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THE MARINE ALGAE OF AUSTRALIA

H. B. S. Womersley

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THE BOTANICAL REVIEW

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THE MARINE ALGAE OF AUSTRALIA

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HISTORICAL ASPECTS

The history of collections and studies of Australian marine algae covers three overlapping periods:

1. The period during which small collections were made by early expeditions which were concerned chiefly with the discovery and mapping of the Australian coastline (1791—1840).
2. The period of collections by Australian naturalists (and by W. H. Harvey from Dublin) and their description by British and European algologists (1840—1900).
3. The present century, when studies by Australian algologists have been made.

FRAGMENTARY COLLECTIONS BY EXPEDITIONS (1791—1840)

Most of the expeditions concerned with the discovery and mapping of the Australian coastline carried botanists—or scientific personnel who devoted some time to plant life—but collections of algae, if made at all, were of a very minor nature. In view of the sea approaches of these expeditions and the numerous landings made by some, the lack of algal collections is perhaps surprising, but in the late eighteenth and early nineteenth centuries, knowledge of the algae lagged well behind knowledge and interest in the higher groups of plants.

The following account deals only with those expeditions on which algae were collected. Flinders (1814) reviews expeditions prior to 1801, and an excellent historical account is given by Hooker (1860) in his "Introductory Essay" on the flora of Tasmania.

The earliest description of an Australian marine alga is apparently that of Velley (1800) who described *Conferva umbilicata (Microdictyon umbilicatum)* from New South Wales. The type is in the herbarium of the Public Museum, Liverpool.

The first expedition on which marine algae were collected was apparently that of Captain Vancouver in 1791 (Vancouver, 1798) in the ships "Discovery" and "Chatham" and with Archibald Menzies as botanist. In Australia, Vancouver discovered and landed at King George's Sound, thereafter passing south of Tasmania to New Zealand. Turner (1808-1819) later described three species of *Fucus* (now *Hormosira banksii, Scytothalia dorycarpa* and *Sargassum linearifolium*) collected by Menzies, and these can have come only from King George's Sound.

Although these are the first species collected in Australia, others collected by Labillardiere in 1792 were described earlier, in 1806.

The French expedition under D'Entrecasteaux (1791-4) (see Labillardiere, 1800), sent in search of La Perouse, and with J. J. Labillardiere as botanist, made landings on the Recherche Archipelago (Willis, 1953) and in south Tasmania ("Cape Van Diemen"). Labillardiere's "Novae Hollandiae Plantarum Specimen" (1806) was the first work (apart from Velley's short paper) to describe Australian algae. Some eight species of common brown algae, including the massive *Durvillea (Sarcophycus) potatorum* [1] and one red alga, all from Tasmania, were described and figured. Labillardiere's specimens are now preserved in the Herbarium Universitatis Florentinae in Florence, Italy.

In 1802, the French expedition under Nicolas Baudin (see Peron, 1809-1814), with a large party of scientists, of whom Francois Peron was the only naturalist to return to France, charted the west coast of Australia from Cape Leeuwin northwards. Some time was spent at Shark Bay ("Baie des Chiens Marines"), where algae were probably collected. They then returned south and, after rounding Cape Leeuwin, sailed for Tasmania, charting the east coast of Tasmania and parts of Bass Strait. Thence Baudin sailed westward and was the first to discover the coast from Cape Banks to Encounter Bay in South Australia where he met Matthew Flinders in the "Investigator". Baudin sailed along much of the coast mapped by Flinders in South Australia, as far westward as the Isles of St. Francis where the very poor state of health of the crew made it essential to return to Port Jackson, the only settlement in Australia at the time. Fearing Bass Strait, though given charts of it by Flinders, Baudin returned by the long route south of Tasmania, and the crew were in such a weak state at the end that Flinders, who was also at Port Jackson, had to tow the French ship into the harbour after she had lain outside for two days. In the following year (1803) Baudin again sailed westward and discovered the south and west coasts of Kangaroo Island, returning to France via the western Australian coast and Timor. In spite of claims made by Peron and his application of French names to much of southern Australia, the only coasts really discovered by Baudin's expedition were from Cape Banks to Encounter Bay and the south and west coasts of Kangaroo Island.

Algae collected by Peron, Leschenault and Leseur on Baudin's expe-

1. Naylor (1953) has shown that *Sarcophycus* is not generically distinct from *Durvillea.*

dition were apparently deposited in the Paris Museum, and no attempt made to describe the collection as a whole. Many were later described by C. A. Agardh (1821, 1824) and by Mertens, Lamouroux, Lamarck and other French biologists, but in many cases the only locality given is "Novae Hollandiae", sometimes qualified by reference to the western

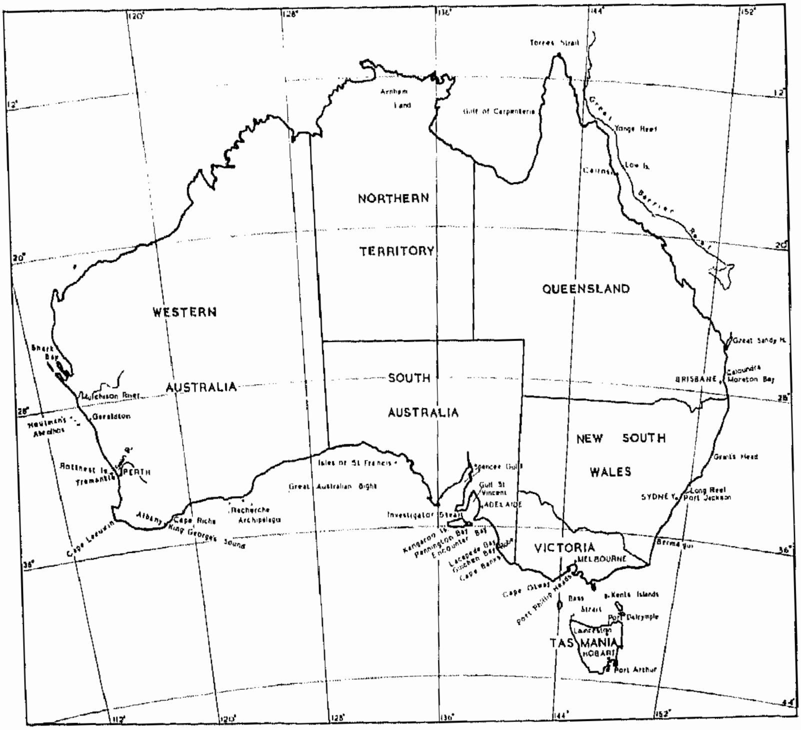

Fig. 1. Australia, showing localities mentioned in the text.

or southern coasts. It seems impossible to discover the type locality of many species collected by the early expeditions.

In 1801-3 the most extensive and important voyage around Australia to that time took place—that of Matthew Flinders (1814) in the "Investigator" with Robert Brown as botanist. This voyage resulted in the accurate mapping of most of the southern, eastern and northern coasts of Australia, and Brown returned with some 3,900 species of Australian land plants. The algae were relatively few (about 31) but constituted the most important collection to that time. A few fresh-water species of *Chara* were described by Brown (1810) in his "Prodromus Florae Novae Hollandiae", and the marine algae were described by Dawson Turner (1808-1819) in his classical "Fuci . . .".

Flinders sailed along the whole southern coast of Australia, landing

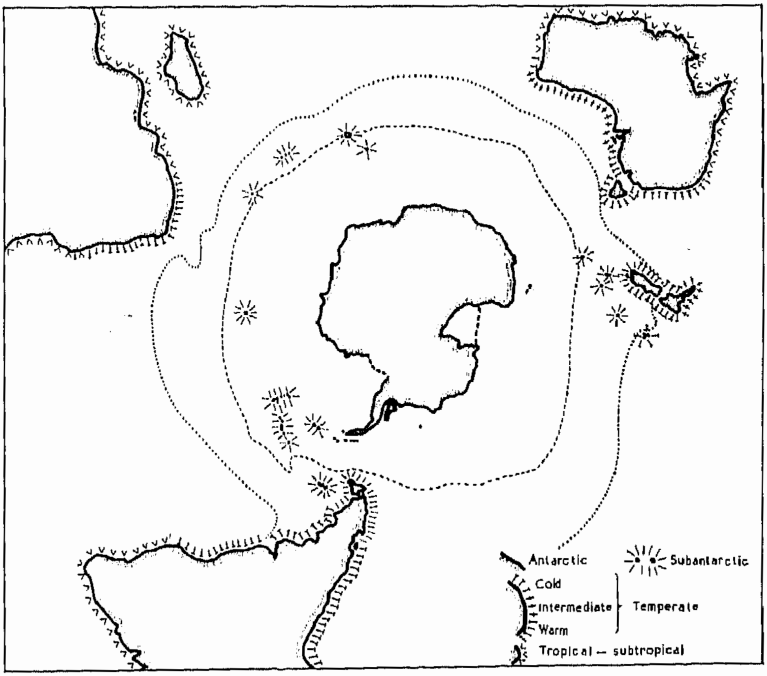

Fig. 2. The southern hemisphere, with provisional classification of intertidal floras and faunas (modified after Stephenson, 1947). The subtropical convergence is shown by a dotted line, and the Antarctic convergence by a line of dashes.

at many places and charting what was then an unknown or little known coast. Passing through Bass Strait and after a stay at Port Jackson, he sailed up the eastern coast (discovered by Cook in 1770) and charted the Gulf of Carpenteria and north-east Arnhem Land. Finding the "Investigator" in a poor state of repair, Flinders returned to Port Jackson via Timor and Cape Leeuwin, keeping clear of the land. When the "Investigator" was condemned in Port Jackson, Flinders set out for England to obtain another ship in which to complete his voyages.

His return to England was singularly ill-fated, as he suffered ship wreck off the Queensland coast and later imprisonment in Mauritius for over six years by the French.

When Flinders left for England, Brown remained to collect in New South Wales, and later spent some time on Kent's Islands, in Bass Strait. About half of the algae described by Turner came from Kent's Islands, some from Port Dalrymple, Tasmania, two from King George's Sound, and the others were labelled simply "south coast" or "north coast" of New Holland.

During the early part of the nineteenth century several French exploring expeditions visited Australia. In 1818-1819, Captain Freycinet in the "Uranie" and "Physicienne" sailed along the north-west coast of Australia spending some time in the Shark Bay region (see Freycinet, 1827). Later Freycinet visited Port Jackson and Botany Bay on the New South Wales coast, but the only algal species collected by the botanist C. Gaudichaud appear to have come from Shark Bay. They were described by C. Agardh (1821; and in Gaudichaud, 1826).

The "Astrolabe" under Dumont D'Urville visited King George's Sound in 1826, then sailed direct to Port Jackson for refitting before visiting New Zealand and various Pacific Islands. She returned to islands off north-west Australia in late 1827 and to Hobart in 1828. The naturalists were A. Lesson and A. Richard, but if collections of plants were made in Australia, they have not been described. The "Coquille" under L. J. Duperrey, with Bory de St. Vincent as naturalist, also visited Port Jackson in 1824, but collected no algae.

The "United States Exploring Expedition" of 1838-1842, under Captain C. Wilkes, visited Sydney on more than one occasion. A few species were recorded from New South Wales by Bailey and Harvey (1874), and the interesting *Notheia anomala* (a parasite on *Hormosira*) was first collected in New Zealand by this expedition.

The "Voyage of Discovery and Research in the Southern and Antarctic Regions, 1839-43", under Sir James Clark Ross, with J. D. Hooker as botanist, brought back to England the finest collection of Antarctic, New Zealand and Tasmanian plants hitherto obtained. The expedition spent two lengthy periods in Hobart, from August to November, 1840, and April to July, 1841, as well as three weeks in Port Jackson. Hooker collected algae as well as land plants in a thorough manner; the former were described by W. H. Harvey (1860) in the magnificent "Flora Tasmaniae" as well as in his "Phycologia Aus-

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The expedition of Ross culminates the first period of Australian phycology and overlaps with the second period which commences with collections sent to Harvey and Sonder from Australia. Expeditions which visited Australia after 1843 contributed little to Australian phycology, though the "Novara" expedition of 1857-59 collected a few species which were reported on by Grunow (1870).

COLLECTIONS BY AUSTRALIAN NATURALISTS AND W. H. HARVEY: THEIR DESCRIPTION BY BRITISH AND EUROPEAN ALGOLOGISTS (1840—1900)

The first collection by a resident of Australia was probably that of Charles Fraser, the colonial botanist of Sydney, from near the Swan River mouth in Western Australia. Several species were described by Greville (1830), to whom Fraser sent the collections.

In the early 1840's several naturalists in Australia commenced collecting marine algae. Information on the distribution of species also became available. In Western Australia, Dr. Ludwig Preiss collected extensively between 1838 and 1842 on the coast between Fremantle and Cape Riche (unfortunately precise localities seem unavailable, but see Gardiner 1926), resulting in the relatively comprehensive account of Sonder (1846).

The arrival of Ferdinand von Mueller in Australia in 1847 marked an upsurge in botanical work. During his first four years residence in Adelaide he collected at nearby beaches, especially on Lefevre Peninsula. In 1852 von Mueller moved to Melbourne where he became Government Botanist, collecting assiduously all groups of plants. The algae were described by Sonder (1852, 1853).

During the 1840's and 1850's several naturalists in Tasmania devoted time to the rich marine algal flora of the island, and sent their collections to W. H. Harvey, Professor of Botany in Dublin. Notable among them were Ronald Gunn (who collected between 1832 and 1850), Charles Stuart, William Archer and the Rev. J. Fereday. In Western Australia, George Clifton of Fremantle provided Harvey with abundant material.

Interest in the numerous collections from his correspondents in

Australia, together with poor health, caused Harvey to embark on an extensive visit to Australia in 1853-4. This marked a turning point in our knowledge of Australian marine algae, when for the first time an expert algologist saw the living Australian algae and collected himself. During Harvey's 18 months in Australia he collected about 600 species and 20,000 specimens, at 13 localities in south-western, south-eastern and eastern Australia. The Western Australian species were described in a preliminary account in 1854 together with ecological notes and comments on their geographical relationships. This was followed in 1858 by the first volume of his "Phycologia Australica" which was completed with Volume 5 in 1863. In these volumes some 300 species of Australian marine algae were described in detail, with locality notes and full synonomy, and a complete list of Australian algae was appended. In 1860 appeared the "Flora Tasmaniae" of Hooker, with Harvey's account of the Tasmanian algae.

Harvey, doubtless because of his field knowledge of the species, formed excellent species concepts, nearly all of which have stood the test of time. In this respect, and on account of his excellent illustrations, Harvey's work was outstanding.

The middle and latter half of the nineteenth century saw the publication of several comprehensive algal floras of the world. In 1848 the Swedish algologist, J. G. Agardh, commenced his "Species Genera et Ordines Algarum", which was to continue to 1901. Agardh described a large number of Australian species; a few were sent to him by Harvey, but most were received from Australian collectors after Harvey's death, in particular from F. von Mueller and J. Bracebridge Wilson in Victoria, and from Jessie Hussey in South Australia. Agardh's publications under the titles of "Analecta Algologica" (1892-1899) and "Till Algernes Systematik" (1873-1890) contain many descriptions of Australian species, and, of more importance, revisions of major groups. Agardh's studies were noteworthy for their morphological contributions, which helped to found the present day classification of marine algae. A particularly important monographic work was that on *Sargassum* J. G. Agardh (1889), though this genus is now in great need of revision (see Womersley, 1954.)

