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Observations on regeneration after fire in the Yule Brook Reserve near Perth, Western Australia

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Abstract

Yule Brook Reserve, a swampy flat, dry in summer and crossed by two sand ridges, has been burnt several times in the past 25 years. This paper is based on notes and photographs taken over this period to record the regeneration after each fire.

On the sandy ridges recovery of the banksia woodland and shrub cover of the almost treeless slopes is rapid as the trees are not seriously damaged and almost all shrub and monocotyledon species sprout from underground parts.

On the wetlands, i.e. *Leptocarpus* sward of the main level of the flats, the *Actinostrobos* mixed scrub and the *Leptospermum-Restio* low scrub, the dominant species of each of the communities are killed by fire and regeneration by seedlings is slow in the difficult habitat, waterlogged through winter and very dry in summer. However, subordinate species, i.e. small perennials and the many geophytes and annuals, with the competition of the dominants reduced, flourish in the first few years of the succession.

In parts frequently burnt there seems to be some reduction in fire sensitive species particularly *Leptospermum ellipticum*, *Actinostrobos pyramidalis* and *Banksia telmatiaea*. A general deterioration of vegetation over the flats has been observed but to what extent this is due to frequent fires, drought, or increased salinity is as yet uncertain.

Introduction

Yule Brook Reserve of 35 hectares is located 20 km south east of Perth (32° S 115° W) on a section of flats on the coastal plain at the foot of the Darling Scarp.

The site is a swampy flat (Fig. 1) crossed by two parallel sand ridges running north and south, the main eastern ridge (Fig. 3) being higher and more extensive than the low ridge (Fig. 2). The soil of the flats is shallow white sand over clay which extends under the deep sand of the ridges. The flats are waterlogged through winter and dry and hot in summer.

A general account of the vegetation was given in the first paper of this series (Speck and Baird 1984) but may be briefly summarised here. Banksia woodland occurs on the crest of the main ridge (Fig. 3) with low shrub undergrowth continuous with the dense low shrub community of the almost treeless slopes (Fig. 3H). The low ridge has similar low shrub cover but no banksia trees. The flats are

covered by a sward of the twine rush *Leptocarpus aristatus* (Fig. 4C). Scattered unevenly through the flats are saline depressions and low shrub covered mounds (Figs. 1, 5H). Intermediate levels at the foot of the ridges have shrub communities dominated by *Leptospermum ellipticum* (Fig. 7E) or *Actinostrobos pyramidalis* (Fig. 7F).

Fires have been frequent on the reserve. In 1958, 1964, 1967 and 1972 (Fig. 1) summer fires burnt big sections of ridges and flats. The southern end of the main ridge has escaped all these fires but most parts have been burnt twice and other parts three or four times in 25 years. Appendix 1 shows the approximate position and extent of these fires.

This paper results from observations and photographs of the regeneration following each of these fires. Later fires are being monitored by present members of the University of Western Australia Botany Department. It is hoped that these notes and photographs may be useful in assessing changes in the area and providing a background for future detailed work.

Regeneration of vegetation

The ridges—woodland and shrub communities.

On the ridges where almost all the undergrowth plants regenerate by sprouting from underground parts, the vegetation rapidly recovers its prefire appearance. As there is no dominance by any one species in the unburnt bush, so there is none in regeneration, although in the first year the more rapid recovery and flowering of some species makes them more conspicuous than those growing more slowly and not flowering until the second year. In general the minor changes in relative proportions of different species of similar life forms alters the overall character of the undergrowth very little. There is a steady build-up of the shrub cover over the years following fires, with some taller species gradually projecting above the general low level of the undergrowth.

Some details of the regeneration on each of the sand ridges is given below and some photographs in Figures 2 and 3.

On the low western ridge (Fig. 2) after the March 1958 fire by May shoots were just visible on most of the burnt off shrubs but the perennial monocoty-

ledons had made far more growth. By August-September *Anigozanthos humilis* in full bloom gave a spectacular display. Also flowering were *Conostylis juncea*, the orchid *Caladenia flava* and the sedge *Schoenus curvifolius*. Through October-November the more massive monocotyledons, *Dasypogon bromeliifolius* (Fig. 2B) and the purple iris *Patersonia occidentalis* were in full bloom with the less conspicuous tall dark flowering stems of *Haemodorum spicatum* and the twisted stems of *Lyginia barbata*. The annual grass *Stipa compressa*, seen only after fires, formed a sparse cover over the ridge (Figs. 2A, B) and the annual composite *Podotheca chrysantha* was abundant. By this time there had been considerable regrowth on the dicotyledon shrubs (Fig. 2C) although few flowered in the first year. Common species included *Eremaea pauciflora*, *Hibbertia hypericoides*, *H. racemosa*, *Bossiaea eriocarpa*, and *Hovea trisperma*.

Certain species flower only (or almost only) after fire e.g. *Stirlingia latifolia*, *Xanthorrhoea preissii*, *Stipa compressa*, *Lyperanthus nigricans*, *Stylidium carnosum*. Other species flower more profusely although not exclusively.



Figure 1.—General view looking east across the flat to the banksia ridge May 1972. The ridge and a strip of the flat was burnt February 1972, the adjacent section of *Leptocarpus* sward and low mound was burnt January 1967; the foreground, a saline patch too bare to carry fire and the zone behind it with shrubs, escaped the 1967 fire. The small dark shrubs on the saline patch are the succulent *Halosarcia*.

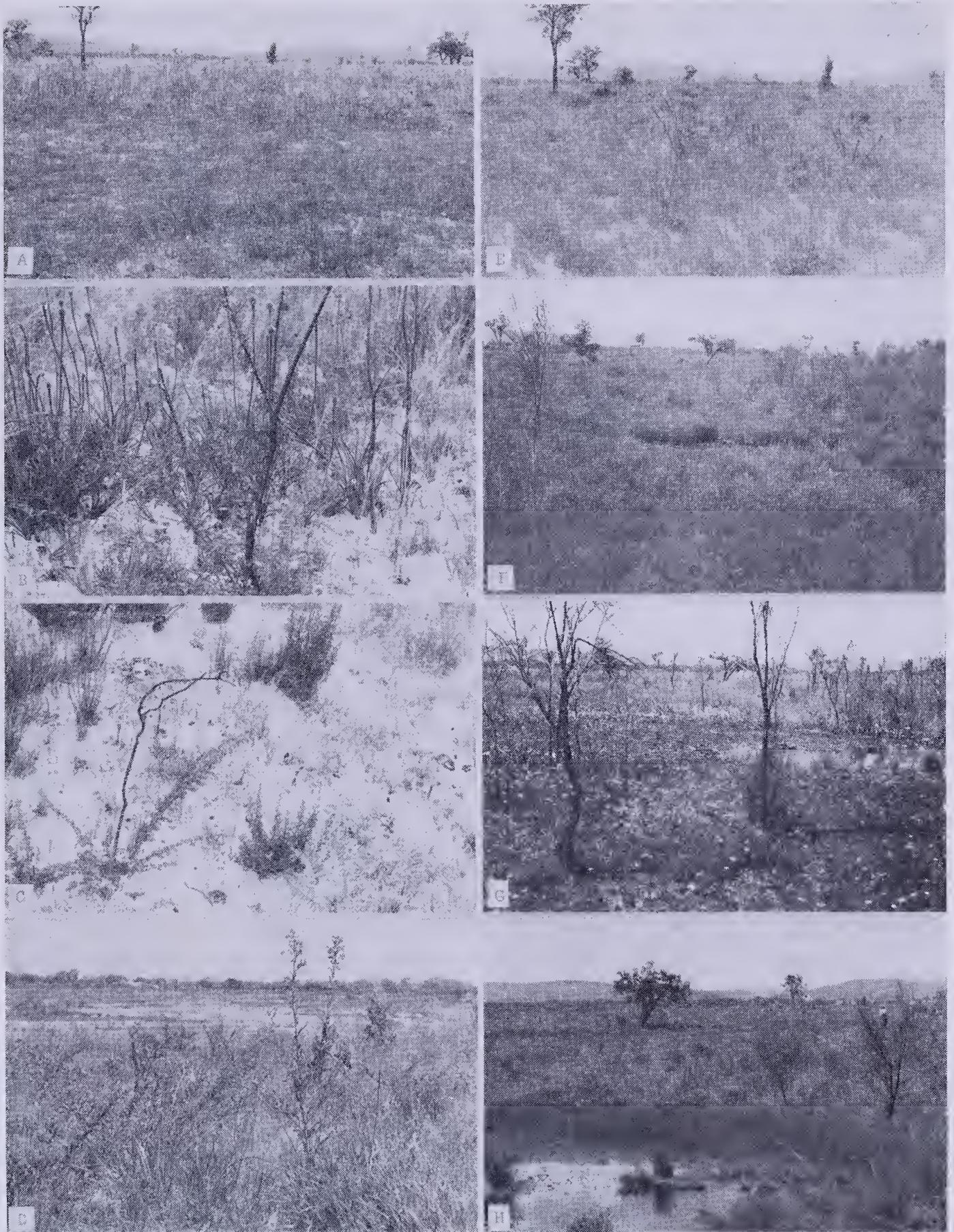


Figure 2.—A-F Regeneration on low western ridge and flat. A—West slope of ridge in October 1958 after the March 1958 fire. *Stipa compressa* showing as light colour on ridge; herbs on flat in foreground; *Nuytsia* trees left, Darling Scarp in distance. B.—Detail of regrowth on ridge. *Dasyopogon bromeliifolius* in bud, wispy *Stipa compressa*, dark flower stems of *Haemodorum* right. October 1958. C.—*Acacia pulchella* with shoots from base of blackened stem, *Hibbertia hypericoides* regrowth right, *Amphipogon* left. October 1958. D.—Second year regrowth on edge of main ridge. *Jacksonia floribunda* projecting. October 1959. E.—Same site as A one year later, low shrub regrowth on ridge. October 1959. F.—Same flat and ridge slightly to right of A. *Viminaria* to right and single plant left. Regeneration in 6th year after another fire in January 1967. *Leptocarpus* restored to flowering stage in foreground. August 1972. G.—Same site as F (cf. forked *Nuytsia* on ridge) in the first spring after another fire in January 1976. *Stipa compressa* covering the ridge, *Tribonanthes variabilis* and *Drosera gigantea* in flower on the flat. September 1976. H.—Same site photographed in 1955, probably burnt in 1949. Photographs looking E to Darling Range on skyline.



Figure 3.—Regeneration on main ridge. A-E Western side, F-H eastern slope. A.—Slope from flat up to the banksia woodland burnt February 1972. May 1972. B.—Recovery in first year after fire in January 1964 epicormic shoots along branches of trees, new foliage on *Xanthorrhoea*, undergrowth with *Stipa compressa* showing pale; dead *Leptospermum* stems in foreground. December 1st 1964. C.—Detail of regenerating undergrowth, *Jacksonia floribunda* left of centre *Haemodorum* and *Patersonia* right of trowel, *Amphipogon* behind. December 1st 1964. D.—Second year regeneration. Tree canopy recovering, shrub regrowth established, *Patersonia* in flower, old spikes of *Xanthorrhoea* which flowered in 1964. October 26th 1965. E.—Regeneration in the sixth year on upper slope, *Eremaea* L.H. corner, dense cover comprising many shrub species, young *Banksia* trees left and right with pale new shoots. December 9th 1969. F.—*Adenanthos* from a 1964 seedling, centre, *Jacksonia*, *Eremaea* and other shrubs behind, *Patersonia* on front margin. December 9th 1969. G.—Part of the shrub cover, *Calytrix aurea* in flower *Conospermum* centre back, *Stirlingia* lower right corner. December 1969. H.—General view looking down eastern slope to *Nuytsia* trees and a group of coppice *Eucalyptus calophylla*. The dense shrub cover restored. December 1969.

By the spring of the second year the low shrub cover was re-established and the plants blooming well. Bare sand still remained to be gradually covered in succeeding years. Some of the bare areas on this ridge were due to remains of old rabbit burrows. Another fire over the same ridge in January 1967 was followed by similar recovery with monocotyledons flowering in the first spring and summer and *Stipa compressa*, not seen in the intervening years, again conspicuous. Figure 2F shows regrowth in the sixth year after the 1967 fire and 2G the same site in the first year after another fire in 1976 with *Stipa compressa* covering the ridge and *Tribonanthes variabilis* and *Drosera gigantea* in flower on the blackened flat.

On the tree crested eastern ridge (Fig. 3) most of the Banksias were defoliated in each of the 1958, 1964 and 1972 fires, the leaves being scorched in the fire and falling subsequently. The extent of crown damage varied along the ridge. Recovery was by growth of epicormic shoots along the upper branches (Fig. 3B). A few seedlings of *Banksia menziesii* and *Banksia attenuata* were found. In 1964 the *Nuytsia* trees on the lower slopes (Fig. 3H) produced a spectacular display of flowers on almost leafless blackened stems. In the following year the foliage had made good recovery but there were few flowers. Similar prolific flowering occurred on trees on the western ridge in the first year after a fire in 1967.

Regeneration of the undergrowth of the woodland and of the almost treeless slopes was similar for that described for the low ridge, with early growth and flowering of monocotyledons and sprouting of almost all shrubs. Figure 3 shows a few stages in the recovery, Figure 3C in December of the first year, 3D in the second and Figures 3E, F, G, H in the sixth year when the dense shrub cover was fully re-established.

Seedlings were few for most of the sprouting shrubs. However, the sprouting *Jacksonia floribunda* (Fig. 2D) produced numerous seedlings. These started with juvenile foliage of true leaves before the adult foliage of leaf like phylloclades. The combination of sprouting from a probably long lived lignotuber and post fire seedling regeneration makes this one of the most fire tolerant shrubs. *Acacia pulchella*, which in the woodland in Kings Park (Baird 1977) is invariably killed by fire, survived and produced shoots from the base of the stem (Fig. 2C) in at least 50% of the plants although there is no lignotuber or thickened tap root which are usual for sprouting species. As in sites where the plants are killed seedlings were numerous.

Few species on the ridge were killed by fire, *Adenanthos cygnorum* a tall grey foliaged shrub was the one species noticeably lacking in the newly burnt areas. However seedlings were numerous and although only 1-4 cm tall after one year grew more rapidly subsequently. Figure 3F shows a 5.5 year old plant. Smaller shrub species killed but regenerating from seed were *Leucopogon conostephioides*, abundant on the wooded eastern ridge, several other epacrids and the legume *Gompholobium tomentosum*.

In 1970 there was on the main ridge a small section long-unburnt at the southern end, a section burnt in 1958 and not since, a big area burnt in

1964 with small incomplete 1967 burns over part of it (Appendix 1). In the unburnt part there was a dense tree canopy including some almost tree size *Adenanthos*, and rather straggly undergrowth with much dead wood. In the 13 year old regeneration the shrub cover was dense with *Leucopogon conostephioides* (ca. 1m) abundant across the ridge, and a lower story including *Hibbertia* (2 spp), *Hovea*, *Bossiaea*, and *Eremaea*. The taller *Acacia pulchella* was mostly dead or dying. The fringe of *Adenanthos* which had been conspicuous outside the banksia before the 1958 fire was in evidence again. In the 1964 extensively burnt area the tree canopy was only partially recovered but the undergrowth was in good condition with the fire sensitive *Leucopogon conostephioides* present again and flowering although the plants were still small (15-20 cm). The shrub cover on the eastern treeless slope (Fig. 3G, H) was almost fully recovered with healthy compact flowering bushes of the sprouting shrubs and persistent monocots. *Adenanthos* plants grown from seed were now sturdy bushes (Fig. 3F). Colonies of *Conospermum* on the upper slopes had regenerated early by many and vigorous long leafy sprouts in the first year and had flowered in the second but had grown progressively more slowly since.

As easily recognisable projection into the flat at the western foot of the main ridge has been photographed since 1958 to show regeneration from a March fire of that year and another in 1972. Figure 6 shows a few stages in the recovery on the flat and slopes.

A tall old paperbark (*Melaleuca preissiana*) was burnt through near its base and the fallen trunk can be seen in the photographs. By November 1958 (Fig. 6A) there had been little growth on the trees and the annual grass *Stipa compressa* was obscuring the early shrub regrowth. On the flat the ground was bare except for the burnt bases of the non regenerating *Leptocarpus* and a few herbs. A year later (Fig. 6B) epicormic shoots on the trees were well developed and there was a dense regrowth of *Acacia saligna*. On the flat seedlings of *Leptocarpus* formed a faint grey film.

Figure 6C in October 1965 gives a more distant view to show the site in relation to the edge of the ridge and part of the flat with the 1964 firebreak. The sward of *Leptocarpus* was restored and there had been massive regrowth from the base of the burnt *Melaleuca*. This is shown more clearly in Figure 6D, November 1970. *Actinostrobilus* regenerated from seed formed a group of slender plants projecting above the *Acacia* scrub.

In 1972 another fire engulfed this site and left it as in Fig. 6E. In the fourth year of recovery from this (Fig. 6F) again there had been a dense regrowth of *Acacia saligna*. The *Leptocarpus* on the flat had regenerated well, much better than on the open flat no doubt because seepage of fresh water from the ridge and drainage along the firebreak checked the development of salinity present on the central part of the flat.

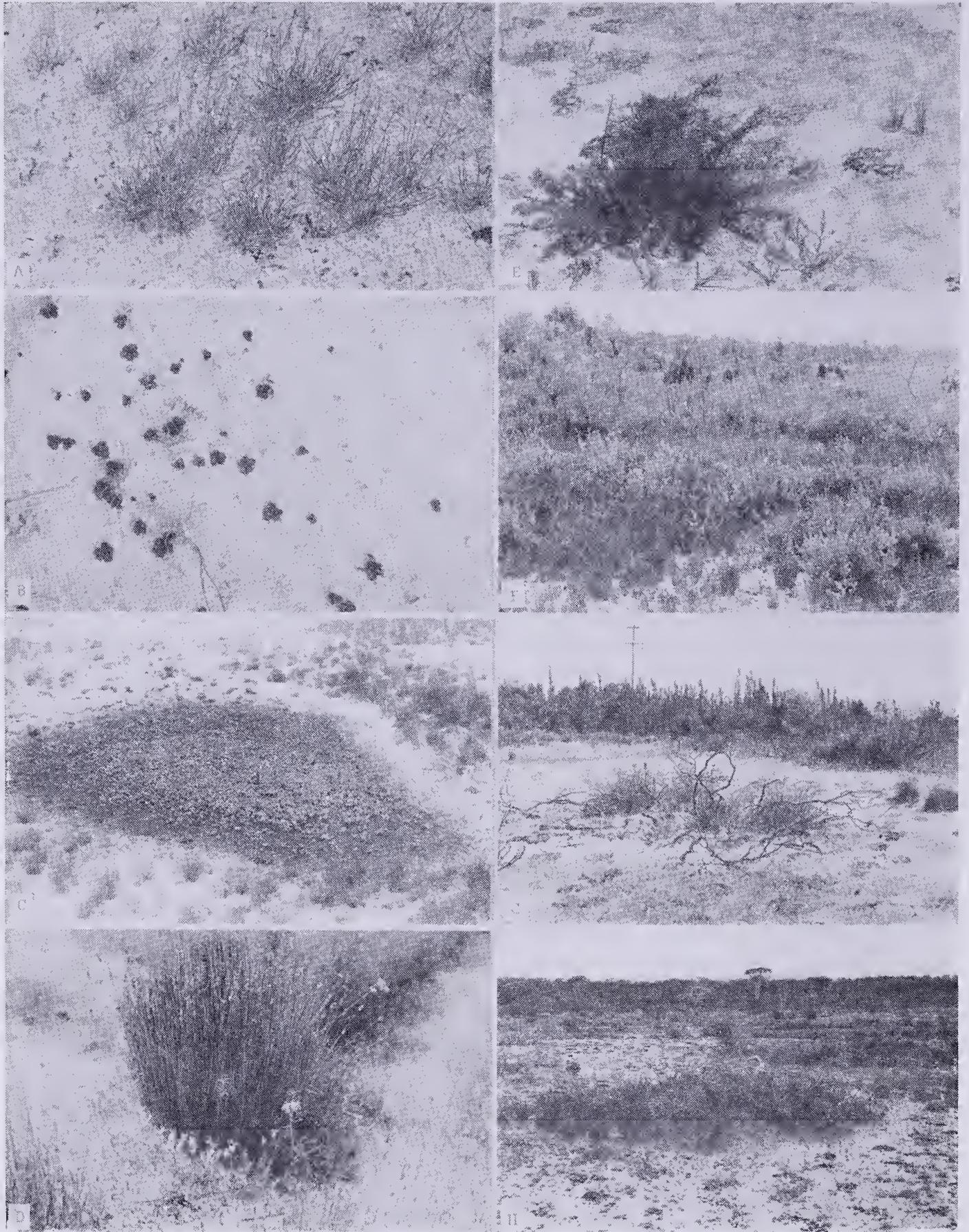


Figure 5.—Species of the flats. A.—*Leptocarpus aristatus* in the 4th year, much bare sand remaining. September 1970. B.—*Drosera bulbosa* on bare white sand after a summer fire. May 1961. C.—*Angianthus stricta* in a slight depression. November 1970. D.—*Stylidium calcaratum* at base of a clump of *Leptocarpus carus*, *Centrolepis aristata* right foreground. October 1967. E.—A sprouting clump of *Grevillea thelemanniana*, *banksia telmatiaea* seedlings two years after fire in March 1958. April 1960. F.—Good seedling regeneration of *Banksia* in sixth year from fire in 1964. December 1969. G.—Two year regrowth of the mound building *Melaleuca bracteosa* on the western flat, unburnt *Actinostrobus* in background. April 1960. H.—Mounds on the central flat in the fourth year after fire in 1967, very poor recovery of the *Melaleuca*. Main sand ridge in background. Tall white stemmed *Melaleuca* and surroundings has escaped all fires. September 1970.



Figure 4.—The main *Leptocarpus* flat with an old cart track across it. A.—The burnt flat after a fire in January, unburnt ridge on left. May 1967. B. In the fourth year of regeneration. Shows the slow recovery of the *Leptocarpus*. The scattered sedge tufts are species which are not killed by fire. September 1970. C.—The *Leptocarpus* sward in its eighth year of regeneration from a fire in 1958. October 1965.

The flats—Leptocarpus sward with depressions and mounds.

Whereas recovery on the ridge is rapid, it is slow on the flats (Fig. 4). The whole appearance of the *Leptocarpus* meadow with its islands of big mound building *melaleucas*, is drastically changed. The dominant *Leptocarpus* is completely killed and the *melaleucas*, although sprouting take many years to regain their former shrub form. For the first year (Fig. 4A) the flats remain bare except for

the occasional tufts of those sedges which are capable of sprouting and the old blackened bases of the burnt-off *Leptocarpus* clumps. The *Leptocarpus* seedlings although present the first year are minute and scarcely project through the loose sand. The seedlings do not grow as single plants but in tufts originating from a fruiting head (Fig. 5A). By the second year of growth they form a faint grey film over the sand and by the third to fifth year some have reached the flowering stage. By the 7th-8th year the meadow-like appearance is restored although the plants have not reached their maximum size (Fig. 4C).

Although the regeneration of the *Leptocarpus* is slow there is no other plant replacing it in the succession. The herbaceous geophytes of the flats, unharmed by fire as they died down before its occurrence, flower as usual in winter and spring and rather more profusely, probably benefiting from the additional nutrient from the ash. These however are more abundant at the levels slightly above the main *Leptocarpus* level.

