil palynomorph *Aglaoreidia cyclops* Erdtman to Ruppiaaceae and Potamogetonaceae, proposing a possible relationship with the extinct fossil fruit genus *Limnocarpus* Reid emend Reid and Chandler. Collinson (1983) supported this, noting that *A. cyclops* pollen

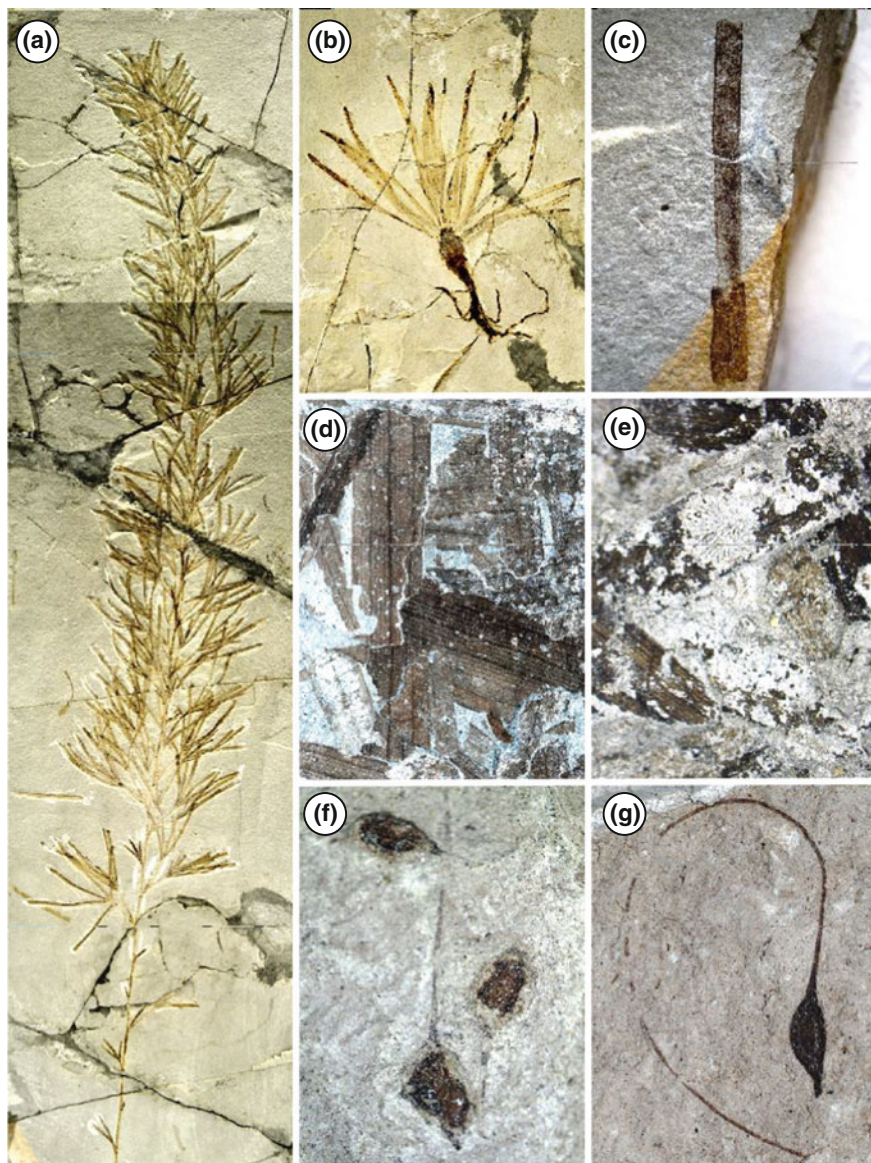
was morphologically intermediate between *Ruppia* and *Potamogeton* and occurs with pollen of other aquatic macrophytes. However, although *A. cyclops* occurs in some Western Australian Upper Eocene lignites (Sanchez Botero et al. 2013), it is absent from Australian and New Zealand Cenozoic sites where pollens have been examined previously (Hill 1994 and papers therein; Raine et al. 2011).

### 1.2.6 ‘Seagrass’ Fossils

The fossil evidence on seagrasses was reviewed by den Hartog (1970) and Larkum and den Hartog (1989) and more recently, as part of the reviews of Alismatales listed above. Seagrass macrofossils are rare, but leaves with cuticular impressions from the Late Cretaceous of Belgium were placed into the extinct genus *Thalassotaenia* R.W. Ham and van Konijnenb and allied to the Cymodoceaceae–Zosteraceae–Posidoniaceae clade (van der Ham et al. 2007). Fossil seagrasses have been described from as early as the Cretaceous, where the genera *Archaeozostera*, *Thalassocharis* and *Thalassotaenia* were present (Koriba and Miki 1931, 1958; Oishi 1931; Voigt and Domke 1955; van der Ham et al. 2007). Brongniart (1828, 1849) described fossil seagrasses from locations of Eocene age in the Paris Basin. Eocene *Cymodocea* and *Caulinites* species were described as seagrasses by Watelet (1866), Bureau (1886) and Laurent and Laurent (1926), although Fritel (1909, 1914) reassigned the *Caulinites* specimens to *Cymodocea* (*Posidonia*) *parisiensis* (Brongt.) Fritel and *Cymodocea* (*Cymodoceites*) *nodosus* (Brongt.) Fritel. Other fossil Potamogetonaceae-like remains attributed to seagrasses by Ascherson and Graebner (1907) were fragmentary and difficult to determine precise affinities.