In Germany, F. T. Kuetzing published his "Species Algarum" in 1849 and later his massive series of 20 volumes of algal descriptions and illustrations, "Tabulae Phycologicae" (1851-71). Kuetzing described numerous Australian species, mostly from the herbarium of O. W. Sonder which is now in the Melbourne National Herbarium.

Apart from the comprehensive accounts of Sonder, Harvey, J. G. Agardh and Kuetzing, and De Toni's "Sylloge Algarum" (1889-1924) which brought together the systematic knowledge of algae to that time, publications on Australian algae in the latter part of the nineteenth and early twentieth centuries consist of lists, sometimes involving new species. These were based on collections sent to various algologists (e.g., Areschoug, 1854; A. and E. S. Gepp, 1906) and some made by expeditions visiting Australia. A number of generic revisions (e.g., Weber van Bosse, 1898, on *Caulerpa;* Kjellmann, 1900, on *Galaxaura;* Barton, 1901, on *Halimeda*) also dealt with Australian species.

Since Harvey's time there have been no accounts published of Western Australian algae until very recently. This lack of interest is remarkable in view of the early studies and the rich and varied algal flora of the Western Australian coast.

In South Australia the most important accounts are those of Reinbold from Investigator Strait (1899) and from Lacepede and Guichen Bays in the south-east of the State (1897, 1898).

In Victoria, J. Bracebridge Wilson, who was Head of Geelong Grammar School, dredged for algae near Port Phillip Heads and in Western Port for a number of years, gathering fine collections which were described by J. G. Agardh. Wilson collected many new species and genera, quite a number of which have never been recollected. Duplicate collections are in the Melbourne National Herbarium and in the British Museum. Wilson published a comprehensive list of his collections in 1892.

Little of importance on Tasmanian algae was published in the latter part of last century, and one of the few contributions on New South Wales algae is that of A. and E. S. Gepp (1906).

From tropical Australia, Montagne (1845) described algae from tiny Toud Island in Torres Strait, but the account of Sonder (1871) was the first major work. This was based mainly on north Queensland algae and was followed by his 1880 census of Australian algae. At the turn of the century several lists of Queensland algae were published by F. M. Bailey, the Queensland Government Botanist, based on De Toni's records and determinations by A. D. Cotton at Kew. Bailey (1913) brought all his Queensland records together.

THE PRESENT CENTURY, WITH STUDIES BY AUSTRALIAN ALGOLOGISTS

The present century saw the first studies of Australian algae by Australian scientists.

In 1909, A. H. S. Lucas[2], a school teacher and naturalist, turned his attention to marine algae, and until 1936 was almost the only student of Australian algae. In 1909 and 1912 he published a list of the marine algae of Australia, extracted from De Toni's "Sylloge Algarum". Unfortunately his list gave no references and distributions were severely abbreviated, making it of very limited value. Lucas later published accounts of certain genera (*Caulerpa* of Victoria, 1931a; *Spongoclonium*, 1927; *Nitophyllum*, 1926) as well as various notes and descriptions of new species. Lucas collected widely, often with his co-worker Mrs. F. Perrin from Launceston, and published in 1928 a list of Tasmanian algae. The algae of Lord Howe Island were described in 1935, and the first part of the "Seaweeds of South Australia" was published in 1936. This was the first descriptive account of any major group of Australian algae for over half a century, and was followed in 1947 by a second part on the red algae, completed by Mrs. Perrin after Lucas' death. This contains little original work, being mainly a translation of the relevant specific descriptions from De Toni, and was consequently out of date when published.

In 1938, Valerie May commenced studies on New South Wales algae, with keys (1938, 1939) to the Chlorophyta and Phaeophyta. These were followed by a number of papers on new geographical records and a revision of the Australian species of *Gracilaria* (1948).

More recently, the present author (Womersley, 1947, 1948, 1950) has studied the very rich algal flora of Kangaroo Island from ecological and systematic viewpoints. These studies have of necessity spread to the whole southern Australian coast, including Tasmania, since this comprises a well defined floristic unit. An account of the known Chlorophyta of this region has been published (Womersley, 1956b) and will be followed by accounts of the Phaeophyta and Rhodophyta. These accounts are founded on a study of the type specimens of nearly all species, together with field knowledge of the species from many localities. Revisions of several other genera have also been published

2. Additional papers by A. H. Lucas and other Australian algologists are listed in Womersley, 1950 and 1956.

(*Rivularia*, 1946; *Dictyopteris*, 1949; *Sargassum* subgenus *Phyllotrichia*, 1954b).

Guiler (1952d) has recently published a list of Tasmanian algae. This list, based only on the literature and on herbarium records, without references and with doubts about many localities, makes little advance on that of Lucas (1928). Cribb (1954a) has reported on economic survey work carried out on the extensive beds of the kelp *Macrocystis* in Tasmania, and later published some new records for the island (Cribb, 1956a).

The tropical coasts of Australia are relatively poorly known. Bailey (1913), in his "Comprehensive Catalogue of Queensland Plants", gave a complete list of the known algae of Queensland. Lucas (1931b) recorded the species of north-east Australia, and in recent years Cribb has studied the southern Queensland algae. Cribb (1954c, 1956b, 1958a,b), has commenced a series of contributions on this area and gives a bibliography of papers on Queensland marine algae. It is to be hoped that such studies on the extensive and interesting Queensland coastline will be extended.

A collection from Arnhem Land (Womersley, 1958) shows that many of the species are typical tropical or sub-tropical representatives, but also that there is a more distinctly Australian tropical element present.

Contributions to Australian algology have been made by overseas workers in recent years, mostly in revisions of groups. The Swedish algologist Kylin has dealt with many Australian species in his revisions of the Chordariales (1940) Gigartinales (1932), Rhodymeniales (1931) and Delesseriaceae (1924), and in his recent monograph on the Rhodophyta (1957). T. Levring, who visited Australia and New Zealand in 1947-8, published an account (1953) of his collections of Bangiales and Nemalionales, contributing to our knowledge of their life histories. De Toni and Forti (1923) have reported on collections from various localities in Australia and Tasmania.

GEOGRAPHICAL RELATIONSHIPS

Australia has long been recognized as possessing a particularly rich marine algal flora—rich in number of species and in unique and endemic genera. This richness, however, is largely confined to the southern coast of Australia where temperate conditions prevail. The northern coast is typically tropical with a relatively large pan-tropical element and a small group of species confined to seas north of Australia.

The algae of tropical coasts of Australia are not well known. Great lengths of coast are more or less inaccessible, on account of their great distance from cities or townships; few expeditions or individuals have collected on these tropical shores. There are no records from the north-west coast, while the north-east (Queensland) coast of over 2,000 miles in length, with the Great Barrier Reef offshore, has been studied only in isolated areas (Lucas, 1931b). Cribb (1954c, 1956b) is studying the south Queensland algal flora. The coastline of New South Wales is better known, due to the researches of Lucas (between 1909 and 1935) and May (1938 onwards).

The majority of algal collections have been made in the southern Australian region, where most of the endemic species and genera occur and where the algal flora is of especial interest. Due to this, and also because of the scanty information available from tropical Australia, this discussion will be largely confined to the southern Australian region.

The first synopsis and census of the Australian algal flora is that of Harvey (1863) who listed 719 species. Sonder (1880) extended this to 923 species, and Lucas (1909, 1912) listed about 1,250 species. Harvey and Sonder both included a few Cyanophyta, and all three authors included some records of freshwater species.

In this discussion the Cyanophyta will be omitted, since nearly all species appear to be cosmopolitan or nearly so. The group is poorly known in Australia but undoubtedly well represented. Womersley (1950) recorded 26 species from Kangaroo Island (a fraction only of those known to occur), and other records appear in the literature.

The southern Australian region, where the majority of species occur, extends from the south-west of Western Australia to about the Victorian—New South Wales border, and includes Tasmania. In analysing the flora of this region, tropical species which just extend south into this region have been excluded, while some typically southern species do extend north of these boundaries. This region is a natural one, from both the environmental and the floristic viewpoints.

A census of the southern Australian marine algal flora shows that about 1,010 species, comprising 94 Chlorophyta, 191 Phaeophyta and 725 Rhodophyta, have been described. In reaching this figure, numerous "species" have been rejected as synonyms as a result of studies of the types by the present writer. Undescribed and unrecorded species certainly number over 100 and may be much higher. It is evident, then, that a very high proportion (perhaps 75%) of the marine algae of Australia is restricted to the southern Australian region.

The relationships of many species, and records of them from other countries, must still be regarded as doubtful. Future taxonomic studies may well show that some of the Australian species recorded from other countries—such as the Arabian Sea, Malay Archipelago and Japan—are not identical but are distinct taxa. However, even though some are shown to be specifically distinct, their close relationship with the Australian species may still warrant comparison. One species in question is *Gigartina radula* (Esper) J. Agardh. The type specimen, collected by Robert Brown in Australia and passed on to Esper by Dawson Turner, is apparently lost. Since then *G. radula* has been reported in South Africa, South America and the sub-antarctic region. That these records apply to a plant identical with the Australian alga is doubtful and will remain so until true *G. radula* is better known. Recent collections of the writer include a plant apparently identical with Esper's illustration of the type, but its variation is not yet understood.

GENERIC RELATIONSHIPS OF THE SOUTHERN AUSTRALIAN ALGAL FLORA

TABLE I
GENERIC RELATIONSHIPS OF THE SOUTHERN AUSTRALIAN ALGAL FLORA

Group	Total number of genera	Number and percentage of endemic genera	Number and percentage of genera endemic to southern Australia and New Zealand
Chlorophyta	27	3 (11%)	3 (11%)
Phaeophyta	63	12 (19%)	17 (27%)
Rhodophyta	239	72 (30%)	80 (33%)
Total	329	87 (26)%	100 (30%)

Table I gives the total number of genera, the number of genera endemic to southern Australia, and the number endemic to southern Australia and New Zealand, for the three main groups of algae. The percentage of endemic genera is also given.

The number of endemic genera of Australian Chlorophyta is small; most genera are widespread, and several are truly cosmopolitan, e.g., *Ulva, Enteromorpha* and *Cladophora.* The three monotypic genera endemic to southern Australia are *Callipsygma* J. Agardh, *Rhipiliopsis* A. and E. S. Gepp and *Apjohnia* Harvey. The 27 genera of Chlorophyta represent nearly half the known genera of marine Chlorophyta. Genera well represented in southern Australia are *Bryopsis* (8 species), *Caulerpa* (19), *Chaetomorpha* (8), *Cladophora* (10 or more species) and *Codium* (14).

In the Phaeophyta, 63 genera occur in Southern Australia, of which 12 are endemic (17 including those extending only to New Zealand). Smith (1955) states there are about 195 genera and 1,000 species of brown algae, while Papenfuss (1953) gives 240 genera and 1,500 species. The genera endemic to southern Australia, with numbers of species in parentheses, are: *Bellotia* Harvey (1), *Carpoglossum* Kuetzing (3), *Chlanidophora* J. Agardh (1), *Encyothalia* Harvey (1), *Lobospira* Areschoug (1), *Myriodesma* Decaisne (8) *Philippia* Kuckuck (1), *Phyllospora* C. Agardh (1), *Polycerea* J. Agardh (2), *Scaberia* Greville (1), *Seirococcus* Greville (1), *Suringaria* Kylin (1).

In addition, *Hormosira* Endlicher (1), *Notheia* Bailey and Harvey (1), *Perithalia* J. Agardh (2), *Ptilopogon* Reinke (1) and *Xiphophora* Montagne are found only along southern Australia, in New Zealand and on associated islands. Two large genera with a majority of species in southern Australia are *Dilophus* J. Agardh (13) and *Cystophora* J. Agardh (23), while the following genera are well represented: *Dictyopteris* Lamouroux (4), *Dictyota* Lamouroux (13), *Halopteris* Kuetzing (8), *Sphacelaria* Lyngbye (12), *Sporochnus* C. Agardh (7), *Sargassum* C. Agardh (30 or more) and *Zonaria* J. Agardh (6).

The southern Australian Phaeophyta are thus noteworthy for a relatively high degree of generic endemism, and possess characteristic genera in the Sphacelariales, Dictyotales, Sporochnales and Fucales. The Dictyotales are often considered a tropical group. However, of some 20 genera and 130 species, 11 genera and 44 species occur along southern Australia where temperate conditions prevail. This is probably a higher number of Dictyotales than in any tropical region.

The highest degree of generic endemism is among the Rhodophyta which are represented by 239 genera, of which 72 (30%) are endemic to southern Australia; an additional eight extend only to New Zealand. Kylin (1957) credits the red algae with 558 genera and 3,740 species. About 43% of the known genera of Rhodophyta are thus found in southern Australia, and the number of endemic genera is remarkably high. Of the 72 endemic genera, 50 are monotypic, ten contain two species, four contain three species, five contain four species, and single genera are known with six, seven and eleven species. In 25 additional genera a majority of the species occur along southern Australia. It is evident that speciation has occurred along southern Australia to such an extent that differences have reached a generic level in many cases. May (1940, in comparing the Australian algal flora with that of other countries, omitted genera represented by two species or less. The above figures show that her conclusions are not justified; they are, in fact, almost opposite to those expressed here.

Genera of Rhodophyta endemic to southern Australia are:

NEMALIONALES:

Ardissonea J. Agardh (1)
Leptophyllis J. Agardh (1)
Tiarophora J. Agardh (1)

CRYPTONEMIALES:

Blastophye J. Agardh (1)
Epiphloea J. Agardh (2)
Gelinaria Sonder (1)
Hormophora J. Agardh (1)
Metagoniolithon W. v. Bosse (3)
Polyopes J. Agardh (1)

GIGARTINALES:

Acrotylus J. Agardh (1)
Binderella Schmitz (1)
Erythroclonium Sonder (4)
Erythronema J. Agardh (1)
Grunowiella Schmitz (1)
Hennedya Harvey (1)
Nizymenia Sonder (1)
Peltasta J. Agardh (1)
Rhabdonia Harvey (11)
Rhododactylis J. Agardh (2)
Stenocladia J. Agardh (2)
Stictosporum Harvey in J. Agardh (1)

RHODYMENIALES:

Bindera Harvey (2)
Gloiosaccion Harvey (1)
Herpophyllum J. Agardh (1)

CERAMIALES:

Ceramiaceae:

Bracebridgea J. Agardh (1)
Gattya Harvey (1)
Heterothamnion J. Agardh (1)
Lasiothalia Harvey (4)
Lophothamnion J. Agardh (1)
Muellerena Schmitz (3)
Ptilocladia Sonder (1)
Rhodocallis Kuetzing (1)
Spencerella Darbishire (1)
Thamnocarpus Harvey (4)
Warrenia Harvey in Kuetzing (1)

Dasyaceae:

Haplodosya Falkenberg (1)

Delesseriaceae:

Chauviniella Papenfuss (1)
Crassilingua Papenfuss (2?)
Halicnide J. Agardh (1)
Heterodoxia J. Agardh (1)
Sarcomenia Sonder (7, 18, sensu stricto)
Sonderella Schmitz
Womersleya Papenfuss

Rhodomelaceae:

Chiracanthia Falkenberg (2)
Cladurus Falkenberg (1)
Cliftonaea Harvey (2)
Coeloclonium J. Agardh (4)
Diapse Kylin (1)
Diplocladia Kylin (1)
Dictymenia Greville (6)
Dolichoscelis J. Agardh
Doxodasya Schmitz (3)
Echinosporangium Kylin (2)
Endogenia J. Agardh (1)
Gonatogenia J. Agardh (1)
Herpopteros Falkenberg (1)
Heterocladia Decaisne (1)
Holotrichia Schmitz (1)
Husseya J. Agardh (1)
Jeannerettia Hooker & Harvey (4)
Lophothalia Kuetzing (2)
Nematophora J. Agardh (1)
Osmundaria Lamouroux (1)
Pithyopsis Falkenberg (1)
Protokuetzingia Falkenberg (1)
Rhodolophia Kylin (1)
Thaumatella Kylin (1)
Trigenia Sonder (2)
Wilsonaea Schmitz (1)

The following genera occur only in southern Australia and in New Zealand: *Aphanocladia* Falkenberg (1), *Areschougia* Harvey (6), *Dasyphloea* Montagne (2), *Echinothamnion* Kylin (4), *Faucheopsis* Kylin (1), *Lenormandia* Sonder (7 of 10 in Australia), *Melanthalia* Montagne (4), *Phytimorphora* J. Agardh (2).