The rather distinctive zone at the foot of the west-facing slopes which normally shows seasonal dominance of *Drosera gigantea* and *Utricularia inaequalis* is particularly spectacular after fire when the *Leptocarpus* which hides the *Utricularia* has been removed. The ephemeral cover of tiny annuals, of which *Centrolepis aristata* is the most abundant and widespread, is much more visible on the fire stripped flats and plants of most species are larger than in unburnt areas. Slight depressions are often densely covered by *Calandrinia granulifera* or, where saline, by *Angianthus strictus* (Fig. 5C).

The larger saline depressions with *Halosarcia halocnemoides* normally escape fires (Fig. 1). The samphires are succulent and are surrounded by more or less bare areas, then by widely spaced *Leptocarpus* clumps before the dense swards of non saline parts. After fires, seedlings from the burnt *Leptocarpus* near the depressions after 4 years graded outwards from plants only 2-5 cm up to 15-20 cm and flowering.

Of the shrubs of the main level and slightly elevated areas of the flats, *Grevillea thelemanniana* (Fig. 5E) *Hakea varia* sprouted early and vigorously. Many seedlings were found of *Grevillea* but few of *Hakea*. *Banksia telmatiaea* was killed but regenerated well from seed. After the 1958 fire, seedlings in the first year grew to 4-5 cm with already well developed proteoid roots. A year later sizes were very varied, but mostly healthy plants 15-20 cm with some branching and, by the third year many were sturdy much branched bushes up to 30 cm tall and similar diameter. A particularly dense even aged stand below ridge still had no flowers in its sixth year and this was also true for plants of similar size and age after the 1964 fire (Fig. 5F). However, one or two plants have been seen with two flowers in their fifth year. *Calothamnus villosus* is also fire sensitive and regenerates from seed.

The mound forming *Melaleuca bracteosa* (Fig. 5G) was not killed but recovered only very slowly so that the mounds for the first few years, with the protection of the large spreading bushes removed, tended to become flattened by erosion. Seedlings from the associated shrubs were spread over a wider area than the original site and developed very differently according to the microhabitat. After the 1958 fire on the central flat, in the first year seedlings

of *Melaleuca*, *Hypocalymma*, *Calothamnus* *Acacia* and *Actinostrobus* were numerous. Over the next few years some flourished and others failed to make satisfactory progress, though few died. Eight years after the 1958 fire, small stunted plants of *Acacia stenoptera*, *Actinostrobus pyramidalis* and *Calothamnus villosus* still survived although only some 5 cm high. This stunting seemed to be associated with increased salinity in the soil. *Acacia stenoptera*



Figure 6.—Series of photographs taken at the same site on the edge of the flat since the fire of March 1958. A.—November 6th 1958—In the foreground bare flat with burnt bases of *Leptocarpus* clumps, some herbaceous growth, left, on the ridge *Stipa compressa*, burnt trees with small epicormic shoots, on the right top of fallen *Melaleuca*, also showing in B, C, and D. B.—October 29th 1959—On the flat a faint grey film of small 2 year old *Leptocarpus*, massive regrowth of *Acacia saligna* on the bank, trees clothed in epicormic shoots. C.—October 1965—A more distant view of the site showing its position in relation to the scraped firebreak put down in 1964. *Leptocarpus* cover restored, dense shrub growth behind fallen *Melaleuca*. D.—November 5th 1970—Slight canopy on the eucalypts, dense bushy regrowth (centre) from the stumps of the burnt off *Melaleuca*; slender thirteen year old *Actinostrobus* (right background). E.—May 1972 after a fire in February 1972—Shows the slope up from the bare at to the eucalypts and adjacent *Xanthorrhoea* plants. F.—October 29th 1975—In the fourth year of recovery, again dense regrowth of *Acacia saligna*, a low but dense growth of *Leptocarpus* on flat.

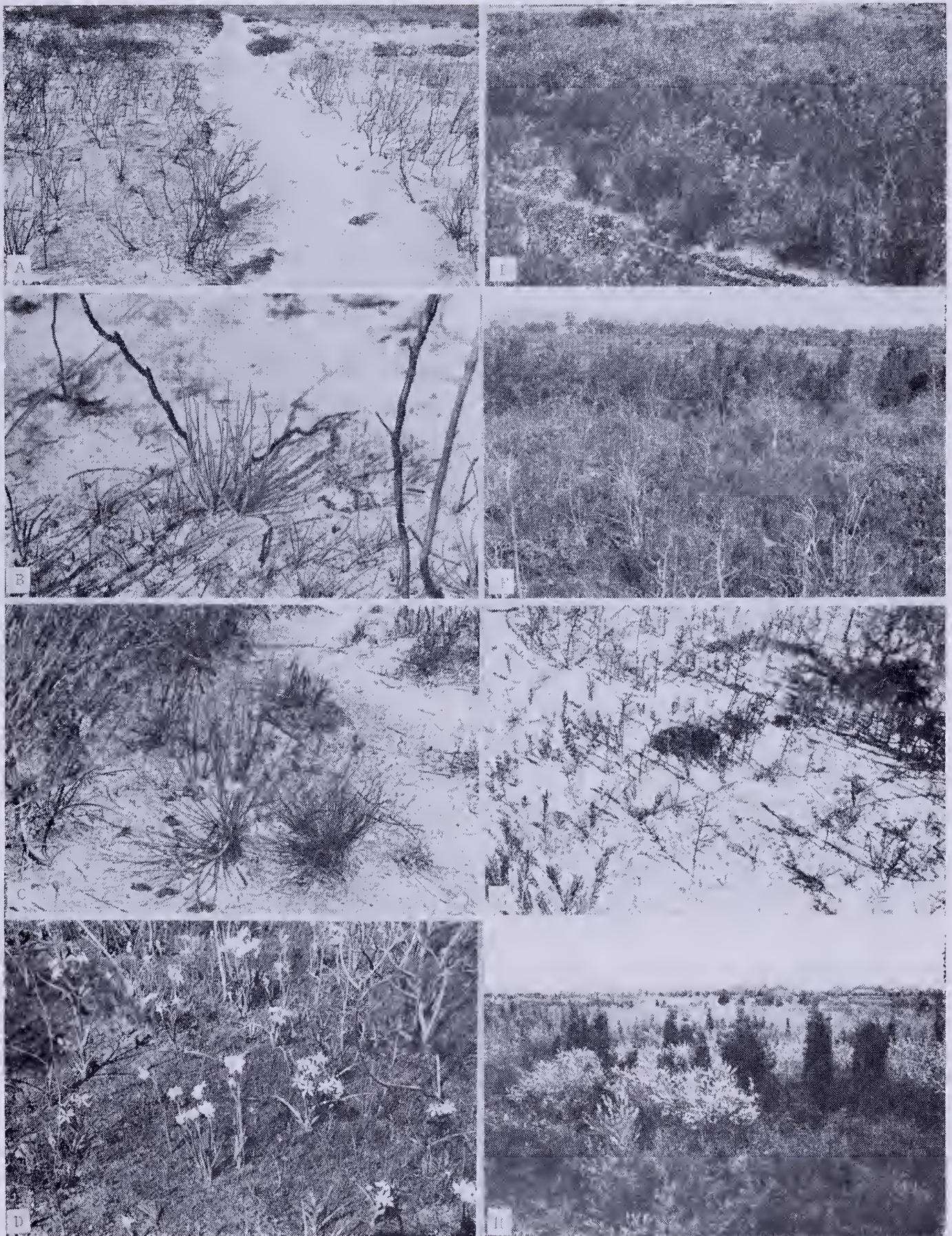


Figure 7.—*Leptospermum* and *Actinostrobos* communities. A.—After a fire in February 1972, dead stems of *Leptospermum*, unburnt *Leptocarpus* sward in background. May 1972. B.—Early regrowth of *Byblis gigantea* at the base of old stems which show the habit of branching; various monocotyledons sprouting in fore-ground. August 1972. C.—*Byblis* in flower, *Conostylis filifolius* right, *Cyathochaetae avenacea*, a sprouting sedge, overhanging left corner. October 1972. D.—*Tribonanthes variabilis* and *Burchardia multiflora* on a site lightly burnt the previous summer. September 8th 1972. E.—Restored community from an earlier fire in March 1958, *Leptospermum* in flower. October 1968. F.—A stand of *Actinostrobos* partly burnt some years earlier (1949), dead stems remaining but no regeneration, on the ground *Leptocarpus* and *Acacia lasiocarpa* in flower. August 1956. G.—Good seedling regeneration in an *Actinostrobos* community. *Actinostrobos* single plant centre foreground and many in background, *Hypocalymma* lower left corner. All are two year old seedlings from a 1958 fire. April 1960. H.—*Hypocalymma angustifolium* in flower in a mixed *Actinostrobos* community. August 24th 1981.

showed the thickening and yellowing so often associated with salt. Regrowth of the large *Melaleuca* bushes continued steadily but slowly and after eight years had reached less than half the prefire height. Build up of the mounds could not be followed for more than nine years as the whole area was burnt again in February 1967. After this fire, the regeneration of the mounds was very poor (Fig. 5H). Where mounds had been burnt in both 1964 and 1967, or in 1958, and 1964, some *Melaleuca* had completely failed to regenerate.

In more favourable situations, although the regrowth of the *Melaleuca* bushes was still slow, associated shrubs flourished. *Acacia lasiocarpa*, common on the mounds, was particularly abundant at the foot of the eastern slope of the western ridge. After the fires of 1958 and 1967, seedlings were very numerous and resulted over the next few years in a dense cover of bright green low bushes yellow with flowers in spring.

Leptospermum communities

In the *Leptospermum* zones (Fig. 7) change in plant cover through early years of the fire succession is shown to a marked degree. In a long unburnt stand the *Leptospermum ellipticum* bushes, (up to 1 m tall), completely overshadow other species. The associated sedge *Restio tremulus*, in which the hanging balls on the male plants give a distinctive appearance, is more conspicuous when the shrubs are smaller. As both of these species are killed by fire (Fig. 7A) the zone is dominated for several years by minor species.

After the 1958 fire, seedlings of *Leptospermum ellipticum* came up in abundance but were not more than 2-3 cm high in September and by the end of the growing season in November were only 3-5 cm with six to eight small leaves above the cotyledons. In spite of the long hot summer mortality was very low and growth accelerated the next season. In the second and third years there was a marked difference between the seedlings in the flatter and lower *Leptospermum-Restio* zone and those on the contiguous better drained slope. In 1960 the seedlings of the lower level were still only about 15-20 cm tall and unbranched while those of the higher level averaged about 30 cm and were branching. By the end of this, the third growing season, a few of these flowered and at the end of the fourth year there was some flowering in the lower level also. Similar rates of growth and similar differences between upper and lower *Leptospermum* zones were observed after later fires, at the western foot of the main ridge.

Restio tremulus, the co-dominant of the lower levels was equally slow to regenerate. Small shoots, recognised as *Restio* by their flattened stems, grew very slowly and few plants had reached the flowering stage by the fourth year. Eight years after the 1958 fire on the steep western slope (Fig. 5C) the whitened stems of the dead *Leptospermum* still pro-

jected above the *Restio* which obscured the small *Leptospermum* plants. Four years later the *Leptospermum* overtopped the *Restio* and the old stems.

Through the early years of the slow growth of the dominants the subordinate species were flourishing in both the lower and upper *Leptospermum* zones. The sprouting shrubs *Hypocalymma angustifolium*, *Daviesia physodes* and *Hakea ceratophylla* grew vigorously and flowered profusely. *Lechenaultia expansa*, regenerating rapidly from seed, flowered particularly well in spring of the 2nd and 3rd year, thereafter gradually waning. *Beaufortia squarrosa* also grew rapidly from seed and some were flowering at 2 years old (April 1960), but in contrast to the more herbaceous *Lechenaultia*, continued to grow into sturdy woody shrubs still flowering well in long unburnt stands. The less frequent slender *Astartea fascicularis* was killed and regenerated from seed.

The herbaceous perennial insectivorous plant *Byblis gigantea* (Fig. 7B&C) sprouted and some plants had one or two flowers in the first year but with particularly good flowering in the 2nd and 3rd years. In the same zone as *Byblis*, *Conospermum huegeli* and *Anigozanthos viridis* were common. Herbaceous geophytes such as the common *Tribouanthes variabilis* and *Burchardia multiflora* (Fig. 7D) and orchids, sundews, and small annuals were conspicuous on the burnt areas.

Actinostrobus communities

Actinostrobus pyramidalis (Fig. 7F) is killed by fire. Mature cones remain unopened on the living plants and seed is released only after death. Numerous seedlings (Fig. 7G) have been found close to the parent plants after each of the fires but survival has been varied. After the March 1958 fire, seedlings with cotyledons and small shoots (2-4 cm) were seen in July and by November had ceased growth at 5-6 cm. In the 2nd year the 3 ranked appressed adult foliage had succeeded the 4 ranked juvenile leaves and heights of 10-15 cm in May and 20-25 cm in October had been reached. In the 3rd year a few plants had tiny cones which would not be ripe for another 18 months. After each fire a few of the biggest plants have had a few ripe cones at 5 or 6 years, most a year or two later. Because of frequent fires along the north west side of the reserve, where most of the *Actinostrobus* occurred before 1960, few plants have survived more than 10-15 years—a short life for a conifer. The plants are scattered through the community or in small groups rather than forming close stands as on a long unburnt site on an adjacent property.

Much of the undergrowth in the mixed *Actinostrobus* stands is similar to that in the *Leptospermum-Restio* community. The sprouting shrub *Hypocalymma angustifolia*, which also produces numerous seedlings (Fig. 7G), is particularly abundant in the repeatedly burnt sections (Fig. 7H). Several species of *Verticordia* are conspicuous after fires but relatively short lived. The annual composite *Brachycome pusilla* is very common.

Discussion

This description is in general terms as no quantitative work has been undertaken and visits to the site have been irregular. All fires were summer ones the earliest in mid or late January and the latest in mid March. The western ridge has been burnt four times at intervals of nine years (1949, 1958, 1967, 1976). This interval would appear to be satisfactory for maintaining a healthy shrub community. The eastern ridge has had fires at different intervals on different sections of the ridge and consequently has different stages of the fire succession in different parts as the example given for 1970.

This is a fire tolerant vegetation as that of most of the south of Western Australia (Gardner 1957, Wallace 1966). Trees are not killed, foliage is renewed from epicormic buds along the branches, e.g. *Banksia attenuata* and most of the shrubs burnt to ground level in fires recover by sprouting from lignotubers or massive tap roots, e.g. *Jacksonia floribunda*. Persistent monocotyledons have rhizomes or otherwise well protected growing apices and the many herbaceous geophytes have inbuilt protection by dying down in summer to underground perennating organs. Species killed by fire regenerate well from seed, e.g. *Leucopogon conostephioides*.

Both ridge and flat species capable of shoot regeneration have the advantage not only of faster vegetative growth but of renewed flowering within one or two years while flowering from seedling plants takes longer. However, early reproduction is a feature of many of the non-sprouting species. The ability of *Actinostrobos* to produce ripe cones on small plants only 5-6 years old is unusual for a conifer and of value in a fire susceptible environment. Fire sensitive species of *Leucopogon*, *Beaufortia*, *Verticordia* and others flower when only 2-3 years old, but other fire susceptible species in the same communities flower much later. Nevertheless, there is some evidence that the frequent fires of the last 20 years have reduced the populations of *Actinostrobos*, *Banksia telmatiaea*, *Leptospermum ellipticum* and some epacrids in parts burnt several times in close succession.

There is an extensive literature on fire in Australian vegetation, much of it listed in recent papers such as Gill (1981) and Purdie and Slatyer (1976). Adaptions such as those described for Yule Brook are well known in sclerophyllous vegetation. Two papers dealing with fire on the Perth coastal plain in vegetation similar to that of the sand ridges at Yule Brook are Whelan & Main (1979) and Baird (1977), one dealing with *Banksia* woodland on deep white sand at Jandacot the other a *Banksia-Eucalypt* woodland on deep yellow sand in Kings Park. In neither site is there underlying clay as at Yule Brook. Although there are differences in species composition on the three sites there are many species in common and the general pattern of regeneration is the same.

For fire regeneration on seasonally waterlogged clay flats like those on the Yule Brook Reserve I can find no published literature.

On this site there is a marked difference between the rapid recovery on the ridges and the much slower regeneration on the flats where the dominants are killed and seedling growth is slow. The *Leptocarpus* swards are replaced effectively though slowly by the very numerous seedlings. Apparent deterioration of the *Leptocarpus* appears to be due to salinity on the flats checking the growth of seedlings.

The scattered shrub mounds have been greatly reduced. These are important ecologically as they provide shelter and stable soil. The fringes of the mounds are a favourable habitat for many of the herbaceous species. The natural succession is for the mounds to increase in height and spread by accession of wind blown sand, plant debris and the addition of further plants in the existing shelter. In the present situation of frequent fires with consequent erosion of the mounds, regression is more evident than succession. Near the eastern boundary there are a few large and complex mounds which have escaped fire. These lend support to the idea given by Speck (1952) in his thesis that the mounds represent an early stage in succession to tall mixed *Actinostrobos* scrub.

Since 1967 the main flat has been very denuded in comparison with its condition 20 years ago. Some of this is due to repeated burning of the *Leptocarpus* which requires 6-8 years for the dense swards to be re-established and some is apparently due to increased salinity. It is as yet uncertain how far fires, drought and changed drainage may have been involved in this apparent deterioration or whether with fewer fires and a succession of wet winters the changes could be reversed.

One of the unfavourable results of repeated fires has been to facilitate the invasion and numerical increase of weed species on both flats and ridges. Fires leave ground open for invasion, and weed cover of annuals which dry off in summer increases the fire danger.

Acknowledgements.—I am indebted to several members of the staff of the Botany Department of the University of Western Australia who have read the manuscript and given helpful advice and criticism, and to Dr N. Marchant for advice on plant nomenclature. I have used some information from student notes from class excursions particularly the class of 1958. I thank Mr. M. Lucks for preparing the photographs for publication.

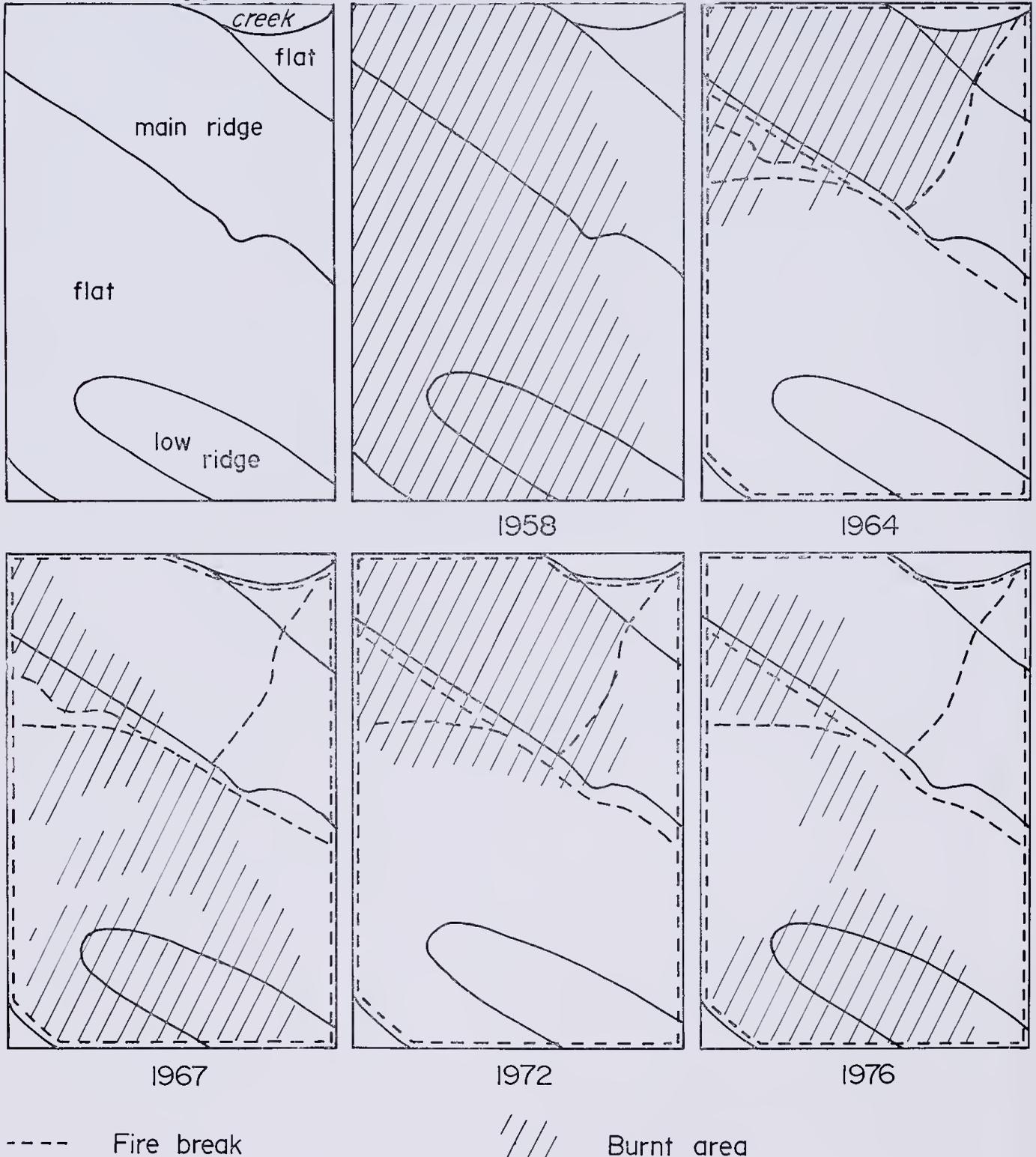
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Appendix 1

Outline of flat showing position of ridges and approximate extent of each of the fires.



Appendix 2

The following lists give the response to fire of some of the more common perennial species. A species list for the reserve is given in the account of the vegetation of the Reserve. (Spek and Baird 1984).

A. Sand ridges—*Banksia* woodland and shrub covered slopes.

Trees—none are killed—sprouting from epicormic buds.

Sclerophyllous shrubs and fibrous monocotyledons.

Sprouting

Eremaea pauciflora
Jacksonia floribunda
Oxylobium capitatum
Hovea trisperma
Bossiaea eriocarpa
Hibbertia hypericoides
H. racemosa
Petrophila linearis
Stirlingia latifolia
Eriostemon spicatus
Conostephium pendulum
Astroloma pallidum
Conospermum sp.
*Casuarina humilis*²
Xanthorrhoea preissii
Dasyogon bromeliifolius
Patersonia occidentalis
Lyginia barbata
Amphipogon turbinatus
Teurariopsis octandra
Schoenus curvifolius
Conostylis spp.
Thysanotus spp.

Killed

Adenanthos cyguorum
Leucopogon conostephioides
Leucopogon sp.
Gompholobium tomentosum

B. Intermediate levels between ridge and flat—*Leptospermum*-*Restio* and *Actinostrobis* communities.

Sprouting

Hypocalymma angustifolium
Hakea varia
Hakea ceratophylla
Daviesia physodes
Viminaria juncea
Byblis gigantea
Anarthria gracilis
Cyathochaeta avenacea
Acanthocarpus preissii
Schoenus sp.

Killed

**Leptospermum ellipticum*¹
 **Actinostrobis pyramidalis*
Hakea sulcata
Astartea fascicularis
Verticordia spp.
Beaufortia squarrosa
 **Restio tremulus*

C. Flats—*Leptocarpus aristatus* sward and shrub mounds.

Sprouting

Hakea varia
Grevillea thelemanniana
Melaleuca bracteosa
Leptocarpus canus
Gahnia trifida
Schoenus sp.