Dixon (1972), Randazzo and Sarooop (1976) and Lumbert et al. (1984) all reported fossils of extant seagrass genera in the Cymodoceaceae (*Cymodocea* K.D. Koenig, *Halodule* Endl., aff. *Ruppia* and *Thalassodendron* Hartog) and Hydrocharitaceae (*Thalassia* Banks ex K.D. Koenig) from the Eocene Avon Park Formation in Florida, although there is some uncertainty of their affinities (Iles et al. 2015). A further Hydrocharitaceae fossil (*Thalassites parkavonenses* Benzecry and Brack-Hanes) was described from the site by Benzecry and Brack-Hanes (2008), indicating that the area had at least seven species of seagrass at the time of deposition (see also Ivany et al. 1990).

The early Eocene Monte Bolca Pesciara limestone contains diverse marine monocots (Wilde et al. 2014; Fig. 1.1), including well-preserved rhizomes, ligulate leaves displaying possible tannin cells and inflorescences, suggesting the presence of several members of the Cymodaceae–Zosteraceae–Posidoniaceae complex. There are also possible Ruppiaceae-like fossil impressions and Najadaceae-like shoots with apparently whorled clusters of finely-toothed leaves. Gregor (1991) described two these fossils as Posidoniaceae: one with reproductive structures as *Posidocea frickhingeri* Gregor and the second (*Posidonia parisiensis* Gregor) from the nearby San Floriano deposit, based on rhizomes; however, the inflorescence structure of *Posidocea* differs considerably from modern *Posidonia* K.D. Koenig



**Fig. 1.1** a–c Examples of seagrass fossils from the Eocene Pesciarìa di Bolca site (Italy); a *Halochloris cymodoceoides*; b *H. veronensis*; c Ligulate *Zostera*-like leaf; d, e Miocene–Pliocene-aged *Enhalus*-like revolute-margined seagrass leaves from New Zealand; d Late Miocene leaves from near Amberley, South Island; e Pliocene leaves with attached crustose algae from Weymouth near Auckland, North Island; f, g *Ruppia*-like long-pedicellate fruits from New Zealand; f Miocene-aged endocarps from palaeo-lake Manuhēria, South Island; g Pliocene-aged endocarp from Ormond, North Island

species and its affinities require further investigation. Nine of the other seagrass-like monocots at Bolca were described as species of *Halochloris* Unger by Massalongo (1859) and Massalongo and Lotze (1859). However, the affinities of most of these fossils are very uncertain and many of them were described previously by Massalongo (1850, 1851, 1852, 1856) variously as species of algae (e.g. *Condrites* Sternb. or *Zonarites* Sternb.) and/or aquatic monocots such as *Ruppia* (Ruppiales) or *Mariminna* Unger (Najadaceae?). There is also the nomenclatural issue that the name *Halochloris* P.J.L. Dangeard (1965), although a later homonym of *Halochloris* Unger (1847), is used for a currently recognised green algal genus in the Chlorococcales (Guiry 2014). More work is therefore needed to sort out the taxonomy and nomenclature of the seagrass-like monocotyledons at Bolca and their diversity and palaeoenvironment are the subject of ongoing study.

In New Zealand, there are currently no published pre-Holocene seagrass fossils (Conran et al. 2015a, b). However, a recent determination that there are late Miocene–Pliocene seagrass fossils from South Island with apparently revolute leaf margins, suggesting affinities to the present day tropical to subtropical Hydrocharitaceae genus *Enhalus*, although pollen at the site indicates that the palaeoclimate at the time was at best warm temperate (Conran et al. unpublished data). The identity and affinities of these fossils are the subject of ongoing research. There are also characteristic, fossilised seagrass limpet shells of the family Lottiidae (Mollusca: Patellogastropoda) present at an Oligocene estuary and palaeoshoreline at Cosy Dell in Southland (Lee et al. 2014; Conran et al. 2014). Based on the biology of living relatives which are obligate grazers on seagrass leaves (Nakano and Ozawa 2007) and their use to infer former seagrass meadows in Onepoto Lagoon, New Zealand 8.1 Ka (Hayward et al. 2002), these Oligocene limpets were regarded as proxy evidence for the presence of Zosteraceae growing in shallow inshore waters at the site (Conran et al. 2014).