Other genera with all or a majority of their species in southern Australia are:

NEMALIONALES:

Delisea Lamouroux (3 of 4)

CRYPTONEMIALES:

Codiophyllum Grey (4 of 5)
Polycoelia J. Agardh (2 of 3)
Thamnoclonium Kuetzing (4 of 6)

GIGARTINALES:

Curdiea Harvey (4 of 7)
Dicranema Sonder (2 of 3)
Ectoclinium J. Agardh (2 of 3)
Mychodea Harvey (11 of 11)
Phacelocarpus Endl. & Diesing (5 of 8)
Rhodophyllis Kuetzing (10 of 18)
Thysanocladia Endlicher (5 of 7)

RHODYMENIALES:

Epymenia Kuetzing (5 of 8?)
Erythrymenia Schmitz (2 of 3)
Hymenocladia J. Agardh (8 of 10)

CERAMIALES:

Ballia Harvey (4 of 4)
Cronania J. Agardh (4 of 6)
Dasya C. Agardh (22 of 28?)
Halodictyon Zanardini (3 of 4)
Hypoglossum Kuetzing (9 of 14)
Kuetzingia Sonder (3 of 4)
Platyclinia J. Agardh (3 of 4)
Psilothallia Schmitz (2 of 3)
Spongoclonium Sonder (11 of 13)
Thuretia Decaisne (2 of 3)

Genera widely distributed but well represented in southern Australia include: *Antithamnion* Nageli (14 or more), *Callithamnion* Lyngbye (12 or more), *Callophyllis* Kuetzing (8), *Ceramium* Roth (20 or more), *Champia* Desveaux (6), *Chondria* C. Agardh (10?), *Cory-*

nospora J. Agardh (7?) *Gigartina* Stackhouse (14), *Gracilaria* Greville (7), *Griffithsia* C. Agardh (7), *Herposiphonia* Nageli (5 or more), *Heterosiphonia* Montagne (11), *Lithothamnion* Philippi (15), *Laurencia* Lamouroux (12?), *Lophosiphonia* Falkenberg (4 or more), *Myriogramme* Kylin (5), *Plocamium* Lamouroux (9), *Polysiphonia* Greville (28 or more) and *Spyridia* Harvey (7).

Papenfuss (1953) has listed many of the characteristic Australasian genera, of which detailed studies of life histories and systematic position are needed.

SPECIFIC RELATIONSHIPS OF THE SOUTHERN AUSTRALIAN ALGAL FLORA

TABLE II
Specific Relationships of the Southern Australian Algal Flora

Group	Total number of species	Number of endemic species	Number endemic to southern Australia and New Zealand
Chlorophyta	94	43 (46%)	47 (50%)
Phaeophyta	191	134 (70%)	145 (76%)
Rhodophyta	725	538 (75%)	597 (82%)
Total	1010	715 (71%)	789 (78%)

Table II gives the total numbers, and numbers and percentages of endemic species, for the three main groups in southern Australia.

The uniqueness of the southern Australian algal flora has been recognised since the first descriptions by European algologists. Harvey (1854) discussed the relationships of the algal flora of south-west Australia, commenting on the high proportion of endemic species and the preponderance of red algal species over those of the brown and green groups. Since that time, few attempts have been made to analyse the Australian marine algal flora, apart from the paper by May (1940).

Okamura (1930) analysed the distribution of marine algae in the Pacific region. While the regions he took are in several cases too wide (e.g., the Australian region includes the whole of Australia, New Zealand and associated islands, and the sub-antarctic islands), his conclusions show the distinctiveness of the Australian region and its very high degree of endemism. Okamura listed 1,610 species from the Australian region, of which 925 were endemic. The great majority of these are confined to southern Australia, as is shown by Table II where, of

1,010 species, 715 (71%) are endemic. From the whole western coast of North and South America, Okamura listed 1,185 species with 715 (60%) endemic, and only 36 endemic genera compared with 103 from his Australian region. Dawson (1947) records 323 genera and 1,262 species of green, brown and red algae from the Pacific coast of North America. This coast covers 6,500 miles from the cold waters of the Aleutian Islands to the tropical waters of the Gulf of Panama, yet the numbers of both genera and species are closely comparable to those from southern Australia. There are, however, some striking differences in the numbers of genera in different taxonomic groups. In the Phaeophyta, the Pacific North American coast is noted for the numerous small genera of Laminariales, whereas southern Australia has very few Laminariales but several distinctive genera of Fucales. In the Rhodophyta, the Pacific North American coast is particularly rich in Cryptonemiales and Gigartinales, whereas southern Australia is poorly represented in these groups but rich in Ceramiales. The eastern coast of North America is much poorer in genera and species of marine algae. Taylor (1957) records only 171 genera and 402 species from this region. Okamura credited the relatively distinct Japanese region with 864 species, of which 310 (36%) were endemic and only 12 endemic genera.

Okamura considered Australasia "a very distinct region surpassing all others in the astonishing number of endemic genera and endemic species and in the great number of species". Okamura's conclusions are amply supported by the present analysis, and it is further evident that southern Australia is the region of greatest endemism. The degree of endemism here is probably higher than in any other part of the world.

Okamura also listed the number of species common to the Australian region and other parts of the world. In doing so he included cosmopolitan or widely distributed species. A better index of the relationships of the southern Australian algae with other regions is obtained if such widely distributed species are eliminated, leaving only the typically Australian species found also in other regions. This has been done below, but relationships within Australia will first be discussed.

RELATIONSHIPS OF THE MARINE ALGAL FLORA WITHIN AUSTRALIA

The algal flora of northern Australia comprises a large pan-tropical element and a small element of species restricted to seas north of Australia (Sonder, 1871; Womersley, 1958). This latter group includes *Anadyomene brownii* (Gray) J. Agardh, *Avrainvillea erecta* (Berkeley) A. and E. S. Gepp, *Dasycladus australasicus* (Sonder) Cramer, *Padina australis* Hauck, *Sargassum decurrens* (R. Br.) C. Agardh, *S. fissifolium* (Mert.) J. Agardh, *S. flavicans* (Mert.) C. Agardh, *S. fragile* J. Agardh, *S. godeffroyi* Grunow, *S. peronii* (Mert.) C. Agardh, *Scinaia moretonensis* Levring and *Hypnea divaricata* (Turner) Greville.

Sonder (1871) recorded 168 species from north Australia, comprising 41 Chlorophyta, 43 Phaeophyta and 84 Rhodophyta. Probably some 200 species could now be recorded from these coasts. The proportions of the three main groups show marked differences from those in southern Australia—that of the Chlorophyta being higher and that of the Rhodophyta much lower. Sonder recorded a number of southern Australian species from tropical Australia, but all such records need re-examination. A few instances of tropical species occurring in isolated areas along southern Australia are discussed below.

The algal flora of the coast of western Australia north of Fremantle is poorly known, since only fragmentary collections have been made. Many of the typically southern Australian species do not reach Fremantle—Cape Leeuwin or Cape Naturaliste may be limiting points in some cases—though a few reach as far north as Geraldton. Several tropical species (e.g., *Eucheuma speciosum*) reach south to Rottnest Island and a very few extend south as far as King George's Sound (*Caulerpa racemosa* var. *laetevirens*, *Halimeda cuneata*). Most of the species of the south-west corner of Western Australia, however, appear to be typically southern Australian. Farther north, at Geraldton, the flora is sub-tropical, while at the Abrolhos Islands (some 60 miles off the coast from Geraldton) typical coral reefs are found. A detailed analysis of the algal flora of the whole west Australian coast would be of considerable interest.

The eastern coast of Australia is better known than the west, due to the work of F. M. Bailey and A. B. Cribb in Queensland and of A. H. S. Lucas and V. May in New South Wales. The Queensland coast is tropical or sub-tropical, but few areas have been studied in any detail. Along the New South Wales coast, a grading occurs from the Victorian to Queensland border. Many southern Australian species do not extend into New South Wales. Others, e.g., *Durvillea potatorum*, extend a short distance, while *Phyllospora comosa* occurs as far north as Grants Head and *Ecklonia radiata* as far as the Queensland border. (Dakin, Bennett and Pope, 1948). The New South Wales coast is, in general, warm temperate under the influence of the warm Notonectian current. Adequate data are not available for a more detailed analysis of the algal flora of eastern Australia.

RELATIONSHIPS OF THE ALGAL FLORA WITHIN SOUTHERN AUSTRALIA

TABLE III

RELATIONSHIPS OF SPECIES WITHIN THE SOUTHERN AUSTRALIAN REGION

Group	Total	"Cosmo-politan"	Southern Australian	Eastern	Western	Endemic to So. Aust.
Chlorophyta	94	22 (23%)	25 (27%)	28 (30%)	11 (12%)	8
Phaeophyta	191	24 (13%)	56 (29%)	87 (46%)	24 (13%)	?
Rhodophyta	725	39 (5%)	240 (33%)	312 (43%)	130 (18%)	4+
Total	1010	85 (8%)	321 (32%)	427 (42%)	165 (16%)	12+

Table III gives an analysis of the southern Australian algal flora, divided into the following elements:

1. A cosmopolitan element of widely distributed, though rarely truly cosmopolitan, species which occur generally along southern Australia.
2. A "southern Australian element" of species restricted to southern Australia and found generally from south-west Western Australia to Victoria and/or Tasmania.
3. An "eastern element" of species apparently confined to the Victorian—Tasmanian region, often extending as far as Robe in South Australia or to Kangaroo Island.
4. A "western element" of species confined to the western regions; some extend as far east as Kangaroo Island, but not into Victoria.
5. A small group of species known only from South Australia. Several species of Phaeophyta and Rhodophyta in this group have yet to be described. Future collections may well place many of these species in either the eastern or western groups.

Of the cosmopolitan species, the Chlorophyta contain the highest proportion, and the Rhodophyta the lowest proportion but the highest number. The 85 cosmopolitan species form a small proportion (8%) of the total number of species.

The southern Australian element comprises a somewhat similar proportion in each group, and coupled with the cosmopolitan group shows that some 40% of the total number of species occur generally along southern Australia.

The eastern element is the largest, comprising 46% of the Phaeophyta, 43% of the Rhodophyta and 30% of the Chlorophyta. This may be correlated with the slightly cooler sea temperatures on the Victorian and Tasmanian coasts. Together with the cosmopolitan and southern Australian elements, about 82% of the total algal flora occurs in the eastern part of the southern Australian region. The extreme richness of this eastern region is apparent.

There seems to be no justification as yet for separating the Victorian and Tasmanian coasts, as most species live in both States. Southern Tasmania probably has a small group of more restricted species, e.g., *Codium dimorphum* Svedelius.

The western element is relatively small but still appreciable, amounting to some 16% of the total. Thus about 56% of the southern Australian algal flora occurs in the western half of southern Australia.

Very few species appear to be endemic to the central part of southern Australia. Several Chlorophyta have been described recently (Womersley, 1955) and some 30 or 40 Phaeophyta and Rhodophyta remain undescribed. It is likely, however, that many of these will prove to be more widely distributed.

It is evident, then, that the southern Australian region shows a very high degree of endemism in its rich algal flora. A high proportion of the species occurs all along southern Australia, a large element is confined to the eastern half where sea temperatures are lower, and a smaller element is confined to the western half. The eastern and western elements overlap in the region of Kangaroo Island, which has a particularly rich marine algal flora (Womersley, 1947, 1950).

RELATIONSHIPS OF THE SOUTHERN AUSTRALIAN ALGAL FLORA WITH OTHER PARTS OF THE WORLD

Small but appreciable numbers of species of the southern Australian algal flora are also found in other parts of the world. Table IV gives the numbers of species recorded from other regions of interest, after eliminating cosmopolitan species. In certain cases, these records may be due to faulty identification, but this is unlikely to diminish the numbers very much. Even though future study shows some records incorrect, close specific relationships may still be apparent.

TABLE IV

SOUTHERN AUSTRALIAN SPECIES RECORDED FROM OTHER PARTS OF THE WORLD, EXCLUDING COSMOPOLITAN OR WIDELY DISTRIBUTED SPECIES

Group	Sub-antarctic	So. Africa	Arabian Sea	Malay Archipelago	Japan	Tropics	New Zealand
Chlorophyta	3	5	1	5	5	3	8
Phaeophyta	6	6	4	7	3	2	17
Rhodophyta	12	12	22	23	26	9	70
Total	21	23	27	35	34	14	95

Species with Sub-Antarctic Distribution

The following sub-antarctic species occur mainly in the eastern part of the southern Australian region, though a few extend along most of the coast. The element is a small one, and most species are at the northern limit of their distribution.

CHLOROPHYTA: *Codiolum kuckuckii* Skottsb. and Levring, *Enteromorpha bulbosa* (Suhr.) Mont., *Chaetomorpha darwinii* (Hook.) Kuetz.

PHAEOPHYTA: *Halopteris funicularis* (Mont.) Sauv., *H. hordacea* (Harv.) Sauv., *Adenocystis utricularis* (Bory) Skottsb., *Scytothamnus australis* (J. Ag.) H. and H., *Macrocystis pyrifera* (L.) Ag.

RHODOPHYTA: *Porphyra columbina* Mont., *Delisea pulchra* (Grev.) Mont., *Chaetangium fastigiatum* (Bory) J. Ag., *Lithothamnion antarcticum* (H. and H.) Heydr., *L. patena* (H. and H.) Heydr. *Griffithsia antarctica* H. and H., *Ballia callitricha* (Ag.) Mont., *B. scoparia* (H. and H.) Harvey, *Lophurella hookeriana* (J. Ag.) Falk., *Polysiphonia abscissa* H. and H., *Dipterosiphonia dendritica* (Ag.) Falk., *D. heteroclada* (J. Ag.) Falk.