Killed

Banksia telmatiaea
Calothamnus aff. *villosus*
Acacia lasiocarpa
 **Leptocarpus aristatus*

D. Geophytes.

In all communities geophytes which die down and perennate through summer as underground corms tubers etc. are not killed. A few common geophytes of the wetlands are:—

Burchardia multiflora
Iribonanthes variabilis
T. brachypetala
Philydrella pygmaea
Drosera gigantea
D. bulbosa
D. heterophylla
D. neesii
Diuris spp.
Pterostylis nana

Notes:

* denotes dominant species.

¹ *Leptospermum ellipticum* has been renamed *Pericalymma ellipticum* (Thompson, J. (1983).—Redefinition and nomenclatural changes within the *Leptospermum* suballiance of the Myrtaceae. *Telopea*, 2(4): 379-383.)

² *Casuarina humilis* has been renamed *Allocasuarina humilis* (Johnson L. A. (1982).—Notes on Casuarinaceae 2. *J. Adel. Bot. Gardens*, 6: 73-87.)

Basins and barrels: the geological background to the search for fossil fuels in Western Australia

Presidential address—1983

by A. E. Cockbain

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Abstract

Fossil fuels, i.e. petroleum and coal, occur in (mainly Phanerozoic) sedimentary basins. The geology of these basins can best be understood in terms of plate tectonics—a concept which has revolutionised geological thinking. Western Australia was once part of Gondwana and the architecture and history of the Phanerozoic sedimentary basins were largely determined by the breakup of that supercontinent. Different types of basin can be recognised and related to the plate tectonic model. Most of the oil and gas in the State occurs in pullapart basins (e.g. Perth and Carnarvon Basins) which formed along the breakup zone. The State's only coalfield is in a rift basin (Collie Basin). Experience elsewhere in the world suggest that downwarp (Bonaparte Basin) and complex (Canning Basin) basins are highly prospective for petroleum. Rift and pullapart basins probably have the best potential for coal.

Introduction

Petroleum, that is oil and natural gas, and coal provide the bulk of the world's energy, e.g. in 1980 they supplied 90% of the energy in the OECD countries (International Energy Agency 1982). Together they comprise the fossil fuels which are those derived from fossil organisms, mostly single-celled marine plants and animals in the case of oil and gas, and land plants in the case of coal. Since fossil fuels are derived from organisms it is natural to explore for them in those rocks which contain abundant organic remains. Such rocks were laid down in sedimentary basins and more especially sedimentary basins formed during the Phanerozoic Era which started about 570 million years ago. Precambrian rocks, while not obviously fossiliferous, do contain evidence of life in them and should not be excluded entirely in the search for fossil fuels.

In following the theme of basins and barrels I shall look first at continental drift and then at the change in thinking about the earth called plate tectonics; then I shall say something about the Gondwana supercontinent by way of setting the scene for a survey of the sedimentary basins of Western Australia, which was once a part of Gondwana. Finally I shall briefly examine the fossil fuel potential of the State's sedimentary basins.

Continental drift

The earth has variously been thought of as a rigid and permanent, with continents and oceans fixed in their present position for all time, expanding, or contracting. The folded rocks seen in mountain chains such as the Alps suggested contraction, to some, by analogy with the wrinkled skin on a drying apple. Contraction ideas usually went hand

in hand with the so-called tetrahedral theory (see Holmes 1964, Carey 1976). A sphere, which has the greatest volume for a given surface would, it was reasoned, contract to a tetrahedron, which has the smallest volume for a given surface. The tetrahedron was usually oriented with one face uppermost representing the Arctic Ocean; the other faces are the three great oceans (Pacific, Atlantic and Indian). The edges and corners represent the land masses. One of the most recent supporters of the theory was W. G. Woolnough (1946), the first Professor of Geology at the University of Western Australia. The theory has no followers today, although it does epitomize the asymmetrical distribution of land and sea.

Earth expansion is associated particularly with one of this Society's members, Professor S. W. Carey of Tasmania. While there are certain attractions to the idea of an expanding earth (Carey 1976), the physical difficulties entailed are formidable and the theory is not widely held.

A fixed diameter earth is by far the simplest model to adopt. Again, simplicity suggests that continents and oceans have always been as they are today—witness the lack of granite in ocean basins and the absence of true deep sea sediments on the continents. But the idea of continents moving over the face of the earth—continental drift—has always fascinated some. In its fully developed form the theory is associated with the German meteorologist Alfred Wegener who published "Die Entstehung der Kontinente und Ozeane" in 1915, later translated as "The origin of continents and oceans" (Wegener 1966). However, the idea appears to go back to Francis Bacon (Holmes 1964). The evidence in support of continental drift includes:

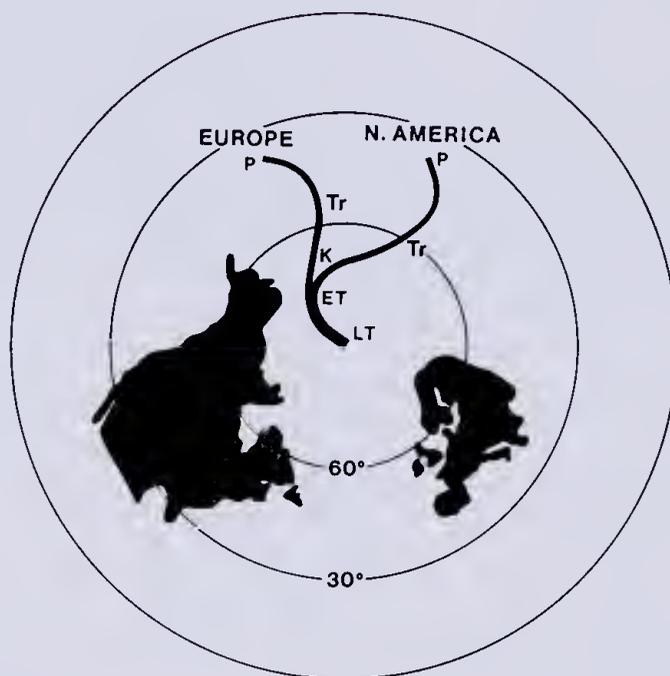
- a. the fit of the continents like pieces from a jig-saw puzzle, the best example being the fit of Africa and South America.
- b. various geological similarities on the continents. As Arthur Holmes (1964), in his class text on physical geology remarks “. . . the westward convergence across Europe of the outer Caledonian and Hercynian fronts, until they almost meet in the south-west of Ireland, is continued in North America, where the fronts eventually cross”. The many similarities between the geology of the southern continents are mentioned below.
- c. past climates; for example there is abundant evidence of glaciation in what are now tropical latitudes.
- d. plant and animal distributions; these are often much easier to understand if distant continents were once closer together. For example, the Early Cambrian trilobite faunas of North America and Europe; north west Scotland has an “American” fauna, while east Newfoundland and Nova Scotia have a “Welsh” fauna. (Cowie 1971).

While the evidence may be suggestive, the lack of a convincing mechanism to move the continents was a problem. Wegener invoked the gravitational attraction of the equatorial bulge to account for the Polflucht or Flight from the Pole of the continents and the breakup of Pangaea—the one landmass into which he believed all the continents were aggregated. However, physicists, especially Sir Harold Jeffreys (see Jeffreys 1976), pointed out that the force was many times too small. And so, for much of the pre-war years continental drift was out of favour.

Plate tectonics

After the second world war two important developments took place, which helped to change this; palaeomagnetism and marine geology.

Palaeomagnetism is the study of fossil magnetism (Irving 1964). Through a variety of techniques the remnant magnetism of a rock can be determined; this is the magnetic polarity imposed on a rock when the contained iron minerals formed or were deposited. From the measurement of the remnant magnetism the latitude of the magnetic pole at various times in the past can be determined. It was shown by this work that the magnetic pole has not always been where it is now. In fact polar wandering paths can be drawn showing how the position of the pole has changed systematically during time. Moreover, the polar wandering paths for North America and Europe differ and differ more markedly the further back in time one goes (Fig. 1). This led Runcorn to suggest that North America and Europe must have been closer together in Permian times and gradually moved apart in the Mesozoic and Tertiary to their present positions (see Hospers and Van Andel 1970). Another feature is that magnetic polarity has not remained constant but that periods of normal (present day) polarity have alternated with periods of reversed polarity (when the north pole has flipped to become the south pole).



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Figure 1.—Apparent polar-wandering paths for Europe and North America. P., Permian; Tr, Triassic; K, Cretaceous; ET, Early Tertiary; LT, Late Tertiary (after Irving and Robertson 1969).

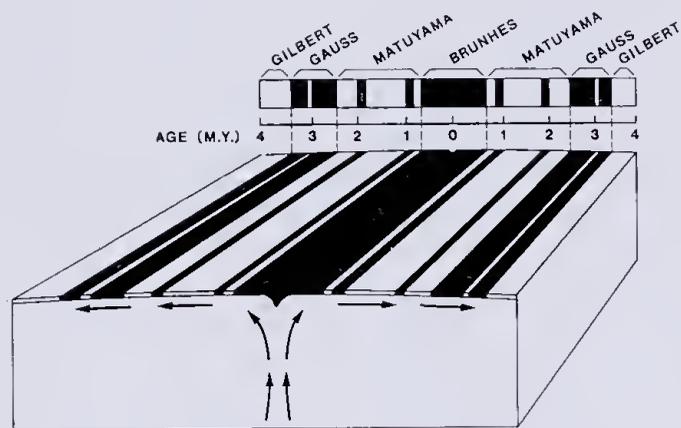
Marine geology, like most oceanography, can be said to have started with the 1873-76 expedition of HMS Challenger, which called in at Fremantle on its epic voyage around the world. However, the science developed dramatically in the 1950s and 60s. Amongst the many interesting findings the following are pertinent.

Heezen, Ewing and others mapped a world-wide oceanic ridge system (Heezen and Fox 1966). This is best developed in the Atlantic Ocean, a submarine mountain chain which occasionally rises above sea level e.g. in Iceland, the Azores, St Paul's Rocks, Ascension. There is a rift valley running along the axis of the ridge and heat flow beneath the axis is much higher than elsewhere in the ocean; the ridge is also a focus of seismic activity.

The ocean basins were found to be quite young. No rocks older than Jurassic were discovered on the ocean floor. An earlier observation was confirmed, namely that the deepest parts of the oceans were the trenches which were situated at the margins of the ocean basins.

All this led Hess (1962) to put forward the idea of sea-floor spreading. In each ocean the mid oceanic ridge is the site of the ascending limb of a convection cell in the mantle which then turns and flows under the oceanic crust carrying the ocean floor with it as on a conveyor belt, and descends into the mantle under the marginal trench.

This idea was confirmed in a remarkable way by the magnetic stripes (Fig. 2). These are linear bands of alternate positive and negative magnetic



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Figure 2.—Sea-floor spreading and the magnetic polarity time scale (after Cox *et al.* 1967).

anomalies which were mapped on the sea floor parallel to the axis of the oceanic ridge system (Vine and Matthews 1963). It was hypothesised that these anomalies are a record of the successive magnetic reversals, alluded to earlier, and that they can be used to determine the age of the oceanic crust. Many workers have subsequently documented the magnetic anomalies and age of the crust throughout the world's oceans (see McCracken 1979 for a map of the magnetic anomalies around Australia).

The last contribution I shall mention is that of J. T. Wilson (1965) who recognised a new type of fault he termed a transform fault. These are linear discontinuities which offset the oceanic ridge system and magnetic stripes. They resemble transcurrent (lateral displacement) faults but movement along them is in the opposite direction to transcurrent movement. Subsequently, studies of earthquakes along the oceanic ridge system demonstrated that this paradoxical sense of motion was correct; this is because the sea floor itself is moving (spreading) on either side of the transform.

Around 1967 these observations were integrated into a unified theory which has come to be called plate tectonics and is associated with the names of Morgan, McKenzie and Le Pichon (see Hallam 1973). The earth is divided into a number of rigid plates (six in the simplest version of the theory, Figure 3). The margins of the plates (Fig. 4) are either spreading centres (oceanic ridges where new crust is formed), subduction zones (trenches where crust is consumed) or transform faults (where plates slide past each other). Any three plates meet at triple junctions which are various combinations of spreading centres, subduction zones and transform faults meeting at a point.

The theory provides an elegant explanation for a number of puzzling features. It explains why the ocean basins are young—they have only recently been formed; ancient oceanic crust has disappeared into the mantle being consumed in the so-called subduction zones beneath the trenches. Mountain chains form where two plates collide, indeed they

represent the suture lines along which plates have joined e.g. the Alps were formed when the African plate collided with the European plate. Finally it provides a mechanism for continent to drift—on the back of plates, driven as it were, by convection cells in the mantle.

While the theory is a powerful one it does have its critics. The Meyerhoffs have written at length detailing palaeoclimatological and plant and animal distribution data which are hard to fit into the plate tectonic model (Meyerhoff and Meyerhoff 1972). Carey (1976), while supporting (and indeed anticipating) some aspects of plate tectonics does not accept the trenches as subduction zones. Of course with an expanding earth, as he advocates, there is no need for subduction zones where crustal material is destroyed.

Retrospect

Plate tectonics has brought about a new way of looking at the earth—the “new global tectonics”—so much so that text books which do not mention the theory are considered dated if not obsolete.

Thomas Kuhn (1962), the philosopher of science, has characterised science as progressing not gradually but through a series of revolutions which overturn, as it were, previously established viewpoints (or paradigms as he calls them) and substitute a new one. Typical examples of revolutions are the Copernican theory that the sun is the centre of the universe and Darwin's theory of evolution through natural selection. In this sense plate tectonics can be regarded as a revolution, although as Hallam (1973) observes it is not entirely clear what paradigm was replaced by the theory although it was probably some notion of continent and ocean permanency. From the philosophical point of view it is interesting to observe, with Hilary Putnam (1974), that Kuhn's idea of science implies that some scientific theories cannot be overturned by data alone but only by alternative theories.

The revolutions are separated by periods of relative tranquillity. In Kuhn's words “Each intervening period of relative tranquillity, each period of “normal science”, is characterised by widespread adherence to whatever theory is current and by the engagement of almost all the scientists in the exploration and articulation of that theory and its ramifications” (quoted in Carey 1976). This “normal science” is well characterised by Sir Macfarlane Burnet (1970) who, in his book “*Dominant Mammal*”, recounts “It is illuminating to watch how, as soon as a new phenomenon is recognised in any field of science there is a swift mobilization of dozens or hundreds of scientists who can cheerfully leave their current research activity to join in the gold rush”.

For all the “dozens and hundreds” of scientists working in the periods of normal science, I suggest there is merely a handful contributing to the revolutions. In Thomas Carlyle's sense these are the Heroes of Science. Indeed one could paraphrase his remark “the history of the world is but the biography of great men” (Carlyle 1840) and apply it to Kuhnian revolutions.

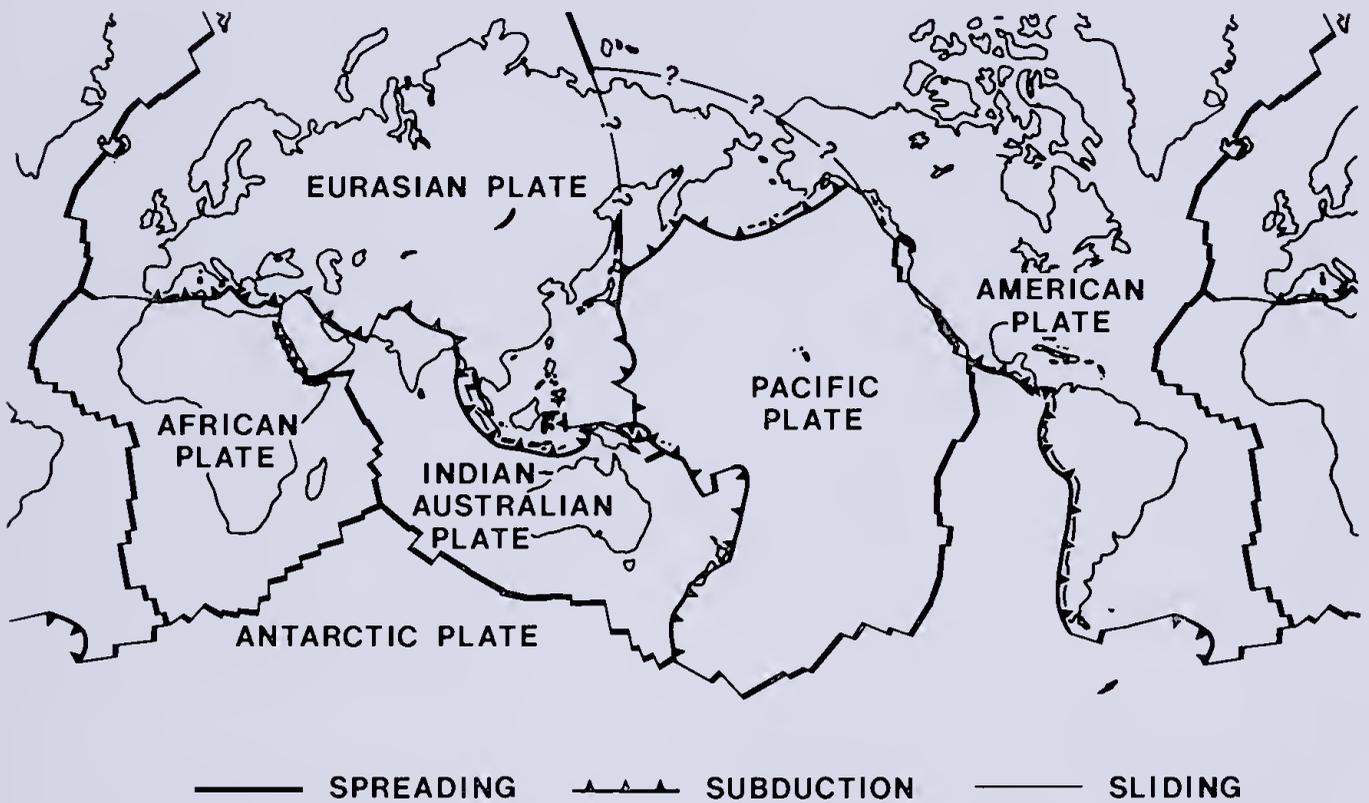
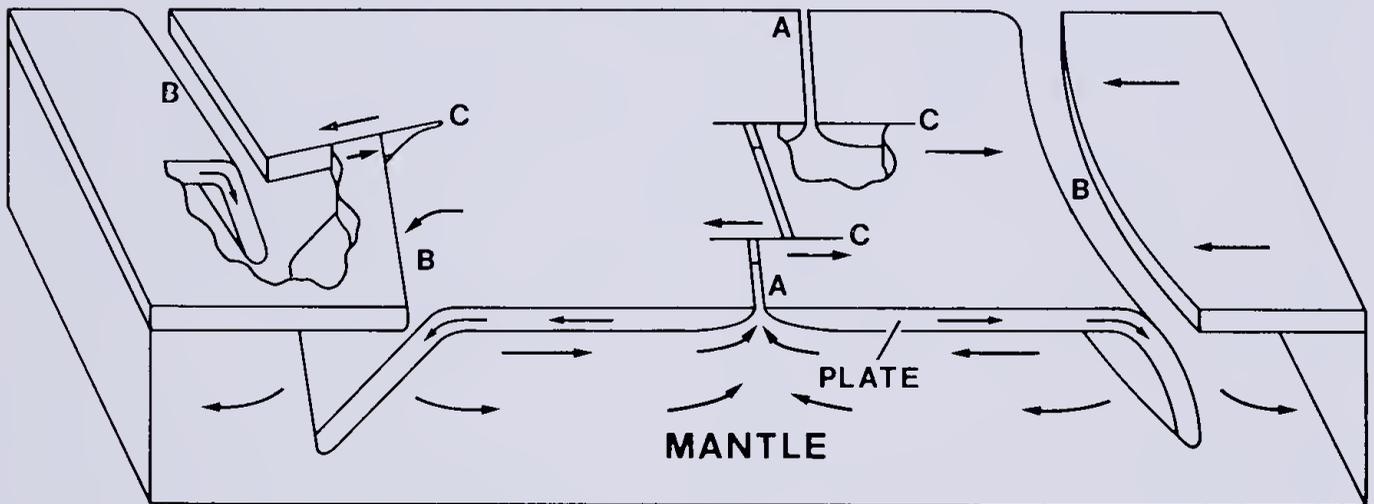


Figure 3.—The six major plates on the earth's surface (after Hamilton 1979).

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Figure 4.—Diagrammatic representation of plate movements at spreading centres (A), subduction zones (B) and along transform faults (C) (after Isaacs *et al.* 1968).

Gondwana

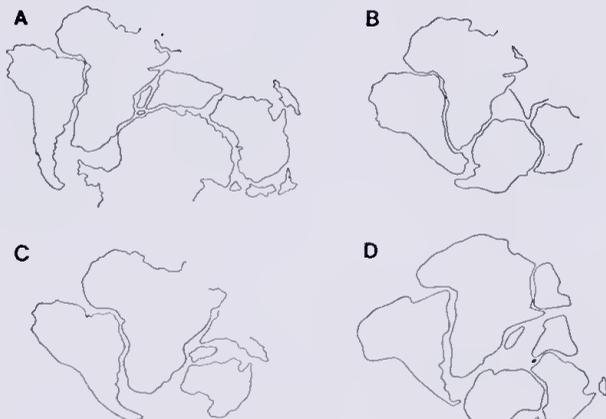
Gondwana—the word means “land of the Gonds” (who inhabited India) and hence the oft-used term “Gondwanaland” is tautologous (Bates and Jackson 1980)—is the name given to the supercontinent embracing South America, South Africa, India, Australia and Antarctica. Curt Teichert, an overseas member of the Society who was at the University of Western Australia in the 1930s and 40s and not

a supporter of Gondwana, has written “... it has always seemed an intriguing coincidence that the Gondwanaland concept was born exactly one hundred years after Captain James Cook had returned (in 1775) from his second voyage around the world. It was on this voyage that the age-old geographical phantasies of a Terra Australis were finally disproved” (Teichert 1958).

But Terra Australis did exist—many millions of years previously.

The name Gondwana is also applied to a series of rocks in peninsular India which are now known to be Late Carboniferous to Jurassic in age. These rocks are remarkably similar to rocks in South America (the Santa Catharina System), South Africa (the Karroo System), Australia and Antarctica (see for example, Kummel 1970). Essentially the sequence in all continents starts with glacial deposits of Late Carboniferous and Early Permian age, passes up into shales with coal seams and then into sandstones of fluvial origin which continue into the Triassic and Jurassic. The widespread Western Australian glacial unit (variously known under the names Nangetty, Lyons, Grant, Paterson and Stockton Formations) belongs to this sequence as do the Collie Coal Measures. Furthermore, the *Glossopteris* flora (well seen in the Collie Coal Measures) occurs in these rocks throughout Gondwana. This flora consists of seed ferns and it was the difficulty of explaining its distribution over continents now widely separated by oceans that led Blanford in 1875 to propose the existence of an Indian Ocean continent. The name Gondwanaland was proposed by Eduard Suess in 1885.

These early authors thought that land once existed over what are now the South Atlantic and Indian Oceans and subsequently founded beneath the waves. But Wegener (1966) and especially the South African geologist Du Toit (1937) envisaged Gondwana as being formed by the southern continents fitting together and later drifting apart. Although the fit of South America and Africa is fairly easy to see, it is not entirely clear how the other continents should be reassembled. In fact a variety of reconstructions is possible (Fig. 5).