Because of the rarity of seagrass fossils, presumed obligately- or strongly-associated proxies are often used to infer their presence in the fossil record, with Brasier (1975) and Eva (1980) using foraminifera to suggest that seagrasses were distributed widely during the Late Cretaceous of the Caribbean. Various groups of molluscs, crustacea, foraminifera and some vertebrates, such as sirenians and certain seahorses are often associated with seagrasses (e.g. Ivany et al. 1990; Teske and Beheregaray 2009; Battley et al. 2011; Unabia et al. 2011) and their abundance as fossils has been used as a proxy for inferring fossil seagrass ecosystems in the absence of actual plant remains (e.g. Domming 2001; Leonard-Pingel 2005; Buchan 2006; Reuter et al. 2011; Velez-Juarbe 2014). We discuss several of the more commonly applied methods of inferring the presence of seagrass ecosystems; however, there are limitations to the ‘proxy equals presence’ approach and some caution is advised (Reich et al. 2015).

### 1.2.7 Foraminiferan Evidence

Wright and Murray (1972) first presented evidence for seagrasses in ancient deposits. This work was continued by Brasier in the Caribbean (see Brasier 1975) and has been continued in the recent studies of Parker and Gischler (2015).

Brasier showed that some shallow tropical foraminiferans have the same geographical distribution as tropical seagrass beds. Some foraminiferans are collocated with characteristic seagrass species, such as *Peneroplis plaanuuatus* with *Cymodocea* spp. in the Caribbean and *Amphisorus hemprichii* and *Sorites marginalis* with *Thalassia testudinum* (Brasier 1975). However, these same foraminifera can be associated with certain algae as well, so the correlation needs to be taken with caution (Heck and McCoy 1979; Eva 1980). Furthermore there is little evidence that similar associations occur in temperate communities.

Despite these caveats, the predictive value of foraminiferan deposits is high, from the Palaeocene–Eocene onwards. Thus Brasier (1975) put forward a coevolutionary scheme based on foraminiferal remains, seagrass fossils and present distributions. Nevertheless, Eva challenged the view that seagrasses did not arrive in the Caribbean until the Oligocene. He suggested that an extensive seagrass population existed in the Eocene, a view supported by the finding of the Eocene seagrass species at Avon Park, Florida (Lumbert et al. 1984; Benzecry and Brack-Hanes 2008). Moreover Wright and Murray (1972) also inferred from foraminiferal remains that seagrass beds (*Cymodocea* and *Posidonia*) were widespread in the middle and late Eocene deposits of the English Channel, supported by the presence of fossil seagrasses in the Paris Basin.

### 1.2.8 Other Associative Evidence

There is evidence from other proxies apart from those that have been used to assess previous seagrass cover. This work has been summarised recently (Reich et al. 2015) and such studies are based in the main on the presence of gastropods, crustose coralline algae and fossil Sirenia.

#### 1.2.8.1 Gastropods

Reich (2014) looked at the gastropod distribution in seagrass-vegetated and unvegetated sand flats in the Bahamas. Multivariate analysis clearly demonstrated that species composition of gastropods was a tool for distinguishing seagrass areas from unvegetated areas. Feeding guild composition based on species richness also differed between the two states. The results suggested that gastropod assemblages are a useful proxy for seagrass meadows in the fossil record. These preliminary results now need to be put to the test in a real fossil situation and Harzhauser (2014)



contemporaneously looked at gastropods associated with putative seagrasses in Miocene deposits of SW India (Kerala).

### 1.2.8.2 Crustose Coralline Algae

Crustose coralline algae (CCA) are a characteristic feature of seagrass structures that grow in the water column, particularly the flat surface of leaves (e.g. Fig. 1.1e). They are an early coloniser and in turn are colonised by other algal epiphytes. As crustose coralline algae also colonise other surfaces that remain exposed it may be difficult to correlate their presence with seagrass beds. However, Beavington-Penney et al. (2004) have shown that CCA colonise seagrass leaf blades and leave behind a characteristic “hooked” form. These “hooked forms have been recognised in modern seagrass deposits and in fossil remains from the Eocene of Oman. Thus this line of research holds out promise for the future.

### 1.2.8.3 Sirenia

Fossil Sirenia also provide insights into the evolutionary ecology of seagrasses on which sirenians are known to be specialist grazers (Domning 1981, 2001). Sirenia (manatees and dugongs) are linked strongly to an association with marine plants and in particular seagrass beds, having co-evolved, as far as current evidence goes, with seagrasses. Indeed the evolution of Sirenia seems to have depended on the presence of seagrasses (Fitzgerald et al. 2013), as unlike herbivorous marine turtles which feed on seagrass leaves but also eat algae, Sirenia feed on both leaves and in some cases the rhizomes, which are rich in carbohydrate reserves (Marsh et al. 2011; this volume, Chap. 19).