Durvillea antarctica (Cham.) Hariot has also been recorded in drift in Tasmania and south-west Australia (Moore and Cribb, 1952), and old fragments have been found on Kangaroo Island coasts, but that it grows on the Australian coastline is very doubtful.

Species in South Africa

Some 21 species in southern Australia are known also from South Africa, including a few sub-antarctic species. In addition, var. *denticulata* of *Caulerpa scalpelliformis* occurs in South Africa while the species is common in southern Australia, and the South African *Martensia elegans* Hering is known from eastern Australia. A second species of the South African genus *Pseudocodium* has also been described recently from Australia (Womersley, 1955).

CHLOROPHYTA: *Cladophora rugulosa* Martens, *Codium duthiae* Silva, *C. lucasii* Setchell, *C. spongiosum* Harvey.

PHAEOPHYTA: *Sphacelaria novae-hollandiae* Sonder, *Zonaria crenata* J. Ag., *Myriogloia sciurus* (Harv.) Kuck., *Splachnidium rugosum* (L.) Grev., *Macrocystis angustifolia* Bory, *Ecklonia radiata* (Turn.) J. Ag.

RHODOPHYTA: *Pterocladia lucida* (R. Br.) J. Ag., *Jania fastigiata* Harvey, *J. natalensis* Harvey, *Polyopes constrictus* (Turn.) J. Ag., *Phacelocarpus labillardieri* (Mert.) J. Ag., *Hypnea episcopalis* Harvey, *H. hamulosa* (Esper) Mont., *Champia compressa* Harvey, *Perischelia glomerulifera* J. Ag., *Botryoglossum cartilagineum* (Harv. and Grev.) Pap., *Placophora binderi* J. Ag.

Species in the Arabian Sea

Borgesen (1934 and earlier papers) has recorded 27 southern Australian species from the Arabian sea region, as well as some from tropical Australia. The majority of these 27 species are Rhodophyta.

CHLOROPHYTA: *Caulerpa scalpelliformis* (R. Br.) Ag. var. *denticulata* (Dcne.) W. v. B.

PHAEOPHYTA: *Dictyopteris australis* (Sond.) Asken., *Myriogloia sciurus* (Harv.) Kuckuck, *Sporochnus radiciformis* (R. Br.) Ag., *S. scoparius* Harvey.

RHODOPHYTA: *Helminthocladia australis* Harvey, *Corallina pilifera* Lamx., *Jania natalensis* Harvey, *Cryptonemia undulata* Sonder, *Sarconema filiforme* (Sond.) Kylin, *Solieria compressa* (J. Ag.) Kylin, *S. robusta* (Grev.) Kylin, *Hypnea hamulosa* (Esper) Mont., *Coelarthrum muelleri* (Sond.) Borg., *Rhodymenia australis* (Sond.) Harvey, *Griffithsia crassiuscula* Ag. *Haloplegma preissii* Sonder, *Ceramium miniatum* Suhr, *Heterosiphonia muelleri* (Sond.) De Toni, *Hypoglossum spathulatum* (Sond.) J. Ag., *Claudea elegans* Lamx., *Martensia elegans* Hering, *Falkenbergia rufolanosa* (Harv.) Schmitz, *Acanthophora dendroides* Harvey, *Laurencia cruciata* Harvey, *L. filiformis* (Ag.) Mont., *L. majuscula* (Harv.) Lucas.

Species in the Malay Archipelago

A comprehensive account of the marine algae of this region is given by Weber van Bosse (1928 for floristic lists) who includes 35 southern

Australian species and also about ten other species from tropical Australia.

CHLOROPHYTA: *Chaetomorpha valida* (H. and H.) Kuetz., *Caulerpa papillosa* J. Ag., *C. scalpelliformis* (R. Br.) Ag., var. *denticulata* (Dcne.) W. v. B., *C. sedoides* (R. Br.) Ag., *C. simpliciuscula* (Turn.) Ag.

PHAEOPHYTA: *Sphacelaria novae-hollandiae* Sonder, *Dictyota apiculata* J. Ag., *D. robusta* J. Ag., *Dictyopteris muelleri* (Sond.) Schmidt, *Zonaria crenata* J. Ag., *Polycerea nigrescens* (Harv.) Kylin, *Sargassum spinuligerum* Sonder.

RHODOPHYTA: *Liagora australasica* Sonder, *Epiphloea bullosa* (Harv.) Schmitz, *Carpopeltis phyllophora* (H. and H.) Schmitz, *Peyssonnelia gunniana* J. Ag., *Ethelia australis* (Sonder) W. v. B., *Melobesia coronata* Rosanoff, *Corallina pilifera* Lamx., *Thysanocladia laxa* Sonder, *Solieria robusta* (Grev.) Kylin, *Hypnea charoides* Lamx., *H. hamulosa* (Esper) Mont., *Rhodymenia australis* (Sond.) Harvey, *Cronania australis* (Harv.) J. Ag., *Wrangelia velutina* Harvey, *Ceramium isogonum* Harvey, *Heterosiphonia muelleri* (Sond.) De Toni, *Hypoglossum spathulatum* (Sond.) J. Ag., *Myriogramme erosa* (Harv.) Kylin, *Claudea elegans* Lamx., *Polysiphonia mollis* H. and H., *Acanthophora dendroides* Harvey, *Laurencia clavata* Sonder, *L. forsteri* (Mert.) Grev.

Species in Japan

Okamura (1930) and later accounts by other Japanese algologists record 34 southern Australian species from Japan. Several of these records, however, need verification.

CHLOROPHYTA: *Cladophoropsis herpestica* (Mont.) Howe, *Codium lucasii* Setchell, *Caulerpa scalpelliformis* (R. Br.) Ag., *C. sedoides* (R. Br.) Ag. *Cladophora rugulosa* Martens is also found in Japan and south-west Australia.

PHAEOPHYTA: *Zonaria diesingiana* J. Ag., *Sporochnus radiciformis* (R. Br.) Ag., *S. scoparius* Harvey.

RHODOPHYTA: *Corallina pilifera* Lamx., *Halymenia harveyana* J. Ag., *Tylotus obtusatus* (Sond.) J. Ag., *Plocamium costatum* (Ag.) H. and H., *P. leptophyllum* Kuetz., *Solieria robusta* (Grev.) Kylin, *Mychodea membranacea* H. and H., *Coelarthrum muelleri* (Sond.) Borg., *Champia compressa* Harvey, *Callithamnion pulchellum* Harvey, *Haloplegma preissii* Sonder, *Antithamnion gracilentum* (Harv.) J. Ag., *Wrangelia velutina* Harvey, *Dasya naccarioides* Harvey?, *D. villosa* Harvey?, *Acrosorium ciliolatum* (Harv.) Kylin, *Chondrophyllum monanthos* (J. Ag.) Kylin?, *Martensia australis* Harvey, *Falkenbergia rufolanosa* (Harv.) Schmitz, *Polysiphonia cancellata* Harvey, *P. mollis* H. and H., *Chondria lanceolata* Harvey, *Laurencia forsteri* (Mert.) Grev., *L. majuscula* (Harv.) Lucas, *Lophosiphonia calothrix* (Harv.) De Toni, *Euzoniella flaccida* (Harv.) Falk.

Relationships with New Zealand

Southern Australia has more species in common with New Zealand than with any other country. The lists of Laing (1926, 1929, 1939), Lindauer (1947) and Chapman (1956) give some 98 southern Australian species occurring in New Zealand, comprising 11 Chlorophyta, 17 Phaeophyta and 70 Rhodophyta. Some of these records may be queried (see Lindauer, 1953: 20), but future studies will probably increase the numbers. While the numbers of species common to southern Australia and New Zealand (excluding cosmopolitan) are larger than elsewhere, they are still less than 10% of the total southern Australian algal flora. It is evident that the separation of Australia and New Zealand by some 1,000 miles of ocean has resulted in their algal floras being isolated to a fairly high degree.

The external distribution of the marine algae of New Zealand was analysed by Laing (1927), but this account is in need of revision in view of recent taxonomic work in New Zealand.

Tropical Species along Southern Australia

Some 14 tropical or sub-tropical species occur in isolated areas along southern Australia, usually on reefs or in rock pools where temperatures in summer may rise to sub-tropical levels (20-25°C) during the day. A few species are widespread along the coastline but best developed where warmer conditions prevail.

CHLOROPHYTA: *Chaetomorpha indica* Kuetzing, *Bryopsis indica* A. and E. S. Gepp, *B. pennata* Lamx.

PHAEOPHYTA: *Pocockiella variegata* (Lamx.) Pap., *Cystophyllum muricatum* (Turn.) J. Ag.

RHODOPHYTA: *Asparagopsis taxiformis* (Del.) Coll. and Herv., *Liagora farinosa* Lamx., *Lithothamnion erubescens* Foslie ?, *L. indicum* Foslie, *Amphiroa anceps* (Lamk.,) Dcne., *Griffithsia tenuis* Ag., *Haloplegma duperreyi* Mont., *Taenioma perpusillum* J. Ag., *Caloglossa leprieurii* (Mont.) J. Ag.

A recently described species of the tropical genus *Dasycladus* (Womersley, 1955) from near the head of the Great Australian Bight also indicates the slight sub-tropical element in the southern Australian flora.

Unusual and Isolated Records

A few species have been recorded from southern Australia which are known only from far distant parts of the world. Such are *Gayella polyrhiza* Rosenvinge from Greenland and Alaska, recently recorded from Kangaroo Island (Womersley, 1956), and *Colaconema americana* Jao from Massachusetts, recorded by Levring (1953) from Kangaroo Island and the Murchison River mouth, Western Australia. Future studies may show such species to be much more widely distributed.

POSSIBLE CAUSES OF THE EXTRA-AUSTRALIAN DISTRIBUTION OF SOUTHERN AUSTRALIAN SPECIES

The occurrence of some southern Australian species in New Zealand and the presence of a few sub-antarctic species along southern Australia present no unusual distribution problems. The presence of southern Australian species in regions across the Indian Ocean and in Japan is, however, of considerable interest. Most of the species concerned were known first from Australia and are common along the southern Australian coastline, whereas many of the records from other countries are based on isolated collections.

It is possible that these species have been common to Australia and other countries for long ages, and their description from Australia first is purely chance. On the other hand, it does appear possible, if not likely, that there has been a spread of southern Australian species across the Indian Ocean to Japan, occurring perhaps in the last hundred years. There seems to be no evidence, however, of characteristic Indian, Malayan or Japanese species being on Australian coasts, but a few South African species (e.g., *Cladophora rugulosa, Botryoglossum cartilagineum, Placophora binderi*) have been found in southern and western Australia in recent years. These South African species are apparently rare in Australia.

If these species have been present in Australia and in other countries for long ages, they may be regarded as cases of discontinuous distribution. Continental drift and former land connections in past geological ages have been suggested as possible causes of such distribution (Svedelius, 1924; Borgesen, 1934; Chapman, 1953). The number of species involved, however, is comparatively small, and it probably is unwise to suggest continental drift as an explanation of the distribution of species living in the oceans connecting land masses.

If this spread of Australian algae has occurred in relatively recent years, the following means may be involved:

1. Transport by Ocean Currents

A surface current (Sverdrup et al, 1942) passes northwards along the Western Australian coast, swings westward to form the equatorial current, then southward to join the Agulhas current on the east coast of South Africa. Many current systems of varying directions are involved north of Australia. Establishment of algae from spores or fragments carried in currents is dependent on two factors:

1. The life of a drifting fragment or spore. Although little is known of this aspect, floating fragments or spores are unlikely to live long. Slow spread of species around coastlines undoubtedly occurs, but spread by currents across wide oceans is most unlikely.
2. The ocean temperature. Tropical waters are usually considered a strong barrier to the spread of species from colder waters. This is generally true and therefore makes the occurrence of southern Australian species in the tropics and northern hemisphere so remarkable.

   Water temperatures along southern Australia range from 10 to 15°C in winter, to 16 to 19°C in summer. South African temperatures show similar ranges, while Borgesen gives an annual range of about 22—25°C for the Arabian sea and refers to the possibility of upwelling of colder water from moderate depths. The Malay Archipelago has tropical conditions, with temperatures much higher than those in southern Australia, while Japanese temperatures are similar to those in southern Australia but show a much greater range.

It seems unlikely that the spread of southern Australian species has been due to ocean currents. Between South Africa and Australia the west-wind drift, with similar sea temperatures throughout, does offer greater possibilities of algal spread, but whether species might survive such passage is undetermined.

2. Carriage by Shipping

It is well known that numerous algal species, particularly cosmopolitan forms, grow on the hulls of ships. A well established case of spread cies involved, however, is comparatively small, and it probably is unwise to suggest continental drift as an explanation of the distribution of species living in the oceans connecting land masses.

If this spread of Australian algae has occurred in relatively recent years, the following means may be involved:

1. Transport by Ocean Currents

A surface current (Sverdrup et al, 1942) passes northwards along the Western Australian coast, swings westward to form the equatorial current, then southward to join the Agulhas current on the east coast of South Africa. Many current systems of varying directions are involved north of Australia. Establishment of algae from spores or fragments carried in currents is dependent on two factors:

1. The life of a drifting fragment or spore. Although little is known of this aspect, floating fragments or spores are unlikely to live long. Slow spread of species around coastlines undoubtedly occurs, but spread by currents across wide oceans is most unlikely.
2. The ocean temperature. Tropical waters are usually considered a strong barrier to the spread of species from colder waters. This is generally true and therefore makes the occurrence of southern Australian species in the tropics and northern hemisphere so remarkable.

   Water temperatures along southern Australia range from 10 to 15°C in winter, to 16 to 19°C in summer. South African temperatures show similar ranges, while Borgesen gives an annual range of about 22—25°C for the Arabian sea and refers to the possibility of upwelling of colder water from moderate depths. The Malay Archipelago has tropical conditions, with temperatures much higher than those in southern Australia, while Japanese temperatures are similar to those in southern Australia but show a much greater range.

It seems unlikely that the spread of southern Australian species has been due to ocean currents. Between South Africa and Australia the west-wind drift, with similar sea temperatures throughout, does offer greater possibilities of algal spread, but whether species might survive such passage is undetermined.

2. Carriage by Shipping

It is well known that numerous algal species, particularly cosmopolitan forms, grow on the hulls of ships. A well established case of spread by shipping is that of the southern Australian *Asparagopsis armata* Harvey, which became established in the Mediterranean in 1925 (see Svedelius, 1933) and has since spread to Britain. This species is well adapted to become attached to the hulls of ships or to other algae already growing on a hull, by means of its spinous branches, and it is known that many Florideae can regenerate from quite small fragments (Fritsch, 1945: 13).

There are direct shipping routes between southern Australia and South Africa, India, Malaya and Japan, by which spores or fragments attached to ships could be transported through the tropical barrier in a short time. The route to South Africa does not involve passing through warmer waters.

Carriage by ships seems to be a more likely means of the spread of southern Australian algal species than any other. It is surprising, however, that species from the Arabian Sea, Malay Archipelago or Japan have not been found in Australia. Future investigations may well reveal such species on the western coast of Australia. An examination during dry-docking of the hulls of passenger liners which cross the Indian Ocean would be of interest in showing species which do become attached.