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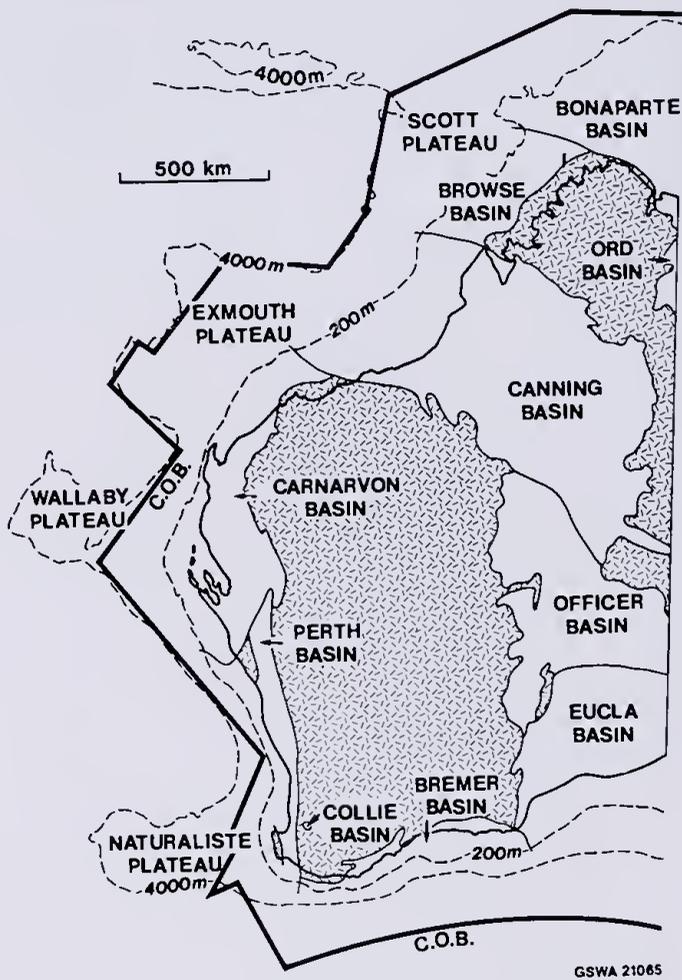
Figure 5.—Reconstruction of Gondwana according to various authors. A, Smith *et al.* (1973) with "Greater India" after Veevers *et al.* (1975); B, Veevers *et al.* (1971); C, Khranov and Petrova (1972); D, Hamilton (1979).

Using several lines of evidence—palaeomagnetism and sea-floor spreading (literally rolling back the sea-floor) it is possible to follow the break up of Gondwana through the Mesozoic. Basically the South Atlantic Ocean started opening in the Early to Mid Cretaceous (Sclater *et al.* 1977), and the Indian Ocean originated in the Late Jurassic to

Early Cretaceous (Falvey and Mutter 1981). Recent work (Cande and Mutter 1982) suggests that Antarctica separated from Australia in the Mid Cretaceous and not in the early Tertiary as previously believed.

Western Australia

Western Australia has a land area of 2.5 million km². Of this 1 million km² are underlain by Phanerozoic sedimentary basins (Fig. 6). In these basins is recorded the history of the Western Aus-



GSWA 21065

Figure 6.—Phanerozoic sedimentary basins of Western Australia. COB, continent—ocean boundary.

tralian part of Gondwana and lies the fossil fuel deposits of my title. The other three fifths of the State is underlain by the Precambrian rocks of the shield areas which form the basement on which the Phanerozoic basins were developed.

As Figure 6 shows the Phanerozoic basins do not end at the coast but extend onto the continental shelf and beyond; in fact they occupy another 1 million km² offshore. The true limit of the basins is at the continent-ocean boundary beyond which oceanic crust created after the breakup of Gondwana occurs (Veevers and Cotterill 1978). Offshore from Western Australia are a number of submarine plateaus, from north to south, the Scott, Exmouth, Wallaby and Naturaliste Plateaus. The Exmouth and

probably the Scott Plateaus are underlain by continental crust, the Wallaby and probably the Naturaliste Plateaus by oceanic crust.

The sedimentary basins of Western Australia fall into two obvious groups, those on the Precambrian shield areas (e.g. Officer Basin) and those marginal to the shield (e.g. Perth Basin) which suggests that we can classify basins into various types. This has been done; unfortunately there are as many classifications as there have been classifiers (see, for example, Bally and Snelson 1980, Klemme 1980, Bois *et al.* 1982, Bally 1982). I shall follow the classification of Klemme (1980) who recognises eight basin types of which three are on the shield or craton, and the others are marginal to it. Five of these basin types are present in Western Australia (Table 1). The main features of the Phanerozoic sedimentary basins in the State are summarised in Table 2 and Figures 7 to 14.

Table 1

Classification of sedimentary basins (Klemme 1980)

Basin type	Examples
A. Cratonic basins	
Interior	Officer (WA) Williston (USA)
Complex	Canning (WA, onshore) Pechora (USSR)
Rift	Collie (WA) Sirte (Libya)
B. Marginal basins	
Downwarp	Bonaparte (WA) Arabian basins
Pullapart	Perth (WA) Newfoundland
Subduction	none in WA Indonesian basins
Median	none in WA Maracaibo (Venezuela)
Delta	none in WA Niger

Table 2

Phanerozoic sedimentary basins of Western Australia

Basin	Area (km ²)	Percentage area	Sediment thickness (m)	Age of sediments	Basin type	No. of petroleum exploration wells (a)	Wells per 1 000 km ²
Perth	95 000	5	25 000 (c)	Proterozoic, Silurian Permian-Cenozoic	Pullapart	90	0.95
Carnarvon	385 000	20	20 000	Silurian-Cenozoic	Pullapart	226	0.59
Canning	530 000	28	15 000	Ordovician-Cenozoic	Complex (onshore) Pullapart (offshore)	127	0.24
Browse	155 000	8	10 000	Permian-Cenozoic	Pullapart	17	0.11
Bonaparte (b)	113 000	6	11 000	Cambrian-Cenozoic	Downwarp	19	0.17
Ord (b)	15 000	1	1 500	Cambrian, Devonian, Cenozoic	Interior	1	0.07
Officer (b)	250 000	13	5 000 (d)	Proterozoic, Cambrian, Permian, Cretaceous, Cenozoic	Interior	9	0.04
Eucla (b)	320 000	17	1 500	Permian, Jurassic, Cretaceous, Cenozoic	Interior (onshore) Pullapart (offshore)	4	0.01
Bremer	62 000	3	200 (e)	Cenozoic (e)	Pullapart	4	0.06
Collie	225	0.01	1 050	Permian, Cenozoic	Rift	0	0.00

(a) drilled to 31/12/1982;

(b) Western Australian part only;

(c) Includes 10 000 m of Proterozoic sediments;

(d) Includes 4 000 m of Proterozoic sediments;

(e) Onshore part only.

The history of sedimentation in these basins is bound up with the history of Gondwana. To the north of the supercontinent lay the Tethys Sea. Marine transgressions across the Western Australian craton from the north started in the Cambrian and continued intermittently until the Cretaceous. Along the western margin of Western Australia rifting occurred in the Late Palaeozoic in the Perth, Carnarvon and Canning Basins and North-west Shelf area. Subsequently these rifts were filled mainly with clastic sediments. Pullapart started in the mid to Late Jurassic in the north and continued into the Early Cretaceous in the Perth Basin as Australia separated from India; by Late Cretaceous times an open marine environment with carbonate sedimentation was established along the whole western margin.

A similar sequence of events, but with slightly different timing, took place along the southern margin

of Western Australia. Rifting probably started in the Jurassic and the pullapart phase commenced in the mid Cretaceous as Australia and Antarctica parted.

The history of the pullapart basins seems to fall into three main phases. These have been called pre-rift, rift and post-breakup by Falvey (1974) and are illustrated in Figure 15. The pre-rift basin is a phase of gentle subsidence. With rising temperature in the mantle, the crust is thinned and rift-valley subsidence begins. The rift valley phase may last a long time and is ended by continental breakup and sea-floor spreading with the formation of new oceanic crust. Cooling of the crust beneath the rift valley causes subsidence with the accumulation of sediments which prograde across the continental margin and form the post-breakup sequence.

Veevers, Jones and Powell (1982) also recognise three phases in the history of the Western Australian basin and have named them pre-Gondwanan, Gondwanan and post-Gondwanan. The pre-Gondwanan phase of early and middle Palaeozoic age they interpret as representing failed rift arms, that is rifts which did not go on to the breakup phase; perhaps the Fitzroy Trough in the Canning Basin and the Collie Basin are examples. The sediments associated with this phase include widespread carbonates (Canning, Bonaparte Basins) and evaporites (Canning, Carnarvon Basins) which suggest deposition in low latitudes. The Gondwanan phase equates with Falvey's rift valley phase and includes the glacial, coals and sandstones of the Gondwana System of Late Carboniferous to Jurassic age, which at least initially were laid down in high latitudes. The post-Gondwanan phase corresponds with Falvey's post-breakup progradation phase.

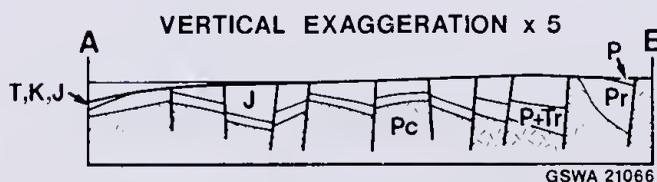
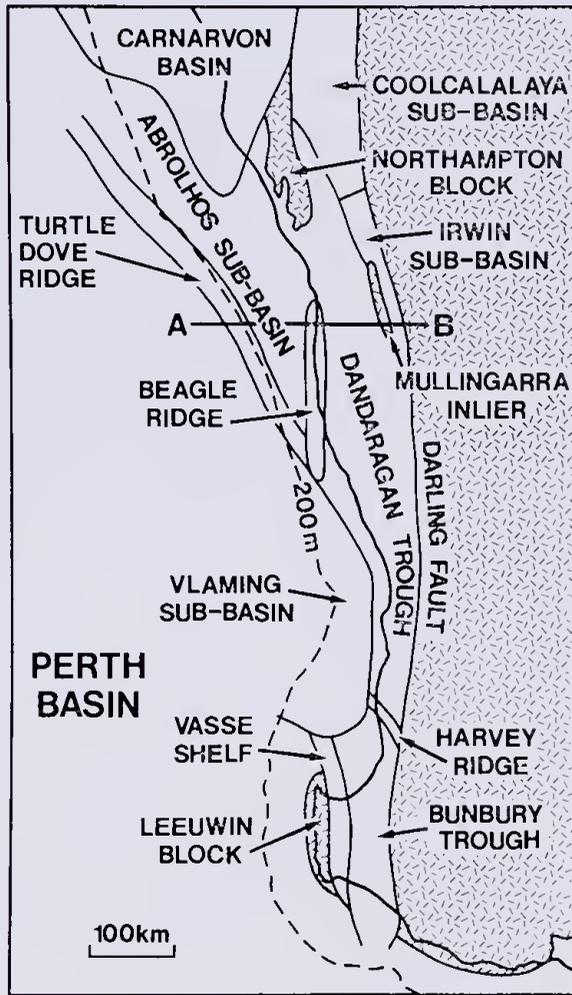


Figure 7.—Perth Basin; subdivisions and cross section (after Playford *et al.* 1976). T, Tertiary; K, Cretaceous; J, Jurassic; Tr, Triassic; P, Permian; Pr, Proterozoic; Pc, Precambrian basement.

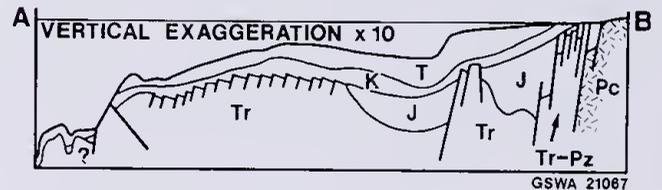
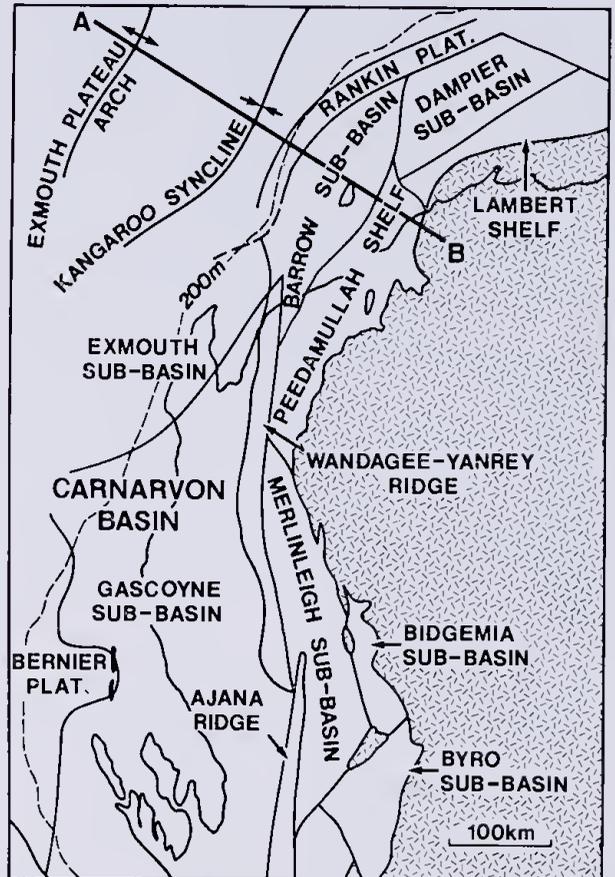


Figure 8.—Carnarvon Basin; subdivisions and cross section (after Falvey and Mutter 1981). T, Tertiary; K, Cretaceous; J, Jurassic; Tr, Triassic; Pz, Palaeozoic; Pc, Precambrian basement.

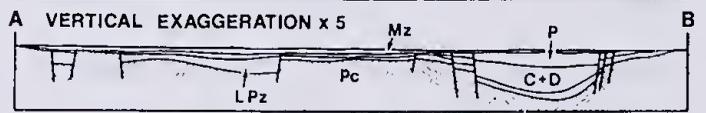
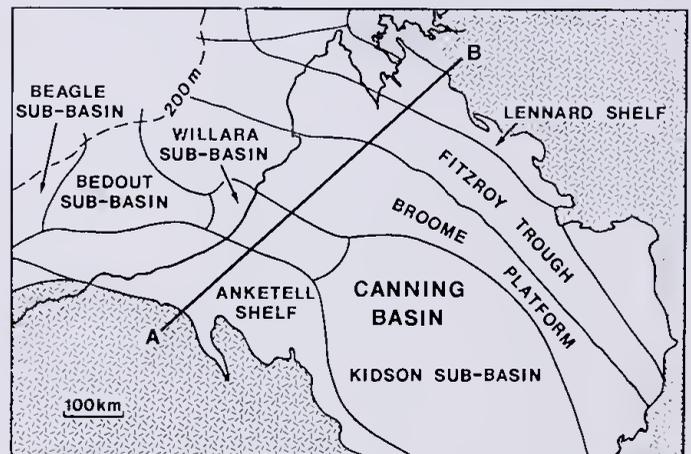
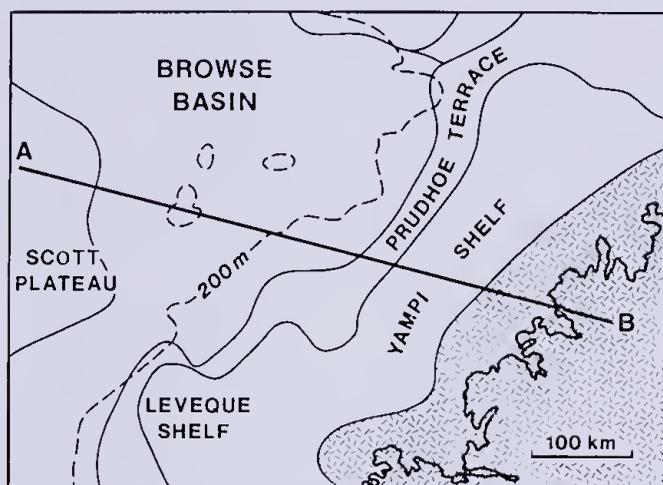
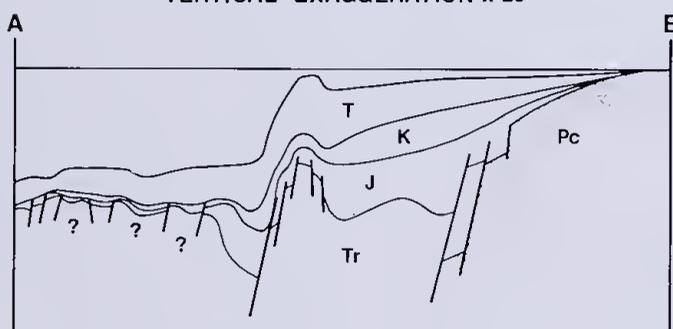


Figure 9.—Canning Basin; subdivisions and cross section (after Playford *et al.*, 1975). Mz, Mesozoic; P, Permian; C, Carboniferous; D, Devonian; LPz, Lower Palaeozoic; Pc, Precambrian basement.



VERTICAL EXAGGERATION x 20



GSWA 21069

Figure 10.—Browse Basin; subdivisions and cross section (after Falvey and Mutter 1981). T, Tertiary; K, Cretaceous; J, Jurassic; Tr, Triassic; Pc, Precambrian basement.

Fossil fuel potential

The fossil fuel potential of Western Australia is summarised in Figure 16 in which the stratigraphic sequence in each basin is outlined and the main oil and gas shows and coal deposits are plotted.

Proterozoic. The thick section of Proterozoic sediments in the Officer Basin includes evaporites and has a number of diapiric structures. There have been minor shows of oil and gas.

Ordovician. Oil shows in the Ordovician Nita, Goldwyer and Willara Formations have been recorded from the Broome Platform in the Canning Basin.

Devonian. Devonian reef complexes in the Canning Basin produce oil at Blina and in the Bonaparte Basin have yielded shows of oil.

Carboniferous. The Blina field also produces oil from rocks of this age and the Bonaparte Basin oil shows referred to previously are partly from carbonates of this age. In the Canning Basin oil shows have also been encountered in the Lower Carboniferous Anderson Formation.

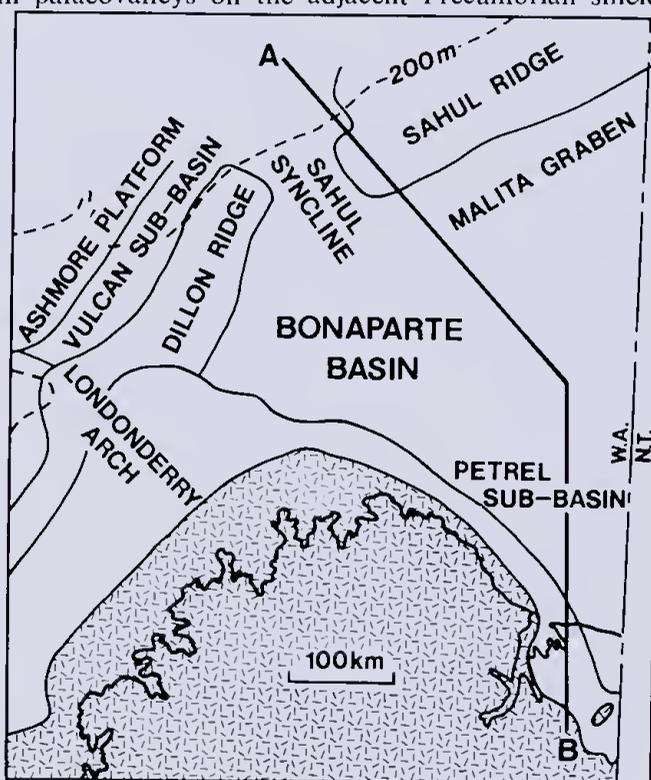
Permian. Again, in the Canning Basin there are oil shows in the Grant Group which is of Late Carboniferous and Early Permian age. Permian rocks are gas reservoirs in the Bonaparte Basin (Hyland Bay Formation in the Tern field) and Perth Basin (Carynginia Formation in the Woodada field, Wagina Sandstone and Irwin River Coal Measures in the Dongara field). The Permian is the main target for coal exploration, the State's only commercial coal-field, at Collie, being in rocks of this age. Permian coal is also known from the Perth, Carnarvon and Canning Basins.

Triassic. The Dongara field in the Perth Basin produces gas from sandstones of Triassic age and the reservoirs in the Rankin Platform (Carnarvon Basin) and in the Browse Basin are also of this age. Oil is also known from these rocks in the Rankin Platform.

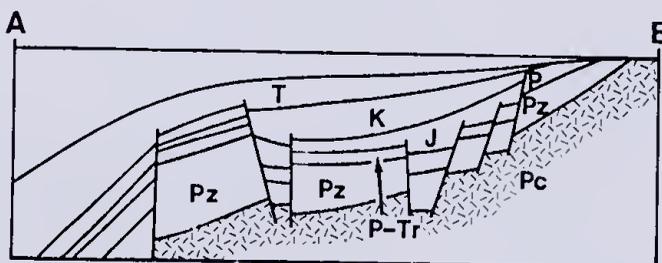
Jurassic. Jurassic rocks are gas bearing in the Perth Basin (mainly Cockleshell Gully Formation), Carnarvon Basin and Browse Basin. The original Barrow Island oil discovery was from the Upper Jurassic, although nearly all the production comes from the Cretaceous. In the Perth Basin coal of this age occurs in the Dandaragan Trough (Eneabba).

Cretaceous. The most prolific reservoirs of Cretaceous age which have been developed are at Barrow Island where the Lower Cretaceous Windalia Sand contains oil. Gas of this age is widely known in the Carnarvon Basin and oil occurs in the Carnarvon and Perth Basins.

Tertiary. Oil and gas are unknown from the Tertiary in Western Australia. Lignite (brown coal) is widespread in the onshore Bremer Basin (near Esperance), western margin of the Eucla Basin and in palaeovalleys on the adjacent Precambrian shield.

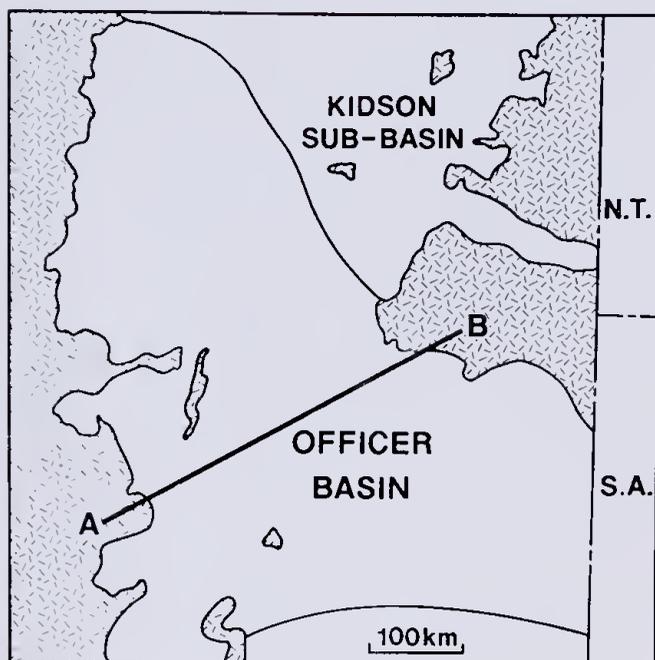


VERTICAL EXAGGERATION x 25

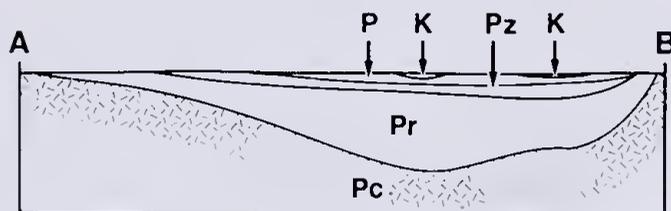


GSWA 21071

Figure 11.—Bonaparte Basin; subdivisions and cross section (after Douch and Nicholas 1978). T, Tertiary; K, Cretaceous; J, Jurassic; Tr, Triassic; P, Permian; Pz, Palaeozoic; Pc, Precambrian basement.