In his seminal review Domning (2001), describes an evolutionary hypothesis that links the fossil record of sirenians, particularly in the tropical Western Atlantic Ocean to a dramatic change in community composition of seagrasses. Indeed, Domning links coevolution of seagrasses and Sirenia throughout the Eocene, through the Palaeocene and to the present time by associating the decline of species diversity in both groups. He suggested that up to 2–3 Ma, around the time of the closure of the Panamanian Isthmus, seagrass ecosystems were largely herbivore-based; however, after that they became detrital-based, which was associated with a great decline in sirenian communities. Domning and coworkers have made many observations in the Caribbean and West Atlantic region describing fossil sirenians and their palaeoecology (e.g. Velez-Juarbe 2014; Springer et al. 2015). Velez-Juarbe (2014) has also discussed possible reasons for the late arrival of sirenians and seagrasses in Australia and South America. Fitzgerald et al. (2013) have presented evidence of a fossil sirenian from New Guinea, which at >11.8 Ma, is the oldest known sirenian from the Indo-Pacific.

Clearly these fragmentary and exiguous pieces of evidence from such diverse methods provide challenging opportunities to gain greater insights into the evolutionary ecology of seagrasses.

### 1.3 Biogeography of Seagrasses

The study of biogeography represents the synthesis of knowledge from disciplines that include understanding species distribution in space and through time. In practice, the models that biogeographic studies test attempt to describe the causal nature of extant and palaeo distributions of species following concepts such as: dispersal-vicariance; centre of origin; track analysis and many others (Crisci et al. 2003). An important additional component to understanding biogeography can be the inclusion of information on the evolutionary origins of species and their relatives. This has led to the growth of a sub-discipline called phylogeography (Avice 2000) that seeks to incorporate phylogenetic information into hypotheses that explain the geographic distributions of species.

Discussions of seagrass biogeography have, in the past, evaluated the fundamental distribution of species as being largely the result of isolation over time (vicariance) as a result of continental drift (den Hartog 1970; Larkum and den Hartog 1989). This concept has been supported by the determination that there is a long evolutionary history of seagrasses (see above). However, newer studies have determined that seagrasses have evolved in four independent lineages (Les et al. 1997) and that these lineages have different evolutionary trajectories (Waycott et al. 2006). There is also the potential that distributions are due to adaptation limits of species such as temperature tolerance limits.

One such hypothesis is that the 'centre of origin' of a species is the region with the highest number of species of a given taxon from which it has spread by radiation to other regions. Thus for seagrasses, if treated as a single lineage, the fact that the region around Malesia (Indonesia, Borneo and New Guinea) has the greatest concentration of seagrass species today might suggest this as the centre of origin of seagrasses in the region (Mukai 1993; Short et al. 2007). However, if the age of seagrasses, their varied evolutionary patterns and geological history are taken into account, this simple hypothesis seems less acceptable and other hypotheses become attractive. For example, a vicariance hypothesis postulates that the current distribution of a region was initially much more widespread and has been constrained by special radiations, plate tectonic movements and local speciation and extinctions. McCoy and Heck (1976) compared the current distribution of corals, seagrasses and mangroves in the Indo-Pacific. They showed that generally these three disparate ecosystems have similar distribution patterns, with the highest number of species occurring in the Malesian region, although smaller areas of increased species number occur on the East African coast. They concluded that a vicariance hypothesis fitted the facts best, based on the widespread occurrence of all groups in the Tethyan seas of the Cretaceous. The vicariance hypothesis has merit

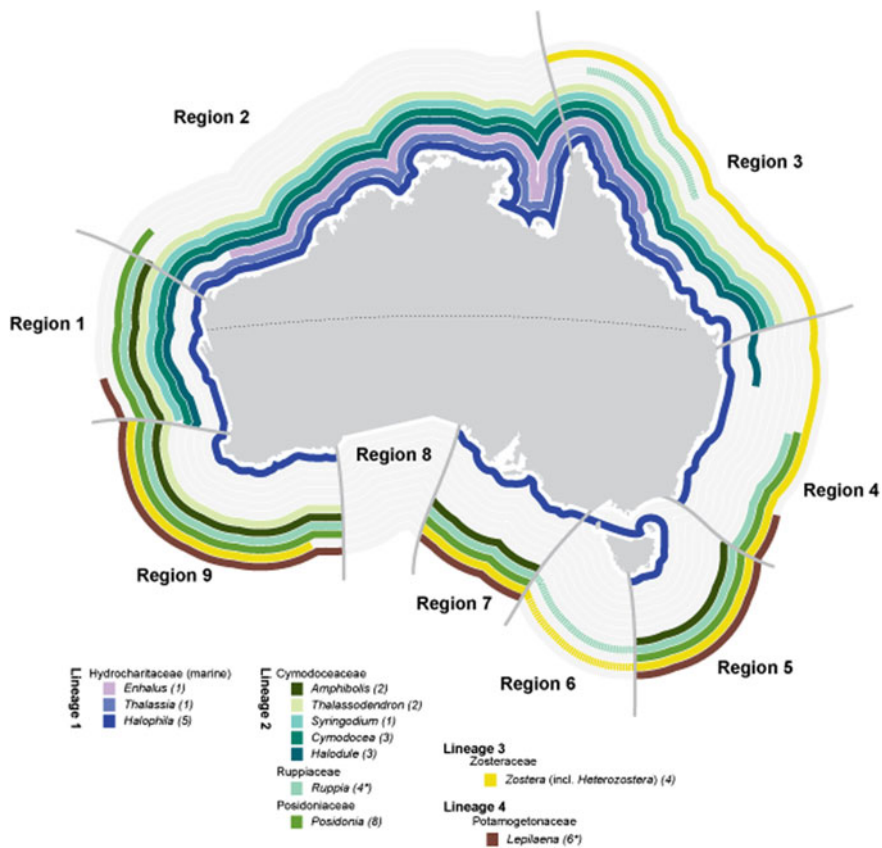
in focusing attention on a number of distribution mechanisms, including plate tectonics and turning attention away from just the present biogeography. However, too strong an adherence to the vicariance hypothesis may itself become dogmatic (Heck and McCoy 1979). Also it should be borne in mind that stochastic events such as the postulated contemporaneous decline of sirenians and seagrasses, due to co-evolutionary destructive interactions (see above) may provide special explanations; in this case for the combined losses of sirenian and seagrass stocks around the world in previous times (before 2 million years ago).