3. Spread by Migratory Sea Birds

Spread by migratory sea birds is a distinct possibility in certain cases, but little is known of it. The occurrence of *Gayella polyrhiza* on Kangaroo Island associated with bird colonies well above high tide level may be due to migratory birds.

INTERTIDAL ECOLOGY

There is little ecological information in early papers on Australian marine algae, though Harvey (1858-63) often gives habitat-notes with his descriptions in "Phycologia Australica." Other papers published before 1920 are almost entirely systematic accounts only.

In recent years intertidal ecology in Australia has developed strongly, though the number of workers in the field is still small. The account by Pope (1943) of the animal and plant communities on a rock platform at Long Reef in New South Wales led to a general account of the coastline (Dakin, Bennett and Pope, 1948). Bennett and Pope (1953) later expanded their surveys to the Victorian coastline.

In South Australia, Womersley (1947) gave a preliminary account of the marine algal ecology of Kangaroo Island, followed by more detailed accounts of Pennington Bay (exposed rock platforms) and American River inlet (calm sandy-muddy tidal flats) (Womersley, 1948, 1956 respectively). Edmonds (1948) discussed the fauna of Pennington Bay rock platforms. A recent paper (Womersley and Edmonds, 1958) gives a general account of the ecology of the South Australian intertidal region.

In Tasmania, Guiler (1950, 1951a, 1951b, 1952a, 1952b, 1952c, 1953a, 1953b, 1954, 1955) published a series of papers on selected areas in the south and south-eastern parts of the island, and Cribb (1954) described the ecology of Port Arthur. A general account of the inter-tidal ecology of Tasmania, as a whole, would be of interest, as nothing is known of the northern and western coasts and of their relation to the Victorian coasts.

Recently Endean, Kenny and Stephenson (1956) have described the intertidal ecology of Queensland rocky coasts, and of certain islands, both continental and coral, off the coast (Endean, Stephenson and Kenny, 1956).

Notes on some aspects of Australian algal ecology are given by Newton and Cribb (1951).

Three facts stand out in marine ecological studies in Australia:

1. A comparatively small amount of the Australian coastline has been studied, few detailed surveys have been attempted, and general accounts are often based on widely spaced areas. This is inevitable when the distances involved are considered, and the studies that have been published are most valuable accounts in view of the difficulties. The marine ecology of the coast of tropical Australia (apart from eastern Queensland) and most of that of Western Australia is virtually unknown, as is that of most of north and west Tasmania. These coasts comprise over half of the total Australian coastline.

2. With the exception of Womersley and Cribb, all authors on intertidal ecology in Australia have been zoologists. As a result, most accounts are somewhat inadequate so far as the algae are concerned. While attempts have always been made to deal with the algae, the accounts range from that of Dakin, Bennett and Pope (1948) on the New South Wales coast to that of Endean, Kenny and Stephenson (1956) in Queensland, who state that they have been "concerned primarily with faunistic elements and, apart from a noting of the position

of the 'algal zone' at each locality, the flora has received a cursory treatment".

The early study by Womersley (1947) of the intertidal ecology of Kangaroo Island was confined to the marine algae, since faunistic studies were not sufficiently advanced. It suffers from lack of a balanced account of the distribution and zonation of both algae and animals, but a general account of South Australian coasts (Womersley and Edmonds, 1958) rectifies this.

Few marine ecological studies anywhere have been undertaken by both competent botanists and zoologists. While this may be unavoidable in many cases, more effort is needed to provide better balanced accounts of intertidal areas.

3. The accounts of the Victorian, New South Wales and Queensland coasts are all confined to rocky coasts and appear to deal largely with the more exposed areas. While rocky coasts may constitute a large proportion of the coastline of these States, accounts of sheltered areas and other sub-strata—bays, estuaries, etc.—are needed to give a comprehensive picture of the eastern and south-eastern Australian coastlines.

Womersley (1955) has described such an area of sheltered coast, with sandy or muddy intertidal flats, on Kangaroo Island, as has Guiler (1951a) in Tasmania. In the State of South Australia, which includes the extensive Gulf Region, sheltered localities are of considerable extent and importance (Womersley and Edmonds, 1958).

An aspect that should receive greater attention is the distribution of organisms below the intertidal region. Most accounts are confined to the region from just below extreme low tide upwards.

In outlining the state of our knowledge of Australian intertidal ecology, the coastline can conveniently be divided into tropical—subtropical and temperate coasts. The studies made within each State, usually by a particular group of workers, will be discussed, and the biogeographical provinces will be described later.

TERMINOLOGY AND NOMENCLATURE

Within the intertidal and sub-tidal regions, three main zones are distinguished on the basis of the organisms present, correlated with tidal factors and the degree of roughness.

The supralittoral zone extends from the top of the littoral zone to the upper limit of marine organisms. On many coasts the lower part of the supralittoral is dominated by littorinid snails.

The littoral zone is essentially the region subject to alternating exposure to air and coverage by water to a degree that is significant to the organisms present. It extends from the sub-littoral to about high water level or to the upper limit of prevalent wave wash. The upper level corresponds on many coasts to the upper limit of barnacles, which is frequently also about the lower limit of littorinids.

Within the littoral, three sub-zones can be conveniently distinguished on most Australian coasts—upper, mid and lower littoral zones.

The sub-littoral zone is normally submerged, and only occasionally, as during a very low tide or the suck-back of waves, are organisms of this zone exposed to the air. The upper limit on many cold temperate coasts is placed at the top of the zone of Laminariales; on other coasts different indicator organisms can usually be used to fix the limit. Often the littoral—sub-littoral boundary corresponds to about mean low water neaps, but it varies with tidal conditions, degree of roughness and air conditions.

In general, the short or momentary degree of air exposure is not significant to organisms which are typically submerged forms. The Laminariales as a group appear to be of this type, and where they occur they are by far the most useful indicators of the littoral—sub-littoral boundary.

In Southern Australia, certain Fucales have been used in fixing the upper limit of the sub-littoral (Womersley and Edmonds, 1958). Various species of *Cystophora* in southern Australia and of *Durvillea potatorum* in Tasmania have been used in this way. The Fucales, however, are a group which is variously adapted to air exposure. In the cold temperate northern hemisphere they are usually thought of as mainly an intertidal group, but in southern Australia only one species is essentially intertidal—*Hormosira banksii*. In New Zealand several Fucales inhabit the lower littoral, notably *Durvillea antarctica, Xiphophora chondrophylla* var. *maxima* and *Carpophyllum maschalocarpum*. Caution is therefore necessary in using Fucales in comparing zonation in different countries.

The uppermost part of the sub-littoral is exposed between waves at low tide on rough coasts or at very low spring tides, and may show a distinctive zone of organisms, the dominants of which are restricted to this region. The term "sub-littoral fringe" was first used by Stephenson (1939: 502) for this zone and was strictly defined as covering only this region (See also T. A. and A. Stephenson, 1949). This fringe zone is a reality on sub-tropical and warm temperate South African coasts, but not on the cold temperate west coast of South Africa (Stephenson, 1944: 330) where laminarians extend down for some distance. The fringe zone is in general not distinct on coasts where Laminariales dominate the upper sub-littoral, but the term has been misapplied to such coasts. This is probably due to the Stephensons' (1949) unfortunate mention of laminarians in their Fig. 3, explaining the terms. In South Australia, very rough coasts do show a distinct sub-littoral fringe dominated by *Cystophora intermedia*, but not calmer coasts, or Victorian and Tasmanian rough coasts where *Durvillea potatorum* dominates the upper sub-littoral to well below lowest tide level.

"Sub-littoral fringe" is a distinctly useful term when strictly applied in the original sense of the Stephensons, but it is clearly not one of "universal" application. It is particularly regrettable that its meaning has been distorted by some authors to be synonymous with "upper sub-littoral."

The terminology used in this paper is applicable to any type of shore sub-stratum, from rocky to muddy.

The vast majority of authors, especially botanists, have used essentially this terminology for many years and there has been little confusion (Womersley and Edmonds, 1952, 1958). In Australia in recent years it has been employed by Dakin, Bennett and Pope (1948) in New South Wales, by Bennett and Pope (1953) in Victoria, by Cribb (1954b) in Tasmania, and by Womersley and Edmonds (1958) and Womersley (1956a and earlier papers) in South Australia. The only dissentant has been Guiler in Tasmania.

T. A. and A. Stephenson (1949) proposed a new nomenclature for the general zonation which has been recognised on many coastlines throughout the world. Womersley and Edmonds (1952) discussed these changes and advocated retaining the previously reasonably well understood nomenclature. They objected in particular to the Stephensons' new use of "mid littoral" which corresponds almost exactly to the "littoral" of most authors on marine ecology. The Stephensons have been supported in part by Chapman and Trevarthen (1953) and Guiler (1953a), and have been followed by some other authors. Hedgpeth (1957a), however, reports that a Committee of the Geological Society of America, after several years of discussion, advocates terminology essentially similar to that used in this account. Doty

(1957) has also discussed at length the zonation of organisms on rocky intertidal surfaces, and analyses the nomenclature and terminology. He supports in large measure the older scheme. Even when the Stephensons' new nomenclature is followed, comments are frequently made, pointing to the advantages of the older scheme (e.g., Batham, (1956) and Dellow, 1955: 20, in New Zealand). Chapman (1956: 335) returns to the older nomenclature but not the following year (1957). In South Africa, Isaac (1949) also uses "littoral" in the older sense.

Differences of opinion between marine ecologists are not with the facts of zonation but mainly with nomenclature, the purpose of which is to facilitate understanding and comparison of different areas. Any names can be applied and not alter the facts, but it is regrettable when new names are introduced with meanings radically different from that of previously well understood terms e.g., "littoral" and "mid-littoral". The older nomenclature supported here is by far the most satisfactory, and it is hoped that it will be generally applied by marine ecologists.

TROPICAL—SUB-TROPICAL COASTS

Here are included the coasts of northern Australia, western Australia as far south as Geraldton (with tropical influence to Fremantle) and of eastern Queensland to a point somewhat north of the Queensland—New South Wales border.

Coral Reefs

Coral reefs occur scattered around tropical Australia, from Houtman's Abrolhos in the west to the southern end of the Great Barrier reef in Queensland. Fairbridge (1950) maps their occurrence, though virtually no information on the algal ecology is available for those in western and northern Australia. Stephenson, Stephenson, Tandy and Spender (1931), however, give a good account of the ecology of selected parts of the Great Barrier reef system. Low Isles, a small vegetated island north of Cairns, was studied in detail. This is an isolated reef within the barrier series, not exposed to the Pacific surf. T. A. Stephenson (1931), in reviewing the Low Isles fauna and flora comments on the absence of anything comparable to the "laminarian zone of colder waters"; there is no fucoid growth at high intertidal levels, though *Enteromorpha* may occur, and, while the pools of the reef contain abundant algae, they are mostly mossy or turf-like forms. At low levels corals are dominant and algal growth weak. In pools, *Sargassum, Cystophyllum, Turbinaria* and *Padina* are the only large algae, while on the windward shelf a *Sargassum* zone is developed, accompanied by *Turbinaria* and *Chlorodesmis comosa.* Lithothamnia are almost ubiquitous at Low Isles in the form of thin crusts or small nodular growths but play only a limited part in reef formation. The variety and abundance of Cyanophyta are striking features of the reef, occurring in almost every type of habitat.

Manton (1935) further discusses the ecology of Low Isles, based on traverses. He found that in certain areas "the abundance of algal species is approximately inversely proportional to the numbers of species of corals. All the major groups of algae are at a maximum in the shallower part of the moat, where temperature and other extremes are greatest. They are fewer on the reef flat and are practically absent outside the Boulder Tract, even where corals are scarce and the water shallow. They decrease in numbers towards the drying flat and in the deeper water of the Moat". Algae are almost absent on the seaward slope. The limiting factors for this distribution are not clear. Manton found that the brown algae are fewer than the reds and greens, while the latter comprise most of the widely distributed species.

Other reefs within the barrier were studied more briefly, and T. A. and A. Stephenson (1953) describe also the ecology of Yonge Reef, part of the outer barrier. As would be expected, considerable differences were found between this reef and Low Isles, though many of the same species were present. A feature of Yonge Reef is the heavy incrustation of nullipores which colour the substratum purplish pink from the Pacific Ocean to the boulder zone. Apart from the nullipores, the outer ridge and outer moat apparently bear few algae, while in shallow pools of the reef crest *Chlorodesmis comosa* is prominent, accompanied by small amounts of *Halimeda* and *Caulerpa.* Farther to the leeward, in the boulder zone, there are loose boulders and sand, with thick patches of *Caulerpa* and *Halimeda.* The algae recorded from Yonge reef are many fewer than those at Low Isles.

Endean, Stephenson and Kenny (1956) also describe and contrast the intertidal ecology of continental and coral islands off the Queensland coast, and demonstrate the paucity of algal growth above mean low water.

The situation on the outer barrier of the Great Barrier Reef (T. A.

and A. Stephenson, 1931) appears to be not very different from that at Funafuti in the Ellice Islands and at Bikini in the Marshall Islands (Taylor, 1950), where lithothamnia form a prominent zone on the windward edge of the reef under heavy surf action. In such areas lithothamnia are the primary reef-building organisms, but corals are stated to be still important in the outer surf zone of the Great Barrier Reef. Whether *Porolithon* (especially *P. onkodes*) is the most important lithothamnion on the outer barrier, as it is on many Pacific atolls, e.g., Bikini (Taylor, 1950) and Raroia (Doty, 1954) is not known. Doty and Morrison (1954, p. 6) suggest that such a species as *P. onkodes* which is unusual in that it grows in brilliant light and develops rapidly under strong surf, might, if it arose and spread rapidly, explain some of the uniform characteristics of coral atolls. The great Barrier Reef Reports also indicate that *Halimeda* is not so important as in the lagoons of some atolls, e.g., Bikini (Taylor, 1950). The situation on Bikini (Taylor, 1950: 8) has been considered to be in marked contrast to that on the Cocos-Keeling Islands, where corals are reported as dominant (Wood Jones, 1910). However, lithothamnia are apparently very important on the windward surf-swept edge, since Wood Jones (p. 156) states ". . . . the barrier runs shoreward as a smooth Nullipore-covered platform", and on p. 159 "In that area on which the surf beats—the seaward edge of the barrier—living coral growth reaches its minimum of individuals as well as of species". As discussed by Marshall (1931) and Setchell (1928), on the outer barrier of most coral reefs lithothamnia are prominent and usually dominant if wave action is heavy but decrease in importance with lessened surf. Coral, on the other hand, is usually best developed away from strong surf action.

Other Tropical Coasts

Included here are coasts other than coral reefs. Certain areas of Arnhem Land are known from a brief account of Womersley (1958). In Arnhem Land algal growth above low tide level is very sparse, being limited to moister depressions; blue green algae, such as *Lyngbya confervoides* and *Isactis plana*, the green *Enteromorpha* and in some areas *Ralfsia* and *Chaetomorpha*, together with encrusting lithothamnia, are the main forms of the lower littoral.