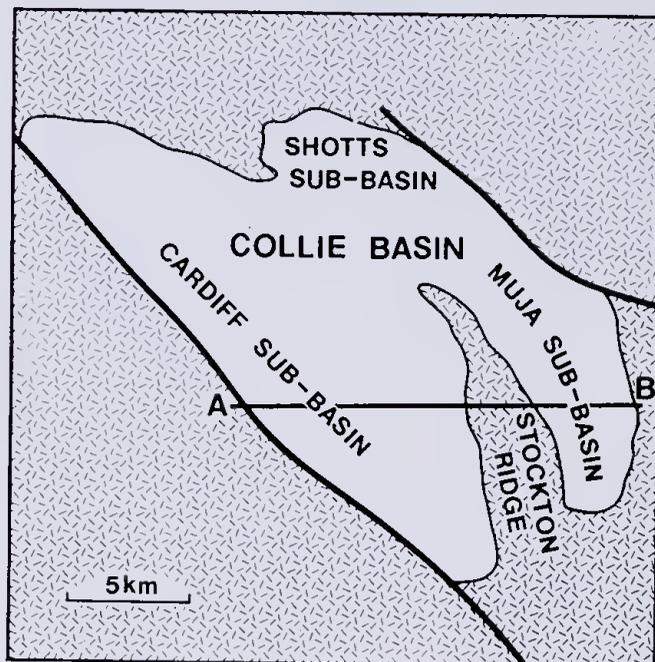


VERTICAL EXAGGERATION x10

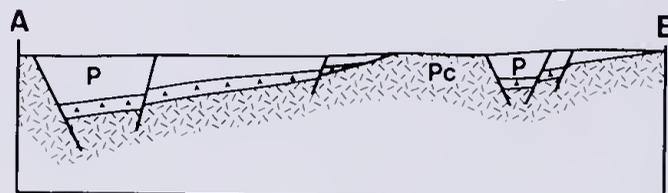


GSWA 21072

Figure 12.—Officer Basin; cross section (after Jackson and van de Graaf 1981). K, Cretaceous; P, Permian; LPz, Lower Palaeozoic; Pr, Proterozoic; Pc, Precambrian basement.

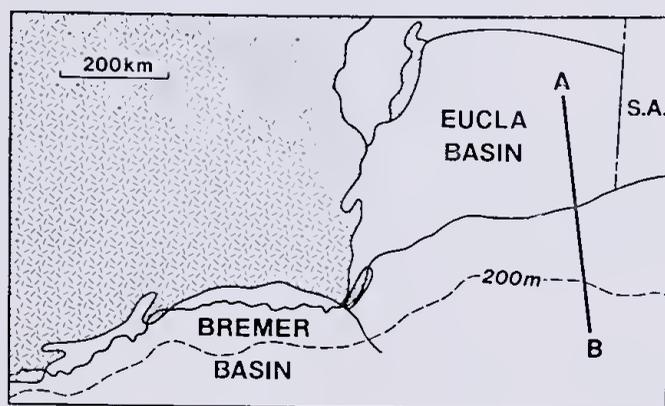


VERTICAL EXAGGERATION x1½

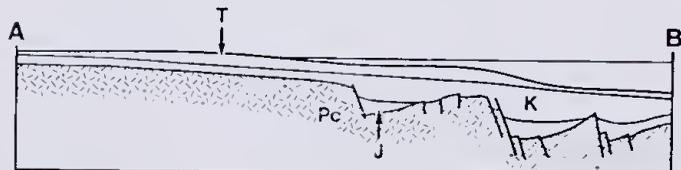


GSWA 21074

Figure 14.—Collie Basin; subdivisions and cross section (after Lowry 1976). P, Permian (triangles denote glacial sediments); Pc, Precambrian basement.



VERTICAL EXAGGERATION x10



GSWA 21073

Figure 13.—Eucla and Bremer Basins; cross section (after Bein and Taylor 1981). T, Tertiary; K, Cretaceous; J, Jurassic; Pc, Precambrian basement.

Prospects

Two oil fields and 11 gas fields or potential gas fields have been discovered so far (July 1983), all in the Perth, Carnarvon, Canning, Browse and Bonaparte Basins; the Ord, Officer, Eucla and Bremer Basins have not been sites of hydrocarbon discoveries to date. The only coalfield known is in the Collie Basin, although potential coalfields occur in the Perth and Bremer Basins. Obviously one is tempted to look for hydrocarbons and coal near where existing deposits have been found—indeed this is one of the cardinal rules of exploration. However, the law of diminishing returns sets in and the success rate declines with time. Giant oil and gas fields are usually found in the early stages of exploration in a basin and the same would be true for coal.

The next step is to look at new areas. Where are the new frontiers? One guide is to see what are the most prospective types of basin. This has been done for petroleum by several workers. Klemme (1980) has calculated what percentage of reserves are in different types of basin and the percentage area occupied by each basin type. In Table 3 the column labelled reserves/area ratio summarises his results; a figure greater than 1 indicates a basin

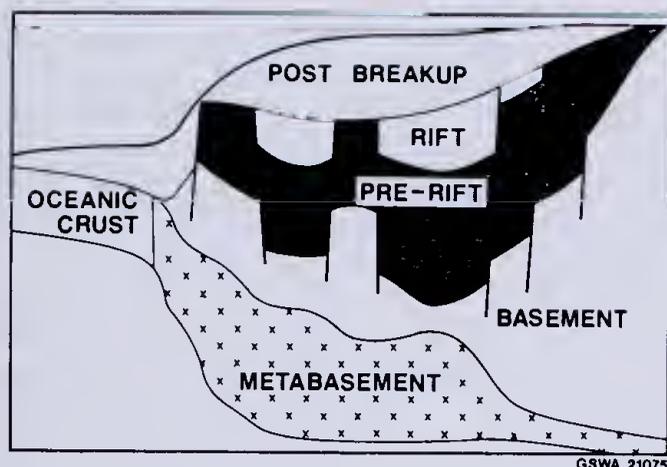


Figure 15.—Diagrammatic cross section of a pullapart basin (after Falvey 1974).

Table 3

Basin types and petroleum reserves (after Klemme 1980)

Basin type	Percentage basin area	Percentage reserves	Reserves/area ratio
Interior	World 18.2	1.5	0.08
	W.A. 31.0	0.0	0.0
Complex	World 27.3	25.0	0.9
	W.A. 22.0	1.0	0.05
Rift	World 5.4	10.0	1.9
	W.A. 0.01	0.0	0.0
Downwarp	World 17.5	47.0	2.7
	W.A. 6.0	2.0	0.33
Pullapart	World 18.2	0.5	0.03
	W.A. 42.0	97.0	2.31
Subduction	World 7.0	7.5	1.1
	W.A. 0.0	0.0	0.0
Median	World 3.7	2.5	0.7
	W.A. 0.0	0.0	0.0
Delta	World 2.6	6.0	2.3
	W.A. 0.0	0.0	0.0

type with a large proportion of the world's petroleum reserves, less than 1 indicates a basin with a small proportion of the reserves. Downwarp basins are by far the most productive, chiefly because they include the giant fields of the Middle East. By contrast pullapart basins are the least productive basins. Yet in Western Australia they have 98% of the oil reserves (the remaining 2% being in complex basins) and 96% of the gas reserves (with only 4% in downwarp basins). Since Western Australia has no delta, subduction, median or rift (except for the non-petroliferous Collie Basin) basins, Klemme's data suggest that downwarp and complex basins are the ones in which exploration

should be concentrated, that is the Bonaparte and Canning Basins respectively. Certainly exploration in the Canning Basin has increased dramatically in the last few years, although the Bonaparte Basin still lags behind somewhat in exploration effort.

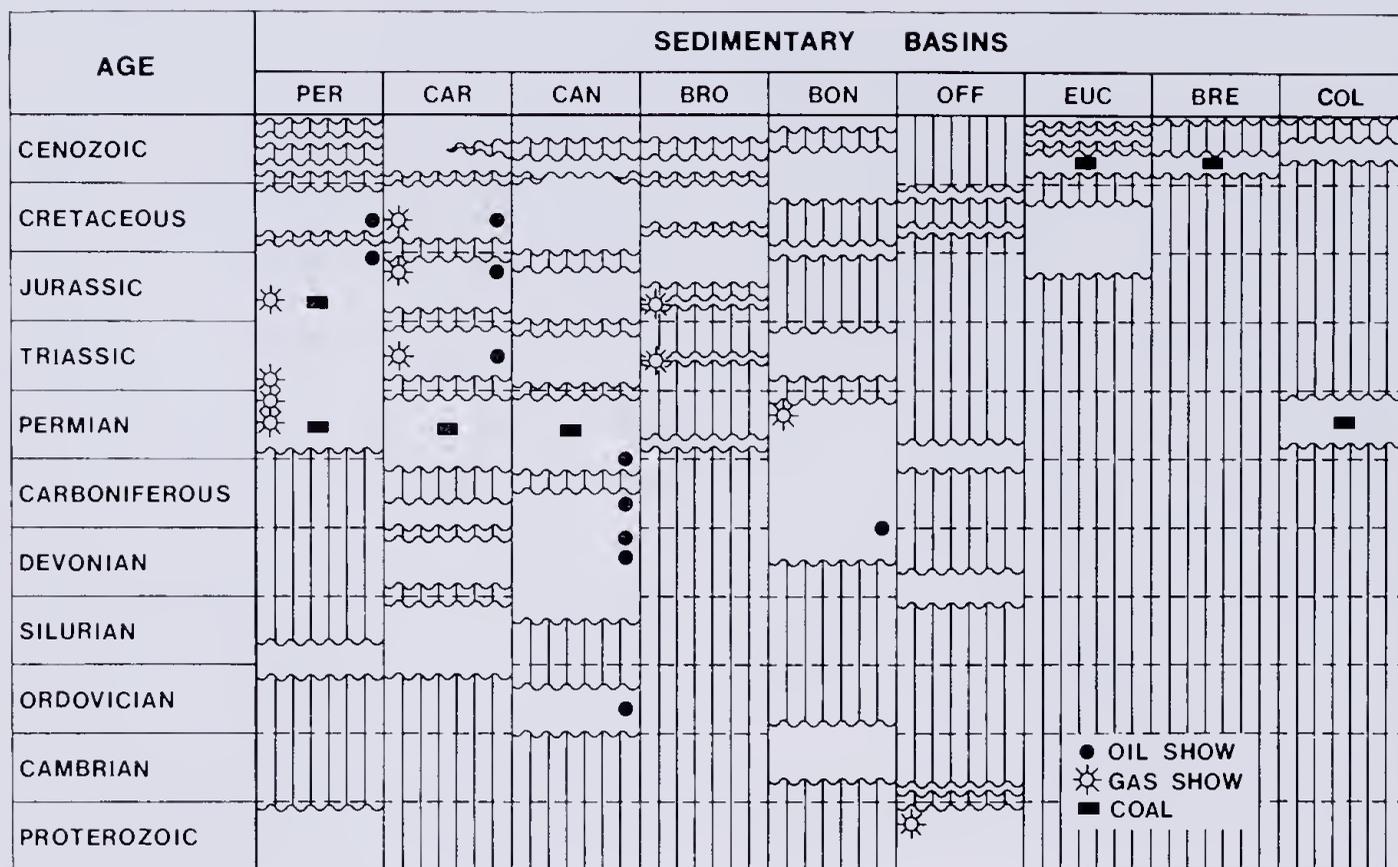
With coal the situation is less easy to quantify and more difficult to fit into any classification of basin types. Rift and pullapart basins have been the most promising so far. In other parts of Gondwana, rift and cratonic interior basins seem to contain the bulk of the Permian coals. Future exploration will be in the pullapart basins—the Perth Basin for Permian and Jurassic coal, the Bremer and Eucla Basins for Tertiary lignite—and the search for other small concealed rift basins like the Collie Basin will continue on the Precambrian shield.

Conclusions

I have sketched the fossil fuel potential of the sedimentary basins of Western Australia against a global backdrop of drifting continents, ever-changing plates and the breakup of Gondwana. In the latter part of my address I have dealt with what Kuhn would call "normal science". I have deliberately refrained from mentioning the names of the many workers who have contributed to our knowledge of the sedimentary basins. There are few of Carlyle's Heroes here. To quote the historian Hugh Thomas (1981), "The men who made history were enabled to survive by... the patient toil of the husbandmen". Normal science is the domain of the husbandman. But this is not to deny that the spirit of creativity is at work here just as it is in times of scientific revolution—for out of the periods of normal science there must arise tomorrow's revolutions.

My immediate predecessor, Professor J. F. Lone-ragan, entitled his address "Curiosity and practicality in scientific research" and spoke of the interplay of pure and applied science. My theme has ranged from the curious global plates which determine the history of the basins to the practical barrels of oil. And yet regardless of the motivation, whether curiosity or practicality, the search for fossil fuels depends on creative ideas.

I should like to finish by quoting a famous American petroleum geologist, Wallace Pratt; although he had oil in mind when he wrote, his message applies to the exploration for all fossil fuels. "Where oil is first found... is in the minds of men. The undiscovered oil field exists only as an idea in the mind of some oil-finder. When no man any longer believes more oil is left to be found, no more oil fields will be discovered, but so long as a single oil-finder remains with a mental vision of a new oil field to cherish... just so long new oil fields may continue to be discovered." (Pratt 1952).



GSWA 21076

Figure 16.—Simplified stratigraphic sequences in the main Phanerozoic sedimentary basins showing the principal oil, gas and coal occurrences. PER, Perth Basin; CAR, Carnarvon Basin; CAN, Canning Basin; BRO, Browse Basin; BON, Bonaparte Basin; OFF, Officer Basin; EUC, Eucla basin; BRE, Bremer Basin; COL, Collie Basin.

Acknowledgement.—I thank three Past Presidents of the Society—J. R. de Laeter, J. F. Loneragan and P. E. Playford—for reading the manuscript and the Mapping Branch of the Mines Department for drafting the diagrams.

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Chromosome numbers in Western Australian plants, II

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Abstract

Chromosome numbers for 76 species are given. The counts on *Cheiranthra* ($n = 12$), *Halosarcia* ($n = 9$), *Pityrodia* ($n = 14$), *Maireana* ($n = 9$), *Cypselocarpus* ($n = 14$) and *Phlebocarya* ($n = 7$) are first records for these genera.

Introduction

This paper documents chromosome numbers for 76 species of flowering plants from Western Australia. These are nearly all new records for these species.

Results

Chromosome numbers, details of collection localities and vouchers are given in Table 1. Abbreviations are as given in Keighery (1978). Vouchers are deposited in Kings Park Herbarium and/or in PERTH.

Materials and methods

These are the same as outlined in Keighery (1978).

Reference

Keighery, G. J. (1978).—Chromosome numbers in Western Australian plants, I. *Roy. Soc. West. Aust.*, 60: 105–106.

Table 1

Miscellaneous species counted

Taxon	n	2n	Locality	Voucher
MONOCOTYLEDONAE				
JUNCAGINACEAE				
<i>Triglochin ninutissina</i> F. Muell.	14	Cannington	GK 1277
COMMELINACEAE				
<i>Cartonema philydroides</i> F. Muell.	12	12 km N. Port Gregory	GK 1766
HAEMODORACEAE				
<i>Phlebocarya ciliata</i> R. Br.	7	10.2 km N. Walpole	GK 679
<i>P. ciliata</i> R. Br.	7	5 km S. Carbanup River Store	GK 691
<i>P. filifolia</i> (F. Muell.)	7	5 km S.E. of Badgingarra	GK 2552
DICOTYLEDONAE				
PROTEACEAE				
<i>Adenanthos cuneata</i> Labill.	13	Gnowangerup Shire Boundary on Ravensthorpe Road	GK 229
<i>A. forrestii</i> F. Muell.	13	Twilight Cove	GK 232
<i>A. gracilipes</i> A. S. George	13	32° 33'S, 120° 20'E	GK 1513
<i>A. obovata</i> Labill.	13	7 km S. Collie	GK 198
<i>A. oreophila</i> Nelson	13	Mt. Ragged	GK 266
<i>A. sericea</i> Nelson ssp. <i>sphalma</i> Nelson	13	Hellfire Bay	GK 474
<i>Grevillea bipinnatifida</i> R. Br.	10	Welshpool Road	GK 1980
<i>G. pterosperma</i> F. Muell.	10	2 km W. Mt. Hampton	GK 23
<i>G. sp. nov.</i>	10	Duladgin Rock	GK 1773
<i>Hakea coriacea</i> Maconochie	10	2 km W. Mt. Hampton	GK 23, a
<i>Persoonia angustiflora</i> Benth.	7	10 km N. Mt. Holland....	GK 1078
<i>P. striata</i> R. Br.	7	3 km W. Tamin....	GK 1984
<i>P. teretifolia</i> R. Br.	7	32° 33'S, 120° 20'E	GK 1512
<i>P. sp.</i>	7	7 km N. Howatharra	GK 185
CHENOPODIACEAE				
<i>Atriplex bunburyana</i> F. Muell.	9	Twilight Cove	GK 228
<i>Sclerolaena drummondii</i> (Benth.) Domin	9	24 km S. Yellowdine	GK 14
<i>Chenopodium pseudo-microphyllum</i> Aellen	9	14 km Ravensthorpe	GK 662
<i>Halosarcia lylei</i> (Ewart et White) P. G. Wilson	9	Mortlock River, Meckering	GK 390
<i>Halosarcia lepidosperma</i> P. G. Wilson....	18	Pallinup River	GK 671
<i>Maireana sclerolaenoides</i> (F. Muell.) P. G. Wilson	9	Karolin Rock	GK 11
<i>M. trichoptera</i> (F. Muell.) P. G. Wilson	9	Karolin Rock	GK 12
<i>Rhagodia preissii</i> Moq.	9	14 km W. Ravensthorpe	GK 663

Taxon	n	2n	Locality	Voucher
GYROSTEMONACEAE				
<i>Codonocarpus cotonifolius</i> Desf.	14	2 km N. Millstream	GK 759
<i>Cypselocarpus haloragoides</i> F. Muell.	14	Bremer Bay	GK 846
<i>Gyrostemon ramulosus</i> Desf.	14	25 km N. Neale Junction	GK 562
RANUNCULACEAE				
<i>Ranunculus colonorum</i> Endl.	8	Mt. Chudalup	GK 683
BRASSICACEAE				
<i>Lepidium linifolium</i> (Desf.) Benth.	16	Quobba	Demarz 3871
<i>Stenopetalum filifolium</i> Benth.	10	10 km S. Waialki	GK 380
<i>S. filifolium</i> Benth.	10	32 km S. Yellowdine	GK 393
PITTOSPORACEAE				
<i>Billardiera floribunda</i> (Putterl.) F. Muell.	12	Augusta	GK 1569
<i>Cheiranthra filifolia</i> Turcz. var. <i>brevifolia</i> Bennett	12	28 km W. Ravensthorpe	GK 665
FABACEAE				
<i>Bossiaea preissii</i> Meisn.	9	2 km W. Israelite Bay	GK 219
<i>Burtonia conferta</i> DC.	9	115 km N. of Perth	GK 364
<i>B. viscida</i> E. Pritzel	9	8 km N. Southern Cross	GK 9
<i>Daviesia croniniana</i> F. Muell.	9	20 km S.W. Marvel Loch	GK 22
<i>D. epiphylla</i> Meisn.	9	Strathmore Road to Cervantes	GK 1793
<i>D. hakeoides</i> Meisn.	9	50 km S. Nannup on Brockman Hwy	GK 353
<i>D. polyphylla</i> Benth. ex Lindl.	9	31 km N. Perth on Toodyay to Calingiri Rd	GK 108
<i>D. preissii</i> Meisn.	9	10 km S. Stuart Rd Brockman Hwy	GK 353
<i>D. striata</i> Turcz.	9	3 km N. Regans Ford	GK 288
<i>D. striata</i> Turcz.	9	16 km along Cadda from Nair Road	GK 1983
<i>Crotalaria cunninghamii</i> R. Br.	8	Karratha	GK 2362
<i>Gompholobium aristatum</i> Benth.	9	131 km N. Perth	GK 355
<i>G. ovatum</i> Meisn.	9	10 km S. Stuart Road on Brockman Highway	GK 352
<i>G. sp.</i>	9	Walyunga	GK 200
<i>Isotropis cuneifolia</i> (Sm.) Benth. ex B. D. Jackson	18	St. Columba College	GK 1819
<i>Jacksonia alata</i> Benth.	9	7 km W. Toodyay	GK 1053
<i>J. furcellata</i> (Bonpl.) DC.	9	7 km N. Howatharra	GK 184
<i>J. horrida</i> DC.	9	Windy Harbour	GK 991
<i>J. namatoclada</i> F. Muell.	9	Charles Gairdner Reserve	GK 325
<i>J. restioides</i> Meisn.	9	7 km W. Toodyay	GK 1052
<i>J. restioides</i> Meisn.	9	7 km E. Mawson	GK 294
<i>J. umbellata</i> Turcz.	9	2 km S. Mt. Ragged	GK 437
<i>J. sp. 1</i>	9	Munglinup	GK 620
<i>J. sp. 2</i>	9	Tarin Rock Siding	GK 368
<i>Kennedia carinata</i> (Benth.) Domin	11	50 km W. Condinup	GK 222
<i>K. glabrata</i> (Benth.) Lindl.	11	Cult—ex Mt. Chudalup	GK sn
<i>K. macrophylla</i> Meisn.	11	Cape Leeuwin	GK 1887
<i>K. stirlingii</i> Lindl.	11	Bindoon Hill	GK 101
<i>Mirbelia dilatata</i> R. Br.	8	South Ironcap	GK 887
<i>Oxylobium lanceolatum</i> (Vent.) Druce	8	2 km W. Two People's Bay	GK 1390
<i>O. parviflorum</i> Benth.	8	Sandalwood Rd, S.E. Stirling Ranges	GK 356
<i>Pultenaea adunca</i> Turcz.	7	47 km S. Ravensthorpe	GK 633
<i>P. capitata</i> (Turcz.) Druce	7	7 km S. Winchester	GK 1057
<i>Swainsona sp.</i>	16	Gnarlbine Rock	GK 500
GERANIACEAE				
<i>Pelargonium australe</i> Willd.	11	Mt. Madden	GK 1938
<i>P. littorale</i> Hueg.	11	Lort River	GK 1389
ZYGOPHYLLACEAE				
<i>Zygophyllum fruticosum</i> DC.	8	Red Bluff	GK 1792
RUTACEAE				
<i>Diplolaena ferruginea</i> P. G. Wils.	14	Cockleshell Gully	GK 202
<i>D. microcephala</i> Bartl.	14	Forrest Beach, Capel	GK 32
BORAGINACEAE				
<i>Halgania lavandulacea</i> Endl.	16	Twilight Cove	GK 238
CHLOANTHACEAE				
<i>Pityrodia terminalis</i> (Endl.) A. S. George	14	16 km E. Mt. Hampton	GK 37
BRUNONIAEAE				
<i>Brunonia australis</i> R. Br.	9	Comet Vale	GK 337

Taxonomic revision of *Isoetes* L. in Western Australia

by E. R. L. Johnson*

(completed by Hj. Eichler** from notes left by Mrs. E. R. L. Johnson)

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Abstract

A taxonomic revision of *Isoetes* L. in Western Australia is presented and eight species are described and illustrated. Six species are endemic of which *I. brevicula*, *I. caroli*, *I. inflata* and *I. mongerensis* are newly described and *I. australis* and *I. tripus* previously known. The remaining two species, *I. drummondii* and *I. muelleri*, are widespread in other Australian States.