The advent of molecular clock testing of biogeographic models of species distributions on a global scale has been successfully applied to seagrasses and other aquatic plants by Les et al. (2003). These authors evaluate the very widespread distribution of many aquatic plant groups, species and genera and essentially test that these ranges have the potential to represent either long-term isolation at the global scale, or long distance dispersal. Among the species pairs assessed, Les et al. (2003) tested the divergence times between *Thalassia* species (from Australia and North America), *Posidonia* species (from the Mediterranean and Australia) and *Zostera* species (from Australia, Europe and North America). In all cases, the disjunction could have been the result of long-term vicariant speciation associated with continental drift and isolation. In all cases, the molecular clock estimate for the divergence time was significantly lower than would have been expected under a continental drift, isolation, vicariance model (Les et al. 2003; see Chap. 5 for additional discussion). Finally, other models of speciation may reflect more ecologically based divergence of seagrasses into tropical and temperate genera through adaptation and selection.; but in general the apparent matching of seagrasses, corals and mangrove distributions in the tropics can be upheld (McCoy and Heck 1976).

### 1.3.1 *The Present Distribution of Seagrasses*

There are currently 11 genera of seagrasses, excluding the genera *Ruppia* and *Lepilaena* and ca. 65 species (Chaps. 4, 5 and Appendix). This number of taxonomic groups adopts the recent view that the genus *Heterozostera* should be merged with *Zostera* (Jacobs et al. 2006) (but see the Appendix). A recent review of geographic regions of seagrasses by Short et al. (2007) provides a broad bioregional classification that allows clustering of species present in thermal and oceanic regions (Fig. 1.2). However the biogeography of seagrasses of the world was well established before 1940 (Ascherson 1876, 1906; Ostenfeld 1915, 1927a, b; Setchell 1920, 1935). The addition of the magisterial opus of den Hartog (1970) generated a significantly enhanced view of the world's seagrass flora. Since that time over 10 seagrass species have been added around the world bringing the total to ca. 65 (see Chap. 5 and Appendix). The majority of early workers set their conclusions on the current geographical limits of species; in particular Setchell (1915, 1920) made the useful contribution of considering the influence of water temperature on distribution patterns. He made the important distinction of defining species distribution





**Fig. 1.2** Australian extent of each seagrass genus indicated by solid, concentric, lines parallel to the coast. Dashed lines indicate areas where members of two genera, *Ruppia* and *Lepilaena* occur but there is uncertainty as to any marine occurrences in the zone indicated. Regions, bounded by grey lines perpendicular to the coast, are numbered arbitrarily and clockwise starting with the major tropical/temperate overlap zone on the West coast. The dashed line across the continent represents the Tropic of Capricorn. Faint grey lines are to provide reference for the zones where genera do not occur. The number of species in each genus is indicated in parentheses next to the genus name in the legend, \*indicates the number of species includes potentially non-marine taxa requiring review. Colours are clustered according to lineage, in particular (and in order), ‘purple’ for the marine Hydrocharitaceae and ‘green’ for the Cymodoceaceae/Posidoniaceae/Ruppiaceae group, ‘yellow’ for Zosteraceae and brown for Potamogetonaceae

according to the mean water temperature of the warmest month (tropical 25 °C; subtropical, 20 °C; temperate, 15 °C; cold temperate, 10 °C) (Setchell 1915, 1920).