At or just below low tide level mats of *Gelidiella* may occur, and an algal turf of species up to six inches or so high is common, including *Padina commersonii, Spyridia filamentosa, Hypnea cornuta, Dictyota* *pardalis, Acanthophthora spicifera* and others. Below low tide level but reaching the surface at low tide, *Sargassum* becomes dominant (*S. baccularia, S. godeffroyi*), often with *Turbinaria ornata, Padina, Halimeda, Laurencia* and others. *Caulerpa* spp. are common in deeper water.

The mainland coast of Queensland is known from an early paper of Johnson (1917) on Caloundra in southern Queensland and a recent general account by Endean, Kenny and Stephenson (1956). This latter account refers only to an "algal zone" below low water neaps. Endean, Kenny and Stephenson do, however, emphasize the paucity of algae above the level of low water neaps, particularly in northern Queensland, and they state also that *Sargassum* is commoner below low tide level in southern than northern Queensland. This may not apply to *Sargassum* in deeper water. They suggest that a zoogeographical boundary near the southern tip of the Great Barrier Reef occurs at about 25°S. It would be interesting to see whether the algal distribution supports this.

On the ocean reef at Caloundra, Johnson describes a *Sargassum*-chiton zone which may be just uncovered at lowest tides. There are several species of *Sargassum* together with *Cystophyllum muricatum, Dictyota dichotoma* and 20 or more other associated species. On the upper edge of this zone is a fringe of *Laurencia obtusa*; *Ulva* and *Enteromorpha* also occur in the littoral, but algal growth above a low littoral level is sparse.

TEMPERATE COASTS

These may provisionally be divided into the warm temperate coast of New South Wales, the cold temperate coasts of Victoria and Tasmania, and the southern Australian coasts from Victoria westwards.

New South Wales Coast

The earliest ecological account of the coast near Sydney is that of Hedley (1915). Pope (1943) later studied Long Reef, some six miles north of Sydney, and this was followed by a general account of the New South Wales coast in 1948 by Dakin, Bennett and Pope. These authors later published a popular account (mainly zoological), "Australian Seashores", which is based largely on the New South Wales coast (Dakin, Bennett and Pope, 1952).

Basic zonation on rocky coasts of New South Wales (Table V) consists of:

a) Supralittoral zone characterised by the littorinid snails *Nodilittorina* and *Melaraphe.*

b) Littoral zone dominated by small barnacles (*Chthamalus* and *Chamaesipho*) in the upper part, larger barnacles (*Catophragmus* and *Tetraclita*) and the polychaete *Galeolaria* in the mid part, and with a basal zone of the ascidian *Pyura.* Superimposed on these zones may occur *Bangia, Ectocarpus* and *Enteromorpha* in the upper part, and *Ulva* at about a mid-littoral level.

Hormosira banksii is often well developed and dominant above *Galeolaria* (i.e., at a mid-littoral level), especially on rock platforms and more sheltered areas at suitable tidal height. This mid-littoral occurrence of *Hormosira* is apparently higher than its occurrence in southern Australia, where it is always in the lower littoral. That *Hormosira* grows higher in relation to the total environment in New South Wales than in southern Australia appears doubtful from the comments of Dakin, Bennett and Pope (1948, p. 22), and further evidence on this is required. It is possible, but not likely, that forms with different physiological tolerances may be involved. *Corallina* also occurs commonly in the lower littoral, though as stunted plants compared to those constantly submerged.

c) Upper sub-littoral (possibly sub-littoral fringe in places) dominated by large brown algae. *Ecklonia radiata* is present throughout the New South Wales coastline, *Phyllospora comosa* south of Grant's Head (about lat. 32°S.), and the giant fucoid *Durvillea potatorum* south of Bermagui (about lat. 36° 30′S.). Species of *Sargassum* and *Cystophora,* and corallines are common, while lithothamnia may colour the rock pink in this zone.

Victorian and Tasmanian Coasts

These are known through the papers of Bennett and Pope (1953) on Victoria and of Cribb (1954) and Guiler (1950, 1951a, 1951b, 1952a, 1952b, 1953b, 1954, 1955) in Tasmania. Observations of the present writer are also embodied in the following account.

VICTORIA. On exposed rocky coasts the basic zonation comprises:

a) Supralittoral zone of the mollusc *Melaraphe* and the lichens *Lichina confina* and *Verrucaria,* which are somewhat variable in occurrence.

	South Australia	Victoria	Tasmania	New South Wales	Queensland (northern).
Supra-littoral	Melaraphe samphires	Melaraphe	Melaraphe lichens	Nodilittorina Melaraphe	Nodilittorina Melaraphe
Littoral — Upper	Chthamalus → gastropods → Bembicium Chamaesipho	Chthamalus (Modiolus) Chamaesipho limpets	lichens Chamaesipho → Bostrychia	Chthamalus Chamaesipho	Chthamalus malayensis
Littoral — Mid	Catophragmus → gastropods → Bembicium (Brachyodontes) blue-green algae Galeolaria	Catophragmus Brachyodontes blue-green algae Galeolaria	(Brachyodontes) → limpets gastropods Catophragmus → lamellibranchs Galeolaria Gelidium	Tetraclita Catophragmus Galeolaria	Crassostrea (oyster)
Littoral — Lower	Balanus coralline-mat → Gelidium-mat Hormosira	Balanus coralline-mat Hormosira	lithothamnia → Hormosira coralline-mat Mytilus Zostera ↓ Laurencia Cystophora torulosa	Balanus → Hormosira Pyura coralline-mat	Tetraclita squamosa
Fringe	Cystophora intermedia → Hypnea Spyridia → Cystophora spp.	Durvillea ↓	Xiphophora → Cystophora Durvillea Sargassum	Cystophora Phyllospora Sargassum	"algae"
Upper Sub-littoral	Zostera ↓ Posidonia ↓	Macrocystis ↓	Phyllospora Phyllospora Macrocystis ↓ Ecklonia Macrocystis ↓	Ecklonia	
	Womersley and Edmonds, 1958	Bennett and Pope, 1953	Cribb, 1954; Guiler, 1952	Dakin, Bennett and Pope, 1948	Endean, Kenny and Stephenson, 1956

TABLE V

ZONAL DOMINANTS ON THE COAST OF EASTERN AND SOUTHERN AUSTRALIAN STATES

Horizontal arrows indicate changes from rough conditions (left of each column) to calm condition (right of each column). Vertical arrows indicate the organism extends into the sub-littoral for some distance.

b) Littoral zone, with barnacles dominant in the upper region, mussels and *Galeolaria* in the mid-littoral (often with *Splachnidium rugosum* super-imposed here in summer), and an algal mat in the lower littoral. Blue-greens, e.g., *Rivularia firma,* may be common in the mid-littoral; also *Ilea fascia* (probably seasonal). *Hormosira* forms a well developed association on horizontal areas of rock at a low littoral level. The algal mat is best developed in fully exposed localities. It is dominated by corallines such as *Corallina* or *Jania,* accompanied by small species, among them being *Pocockiella variegata, Caulerpa brownii* and *Laurencia heteroclada.*

The lower part of the littoral is, according to Bennett and Pope, occupied by a "Poneroplax" or "bare" zone. The large chiton *Poneroplax* is common between the *Galeolaria* and large brown algal zones, but otherwise the rock has a bare appearance. This is very likely due to the destructive effect of the large *Durvillea* fronds moved across the rock by the waves; actually the zone often has a covering of lithothamnia and other small and stunted species. In some localities in eastern Victoria *Pyura* may occur in this zone.

c) Upper sub-littoral zone dominated by large brown algae—*Durvillea potatorum* in particular, also *Phyllospora comosa* and *Ecklonia radiata*, while *Macrocystis angustifolia* occurs in deeper water. Where there is slight shelter, there may be *Cystophora* spp., especially *C. intermedia*, often growing slightly higher than *Durvillea.*

Little information is available on the ecology of inlets and sheltered bays on the Victorian coast. In parts of Port Phillip and Westernport *Zostera* flats are developed, and the ecology is probably similar to that of such localities on the South Australian coast.

TASMANIA. Guiler has described a number of localities on the south-east coast, with emphasis on the fauna. A more adequate account of the zonation of Port Arthur, with emphasis on the flora, is given by Cribb (1954). Port Arthur includes habitats ranging from very exposed cliffs and surf-swept rock platforms to extremely well protected bays with gently shelving sand-mud flats. The algal zonation probably gives a good picture of that on many other Tasmanian coasts.

Cribb, following the usage of A. D. Cotton (1912) on Ireland, and of Womersley (1947) on Kangaroo Island, divides the coast into 'Rocky Shore' and 'Sand and sand-mud' formations, further subdividing the rocky shore into sheltered, semi-exposed and exposed habitats. These divisions are dependent on degree of wave action, and distinguished by characteristic indicator species, especially in the upper sub-littoral zone:

a) Supralittoral. While the littorinid *Melaraphe* is common in the lower supralittoral and upper littoral, bands of lichens are the distinctive feature of these zones. On sheltered rocky coasts, zones of *Parmelia* (probably terrestrial), *Ochrolichina* (extending just below high water springs) and in the upper littoral *Candelariella, Verrucaria* and *Lichina* (with *Bostrychia* where sheltered) form striking horizontal bands. On semi-exposed coasts these bands are extended upwards by wave splash, but on exposed coasts, though the lichens are often present, they do not form conspicuous bands.

b) Littoral. The upper and mid-littoral zones are usually dominated by barnacles or limpets, with algae forming seasonal or local communities. On sheltered coasts *Gelidium* forms an association with *Galeolaria* in the lower part of the mid-littoral, and *Ulva* is often also well developed. On exposed coasts, *Bangia* and *Porphyra* often occur together with *Ulva* and *Scytosiphon*.

The lower littoral is marked by the presence of brown algae on the calmer coasts. In sheltered areas *Hormosira* forms a well defined zone above *Cystophora torulosa,* both with an undergrowth of *Corallina*; in semi-exposed areas *Hormosira* is absent, and *Corallina* forms a band above *Xiphophora* (probably sub-littoral). With exposure to strong surf, the encrusting corallines, including *Lithophyllum hyperellum,* become dominant with a narrow band of *Laurencia* below.

c) Sub-littoral fringe. In sheltered places this is dominated by *Cystophora cephalornithos* and *Sargassum laevigatum*. Below the fringe zone *Phyllospora* occurs, and in deeper water *Cystophora retroflexa, Ecklonia* and beds of *Macrocystis pyrifera* are found. With semi-exposure, *Xiphophora* dominates the fringe zone, with *Phyllospora* and *Macrocystis* below, and on exposed coasts *Xiphophora* occurs below the *Laurencia* but the giant fucoid *Durvillea* dominates the zone just below low water springs, with *Phyllospora* and *Macrocystis* below.

Cribb regards *Cystophora torulosa* as a lower littoral alga; *Xiphophora* also extends above low water springs. These, together with *Hormosira* which is typically lower littoral, are comparatively fleshy brown algae and with cooler and moister air conditions in Tasmania can extend higher intertidally than they do on the mainland coast. *C. torulosa* is better adapted to withstand exposure to air than any other species of the genus. From Cribb's account and his zonation scheme, it is clear that detailed correlation of zones with tidal data is desirable in distinguishing the littoral zone limits.

Algae in the intertidal region are more plentiful on Tasmanian and Victorian coasts than elsewhere in Australia, though the mid and upper littoral levels are still regions of faunistic dominance.

South Australian Coasts

A general account of the intertidal ecology of the State of South Australia has been given recently by Womersley and Edmonds (1958). The coast is subject to wave action ranging from very rough conditions on capes exposed to the Southern Ocean to calm sheltered conditions in Spencer and St. Vincent Gulfs and in several almost land locked bays and inlets. Environmental conditions such as air temperature and humidity in the intertidal zone are more severe in sheltered areas than on open coasts.

The south-eastern coasts of South Australia (from Robe eastwards) are ecologically similar to the Victorian coasts (see above) except in the reduced barnacle population of the mid and upper littoral zones. From Robe westwards into Western Australia comparable habitats are similar ecologically, and the coast may be conveniently sub-divided on degree of wave action and type of sub-stratum. Indicator species have proved useful in comparing degree of wave action.

On coasts exposed to heavy wave action, three types of sub-stratum occur. Palaeozoic rock, usually steeply sloping into deep water, forms the capes and points; calcareous sand-rock platforms at about low tide level occur over extensive areas between the Palaeozoic rock; and sandy beaches are of common occurrence.

PALAEOZOIC ROCK CAPES show the following basic zonation:

a) Supralittoral dominated by *Melaraphe unifasciata*, with sometimes a prominent black band of *Calothrix fasciculata* above the *Melaraphe*.

b) Littoral. This is essentially a barnacle zone, with three sub-zones: upper littoral of *Chamaesipho columna*, mid-littoral of *Catophragmus polymerus* (with some molluscs, *Galeolaria* and blue-green algae) and lower littoral of *Balanus nigrescens*. A dense mat of *Corallina* or *Jania* occurs on the rock of the lower littoral and also covers all except the uppermost *Balanus*. Where wave conditions are less severe, molluscs often become dominant in the mid-littoral and *Balanus* disappears.

c) Sub-littoral, with a fringe zone of *Cystophora intermedia* and an undergrowth of *Corallina* and other small algae.

CALCAREOUS ROCK-PLATFORMS are found along much of the coastline subject to constant surf. They consist of more or less vertical cliffs backing a horizontal platform which lies at about low tide level, then dropping vertically with numerous crevices and frequent undercutting to ten or 20 feet of water. The surface of the platform has numerous pools and shallow channels, and exhibits a remarkable variety of algal growth, especially near the rougher edge.

a) Zones above the lower littoral occur only on the cliffs backing the platforms and are similar to those on Palaeozoic rock. In many places wave action at the back of the platforms is reduced, resulting in both mid and upper littoral zones being dominated by molluscs instead of barnacles. Blue-green algae (*Rivularia firma, Isactis plana, Symploca hydnoides*) are often prominent in the mid-littoral.

b) Lower littoral. This zone occurs both at the base of the cliffs and on higher parts of the platforms, and normally bears a dense and fairly pure association of *Hormoisra banksii*, with *Notheia anomala* epiphytic.

c) Sub-littoral. Ponds and shallow channels on the platforms bear a "mixed *Cystophora* community", comprising *Cystophora uvifera, C. subfarcinata, C. siliquosa, Cystophyllum muricatum* and *Sargassum decipiens*. The larger of these reach two feet in length, with *C. siliquosa* sometimes up to five feet long. Other algae in this community are relatively few, especially where the *Cystophora* fronds wash over the rock.

The sub-littoral fringe on the edge of the platforms is dominated by *Cystophora intermedia*, with a wealth of other algae. Larger associated species include *Cystophora paniculata, Sargassum bracteolosum, Scytothalia dorycarpa* and *Ecklonia radiata*, with smaller species forming an undergrowth. Over 60 species may be collected in an area of two or three square yards in this association.

The deeper sub-littoral zone is rich but is known only from drift material. Well over 300 species may be found along a short length of this type of coast, but up to half are known only from the deeper sub-littoral.