Populations of young sterile plants of *I. australis* and homosporous ones of *I. australis*, *I. drummondii*, *I. mongerensis* and *I. muelleri* are reported. Dimorphic megaspores were found in populations of *I. drummondii*, *I. mongerensis* and *I. muelleri*.

Two keys are provided, one is based on vegetative characters and the other includes features of mature megaspores. Lectotypes are designated, where appropriate, for the names of other Australian *Isoetes* species not occurring in Western Australia.

Introduction

Isoetes L., one of the heterosporous Lycopsidea, was first described from Western Australia in 1864 and 1868 by Alexander Braun. His specimens were collected by James Drummond in 1843 at the Swan River. Drummond's plants were probably included in a collection of cryptogams he sent to Sir William Jackson Hooker at Kew in August 1844 (Erickson 1969). Drummond numbered his *Isoetes* specimens 989 and 990, but no mention of these numbers has been found in a search of the letters he sent to Sir William about that time (Carrick, comm. 1970). In a later letter to Sir William (No. 140, 7 March, 1846) Drummond mentioned finding a third kind of *Isoetes* and commented on its habitat. This was similar to that in which some Western Australian species now occur. He wrote: "I found in shallow pools of rain water on granite rocks in the vicinity of the Wangan" (probably Wongan, auct.) "Hills a third species of this curious genus. It may be called *Isoetes minuata* . . . Small as it is, it is produced in such numbers that it gives a green colour to the bottom of such pools. For 7 or 8 months in the year this little plant is exposed to the most extensive heat of the sun, where there is scarcely enough of dark coloured metallic sand to cover its minute roots. I have unfortunately mislaid the only specimens I collected of this curious little plant." No specimen or other record of this "third species" has since been found.

Drummond's specimens were incorporated in Hooker's and other herbaria, and duplicates are now at Berlin, Kew, Munich, Paris and Vienna. Braun (1864, 1868) described them as two new species, naming No. 989 *I. drummondii*, and No. 990 *I. tripus*. A number of their vegetative and reproductive features were described first in his paper on the Sardinian species of *Isoetes* (1864) and complete descriptions published later (1868). Since then *I. drummondii* is the only species recorded in all lists of Western Australian taxa.

Meanwhile in France Durieu (1864) published the results of his examination of specimens of *Isoetes* from the herbarium of the late Baron

Delessert. Some of these had been collected by Drummond in "Nouvelle Hollande" in 1842 and 1843. The specimens were few and badly preserved, so Durieu, though he recognized three types of megaspores, would describe only one species which he named *I. phaeospora*. He characterized it by brownish megaspores covered with a network of deep sinuous meshes. Earlier in 1864 Braun had used these characters in describing *I. tripus* (Drummond's No. 990), so in 1868 he cited *I. phaeospora* Durieu as a synonym of *I. tripus*.



Figure 1.—General view of flat granite outcrop with rock pools west of Ballidu. *I. caroli* growing submerged. *Borya* sp. and *Cheilanthes* sp. fringing outer edge of a pool. Photo—K. F. Kenneally.

Bentham (1878) reduced the Western Australian species to one by including both *I. tripus* and *I. phaeospora* under *I. drummondii* as he considered they were not distinct because of their similar vegetative characters.

* Died 11 August 1972

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Mueller (1866) referred to *I. phaeospora* as occurring in the western extra-tropical parts of Australia, but omitted it from his Systematic Census (1882) and listed only *I. drummondii*. *I. tripus* was included in his Second Systematic Census (1889) and so restored to two the number of recorded species.

Baker (1880) in his Synopsis and Motelay & Vendryès (1882) in their monograph recorded *I. drummondii* and *I. tripus* for Western Australia and placed *I. phaeospora* as a synonym of *I. tripus*. Kuntze (1891) transferred both *I. drummondii* and *I. tripus* to the genus *Calamaria*, a pre-Linnean name for *Isoetes* which is not now recognized. Sadebeck (1902) placed both species in the genus *Isoetes* and so did Pfeiffer (1922) in her monograph, though she did not examine specimens of *I. tripus*.

Over the last hundred years little has been added to the results of Braun and Durieu. During this period, though many large collections of Western Australian plants have been made, few included specimens of *Isoetes*. Possibly collectors overlooked them because of their small size, sedgelike habit and absence of flowers.

Gardner (1930) in his Census of Western Australian Vascular Plants lists only *I. drummondii*, which is also the only species recorded by Blackall (1954). Willis (1953) who first recorded the *Isoetes* in the Recherche Archipelago as *I. drummondii* (form) emended this to *I. humilior* (1959). Smith (1966) also recorded *I. humilior* from Western Australia. Examination of the material has shown it to be *I. australis*, a species described by Williams (1943) from Western Australia. The publication of it was overlooked until recently, although it was listed by Reed (1953) in his Index.

The three species known to occur in Western Australia prior to the present study are *I. drummondii* A. Braun, *I. tripus* A. Braun and *I. australis* S. Williams.

Material and methods

In August 1958 the late Charles A. Gardner, then Government Botanist of Western Australia, gave to the author a large collection of *Isoetes* he had made near Lake Monger (now known as Mongers Lake). The exact site or sites of this collection is not known as Gardner in his field notes gave only "...near Lake Monger" as the location. This lake is situated between lat. 28°45'-29°56'S and long. 116°48'-117°19'E, its mid-point being about 246 km east-south-east of Geraldton. It is an irregular stretch of water with a long shore line very narrow in some parts and in others never more than 16 km wide.

From a preliminary examination of Gardner's collection and a report by Smith (1966) it was evident that in Western Australia there occurred a number of forms of *Isoetes* which could not be referred to any known species and a study of the genus in Western Australia has been carried out at the State Herbarium of South Australia. Additional material was made available on loan from AD, ADW, B, CHR, K, M, MEL, MO, NY, OXF, P, PERTH, SYD, US, UWA, W and WELT.

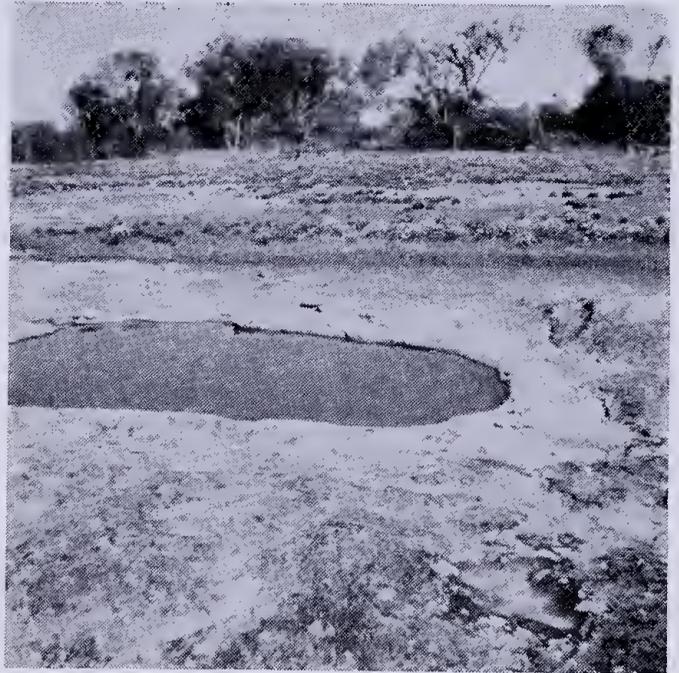


Figure 2.—Shallow pool on a granite outcrop south of Pithara. *I. inflata* growing wholly or partly submerged around its edges. Photo—K. F. Kenneally.

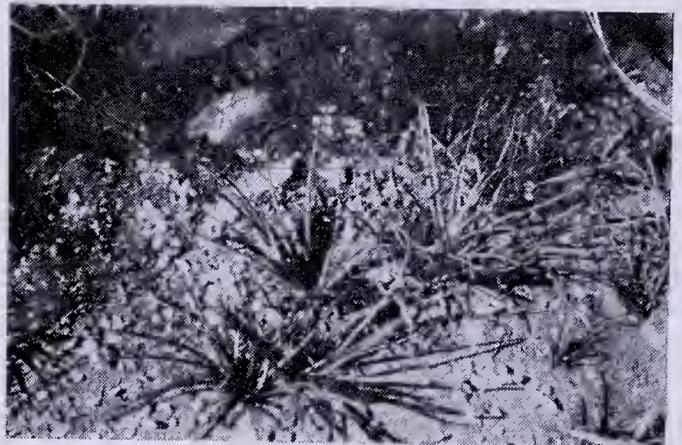


Figure 3.—*I. muelleri* growing submerged in rock pool, Glen Cuming Rawlinson Range. Photo—A. S. George.

The number of collections and sheets examined was 266 of which 189 were of *Isoetes* from 90 different localities in Western Australia and 6 were of small aquatic Angiosperms. The remainder were of *I. drummondii*, *I. muelleri* and other Australian taxa from localities in other parts of Australia.

As this journal is unable to publish long lists of specimens for each species, for the more common species only a selection of those examined is cited. Complete lists of collections examined are deposited at AD, CANB and PERTH. An asterisk denotes that only wet-preserved material (formalin or alcohol) was available. Maps show the distribution of each species in the South-Western and Eremean Provinces which are two of the three Climatic Provinces in Western Australia in relation to vegetation as delimited by Gardner (1942). Spore measurements give the approximate range of spore size. Megaspores were measured dry at $\times 10$ and microspores in water at approximately $\times 400$. Dimorphic

megaspores were counted when found in the same sporangium. Spore colour is that seen when dry megaspores and dry massed microspores are viewed against a white background in daylight or when wet with water.

Keys to the Western Australian species of Isoetes

The first key, based on vegetative characters, may be used to distinguish species at most stages of growth. The second key requires fertile plants with mature dry megaspores.

(a) *Key based on vegetative characters*

- (1) Stock 2-lobed; leaves usually short, 4 cm or less.
 - (2) Leaves \pm terete above the wings, attenuate, sometimes falcate (Fig. 4) 1. *I. australis*
 - (2) Leaves inflated above the wings, acuminate with apiculate apex often dark (Fig. 10) 5. *I. inflata*
 - (1) Stock 3-lobed; leaves short or long ca. 0.4-12 cm.
 - (3) Leaves $<$ 4 cm; wings short above ligule, ending towards middle of adaxial leaf surface.
 - (4) Leaves $<$ 1 cm (Fig. 6) 2. *I. brevicula*
 - (4) Leaves $>$ 1 cm.
 - (5) Leaves \pm divergent, firm, narrow, attenuate (Fig. 12) 6. *I. mongerensis*
 - (5) Leaves \pm upright, soft, terete, broadening about the middle then acuminate (Fig. 8) 3. *I. caroli*
 - (3) Leaves $>$ 4 cm, semi-terete, attenuate; wings long above ligule, \pm lateral, narrowing gradually.
 - (6) Brown scale leaves present (Fig. 9) 4. *I. drummondii*
 - (6) Brown scale leaves absent.
 - (7) Stock small; leaves \pm lax, velum present (Fig. 13) 7. *I. muelleri*
 - (7) Stock prominent, firm, leaves slender, velum absent (Fig. 14) 8. *I. tripus*
- (b) *Key including megaspore characters*
- (1) Stock 2-lobed, mature megaspores \pm black when dry.
 - (2) Megaspores \pm round, smooth or with faint tubercles (Fig. 4) .. 1. *I. australis*

- (2) Megaspores \pm 3-lobed, tubercles small, on distal face often confined to three areas separated by furrows (Fig. 10) .. 5. *I. inflata*
- (1) Stock 3-lobed; mature megaspores not black when dry.
 - (3) Leaves usually $<$ 1 cm long (Fig. 6) .. 2. *I. brevicula*
 - (3) Leaves $>$ 1 cm long.
 - (4) Megaspores with numerous tubercles, crests few mostly short, few confluent.
 - (5) Tubercles and crests crowded (Fig. 9) .. 4. *I. drummondii*
 - (5) Tubercles and crests distant (Fig. 12) 6. *I. mongerensis*
 - (4) Megaspores with few tubercles, crests numerous, many branched and confluent.
 - (6) Crests \pm close, often forming reticulations (Fig. 14) 8. *I. tripus*
 - (6) Crests distant.
 - (7) Crests on distal face \pm rounded (Fig. 8) 3. *I. caroli*
 - (7) Crests on distal face sharp (Fig. 13) 7. *I. muelleri*

1. *Isoetes australis* S. Williams, Proc. R. Soc. Edinburgh, Sect. B, 62 (1): 1-8, fig. 1 and 2, t. 1-3 (1943); Reed, Bol. Soc. Brot. II, 27: 15 (1953).—*Typus*: "collected in 1930 from rock pools in granite outcrops of Bruce Rock, 150 miles inland from Perth, Western Australia." *Lectotypus* (or *neotypus*): Western Australia. Bruce Rock: 1930; *F. R. Drummond and D. C. Swan s.n.* (PERTH lecto or neo (transferred from UWA), AD 97339092). (See note on lectotypification below.)—Figs. 4, 5. [*I. humilior* auct. non F. Muell. ex A. Braun (1853): Willis, Muelleria 1: 98 (1959); Smith, J. R. Soc. W. Austral. 49: 4 (1966).]

Plants small, 1-4 cm tall, rarely 5-9 cm; leaves few, distichous, bases closely overlapping on a laterally elongated stock, roots numerous, long. *Stock* bilobed with a shallow vertical groove between the lobes, leaf-bearing part pale, fleshy, extended laterally by dark desiccated, flattened segments, the remains of stocks of former seasons. *Leaves* 3-6, rarely 6-10, ca. 1-4(9) cm long \times ca. 1-1.5 mm broad, \pm terete, attenuate, sometimes falcate, without chlorophyll towards base; wings broad at base, closely overlapping, firm, short, distal ends truncate or rounded ending on the adaxial leaf surface ca. 2 mm above the sporangium; ligule reniform, margin crenate, on old leaves usually partly within the fovea concealed by the sporangium; labium very short; velum absent; fovea deep, edge

often acute projecting shortly over sporangium; stomata absent; peripheral strands absent. *Megasporangia* \pm circular and flat in face view, 2-2.5 mm diam., deeply sunken in fovea, becoming dark as spores mature; wall firm, hyaline, vertical walls of

epidermal cells slightly thickened, yellowish; megaspores usually few (4-12) per sporangium, rarely 24 or more, ca. 350-500 μ m, immature dark greyish (wet), white (dry), mature black (wet and dry), sometimes with lighter areas, smooth or with faint low

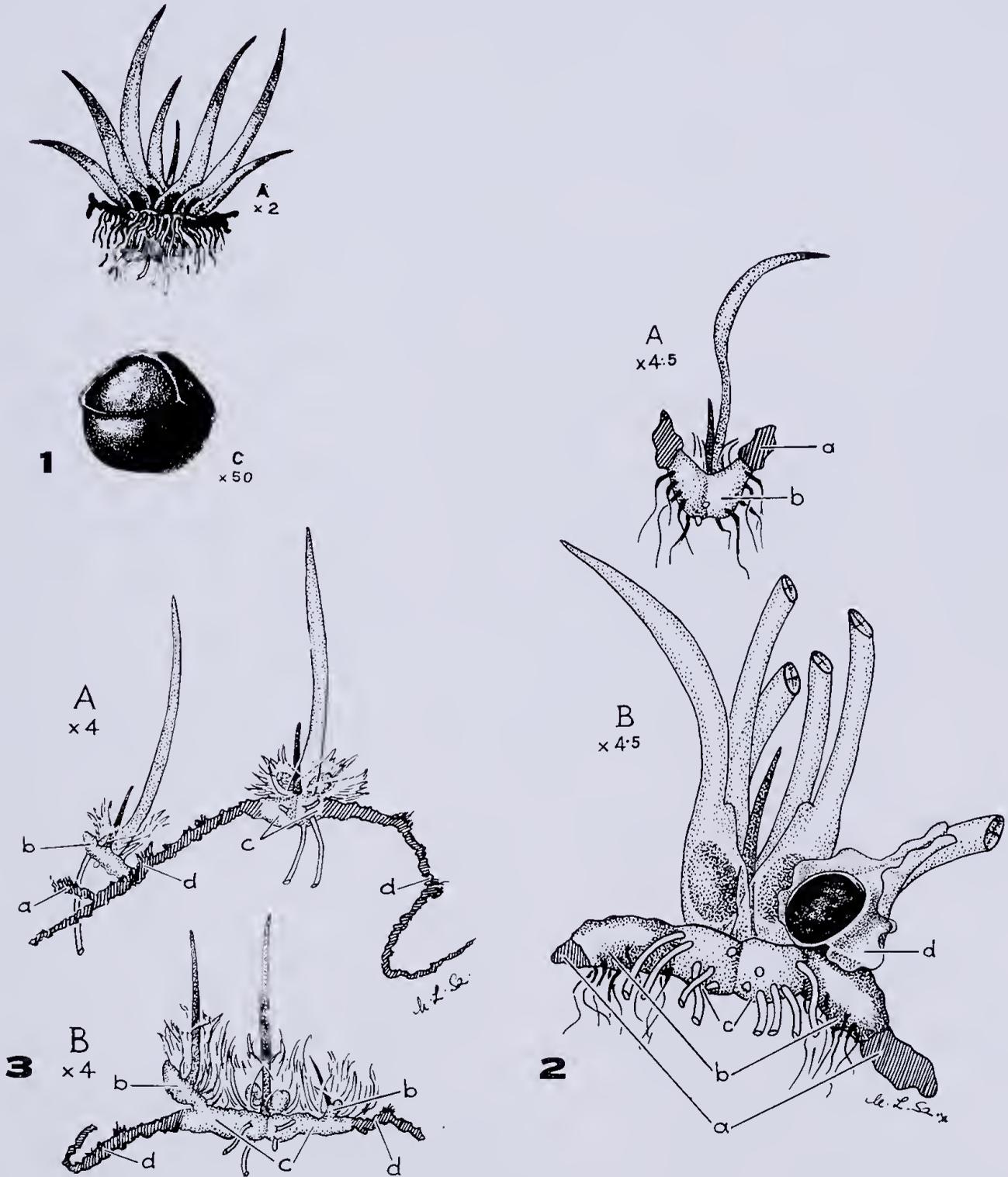


Figure 4.—*I. australis*. 1—*I. australis* Bruce Rock. A. habit; C. mature megaspore. 2—*I. australis* from pools on adjacent granite outcrops, One Mile Rocks, collected mid-November. A. Sterile plant, second growing season; a stock segments of previous season, b fleshy segments of current season. B. Fertile plant, third growing season; a, b, c, stock segments of three seasons; d outermost leaf showing microsporangium. 3—*I. australis*. Lateral stocks (old roots not shown). A. On stock of an earlier season, Stennet Rock. B. Onstock of current season, Albany Highway, 51 km south-east of Perth. a base of old branch, b young lateral stocks, c stock of current season, d lateral desiccated parts of stock segments of earlier seasons.

tubercles, commissural ridges prominent, rounded—brown; lateral view ca. 27-33 μm long \times ca. 18-24 μm deep, wall thick, brown, spinulose, spines pointed or truncate, crests narrow when present, usually absent.

Distribution (Fig. 5): *I. australis* is widely distributed in Western Australia in the central and eastern part of the South-Western Province and in the adjacent south-western part of the Eremean Province acute, equatorial ridge thinner. *Microsporangia* similar in size, shape and structure to megasporangia; microspores in mass immature pale, mature dark below lat. 30°S. Further south it is found in the Eremean Province south of Norseman and in the South-Western Province between Lake King and Ravensthorpe, east of Esperance and on Middle Island, Recherche Archipelago.

Specimens examined (selection only): Western Australia: Nungarin Hill ca. 5 km north of Nungarin; 13.ix.1970; *N. Marchant* 326 (PERTH*).—Yorkrakine Hill; 19.ix.1926; *C.A. Gardner* (UWA*).—24 km east of Jura Railway Siding on Merredin-Bruce Rock line; 1934; *E. T. Bailey* (OXF).—Albany Highway at 31 mile peg; 22.v.1964, 14.vi.1970; *G. G. Smith* (UWA).—Tuttanning Reserve south-east of Pingelly; 5.ix.1971; *A. S. George* 10904 (PERTH).—Boyatup Hill, ca. 110 km east of Esperance; 1.x.1968; *A. E. Orchard* 1274 (AD).—High Island, Duke of Orleans Bay; 2.x.1968; *P. G. Wilson* 8191 (PERTH).—Wittenoom Hills, ca. 50 km north-north-east of Esperance; 4.x.1968; *N. N. Donner* 2893 (AD).—Middle Island, Recherche Archipelago; 22.xi.1950; *J. H. Willis* (MEL).

Observations: Small plants (Fig. 4.1) grow completely submerged in pools on granite outcrops, often so closely massed that they form a green underwater sward. Depth of water in the pools is from 3 to 10 cm, in a few cases 15 to 40 cm. The OXF sheet of E. T. Bailey's Bruce Rock collection of 1934 was annotated by Professor T. G. B. Osborn "—habitat rock pools 2 sq. ft to $\frac{1}{2}$ acre, water to 18" but plant rarely found below 6". Only in a few of the collections cited was the depth of water in which the plants were growing stated, though the depth of the pools was noted. The average leaf length was about 2 cm. Longer leaves 4-9 cm long were on plants growing in a pool 30 cm deep on the top of Boyatup Hill and they were 3-7 cm on plants from Middle Island, but no depth of water was recorded. Pools with shallow water gradually dry out in the late spring and by December or earlier are completely dry. During this time the leaves die down and stocks with leaf bases and sporangia become desiccated and mixed with the detritus left on the rock surface. During the summer, this is exposed to periods of extreme aridity and high insolation, and the occasional summer rains, if any occur, provide only temporary water in the depressions. Regrowth of the stock does not take place during such short wet periods but recommences after the pools become permanent following the beginning of the next winter rains about April or May. In the laboratory growth from dry stocks as well as sporelings appeared after about four week's immersion in rain water.

Table 1

I. australis—Homospory and Heterospory in collections of young plants.

Locality	Date Collected	Sterile	Fertile	Homosporous		Hetero- sporous	Mega- spor- angia small	Aborted spor- angia	Loose spores and sporelings	Notes
				microsp.	megasp.					
Albany Highway 40 mile peg	July, 1963	0	0	few	microsporangia may have developed later in season
Mt. Hampton	Sept., 1964	0	0	0	numerous	fertile plants in third growing season
Jilakin Rock	Aug., 1970	0	0	plants all young
Durgacutting Rock	Sept., 1970	0	0	0	0	0	0	few	microsporangia large
Mt. Stevens	Sept., 1970	0	0	0	0	few	fertile plants few, sterile in first growing season
Mt. Madden (498)	Sept., 1970	0	0	0	few	rare	plants in drying pool, most in first growing season
Mt. Madden (499)	Sept., 1970	0	0	0	few	rare	numerous	plants in a deep pool, of different ages
One Mile Rocks (10489)	Nov., 1970	0	a few spores	plants in drying pool, near end of second growing season
One Mile Rocks (10491)	Nov., 1970	0	0	few	rare	numerous megaspores	plants all fertile, some old ones present
Bald Rock	Sept., 1971	0	0	0	few	rare	a few older plants pres- ent

Table 2

I. australis—Distribution of sporangia in a population of young plants from Durgacutting Rock.
Numbers of plants in brackets ().