The evolutionary stability and fitness of seagrasses are topics of importance but which have been only tentatively explored until recently (e.g. Williams 1995; Reusch 2001a, b; Reynolds et al. 2012). In terms of species persistence through geological time, seagrasses may be viewed as highly successful. The reproductive

strategies of seagrasses enable their survival; the advent of modern molecular genetic and analytical techniques has enabled an improved understanding of influences on their survival (e.g. Waycott 1995; Reusch 2001a, b; Waycott et al. 2006; van Dijk et al. 2009; Kendrick et al. 2012; McMahon et al. 2014). Further exploration of these factors in seagrass adaptation are presented throughout this book (see Chaps. 5, 6, 8, 10, 6, 12, 15, 21, and 22).

### 1.3.2 *Seagrass Distribution and Biogeographical Regions*

There have been six global seagrass bioregions established that capture the nature and scale of seagrass communities, and their associated floras (Short et al. 2007). Seagrass genera are typically affiliated with tropical or temperate environments (Short et al. 2007; Waycott et al. 2004, 2014). Tropical seagrasses have a greater proportion of taxa within them, seven of the 11 current genera of seagrasses have a tropical distribution: *Halodule*, *Cymodocea*, *Syringodium*, *Thalassodendron*, *Enhalus*, *Thalassia* and *Halophila*. The other four are confined to temperate waters: *Zostera*, *Phyllospadix*, *Posidonia* and *Amphibolis*. In addition, there are two genera that are sometimes not discussed when considering as seagrass biogeography, *Ruppia* and *Lepilaena*; however, they can co-occur with seagrass species, in marine habitats so are included here (Waycott et al. 2004, 2014). These are both typically temperate groups although *Ruppia* has a particularly widespread distribution globally and is found in tropical latitudes although more commonly and with higher diversity in temperate regions.

There is an overlap of tropical and temperate groups in the seagrass floras on the West Australian coast (Fig. 1.2, Region 1). This overlap is associated with north/south flowing currents of warm or cold water, along the West coast of Australia, predominated by the south flowing Leeuwin current. The Leeuwin current provides warmer waters much further to the south than would otherwise occur facilitating the broader distribution of tropical seagrasses (Walker 1991). In fact, this region is unusual in a global context as most of the western coasts of continents have depauperate seagrass floras due to poor habitat including colder waters from deep ocean upwellings (den Hartog 1970; Green and Short 2003). In contrast, on the east coast of Australia, there is a distinct region depauperate of seagrass species south of the major north-eastern facing bays of Queensland, and the presence of the widespread temperate species that occur in sheltered bays along the NSW coastline (Fig. 1.2, Region 4). Interestingly this contrasts with a region of high diversity, and overlapping temperate and tropical floras terrestrially in this same region (Burbidge 1960; Ebach et al. 2015). The western coast of Tasmania, and the ocean-facing coast of Victoria have only a few seagrasses: only those that occur in estuarine systems, i.e. *Zostera*, *Halophila* and *Ruppia* species (Fig. 1.2, Region 6). The Great Australian Bight is distinctly lacking in a seagrass flora although occasional records, most likely drift, have been described (Kirkman 1997). This depauperate seagrass flora is likely due to the fact that this region is exposed to very

high-energy, deep swells from the Southern Ocean and the fine silica grained sands that are highly mobile (Carruthers et al. 2007). Indeed the significant limitation to the existence of seagrasses in temperate Australian ecosystems is where exposure to high energy waves/oceanic conditions is at its extreme.

There are variable broad scales of distribution geographically among seagrass species within genera. In Australia, for example, *Halophila ovalis* stretches from northern Queensland to southern New South Wales on the East coast, and to the lower corner on the south-west coast, where in both regions it is replaced by *Halophila australis*. *H. australis*<sup>1</sup> has a restricted, temperate Australian endemic distribution from the South West of Western Australia to southern Tasmania and a small section of the east coast of Australia. *Halophila ovalis* is highly eurythermic in general and in other parts of the world it is found in Japan and across the Indian Ocean as far north as the Suez canal (e.g. Waycott et al. 2004). It is worth noting that in general for *Halophila* species, most are tropical and it is only in the case of *H. australis*, in Australia that a purely temperate species has evolved. There are at least two tropical genera that have produced species that are now restricted to sub-tropical or warm temperate waters, both in Australia, viz. *Cymodocea nodosa* (found in the Mediterranean Sea and the West coast of Africa) and *Thalassodendron pachyrhizum* (found in Western Australia). On the other hand at least four species of the temperate genus *Zostera* (subgenus *Zosterella*) extend, in different regions, into tropical/sub-tropical waters: viz. *Z. capensis*, *Z. muelleri*, *Z. japonica* and *Z. noltii*.