SHELTERED COASTS, subject only to moderate wave action except under storm conditions (e.g., lower parts of the Gulfs and north coast of Kangaroo Island) show similar supralittoral (*Melaraphe* dominated) and upper-mid-littoral zones (barnacle and mollusc dominated) to those on somewhat rougher coasts. The density of organisms, however, is usually considerably less. Prominent differences from rougher coasts occur in the lower littoral and upper sub-littoral.

a) Lower littoral. This comprises a dense algal mat up to two centimeters thick of *Corallina* (*C. cuvieri* or *C. officinalis*) and often *Jania*, or of *Gelidium pusillum;* in some areas *Corallina* and *Gelidium* occur mixed. On rock platforms and sloping rock, *Hormosira banksii* is often dominant.

b) Upper sub-littoral. This zone is marked by an absence of *Cystophora intermedia* and instead is dominated by other species of *Cystophora* (*C. subfarcinata, C. retorta, C. polycystidea, C. spartioides*), *Ecklonia radiata, Sargassum bracteolosum, S. decipiens, S. lacerifolium* and other species. This assemblage extends down for six to 20 feet and no distinct fringe zone to the sub-littoral is present. Coralline algae, both articulate and crustose, are common under the large sub-littoral algae.

CALM, SHELTERED SAND-MUD FLATS. In the upper parts of Spencer and St. Vincent Gulfs and in enclosed bays, where gently shelving sandy or muddy tidal flats prevail, zonation is quite different. Womersley (1956) has described in detail the ecology of American River, an almost landlocked inlet (not a river) on the north coast of Kangaroo Island. Here conditions are normally a flat calm, with tidal flats flanking a channel two to three fathoms deep. A rocky sub-stratum occurs only as outcrops in the upper littoral and supralittoral; elsewhere are sandy or shelly beaches.

a) Supralittoral. This varies from a loose sandy beach bare of macroscopic organisms to dense "swamps" of the samphires (*Salicornia* and *Arthrocnemum*) on deeper mud or to extensive areas of mangroves *Avicennia marina* var. *resinifera*) in the upper parts of the Gulfs. The samphires and mangroves extend down into the littoral zone, the latter almost to the lower littoral. On firm mud under the samphires, *Gelidium pusillum, Bostrychia mixta, Chaetomorpha capillaris* and *Vaucheria* sp. have been found.

b) Littoral. The upper and mid-littoral are scarcely distinct zones, being dominated by the mollusc *Bembicium melanostoma*; patches of the mussel *Modiolus* and of *Enteromorpha* sp. also occur. The lower littoral usually bears a well developed community of Hormosira banksii, usually growing on large mussels. *Hormosira* here is of a very different ecological form to that on rough coasts, being much branched, with large, spherical vesicles.

c) Upper sub-littoral. Here large brown algae are absent unless local water movement occurs, e.g. tidal currents. Instead one finds a sub-littoral fringe zone dominated by the red algae *Hypnea musciformis* and *Spyridia biannulata.* At the same level and extending down about ten feet, the angiosperm *Zostera muelleri* forms extensive "meadows" over large areas of the tidal flats; and from one foot below low tide to five or six fathoms, *Posidonia australis* is dominant.

Western Australian Coasts

Very little published information is available on the inter-tidal ecology of Western Australian coasts. Harvey (1854) gave ecological notes on the algae of King George's Sound and Rottnest Island; since then only a short paper mentioning some of the algae of the Swan River Estuary (Thomson, 1946) and comparative notes in Womersley and Edmonds (1958) have been published. However, an unpublished account by G. G. Smith (1952) describes the algal ecology of the Rottnest Island and Cockburn Sound area near Fremantle.

The coastal topography near Fremantle consists of sandy beaches and calcareous rock platforms. The tide is predominately diurnal, with a range not exceeding three feet, and is much affected by wind. The rock platforms are similar to those on South Australian coasts, but many show a raised outer edge ("lithothamnion rim") which results in shallow "lagoonal" conditions on much of the platform. This rim is from six inches to 18 inches high and about a foot broad at the base, but consists of calcareous rock with only a covering of lithothamnion up to two inches thick. It is therefore not strictly comparable to the lithothamnion rim of tropical coral reefs.

The general ecology and communities recognised by Smith are similar to those on South Australian rock platforms (Womersley, 1948), but genera such as *Sargassum* and the lithothamnia are of greater importance, *Cystophora* is of much less importance and *Hormosira* is absent. A few sub-tropical species, among which are *Halimeda cuneata, Caulerpa racemosa* f. *cylindracea* and *Cystoseira abrotanifolia*, also appear on Western Australian platforms. Otherwise the floristic composition is remarkably similar to that on South Australian rock platforms.

Womersley and Edmonds (1958) point out some interesting changes, affecting mainly the fauna, along the south coast of Western Australia. The most striking difference from South Australian coasts appears to be the absence of barnacles in the upper and mid-littoral zones, though *Balanus* may be prominent in the lower littoral. Among the algae, the most noteworthy change is the disappearance of *Hormosira banksii* west of Albany.

SUMMARY OF INTERTIDAL ZONATION ON AUSTRALIAN COASTS

Intertidal zonation on rocky coasts of various parts of Australia (Table V) may be summarized as follows.

a) Supralittoral: a typical littorinid zone, dominated chiefly by *Melaraphe* but with *Nodilittorina* in warm temperate and sub-tropical regions.

b) Littoral: this zone is usually divisible into three sub-zones:
Upper littoral; usually dominated by barnacles (*Chthamalus, Chamaesipho*) unless under calm conditions where gastropods or lichens may be prominent.

Mid littoral, dominated by barnacles (*Catophragmus*) (and *Tetraclita* in New South Wales) in rough places or by molluscs, *Galeolaria* and blue-green algae under moderate or slight wave action in temperate regions. In Queensland the mid-littoral is an oyster zone (*Crassostrea*).

Lower littoral, characteristically an algal zone. Under very rough conditions on temperate coasts *Balanus* is frequent but gives way with less rough conditions to a dense mat or turf of articulated coralline algae or of *Gelidium pusillum*. *Hormosira* and lithothamnia are common along southern Australia, while *Pyura* is often dominant on the warm temperate New South Wales coast. In sub-tropical Queensland *Tetraclita* is the most important lower littoral organism, algae being limited to the sub-littoral fringe.

c) Sub-littoral: this is invariably dominated by algae where wave action is appreciable. On temperate coasts the Fucales are very conspicuous at and below the top of the sub-littoral (*Cystophora* spp., *Phyllospora, Sargassum* spp., *Durvillea*) with the kelp *Ecklonia* occasionally important and *Macrocystis* forming extensive beds in Tasmanian and Victorian waters. In calm, sheltered areas large brown algae disappear and are replaced by red algae (e.g. *Hypnea, Spyridia*) and by marine angiosperms. A sub-littoral fringe zone can be recognised on several coasts. On sub-tropical coasts algae dominate the upper sub-littoral, but *Sargassum* is the most important of the Fucales.

MARINE BIOGEOGRAPHICAL PROVINCES OF THE AUSTRALIAN COAST

The marine biogeographical provinces of Australia have been described almost entirely on a faunistic basis. Older accounts were based largely on the distribution of particular animal groups, but more recently the whole intertidal biota has been considered.

Hedley (1904) first proposed the following provinces based on distribution of molluscs:

ADELAIDEAN: from Melbourne along southern Australia to Geraldton in Western Australia. Cotton (1930) substituted the more appropriate name FLINDERSIAN for Hedley's Adelaidean, and this has been followed by later authors.

PERONIAN: the east coast of Tasmania, eastern Victoria and New South Wales.

SOLANDERIAN: the eastern Queensland coast from Moreton Bay to Torres Strait.

DAMPIERIAN: tropical Australia from Houtman's Abrolhos to Torres Strait.

Important modifications since have been made by Ashby (1926) who suppressed the Solanderian within the Dampierian. This is supported by Endean (1957) on the basis of echinoderm distribution. Insufficient is known of the algae of tropical Australia to comment on this, but the few distributions known do not disagree with the recognition of one Australian tropical-sub-tropical province.

Whitley (1932) first recognised the Great Barrier Reef as a province distinct from the mainland coast of Queensland but he "restricted" Solanderian to the reef and renamed the mainland province "Banksian". In view of Hedley's explicit use of "Solanderian" for the mainland coast of Queensland, Whitley's action was unjustified. Endean, Stephenson and Kenny (1956) and Endean (1957) have shown that the Barrier Reef fauna is distinct from that of the mainland, but have followed Whitley's names. Wood (1954), in describing the dinoflagellate distribution of waters off Australia, maintains both Dampierian and Solanderian, restricting the latter, however, to waters of the Coral Sea outside the Great Barrier Reef, and using "Banksian" for waters inside the reef. Bennett and Pope (1953), however, have correctly applied "Solanderian" to the Queensland coast.

Ashby (1926) also suggested that the Peronian extends northwards to Great Sandy Island, and this is well supported by Endean, Kenny and Stephenson (1956) who fix the limit at about lat. 25°S. The latter authors show that a major change in the fauna occurs here, and, while the algal distribution is not yet adequately known, it does seem to show this change.

The Peronian province was originally considered to cover the coast of New South Wales and extend to the east coast of Tasmania. The east coast of Tasmania was designated by Iredale and May (1916) as the Maugean region, since the chiton fauna is distinct from that on the north coast of Tasmania which is Adelaidean (Flindersian) in affinity. Bennett and Pope (1953), however, extend the Maugean province to include all of Tasmania and Victoria, which are of cool temperate affinity in contrast to the warm temperate Peronian of the New South Wales coast. The Maugean province is marked by the presence of the giant brown algae *Durvillea potatorum* and *Macrocystis* (*M. pyrifera* and *M. angustifolia*) in the upper sub-littoral.

The recent account of Womersley and Edmonds (1958) shows that the intertidal ecology and algal distribution do not support separation of the Maugean province as distinct from the Southern Australian Flindersian. The differences are not of comparable order to those separating the Peronian from either the Dampierian or the Flindersian. The Flindersian is considered to extend along the whole of southern Australia, and the Maugean to comprise a region of sub-provincial status showing distinct cold temperate affinities. The Flindersian from Robe in South Australia westwards is considered by Womersley and Edmonds as a region intermediate between cold temperate and warm temperate conditions. *Durvillea* and *Macrocystis* are absent, but the intertidal zonation is otherwise very similiar to that in Victoria. The total algal distribution strongly supports recognition of one province along most of southern Australia, and the distribution of most animal groups appears to support this. There is some doubt, however, as to the south-east part of Tasmania where colder water species are more prominent. Sea temperatures along most of Southern Australia do not differ by more than 3 or 4°C.

The Flindersian has usually been considered to grade around the south-west corner of Western Australia with the sub-tropical Dampierian. Some species characteristic of southern Australia, especially animals, extend as far north as Geraldton, while some sub-tropical species extend south to near Fremantle or in a few cases around to Albany. Noteworthy sub-tropical algae found near Fremantle are *Halimeda cuneata, Penicillis nodulosus* and *Caulerpa racemosa* f. *cylindracea.* However, the flora of rock platforms near Fremantle is still largely of southern Australian affinity (155 of 196 species listed by Smith (1952) are southern Australian), but the sub-tropical forms present are more conspicuous.

Insufficient evidence is available of algal distribution and of most animal groups to follow the change around south-west Western Australia, but it appears likely that there is a grading over a long distance, as recognised by Hedley (1904) and by Bennett and Pope (1953). The limits of some intertidal organisms are discussed by Womersley and Edmonds (1958). Ashby (1926), however, on the basis of chiton distribution, introduced an "Indo-Australian" region, extending from the Abrolhos Islands around to the Great Australian Bight, and overlapping with the Flindersian in southern Western Australia. Kott (1952) proposed a more restricted province, the Baudinean, to describe the ascidian fauna of the coast from Fremantle to Albany. What is known of the algal distribution and intertidal ecology does not support recognition of a distinct province in this restricted region.

The only broad study on Australian phytoplankton is that of Wood (1954) on dinoflagellates. Wood recognises a number of sub-areas within the main Australian marine provinces, the limits of which often differ significantly from limits based on benthic organisms. For instance, Wood limits the Maugean region to Bass Strait from Cape Otway eastwards and the east coast of Tasmania. Wood also shows that sub-tropical dinoflagellates occur in waters south of the continental shelf of southern Australia and extend as far east as the west coast of Tasmania. This supports Halligan's description (1921) of a sub-tropical surface current from south-west western Australia flowing eastwards some distance offshore. Whether any element in the benthic algal population of western Tasmania supports this is unknown.

The present evidence for marine biogeographical provinces around the Australian coast, based largely on faunistic distribution in northern australia but with adequate floristic evidence in southern Australia, supports the following:

DAMPIERIAN province of tropical—sub-tropical affinitives, extending from the Abrolhos Islands (grading south of this) in Western Australia around north Australia to about lat. 25°S. on the Queensland coast. This includes the Solanderian of Hedley (Banksian of others) which might be recognised as a sub-province.

GREAT BARRIER REEF province of tropical affinities.

PERONIAN province of warm temperate affinities, including the coasts of Queensland south of lat. 25°S., New South Wales and eastern-most Victoria.

FLINDERSIAN province of southern Australia, from the south-west corner of Western Australia (where it grades with the Dampierian) to Victoria and Tasmania. The Maugean sub-province, of cool temperate affinities, includes the coast east of Robe in South Australia, Victoria and Tasmania.

ECOLOGICAL COMPARISONS WITH OTHER COUNTRIES

No attempt will be made here to give a thorough comparison of Australian intertidal ecology with that of other parts of the world, since this merits a review in itself. Certain general features will be described and brief comparisons made with other southern hemisphere regions, particularly New Zealand. Chapman (1957) has reviewed the previous ten years progress in marine algal ecology, while Cribb (1954b) and Guiler (1952b) have briefly compared Tasmanian intertidal ecology with that of New Zealand, South America and South Africa. Southward (1958) has reviewed zonation on rocky coasts in many parts of the world, but his account of Australasian shores is based on inadequate information.

Tropical and sub-tropical regions of the world show many similarities in their intertidal ecology, and northern Australia provides no striking exceptions as far as can be judged from the little information available. Algae are largely confined to below a very low littoral level, and *Sargassum* is the most important brown algal genus in the upper sub-littoral. In contrast to temperate regions, animals, particularly corals, tend to dominate much of the sub-littoral.

Were it not for the many accounts of the intertidal region of colder northern hemisphere coasts, an algologist from the southern hemisphere would be amazed at the great development of algal species throughout the intertidal region there. This is often made more striking by the relatively great tidal range. In temperate parts of Australia there are few conspicuous algae above the lower littoral zone (i.e., about the lower quarter of the intertidal zone), and when present they are mainly blue-green algae such as *Rivularia* and *Symploca.* Even in the lower littoral the perennial algae are predominately mat- or turf-like forms—*Corallina, Jania, Gelidium*—or algae such as *Hormosira* which is clearly adapted to some desiccation with its water-holding vesicles. *Hormosira* is the only member of Fucales which grows in the lower littoral except in Tasmania where *Cystophora torulosa* and perhaps *Xiphophora gladiata* grow above mean low water (Cribb, 1954b). These latter have more fleshy thalli than most sub-littoral Fucales. A few winter species do occur at a mid-littoral level in southern Australia—*Ilea fascia, Splachnidium rugosum, Bangia fuscopurpurea, Porphyra columbina* and *P. umbilicalis,* while *Entermorpha* spp. may also be found. Most of these are cosmopolitan species.