Sporangia	No. of plants	Sporangia per plant		Aborted	Megaspores per sporangia μm
		micro-	mega-		
Microsporangia only	36	1 (4) 2 (16) 3 (12) 4 (4)		
Microsporangia and small megasporangia	15	1 (6) 2 (7) 3 (2)	1 (13) 2 (2)	4 (4) 8 (7) 12 (3) 16 (1) 16 (2)
Microsporangia and aborted sporangia	11	1 (1) 2 (6) 3 (2) 4 (2)	1 (8) 2 (3)	
Total	62	141 (62)	17 (5)	14 (11)	

Two periods of growth in the season 1971 were shown by plants from Newcarlbeon Soak and Stennet Rock. On the distal parts of the stocks were the remains of leaves, mature sporangia and shrivelled roots, and in the central parts developing leaves and roots, (Fig. 4.3), the former had the appearance of plants at the end of a growing season and the latter like those at the beginning of one. Field notes stated that at Newcarlbeon Soak the "pool had apparently dried out during the spring and refilled after recent rains" and at Stennet Rock in mid-November "water in the pool was 3.5 cm deep." Rainfall statistics show that dry periods occurred in both localities earlier in that season and in late spring rainfall was more frequent and heavier. These observations suggest that in shallow pools a falling water level may be one of the factors involved in spore maturation and cessation of growth towards the end of a growing season. In both cases active growth was resumed without the usual summer period of rest and exposure to high temperatures and aridity. Burbank and Platt (1964) have reported the same type of cessation and renewal of growth in *I. melanospora* from Georgia when growing under similar environmental conditions.

Spore production was observed to commence in one plant's third growing season. The younger sterile plants (Fig. 4.3A) were small with few leaves and fleshy swollen stocks often with slightly shrunken segments of the previous season attached to their distal ends. Young fertile plants (Fig. 4.3B) had 4 to 6 leaves and 1 to 4 large microsporangia. The outer leaves, if present, were sterile or bore one, rarely two, small megasporangia with few small spores, or aborted sporangia.

Larger megasporangia with microsporangia typical of older heterosporous plants were found in only two populations of young plants from Jilakin Rock and Mt. Hampton. Details of the different types of spores in a number of young populations are given in Tables 1 and 2. These indicate that heterospory is variable in young fertile plants and that they tend to be wholly or potentially homosporous (microsporangiate).

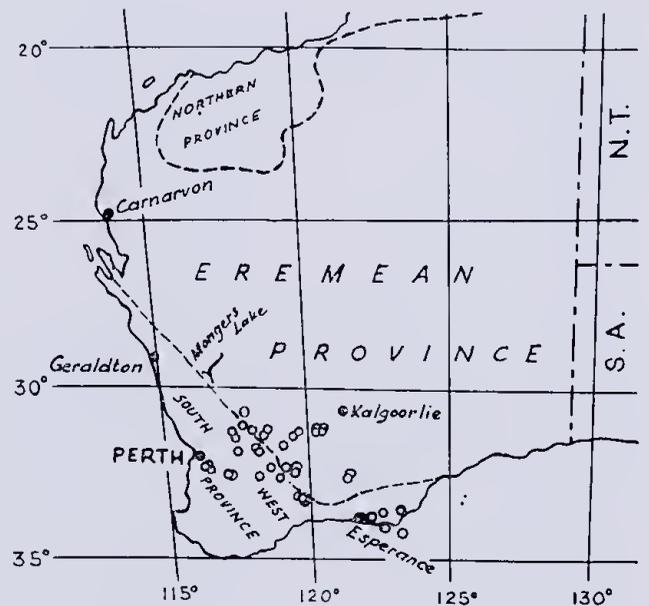


Figure 5.—Distribution of *I. australis*, O.

On a number of plants were small lateral fleshy stocks associated with the axils of the leaves (Fig. 4.2). The smallest one seen was a small fleshy outgrowth from the upper surface of the main stock, with a rounded distal end, a single small leaf near the mid-point of its abaxial surface and no roots. Larger stocks had two longer leaves and young roots. These differ in position and development from the small apogamous leafy shoots, on which stocks and roots develop later, which replace the sporangia in *I. lacustris* and *I. echinospora* (Goebel 1879). The structures in *I. australis* appear to be small axillary branches on which leaves and then roots develop. Pfeiffer (1922) refers to the branching of "the corm" being rare, but does not cite any examples. In *I. australis* the young lateral stocks were frequent in two collections and would be a means of vegetative reproduction.

A submerged species common in rock pools on granite, characterized by its bilobed stock bearing few, often falcate, leaves and mature megaspores which are smooth or faintly tuberculate, black or dark greyish-black.

Note on lectotypification: Dr Samuel Williams did not designate a type specimen when he published the description of *I. australis* in 1943. He saw specimens collected at Bruce Rock in 1930 and sent to Professor J. Walton at Glasgow in 1934 by Miss Alison Baird of Perth, and from Professor T. G. B. Osborn air dried plants, grown in his laboratory at Sydney, and collected by E. T. Bailey in 1934 near Bruce Rock, and herbarium specimens also collected at Bruce Rock by Bailey. The specimens on which Williams based his description, for which a search was made at Glasgow and Edinburgh (E), have not been found. Williams stated that his "description is mainly based on Miss Baird's material". According to information from Miss Baird, this was collected in 1930 at Bruce Rock by F. R. Drummond and D. C. Swan, and at least part of it is still held in the Botany Department of the University of Western Australia. A sheet in Oxford (OXF) bearing a series of plants annotated by Osborn as "coll. E. T. Bailey" without date at "15 m E of Jura Railway Siding on Merredin-Bruce Rock line, W.A." is noted as part of the original sheet sent to the British Museum (BM). A photograph of a small collection at BM shows that it was also made in 1934. There is no evidence that Williams saw either the OXF sheet or the BM specimens. I have examined from UWA a collection made in August 1930 at Bruce Rock by F. R. Drummond and D. C. Swan which represents part of the collection of which Miss Baird sent at least a portion in 1934 to Glasgow. Although it is uncertain whether Williams actually saw the part I examined (it may have been retained at UWA or returned by Williams after examination), I designate this portion of the syntype collection on which Williams mainly based the description of *I. australis* as the lectotype of this name. However, for purists who request the lectotype to be chosen from among elements that were definitely studied by the author (I.C.B.N. 1978, p. 75, Guide to the Determination of Types: 4, a) and who may claim that Williams possibly did not see UWA material I

examined, and that for the same reason none of the existing specimens (OXF, BM, and UWA) qualify as lectotypes (all syntypes being lost), I designate the UWA material alternatively as neotype of *I. australis*. The type material has now been transferred to PERTH; AD received a portion of this collection from UWA which accordingly is an isolectotype or isoneotype.

2. *Isoetes brevicula* E. R. L. Johnson, sp. nov.—Figs 6 and 7. Caudex trilobus. Folia 4-8 mm longa, 1-1.5 mm diametro. Megasporae (immaturae?) leaves vel modice sulptae.—*Typus:* Western Australia. Graham Rock, 17.6 km east of Hyden, in shallow pools on granite, water 3-6 cm deep; 21.ix.1971; *N. Marchant* 71/622 (PERTH holo, AD).

Plants (Fig. 6) very short to 1 cm tall with tuft of spirally arranged dilated shortly pointed leaves on a well-developed stock. Stock dark, prominent, 3-lobed, fleshy, 2-4.5 mm wide \times 1-3 mm deep, abscission caps present. Leaves 4-8, 4-8 mm long \times 1-1.5 mm diam. near mid-point of blade, fleshy, inflated \pm terete flattened adaxially distally, apex acute often dark; wings short ca. 2.5 mm long, fleshy, at base 2.5-3.5 mm wide, narrowing above region of ligule, ending near middle of adaxial leaf surface; ligule on young leaves triangular, cordate at base, \pm reniform on older ones; labium short, broadly triangular; velum absent, stomata absent; peripheral strands absent. *Megasporangia* immature, circular ca. 1.2 mm diam., adaxial surface flat; wall hyaline, slightly brown; megaspores 4-16 per sporangium, ca. 300-400 μ m, pale to dark brown (wet), greyish-white (dry); proximal faces sculpturing absent or faint, tubercles low, variable in number, size and shape; distal face few small low crests and tubercles; commissural ridges prominent \pm rounded; equatorial ridge thinner. *Microsporangia* similar to megasporangia, sometimes \pm oval; microspores light brown, in lateral view \pm 27-30 μ m \times 18 μ m without crest, wall thick, crests present or absent.

Distribution (Fig. 7): *I. brevicula* is known only from Graham Rock (32° 28' S 119° 02' E) in the Eremaean Province near its south-western boundary with the South West Province.

Observations: A collection of 15 plants growing submerged in a shallow rock pool on granite. All were heterosporous, with immature spores, except one which was sterile. This appeared to be in its second growing-season and had a well-developed fleshy stock bearing five leaves and three very small dark abscission caps.

Plants are distinguished from those of other species with 3-lobed stock by their small size, inflated leaves and smooth or faintly sculptured megaspores. It differs from *I. inflata* in its habit and 3-lobed stock.

3. *Isoetes caroli* E. R. L. Johnson, sp. nov.—Figs 1, 7 and 8. Caudex trilobus. Folia teretia, 2-4 cm longa, acuminata, lenia, plus minusve erecta, ad medium incrassata. Megasporae tuberculis paucis, cristis numerosis distantibus in superficie distali plus minusve rotundatis.—*Typus:* Western Australia. Near Lake Monger (now Mongers Lake), in granite rock pool; August 1958; *C. A. Gardner s.n.* (AD 97134006 holo, AD, PERTH.)

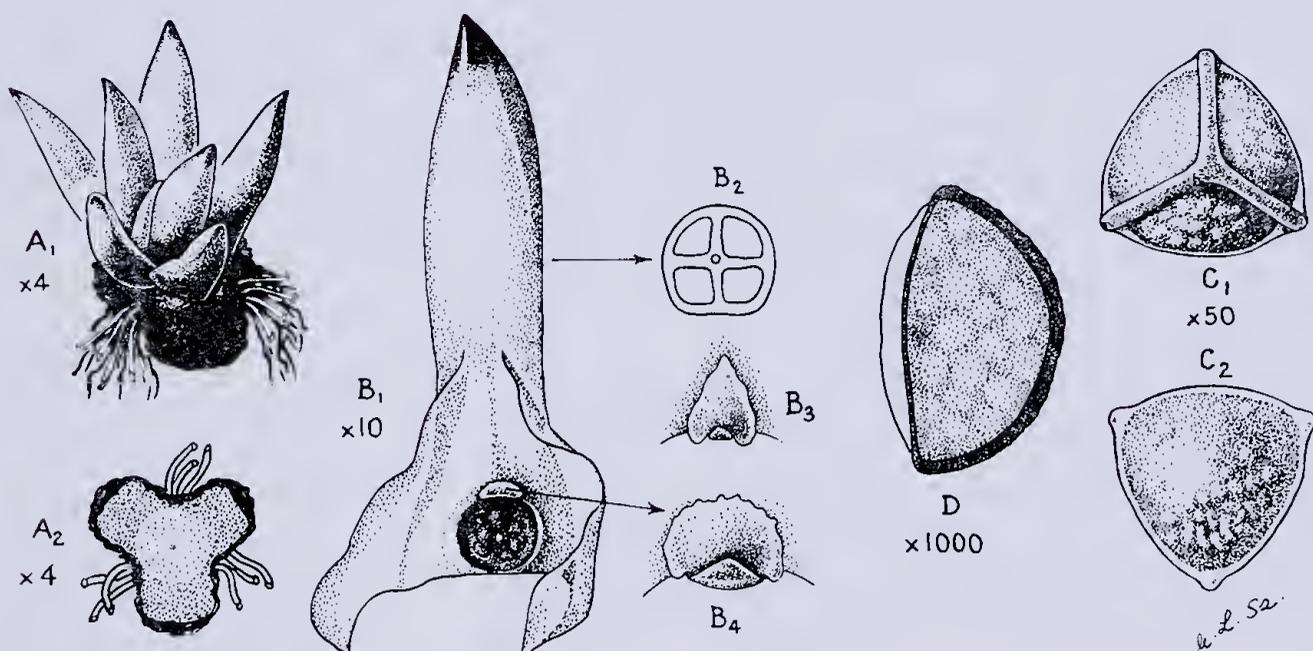


Figure 6.—*I. brevicula*, Graham Rock. A₁ habit, A₂ T.S. stock; B₁ megasporophyll, B₂ T.S. blade, B₃ ligule and labium on young leaf, B₄ ligule on mature leaf; C₁C₂ megaspore proximal and distal faces; D microspore, lateral view, optical section.

Plants (fig. 8A) small, (1)2-4(5) cm tall with a tuft of spirally arranged leaves on a well developed stock. *Stock* brown, 3-lobed, firm ca. 5 mm wide, abscission caps present, sometimes indistinct. *Leaves* (4)10-15(20), (1)2-4(5) cm long × 1-2 mm diam. in the lower and middle part, soft, terete, erect, sometimes ± falcate, tapering into the acuminate apex, with chlorophyll in the upper half or third of its length; wings thin, firm and fleshy, ca.(4)5-6(8) mm across at the base, narrowing gradually onto the adaxial leaf surface to about 8 mm above the ligule; ligule short, 0.25 mm long, reniform; labium small; velum absent; fovea deep with acute edges; stomata absent or sparse in upper part; peripheral strands absent. *Megasporangia* ± circular to broad-ovate, 2-3 × 1.8-2 mm, adaxial

surface flat; wall brownish, firm, thickened; margins rounded; megaspores 8-36 per sporangium, 350-400 μm, dark grey (wet), greyish-white (dry); proximal faces with few low and faint markings; distal face with numerous mostly low tubercles and some branching and anastomosing crests; commissural ridges prominent, broad, rounded; equatorial ridge thinner. *Microsporangia* ± ovate 3.5 × 2 mm, dark, adaxial surface flat, slightly margined, wall firm, opaque; microspores dark brown (wet), 15-18 × 30-53 μm, some crested, walls most by smooth or slightly crenulated and shortly and finely spinulose.

Distribution (Fig. 7): *I. caroli* is widespread in the South-West Province of Western Australia where it is restricted to seasonal granite rockpools.

Specimens examined (selection only): Western Australia: 3 miles east of Wubin on Payne's Find Road; viii. 1964; G. G. Smith (AD, UWA379).—7.5 miles west of Ballidu on Bindi-Bindi—Ballidu road; 26.ix.1971; K. F. Kenneally (AD, UWA). Granite flats just southeast of Ballidu, in or close to shallow pools; 4.v.1960; A. S. George 838 (PERTH). Yerritup Creek ca. 75 km west of Esperance; 27.ix.1968; H. Eichler 20005 (AD).

Note: The epithet 'caroli' (from Latin *Carolus* = Charles) refers to Charles Austin Gardner (1896-1970), the collector of the type.

4. *Isoetes drummondii* A. Braun, Monatsber. K. Akad. Wiss. Berlin 7 Dec 1863:573, 593-595 (1864); 13 Aug 1868:528-530, 534, 542-544 (1868); Bentham, Fl. Austral. 7:672 (1878); Baker, J. Bot. 18:65, 70 (1880); F. Muell., Syst. Census Austral. Pl. 1:136 (1882); Mot. & Vendr., Actes Soc. Linn. Bordeaux 36:379, t. 13:4, 5 (1882); F. Muell., Sec. Syst. Cens. 1:228 (1889); Sadeb. in Engler & Prantl, Nat. Pflanzenfam. 1/4:777 (1902); Osborn, Trans. R. Soc. S. Austral. 42:1, 5, 10, fig. 3 (1918); Pfeiffer, Ann. Missouri Bot. Gard. 9:125, t. 15:15

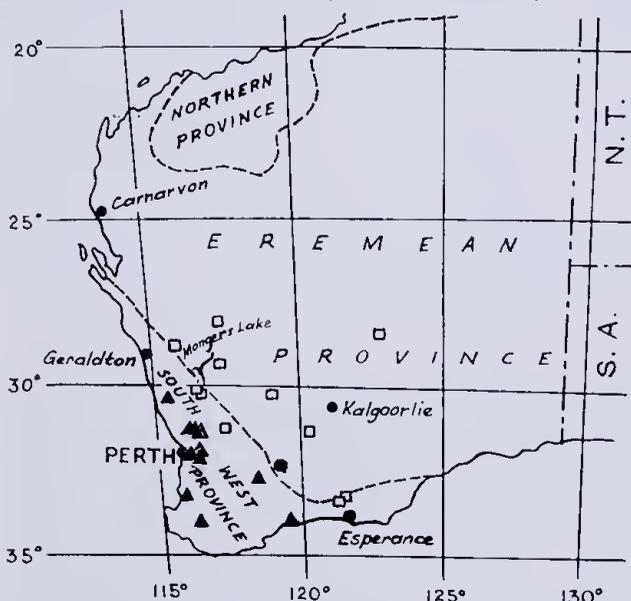


Figure 7.—Distribution of *I. brevicula*, ●; *I. caroli*, □; *I. drummondii*, ■.

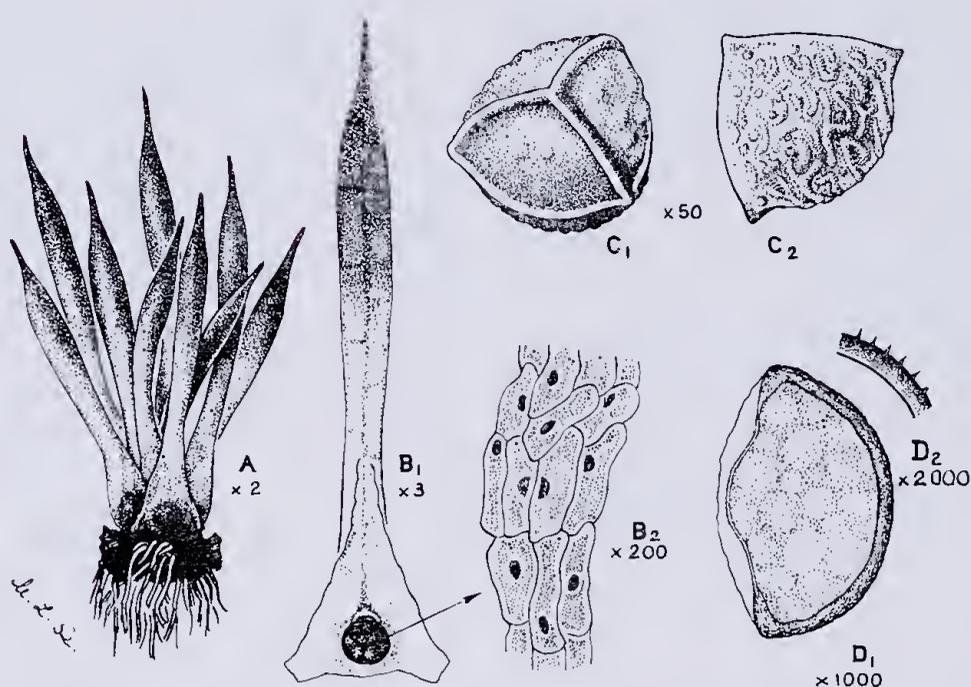


Figure 8.—*I. caroli*, Lake Monger. A habit; B₁ megasporophyll, B₂ sporangial wall hyaline cells; C₁C₂ megaspores proximal and distal faces; D₁ microspore, D₂ wall of older microspore (Wubin collection).

(1922); Osborn, Ann. Bot. 36: 41-54, fig. 1-15 (1922); Williamson, Vict. Nat. 44:228, fig. F (1927); Gardner, Enum. Pl. Austral. Occid.: 3 (1930); Reed, Bol. Soc. Brot. II, 27:20 (1953); Blackall, How to know W. Austral. Wildflowers 1:4 (1954); Wakefield, Ferns Vict. Tasm.: 65, fig. F (1955); Willis, Handb. Pl. Vict. 1:53 (1962); Smith, J. R. Soc. W. Austral. 49(1):4 (1966).—*Calamaria drummondii* (A. Br.) Kuntze, Revis. Gen. Pl. 2:828 (1891).—*Typus*: "... in herb. Vindob. et Hook. 1863 ... Ad flumen Swan River Novae Hollandiae australi-occidentalis I. Drummond 1843 (no. 989)." (W lecto, AD photo; K, P (mixed with *I. tripus*), W (the only sheet bearing Drummond's number label)). (See note on lectotypification below).—Figs. 7 and 9.

Plants (Fig. 9A) 4-10 cm tall with firm spreading leaves closely overlapping at the slightly bulbous base. *Stock* ± 1 cm broad × 2-5 mm deep, dark, 3-lobed, each lobe with a prominent persistent abscission cap. *Leaves* 9-10(18), 6-10 cm long × 1-1.5 mm broad near mid-point of blade, firm, semiterete, attenuate, green almost to the base; wings 6-10 mm broad at base, gradually narrowing above the level of the ligule, ± lateral; ligule triangular, cordate at base to 4 mm long × 2 mm across base, often shorter or damaged; labium short, firm, broadly triangular; velum absent; stomata present, sometimes sparse; peripheral strands absent; scale leaves small, hard, dark brown, shiny, acute, 2-3 mm long × 1-2.5 mm broad at base; mucilage cells in basal tissue of mature leaves; heavily thickened cells from dark brown area behind fovea. *Megasporangia* circular, oval or obovate, ca. 3-6 mm long × ca. 2-3.5 mm broad, adaxial surface flat, margined when mature; wall firm, immature pale, mature dark brown, epidermal cells thick walled, outer walls brown, inner very thick almost colourless, lumina narrow; megaspores ca. 300-400 μm, few ca. 500 μm,

mature dry greyish-white; proximal faces covered with numerous small low tubercles, crests few, short; distal face crests numerous few-branched or confluent, tubercles fewer; commissural ridges low, rounded; equatorial ridge thin, acute. Dimorphic megaspores occasional in same sporangium, size difference ca. 150-200 μm. *Microsporangia* similar to megasporangia in size, shape and structure; microspores immature pale in mass, mature dark greyish-brown, densely spinose, in lateral view ca. 30-33 μm long × ca. 18-24 μm deep, not crested.

Distribution (Fig. 7): A species occurring in Western Australia mainly in the western part of the South West Province below lat. 30°S. A single collection was made by Diels in 1901 about 64 km west of Esperance near the Hamersley River between Ravensthorpe and Jerramungup. No other collection has been made from or near this locality. The site "Ad flumen Swan River" of Drummond's type collection is not known. Recent collections at Cannington and Toodyay, both near the Swan River, are about 80 km apart. *I. drummondii* is also known from the southern and south-eastern parts of Australia.

Specimens examined (selection only): Western Australia: Cannington Swamp; 22.viii.1947; C. M. Eardley (ADW).—Brookton-Armadale Road ca. 83 km from Perth; 10.xi.1960; G. G. Smith (UWA 483).—Tuttanning Reserve southeast of Pingelly; 5.ix.1971; A. S. George 10908 (PERTH).—Harvey; 26.ix.1950; R. D. Royce 3343 (PERTH).—South West Highway 20 km south of Bridgetown; 23.x.1962; W. A. Loneragan (PERTH, UWA 723).—Kent, östlich von Hamersley River; 12.x.1901; L. Diels 4906 (B).