The tropical seagrasses are not distributed homogeneously, but are concentrated into two large, but widely separated areas globally. The Indo-West Pacific contains all seven of the tropical genera. *Thalassodendron* and *Enhalus* are endemic and *Cymodocea* is largely confined to that area (i.e. *C. nodosa*). Four of these genera occur in the Caribbean area as well as the Indo-West Pacific: viz. *Halodule*, *Syringodium*, *Thalassia* and *Halophila* and two of these (*Halodule* and *Halophila*) also occur on the central west Pacific coast of South America. However, it should be pointed out that this region is little explored and highly disturbed by riverine inputs (Creed et al. 2003). The three species that have been reported there: viz. *Halodule wrightii*, *H. beaudettei* and *H. baillonis*, also have a wide distribution in the Caribbean and likely migrated to the West when the two Americas were still separated (Creed et al. 2003). *H. wrightii* has also been reported as far North as the Gulf of California (McMillan and Phillips 1979). The tropical Atlantic does not have any endemic genera, but its species are different from those of the Indo-West Pacific, suggesting ancient speciation in these genera. The exceptions here are *Halophila decipiens*, which is a very widely distributed pan-tropical species (see

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<sup>1</sup>Current distributions of species of seagrasses in Australia are inferred from data available on Australia's Virtual Herbarium (avh.ala.org.au), published accounts including Green and Short (2003), Carruthers et al. (2002, 2007a, b), IUCN Redlist distributions (iucnredlist.org see Short et al. 2011), regional mapping and field guide resources (Carter et al. 2016; Waycott et al. 2004, 2014; seagrasswatch.org).

McMahon and Waycott (2009) for extension into Kenya) and *Halodule wrightii*, which has a centre in the Caribbean, but also may occur on the coast of East Africa.

The high species diversity in the Indo-West Pacific means that there can be up to 12 seagrass species in any one location (Green and Short 2003) and 35% (17) of the total number of seagrass species occur here. Most of these species have a wide distribution, but six have a more restricted range. These are *Halodule pinifolia*, *Thalassodendron ciliatum*, *Halophila stipulacea*, *H. beccarii*, *H. spinulosa*, *H. tricostata*, *H. capricorni* and *H. sulawesi* (and now *H. nipponica*, *H. major*; Uchimura et al. 2008). This pattern was the basis for the Malaysian and East African seagrass groups that were distinguished originally by Ostenfeld (1915), but with more complete records these geographic groupings can no longer be maintained. *Thalassodendron ciliatum* has a disjunct distribution (East African coast, Eastern Indonesia, Northern Australia, New Guinea, the Philippines and rarely in the Solomon Islands) and *Thalassodendron leptocaula* has recently been distinguished from *Thalassodendron ciliatum* as a separate species on the East African coast (Duarte et al. 2012). *Halophila stipulacea* occurs only in the Western part of the Indian Ocean (although since the opening of the Suez Canal it has spread extensively in the Mediterranean, den Hartog 1970) and thus it may well have suffered extinctions in recent times. More recently, *H. stipulacea* has been found in the Caribbean and is now recognised as having the capacity to disperse globally (Willette and Ambrose 2009).

In the Atlantic there are only four seagrass genera and nine species and these are less homogeneously spread in comparison to the Indo-West Pacific. The main region of biosiversity is in the Caribbean, where three genera are represented by one species each and *Halophila* by four species, including *H. johnsonii* (Eisenman and MacMillan, 1980) whose taxonomic status remains controversial (Waycott et al. 2002; Short et al. 2010). The Atlantic coastal areas South of the Equator have a very depauperate flora. The West coast of Africa has only one species (*Cymodocea nodosa*) and the coast of Brazil has four species from only two genera (*Halophila* and *Halodule*). It is possible to hypothesise that the tropical species of seagrass had a more pan-tropical distribution before the upheaval of the Central American Isthmus in the Miocene. After this it is possible that the species diverged to give rise to the so-called twin species, which have only slight morphological differences but are widely separated from each other. The three sets of twin species proposed by den Hartog (1970) are:

Indo West Pacific	Tropical Atlantic
<i>Halodule uninervis</i>	<i>Halodule wrightii</i> (syn. <i>beaudettei</i> )
<i>Syringodium isoetifolium</i>	<i>Syringodium filiforme</i>
<i>Thalassia hemprichii</i>	<i>Thalassia testudinum</i>

These twin species are most likely the result of a broader geographically distributed progenitor that became subsequently isolated and have diverged through isolation (i.e. vicariance). Across these major biogeographic regions there has also

been loss of species (especially as a result of the probable sirenian/seagrass dieback (see above) in the tropical Atlantic region in particular, which in the Eocene appeared to have *Thalassodendron* and *Cymodocea* present based on high quality fossils (Ivany et al. 1990).

The Australian region shows a great diversity of species and likely represents the greatest endemism of any region in the world and is discussed extensively elsewhere in this book (see Chaps. 2–6). The distribution of seagrass genera around Australia is shown in Fig. 1.2. Very broadly, a distinction can be made between the tropic/subtropical regions and the southern temperate zone, with a rather distinct transition point at about 25°S on the West coast and 30°S on the East coast. The difference between latitude cutoffs on the West and East coast, as well as the exceptions of *Zostera muelleri* and several species on the West coast (Fig. 1.2), has not been successfully explained. A reasonable working hypothesis is that the edges of the ranges of these species are dispersal limited and relate to the overall movement ecology of each species (i.e. Kendrick et al. 2012; McMahon et al. 2014).