In general, on temperate Australian coasts, the fauna is dominant above the lower littoral, while algae or marine angiosperms are dominant below this level. Lack of algae above about a mid-tide level is a feature of many of the world's coasts, and contrasts strikingly with the situation in colder northern hemisphere countries. The cause of this difference lies partly in the colder and more humid conditions in the northern hemisphere and also in the absence of species adapted to withstand desiccation in the tropics and southern hemisphere. *Fucus* and *Pelvetia,* such important littoral genera in the northern hemisphere, are unknown in the southern hemisphere. The Fucales may be considered a littoral group in colder northern waters, but they are largely a sub-littoral group in the southern hemisphere. *Hormosira, Durvillea antarctica* and *Xipophora chondrophylla* var. *maxima* are the most important littoral Fucales in the Australasian or subantarctic regions.

Australian coasts show basic similarities with those of other southern hemisphere countries. Three basic zones—supralittoral, littoral and sub-littoral—can be defined by the limits of similar organisms, and the littoral can conveniently be sub-divided into three zones.

Comparisons of the zonation given by different authors is not always easy. The zonation on different Australian coasts can be fairly readily compared, but correlation of upper, mid and lower littoral zones in South Africa and New Zealand with the same zones in Australia is sometimes uncertain. In particular, when similar organisms appear to occur at different intertidal levels, this may be due to distinct ecological habitats of different species, but the possibility of discrepancies between workers cannot be overlooked. Table VI gives the comparative zonation

	SOUTH AFRICA			NEW ZEALAND		SUB ANTARCTIC
	West Coast (cool temperate)	South Coast (Warm temperate)	East Coast (sub-tropical)	Cold temperate (central coasts)	South Coast — Stewart Is.	South of South America
Supra-littoral	Littorina knysnaensis ↑	L. knysnaensis L. africana (Porphyra)	L. africana (L. obesa) (Tectarius)	Lichens blue-green algae Melaraphe cincta, M. oliveri Porphyra (winter) ↓	Melaraphe Bostrychia	↑
Littoral: Upper	Porphyra (Chastangium) Patella granularis	Chthamalus Octomeris Tetraclita (Limpets – Patella)	Ostrea Chthamalus Tetraclita Gelidium Caulacanthus Pomatoleios	Bostrychia arbuscula ↑ Modiolus neozelanicus Chamaesipho columna	Bostrychia ↘ ↑ Apophloea lyallii Chamaesipho columna	Hildenbrandtia lecannellieri Bostrychia Chaetangium
Littoral: Mid	(barnacles) (Gunnarsa) Aeodes Splachnidium lithothamnia	↑ Mytilus ⟶ Pomatoleios (Gunnarea) Gelidium (Splachnidium) ↓	coralline turf zoanthids (Mytilus)	Pomatoceros Elminius plicatus Ostrea Mytilus planulatus ↓ Splachnidium Hormosira	Modiolus Scytothamnus Elminius Adenocystis ↓ Pachymenia Gigartina lithothamnion corallines	Porphyra
Littoral: Lower	Patella cochlear (Bifurcaria) Gigartina Champia P. argenvillei	Patella cochlear algal turf (corallines Laurencia) Mytilus	zoanthids Hypnea spicifera	Xiphophora corallines Durvillea antarctica Cystophora torulosa Carpophyllum D. willana C. scalaris Mytilus canaliculatus ↓ ↓	Hormosira Xiphophora Durvillea antarctica Cystophora scalaris (Mytilus canaliculatus)	Iridaea corallines Durvillea antarctica Adenocystis Scytosiphon Cladophora Monostroma
Fringe	(Pyura) Ecklonia buccinalis ↓ Laminaria pallida ↓	Pyura Plocamium Caulerpa	(Pyura) Hypnea, Gelidium, Rhodymenia	Lessonia variegata ↓ Ecklonia ↓ red algae	Lessonia ↓ Ecklonia ↓ Carpophyllum flexuosum	Durvillea harveyi Macrocystis ↓ Lessonia ↓
Sub-littoral	Macrocystis angustifolia ↓	Sargassum (Ecklonia radiata)		Macrocystis pyrifera ↓	Marginariella urvilleana Macrocystis pyrifera ↓	Macrocystis pyrifera ↓
	Stephenson, 1944			Knox, 1958		Skottsberg, 1941

TABLE VI

ZONAL DOMINANTS ON SOUTH AFRICAN, NEW ZEALAND, SOUTH AMERICAN—SUB-ANTARCTIC COASTS. Horizontal and vertical arrows are used as in Table V.

on South African and New Zealand coasts, with a brief record from the Sub-Antarctic. Unfortunately no adequate information is available from most of the west coast of South America. Guiler (1952) and Chapman (1957) furnish a broad zonation scheme for Chile, but this gives little for comparison, and "*Durvillea*" is almost certainly wrongly placed in the sub-littoral fringe.

COMPARISONS WITH NEW ZEALAND

Information concerning the marine ecology of New Zealand coasts is limited to studies on restricted areas, mainly in the North Island (e.g., Cranwell and Moore, 1938; Beveridge and Chapman, 1950; Dellow, 1955), but with two accounts from the South Island (Knox, 1953; Batham, 1956). A general account (in press) by G. Knox (1958) of the interidal ecology of South Island, however, enables more adequate comparisons with the Australian coast to be made[3].

Chapman (1957), in reviewing marine algal ecology over the previous ten years, gives a "New Zealand" zonation in comparing New Zealand coasts with those elsewhere in the world. This zonation is most misleading and represents little more than an example of zonation in the warm-temperate Hauraki Gulf (Dellow 1955) on which Auckland is situated[4]. Chapman's statement (p. 326) that "the predominant fucoids of the Southern Hemisphere are all species that require total, or almost total, submergence" also needs modification, especially in relation to New Zealand. Here *Carpophyllum maschalocarpum,* at least in the South Island, is mainly lower littoral; *Xiphophora chondrophylla* var. *maxima* is definitely lower littoral, while *Cystophora torulosa* and *Cyst. scalaris* are largely so, and *Durvillea* (*antarctica* and *willana*), not cited by Chapman, are also definitely lower littoral, the whole *Durvillea* zone being exposed at a good low tide (apart from the floating ends of the fronds.) *Hormosira banksii*

3. The author is greatly indebted to Mr. George Knox, Department of Zoology, University of Canterbury, for discussions on New Zealand marine ecology while in New Zealand in early 1958, and for permission to see and refer to his paper before publication.

4. *Chthamalus* is not known from New Zealand, this barnacle having been renamed *Chamaesipho brunnea* (Moore, 1944). *Hermella* has been corrected to *Sabellaria* (Dellow, 1955: 22). The oyster *Saxostrea* (*Ostrea* in South Is.) is an inhabitant of harbours and sheltered inlets only, and an oyster belt is not "characteristic of New Zealand" (Chapman, p. 327). *Durvillea* and *Carpophyllum* are distinctly lower littoral inhabitants, though the latter appears to occur lower in the Hauraki Gulf than farther south.

is, of course, the highest growing of any Fucales in the Australasian region.

CENTRAL COASTS OF NEW ZEALAND

The southern Australian coast, including that of Tasmania, can be compared to the central coasts of New Zealand (Intermediate and Central Provinces of Moore, 1949) which Knox has shown to be cool temperate in affinity. This actually includes most of the New Zealand coast, since only the area north of East Cape can be considered warm temperate (Dellow, 1955), and the southern-most coast, south of Dunedin, is sub-antarctic in its affinities.

The cool temperate coasts of New Zealand and Australia show similarities but also some striking differences in the zonation pattern. This is in part due to the presence of different species in common genera, to the absence of certain genera and species of Fucales from Australian coasts, and perhaps to the cooler atmospheric conditions and the greater, more regular, tidal fluctuations in New Zealand waters. Most of the intertidal algae common to both countries are either cosmopolitan or seasonal species, and there are few animals in common, one important exception being *Chamaesipho columna*.

Supra-littoral

Melaraphe is the dominant genus in both countries but with distinct species (*M. cincta* and *M. oliveri* in New Zealand). Above the *Melaraphe* band, blue-green algae, e.g., *Calothrix*, may occur.

Littoral

The upper littoral on rough southern Australian coasts comprises a barnacle zone dominated by *Chamaesipho columna* and *Chthamalus antennatus*, changing to the mid-littoral characterised by *Catophragmus* in the roughest places and by molluscs, *Galeolaria* and blue-green algae in calmer areas.

In New Zealand *Chamaesipho columna* (and *C. brunnea* in the North Island) dominates the upper littoral, but *C. columna* extends well below this through the mid-littoral. Why this barnacle should extend lower in New Zealand than in Australia is not clear; competition can be only a partial cause if any at all. The larger barnacle *Elminius plicatus* is important in the mid-littoral in rough areas in New Zealand, occupying a niche similar to that of *Catophragmus* in Australia. Mussels are a more prominent feature on much of the New Zealand coast than along southern Australia. While they are most marked in the mid-littoral, often being co-dominant with barnacles in New Zealand, *Modiolus neozelanicus* extends to the top of the littoral and *Mytilus canaliculatus* down to the sub-littoral. The corresponding species in Australia are *Modiolus pulex* and *Brachyodontes rostratus* with *Mytilus planulatus* also in Tasmania.

Bostrychia arbuscula often forms a conspicuous brand near the top of the littoral in New Zealand. Such a *Bostrychia* band is not found in southern Australia, though *B. mixta* and *B. simpliciuscula* occur in shaded habitats at the same height.

Serpulids occur at much the same mid-littoral level in Australia and New Zealand, and are of considerable importance. *Galeolaria caespitosa* prevails in Australia, *Pomatoceros coeruleus* in New Zealand.

Seasonal algae of the mid-littoral are similar in both countries, though somewhat more prominent in New Zealand. *Porphyra* is particularly conspicuous in the upper littoral in Tasmania and New Zealand, while *Splachnidium rugosum, Adenocystis utricularis, Ilea fascia* and *Scytosiphon lomentarius* are important. *Scytothamnis fasciculatus* and *S. australis* are often conspicuous in the New Zealand mid-littoral throughout the year, but only *S. australis* occurs in Victoria and Tasmania.

The change from mid-littoral to lower littoral is marked by a sudden transition from a region of animal dominance above to one of algal dominance below. This change occurs at a similar environmental height in both southern Australia and temperate New Zealand.

In southern Australia the lower littoral is predominantly a coralline-mat zone with *Gelidium pusillum* in calmer areas and *Hormosira* mainly on platforms. Only in Tasmania and parts of Victoria are any other Fucales present; here *Xiphophora gladiata* and *Cystophora torulosa* are lower littoral species (Cibb, 1954b).

In New Zealand, however, the lower littoral in rough areas displays a magnificent belt of *Durvillea* (*D. antarctica* with *D. willana* usually lower and on rougher points). At the same level in less rough places *Carpophyllum maschalocarpum* forms a well defined belt; scattered plants often extend well below low water. *Xiphophora chondrophylla* var. *maxima* forms a narrow belt fairly high in the lower littoral; *Cystophora torulosa* and *C. scalaris* are also common under moderate to fairly calm wave conditions. In certain areas, as on Littleton Harbour breakwater, an unusual situation is found, the Fucales being replaced by various red algae, e.g., *Gigartina* spp., *Epymenia wilsonis* and *Laurencia* sp., with an undergrowth of *Corallina*.

Under the larger brown algae of the lower littoral, articulated or crustose coralline algae are usually plentiful, and in restricted fairly shelterd areas a fairly pure coralline mat, directly comparable to that in southern Australia, occurs. On rock platforms under moderate to calm wave action a *Hormosira—Corallina* association may be developed.

Upper Sub-littoral

The upper sub-littoral in southern Australia and New Zealand presents differences somewhat the reverse of those in the lower littoral. In both countries members of the Laminariales mark the upper boundary of the sub-littoral, but in many areas (especially in Australia) they are far from plentiful. The most important genus is *Macrocystis* (*M. pyrifera* in New Zealand and Southern Tasmania, *M. angustifolia* in northern Tasmania and Victoria), which extends from a level where the holdfasts may be momentarily uncovered at low tide to a depth of many fathoms. *Ecklonia radiata* is common to both countries but only rarely does it become dominant. *Lessonia corrugata* occurs in Tasmania as a component of the upper sub-littoral, but in New Zealand *Lessonia variegata* is frequently the dominant alga under rough conditions.

These members of the Laminariales (kelps) parallel the occurrence of *Laminaria* and other genera in the northern hemisphere, and in New Zealand they occur distinctly below the very striking zone of Fucales (*Durvillea, Carpophyllum*, etc.). Whereas the latter are subject to a considerable degree of exposure at a very low tide, the Laminariales are just exposed only at extreme low tide or during the suck-back of waves.

On Victorian and Tasmanian coasts (Maugean sub-province) the upper sub-littoral where rough is dominated by *Durvillea potatorum* which grows at a level where it is exposed to the air only between waves. It extends downward well below low tide (Cribb, 1954b: 32). Thus this species inhabits a zone quite different to that of the *Durvillea* species in New Zealand. This fact has not always been recognised in the past and has resulted in confusion in comparing Australian and New Zealand intertidal ecology.

In New Zealand, apart from the Laminariales, certain other Fucales (e.g. *Cystophora retroflexa, Marginariella, Landsburgia*) may be common in the upper sub-littoral, but they are not dominant in this zone to the extent that Fucales are on the southern Australian coast. In some parts of New Zealand, rock below the *Durvillea* may be relatively bare of algae, except articulated corallines. Often *Mytilus canaliculatus* is dominant here and excludes algae.

In many parts of New Zealand there is no distinct fringe zone to the sub-littoral. The lower littoral belt of *Durvillea* etc. has sometimes been referred to incorrectly as the sub-littoral fringe (Chapman, 1957; Southward, 1958), but this zone is not comparable to the fringe on South African coasts, as it occurs at a distinctly higher environmental level.

Knox also shows that there are marked differences between the east and west coasts of the south Island of New Zealand. Many of the algal dominants of the east coast, such as all *Carpophyllum* and *Cystophora* species, *Xiphophora, Hormosira, Ecklonia* and *Lessonia*, are absent from or rare on the west coast. The reasons for this difference are not clear.

Mud flats, in sheltered conditions, present a very different appearance in South Australia and New Zealand. Whereas in South Australia the marine angiosperm genera *Zostera* and *Posidonia* dominate most of the lower littoral and sub-littoral zones, they are absent from New Zealand apart from limited occurrence of *Zostera*, resulting in pure mud flats with little plant life.

NORTHERN COASTS OF NEW ZEALAND

These, north of the East Cape, are regarded by Dellow (1955) as warm temperate largely on the basis of water temperature and are usually recognised as a distinct "Auckland" province (Moore, 1949). Dellow compares these coasts to the warm-temperate New South Wales coast. While certain intertidal species are confined to the Auckland province, several of the dominants are those found farther south. The difference between cold temperate New Zealand and the Auckland province is perhaps comparable to the difference between the sub-provincial Maugean region and the rest of the Flindersian province in southern Australia, i.e., the Auckland province is of intermediate cold-temperate-warm temperate affinities.

SOUTHERN-MOST COASTS OF NEW ZEALAND

These are shown by Knox and others to form a distinct Forsterian province of sub-antarctic affinities. Here are several species which do not extend north of Dunedin, and the general aspect of the intertidal