The subtropical/tropical seagrasses of Australia belong to the members of two lineages, the Cymodoceaceae and Hydrocharitaceae, representing an Indo-Pacific group (Fig. 1.2). Two tropical genera have species endemic to Western Australia: *Cymodocea angustata* and *Thalassodendron pachyrhizum*. The genus *Thalassodendron* is particularly interesting because it has a disjunct distribution in the Indo-Pacific, one a tropical species, *T. ciliatum* occurring right around from Queensland and the northern Territory to the far North of Western Australia, with the endemic *T. pachyrhizum* occurring only south of 25°S on the Western Australian coast. The genus *Thalassodendron* is known to have had a much wider distribution in Eocene times (Lumbert et al. 1984) and *T. pachyrhizum* may well be a relict of a wider, former distribution. The situation for *Cymodocea angustata* (see above) may be a similar.

The temperate seagrasses of Australia divide into several, broad groups:

1. Restricted to the West coast and not reaching the Great Australian Bight; viz. *Cymodocea angustata*, belonging to a genus with tropical affinities.
2. Restricted to the West coast, each side of the Great Australian Bight, South Australia, Victoria and Tasmania viz. *Amphibolis antarctica* and *A. griffithii*, the *Posidonia* complex, apart from *P. australis*, *Thalassodendron pachyrhizum* and *Zostera muelleri* (den Hartog 1970; Cambridge and Kuo 1979; Kuo and Cambridge 1984).
3. Present in all temperate regions, including the East coast; viz. *Zostera tasmanica*, *Z. muelleri* (which also extends into Queensland), *Posidonia australis*.
4. Restricted distribution across southern temperate Australia—South Western Australia, Victoria, Tasmania and parts of southern NSW; viz. *Halophila australis* (Waycott et al. 2014).

It should be noted that prior to the merger of *Zostera capricorni*, *Z. muelleri*, *Z. mucronata* and *Z. novazelandica*, two previous species would have had restricted

distributions: *Z. capricorni* from the East coast to Victoria and *Z. mucronata* to group (ii) (den Hartog 1970). Now any taxonomic differentiation must be ascribed to local sub-species which follow a general trend of *Z. muelleri* subsp. *capricornii* in the tropics subsp. *novazelandica* in New Zealand and subsp. *mucronata* in western and southern Australia. The general distributions described above strongly suggest a general radiation from West to East, with *Zostera muelleri* and *Halophila decipiens* being the exceptions. Another exception is *Halophila ovalis*, which occurs off all coasts around Australia, with the exception of the Great Australian Bight, where it is replaced by *H. australis* (den Hartog 1970).

The zoological provinces in southern Australia were set out by Knox (1963), who described West Australian, Flindersian and Maugean Provinces. It is possible to see correlations with seagrass distributions in these regions. Sea level changes during the Pleistocene and Holocene Epochs help to explain the distributions in terms of a long-term land bridge between Tasmania and the mainland during this period. For example, the absence of *Posidonia australis* in most of Victoria despite its presence in New South Wales on the one hand and in Tasmania and South Australia on the other, may be the result of recent land emersion and unsuitable sites in Victoria. The slow colonisation rates in this region (Larkum and West, 1983; Meehan and West 2000) are consistent with this view and again relate to the movement ecology of these species (McMahon et al. 2014). Those species present in Port Phillip Bay and Western Port (*Amphibolis antarctica*, *Zostera tasmanica* and *Z. muelleri*) are all fast growing and able to colonise unstable habitats.

Global climate change is expected to affect the future distribution of seagrass species in Australia. Discussion of predicted changes is given in Chap. 21.

## 1.4 New Zealand, Our Close Neighbour

In striking contrast to Australia, New Zealand has only one species of seagrass, *Zostera muelleri*. Formerly two species were recognised, *Z. capricorni* and *Z. novazelandica* (den Hartog 1970); however, the latter is now recognised as a sub-species (Jacobs et al. 2006). Thus, despite having separated from Antarctica at about the same time as Australia (~80 Ma) and just at the time that many seagrass species originated (the Late Cretaceous), the seagrass floras are strikingly different. If, as stated for temperate Australia the majority of species migrated from Western Australia and those that came down the east coast were late arrivals, this may provide some explanation for the paucity of species in New Zealand. Together with the fact that New Zealand has undergone considerable climate change and tectonic effects and significant land area reduction on at least one occasion, over the same period that Australia has been fairly stable, are powerful reasons that seem to explain the differences (see Lee et al. 2001). A recent study of the genetic connectivity between Australian and New Zealand populations of *Zostera muelleri* (Ticli 2014) has demonstrated that the New Zealand populations likely represent a long distance dispersal event from the East coast of Australia.