Observations: Plants are semi-aquatic and grow in swampy sandy or clayey loam subject to seasonal flooding and extreme dryness in summer. Complete submergence is rare but the stock and lower parts of the leaves may grow in 2-5 cm of water. A series of collections of plants from Cannington showed that Braun's (loc. cit.) description of the sporangium as "...immarginatum (margine rotundum), pallidum, sclerenchymate carens" was of an immature one as it appears about half-way through the growing season. When mature at the end of the season (November-December) it is margined, dark brown, with heavily thickened epidermal cells. Also present are a thickened dark brown area in the leaf base

of September and only megasporangia, without any developing microsporangia, were on plants collected at Scrivener's Soak and Hamersley River late in the growing season.

Dimorphic spores occurred on plants from York Road (UWA 721) and south of Bridgetown. On plants from Scrivener's Soak were some abnormal megaspores, in polar view up to 500 μm long, oval in shape and with more than three proximal faces and commissural ridges. Braun (1868) noted two sizes of megaspores and the abnormal appearance of others in the Swan River plants.

A specimen from Toodyay (NY) recorded by Pfeiffer (1922) as *I. drummondii* "...coll. O.W.F." is emended to *I. tripus* coll. Oldfield. Its habit and megaspores are characteristics of *I. tripus* and O.W.F. was an incorrect interpretation of the pencilled abbreviation of Oldfield's name on the label.

On a P sheet were two specimens under Drummond's No. 989 referred to *I. drummondii*. Both, somewhat similar in habit, were immature. The left-hand specimen showed features characteristic of *I. drummondii* and the right-hand one those of *I. tripus*. Possibly before being mounted Drummond's number label (990) for *I. tripus* was lost or the specimens had become mixed.

Plants of this semi-aquatic species are distinguished by a few small brown scale leaves outside a tuft of firm tapering green leaves, the lower parts of mature sporophylls thickened and brown with internal mucilage cells and brown margined sporangia.

Note on lectotypification: In the first valid publication (1864) of the name *Isoetes drummondii* A. Braun does not give any indication of a type. In the second paper (1868) he lists "Ad flumen Swan River Novae Hollandiae australi-occidentalis *I. Drummond* 1843 (no. 989)" and gives the location "herb. Windob. et Hook." (= W and K). I have seen both specimens and designate the W sheet as the lectotype and the collection at K as isolectotype. Both collections are annotated by A. Braun and of equal quality. The W sheet bears only *I. drummondii* (Drummond 989) whereas on the K sheet is mounted also a collection of *I. tripus*. On a B sheet in a packet annotated by A. Braun "Isoetes tripus mihi" were two small packets labelled by A. Braun "*I. drummondii*". One of these was empty and the other contained part of a leaf which was insufficient to verify the species. Other isolectotypes, not annotated by Braun, were seen from P and W.

5. ***Isoetes inflata*** E. R. L. Johnson, sp. nov.—Figs 2, 10 and 11. Caudex bilobus. Folia 0.5-1 (2) cm longa, supra alas inflata, acuminata, apex apiculatus, saepe atratus. Megasporae plus minusve trilobatae; tubercula parva in superficie distali plerumque ad tres areas ab sulcis separatas limitata. —*Typus:* Western Australia. Near Lake Monger [now Mongers Lake], in mud of granite rock pool; August 1958; C. A. Gardner s.n. (AD 9713004 holo, AD, PERTH).

Plants (Fig. 11aA) small, 1-2 cm tall, partly or wholly submerged. Stock flat, 2-4 mm wide, 0.5 mm deep, two-lobed with shallow central vertical groove and persistent lateral strap-shaped 1-6 cm long extensions of previous years stock with brown leaf scars and long roots. Leaves (4)5-9(15) in

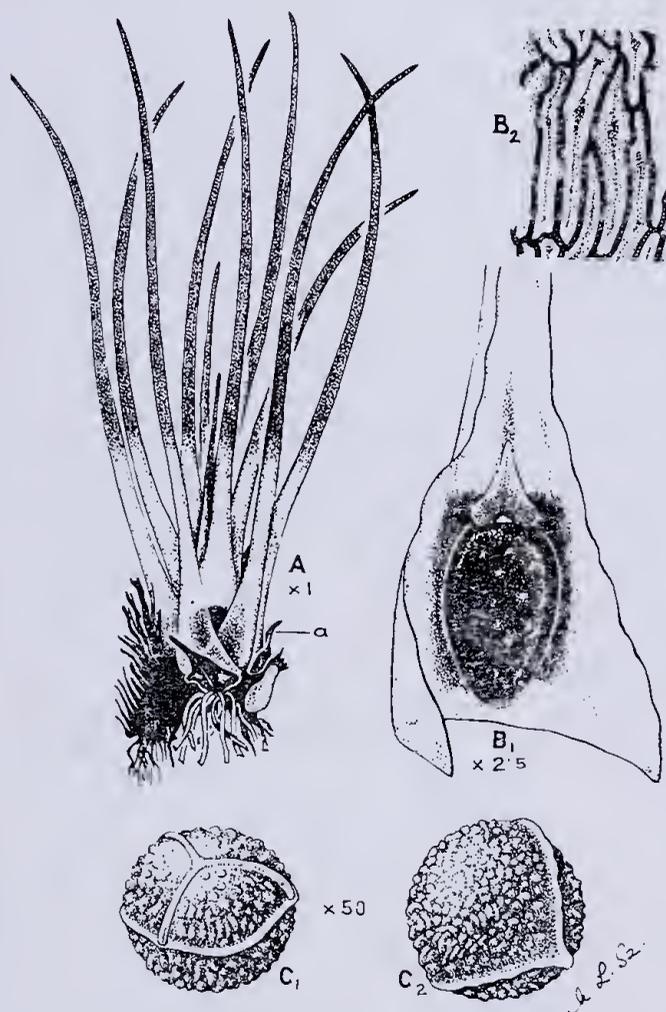


Figure 9.—*I. drummondii*, Cannington. A habit, a scale leaf; B₁ micro-sporophyll, mature microsporangium with thick wall and margin, dorsal area of sporophyll thickened, B₂ thick walled epidermal cells of sporangial wall; C₁C₂ megaspore proximal and distal faces.

behind the fovea, internal mucilage tissue and dark scale leaves around the growing apex. Osborn (1922) described similar structural changes in *I. drummondii* from South Australia and showed that the mucilage tissue functioned in spore dispersal at the beginning of the next wet season. Spore dispersal has not yet been observed in Western Australian plants.

In most collections plants were heterosporous. Homosporous ones with large mature and immature microsporangia were collected at Harvey at the end

opposite rows, stout, almost terete, 0.5-2 cm long \times 1-2.5 mm diam. at the widest point near the middle, tapering rather abruptly into a short, dark, bluntish tip, whitish opaque in lower part, green in upper 2/3-3/4 of length above the wings; wings short, fleshy membranous attached at the broad base to the stock for most of the width, overlapping the next younger ones so as to enclose the sporangium, narrowing above and gradually tapering and ending on adaxial surface to 2-3 mm above the fovea, or with an almost truncate end; edge of fovea acute, slightly extended as a rim around the sporangium; ligule thin, reniform, very short, 0.3-0.5 mm long \times 2 mm broad; labium

firm, short, rounded or pointed; velum, stomata and peripheral strands absent. *Megasporangia* oval to almost circular, 1.5-2 mm diam., adaxial surface flat; wall firm, thin, hyaline, sometimes with groups of brown cells in the inner layer; megaspores white, grey or black, \pm three-lobed, 300-500 μ m diam.; tubercles small, rounded, those on distal face often confined to three raised areas which are separated by furrows, those on proximal faces scattered; commissural ridges prominent, \pm rounded; equatorial ridge thinner. *Microsporangia* similar to megasporangia, oval, 2 \times 1.5 mm. Microspores dark brown, 30-36 \times 18-24(28) μ m, spinulose, crested.

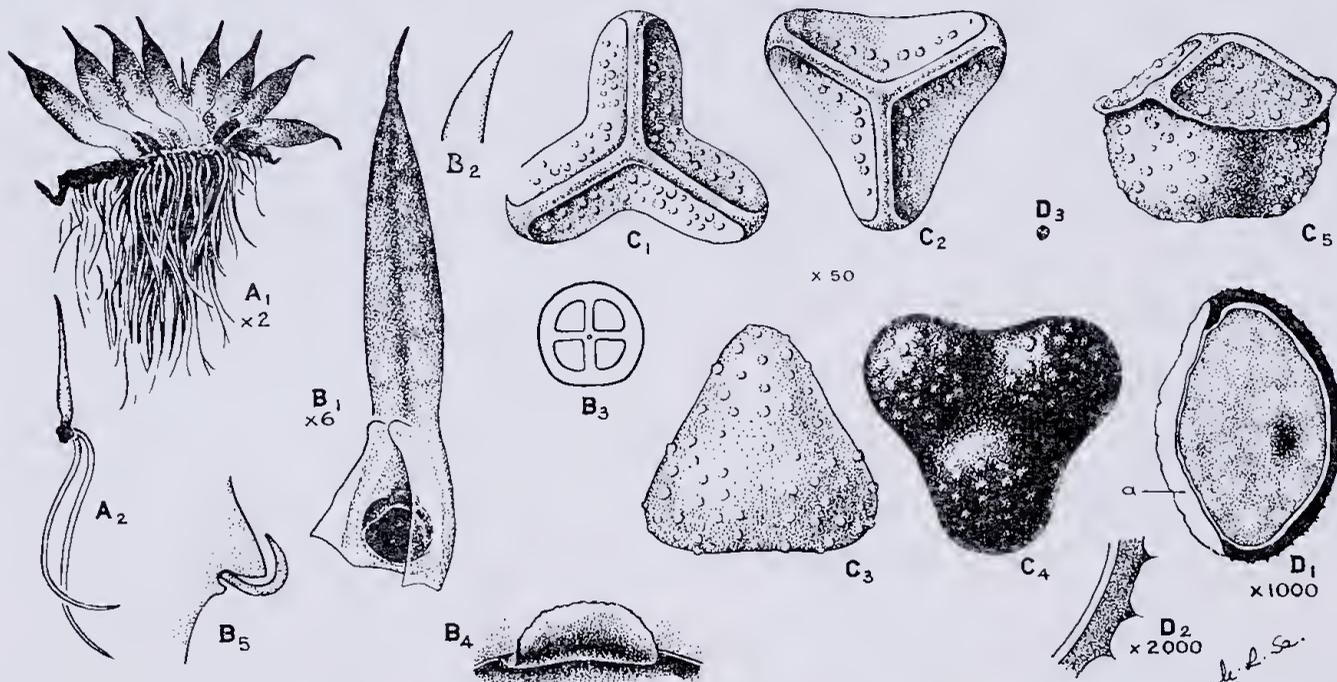


Figure 10.—*I. inflata*, Lake Monger. A₁ habit, A₂ sporeling; B₁ mature leaf, dark tipped, B₂ tip of young leaf; B₃ T.S. terete part of leaf, B₄ reniform ligule, B₅ diagram ligular pit in fovea; C₁-C₄ megaspores showing variation in shape and sculpture, C₄ distal face of mature black trilobate spore, C₅ lateral view megaspore; D₁ microspore, D₂ spinose wall, D₃ microspore \times 50.

Distribution (Fig. 11): *I. inflata* occurs in granite rock pools in inland areas in the southwestern part of the Eremean Province and in an adjacent area of the South-West Province around Pithara.

Specimens examined (selection only): Western Australia: 18 miles northwest of Morawa; 27.vii.1964; D. Yates (UWA 720).—Wannarra; 23.viii.1957; C. A. Gardner (PERTH, UWA).—8.8 miles from junction of Pithara-Kalannie road and Great Northern Highway; viii.1964; G. G. Smith (UWA 378).—17 miles east of Pithara; 23.vii.1971; N. Marchant 71/304 (AD, PERTH*).—Granite rock near Coward Homestead about 50 miles northnorthwest of Bullfinch; 11.ix.1964; S. James & J. Courtney (UWA 406b).—Elachbutting, east of Muckinbudin; 16.ix.1962; N. Marchant (AD, UWA 329).—292 mile peg Great Eastern Highway, near Boondi; 5.ix.1964; J. Courtney & S. James (UWA 422).

Note. The epithet (Latin *inflatus* = swollen) refers to the leaves which appear swollen above the wings. The species differs from others in its megaspores being three-lobed.

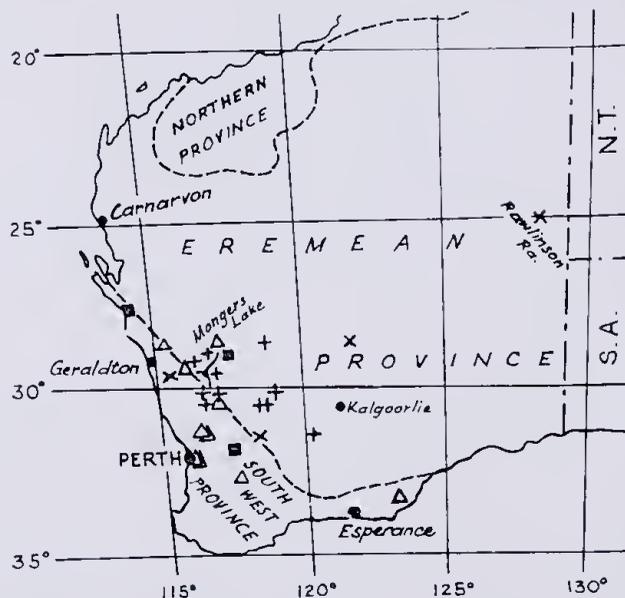


Figure 11.—Distribution of *I. inflata*, +; *I. mongerensis*, ■; *I. muelleri*, x; *I. tripus*, Δ.

6. *Isoetes mongerensis* E. R. L. Johnson, sp. nov.— Figs 11 and 12. Caudex trilobus. folia teretia sed parum quadrangularia, 1-1.5 cm longa, attenuata, ad medium 0.8-1 mm diametro, firma, plus minusve divergentia. Megasporeae tuberculis numerosis dispersis et cristis paucis plerumque brevibus.— *Typus*: Western Australia. Near Lake Monger [now Mongers Lake], in granite rock pool; August 1958; C. A. Gardner s.n. (AD 97134005 holo, PERTH).

Plants small ca 1.5 cm tall (Fig. 11b). *Stock* firm, dark, 3-lobed to 1 cm wide \times ca. 0.5 cm deep, abscission caps prominent, upright remains of old leaf bases with a few small dark scale leaves closely investing the broad bases of the narrow spreading leaves. *Leaves* 6-12, 1-1.5 cm long \times 0.8-1 mm diam. near mid-point of blade; blade rigid, narrowing abruptly above the concealed broad base, tapering apex acute, T.S. 4-angled; wings firm, short, ca. 4 mm long \times 3 mm wide at base narrowing gradually to end a short distance above the ligule on the adaxial leaf surface; ligule variable, short and broad, apex pointed or rounded; labium very small or absent; velum absent or narrow, thin (Fig. 12 B₁a); stomata sparse; peripheral strands absent. *Megasporangia* immature, circular-oval in face view, ca. 1.5-3 mm long \times 1.5-2 mm wide; wall firm, hyaline, light yellowish, brown as walls become thickened, not margined; megaspores to 48 per sporangium, dimorphic, ca. 200-300 μ m and 350-450 μ m, dark (wet), greyish-white (dry); proximal faces tubercles prominent, scattered, irregular in shape, crests few, short, some confluent; distal face crests prominent, scattered, tubercles few; commissural ridges rounded-acute, on small spores slightly sinuous; equatorial ridge thin, acute. *Microsporangia* rare, immature, circular ca. 2 mm diam. similar in structure to megasporangia; microspores cream-brownish in mass, in lateral view ca. 36 μ m long \times 20 μ m deep; wall thick, brownish almost smooth, crest absent.

Distribution (Fig. 11): First collected near Mongers Lake. Later two collections were made from isolated stations in the South-West Province, one in its northern part in the Kalbarri National Park and the other about 600 km south-southwest on Kwolyin Rock.

Further specimens examined: Western Australia: Kalbarri National Park ca. 120 km north of Geraldton; 26.vii.1969; P. G. Wilson 8316 (PERTH).— Kwolyin Rock ca. 40 km east of Quairading; 12.ix.1979; N. Marchant 270 (PERTH*).

Observations: Plants grow submerged in rock pools on granite. The largest ones, 2.5 cm tall with stocks about 1 cm, were on Kwolyin Rock in water 10 cm deep and also in the Kalbarri collection. On leaves of different ages, often on the same plant, the ligule varied in shape from triangular to almost reniform. On plants from Kwolyin Rock the velum was present as a thin hyaline membrane and varied in size on the same plant from very narrow to one-half or three-quarters the length of the sporangium. No firm, complete velum, as in *I. muelleri*, was seen. Also on the walls of the immature sporangia were brownish flecks due to groups of cells with slightly thickened walls interspersed with thin-walled ones, a type of structure characteristic of *I. tripus*. As their other characters differ from those of *I. tripus* and are similar to those of the type of *I. mongerensis*, they are referred to this species.

The Mongers Lake plants were homosporous, microsporangiate ones being rare. Those from Kwolyin Rock were megasporangiate, from Kalbarri heterosporous with microspores in an early stage of development. No plants bore mature spores. Old megaspores and sporelings were among the roots of plants from Kwolyin Rock and Kalbarri. Joined and dimorphic megaspores occurred in a single sporangium on a Mongers Lake plant (Fig. 12C₄). This contained 41 spores, 10 joined in pairs by tubes from their proximal faces and 7 had the broken ends of tubes projecting from theirs. Pant and Srivastava (1962) reported spores joined in a similar way in 6 Indian species and stated this type of tubular connection is only known to occur in *Isoetes*.

Plants of this species are distinguished by their narrow, angular spreading leaves, prominent firm 3-lobed stocks bearing the remains of old leaves which closely invest the broad leaf bases.

7. *Isoetes muelleri* A. Braun, Monatsber. K. Akad. Wiss. Berlin 13 Aug 1868: 528-530, 541 (1868); Luerssen, J. Mus. Godeffroy 3:121 (1875);

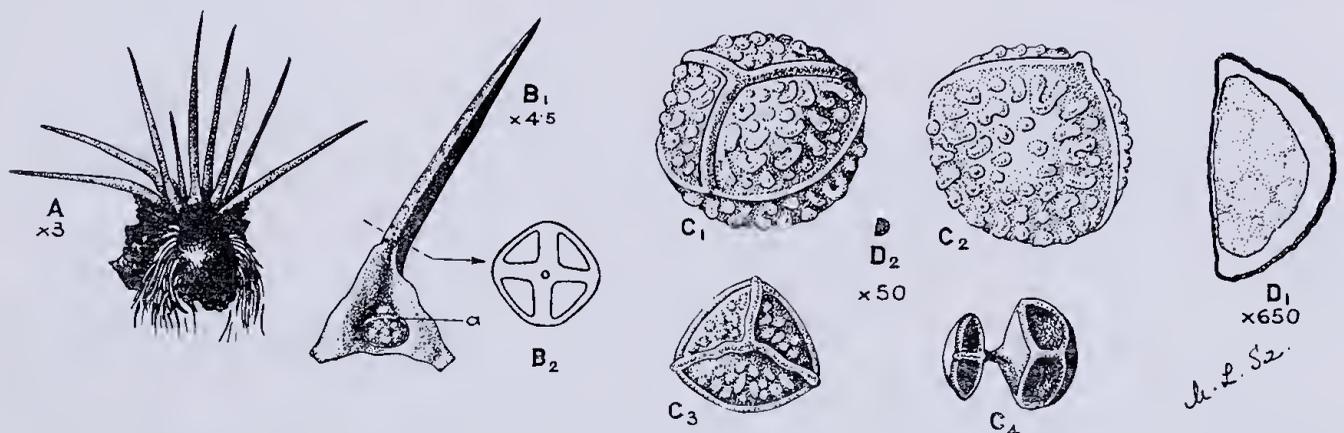


Figure 12.—*I. mongerensis*, Lake Monger. A habit; B¹ megasporophyll, a short extended edge of fovea, B₂ T.S. angular blade; C₁C₂ megaspores proximal and distal faces, C₃ small megaspore, commissural ridges sinuous, C₄ joined spores; D₁ microspore, D₂ microspore \times 50.

Baker, J. Bot. 18:65, 69 (1880); F. Muell., Syst. Census Austral. Pl. 1:136 (1882); Bailey, Syn. Queensl. Fl. 672 (1883); Mot. & Vendr., Actes Soc. Linn. Bordeaux 36:389 (1882); Baker, Handb. Fern-Allies: 127 (1887); F. Muell., Sec. Syst. Census Austral. Pl. 1:228 (1889); Bailey, Catal. Pl. Queensl.: 58 (1890); Bailey Queensl. Fl. 6:1923 (1902); Sadeb. in Engler & Prantl, Nat. Pflanzenfam. 1/4:777 (1902); Pfeiffer, Ann. Missouri Bot. Gard. 9:127 (1922); Reed, Bol. Soc. Brot. II, 27:41 (1953).—*Calamaria muelleri* (A. Braun) Kuntze, Revis. Gen. Pl. 2:828 (1891).—*Typus*: "Locis humidis ad Rockhampton Australiae orientalis tropicae legit P. O'Shanesy 1867 comm. Ferd. Müller." (B holo).—Figs 3, 11 and 13.

[*I. tenuissima* F. Muell. ex A. Braun, Monatsber. K. Akad. Wiss Berlin 13 Aug 1868: 541 (1868) pro syn. (non Boreau, Bull. Soc. Ind. d'Angers 21:269 (1850), n.v.; Mot. & Vendr., Actes Soc. Linn. Bordeaux 36:351 (1882)).]

Plants 3.5-12 cm tall; leaves rather lax and spreading, bases slightly bulbous. *Stock*: small, 3-7 mm wide, firm, 3-lobed, lobes short, abscission caps small, sometimes persistent. *Leaves* 8-25, slender, semi-terete, attenuate, up to 12 cm long \times 1 mm broad near middle of blade, \pm colourless towards base; wings narrow, thin, narrowing along margins of blade above ligule; ligule 1-2 mm long, \pm triangular, base sometimes broad and cordate; labium very short; velum present, firm, pale, usually complete; stomata present; peripheral strands absent. *Megasporangia* circular or oval in face view, ca. 2-3 mm long \times ca. 2 mm broad, not margined; wall (mature) brown, epidermal cells with walls yellowish-brown, slightly thickened, lumina large; megaspores dimorphic, ca. 200 μ m and ca. 300-450 μ m, immature white to greyish-white dry, creamy-dull brown wet, mature darkish-grey dry, dark but not black wet; proximal faces with short and branching crests, few tubercles; distal face crests predominant, sharp, sinuous, branched often confluent; commissural ridges \pm low, rounded; equatorial ridge thinner; sculpturing may be absent near ridges; abnormal spores (Fig. 13 C₃C₄) present, in lateral view ca. 500 μ m \times 350 μ m deep, numbers of proximal and distal faces and ridges vary. *Microsporangia* similar in size and shape to megasporangia; wall brown, firm. Microspores immature creamy in mass, fawn-brown as they mature; in lateral view ca. 30-33 μ m long \times 18-21 μ m deep, usually shortly spinose, sometimes almost smooth, crests rare.

Distribution (Fig. 11): A new record for Western Australia. Collections are from four widely separated localities. Two are in the Eremean Province, the furthest inland and most northern near the Northern Territory border at Glen Cuming and the second about 800 km to the south-west near Morgans. A third locality is in the northern part of the South-West Province at Mingenew about 640 km west of Morgans and the fourth, near Merredin, a further 480 km to the south-west near its eastern boundary with the Eremean Province. This discontinuous distribution may be due to the low number of collections made. Though formerly known only from Queensland this species has been found to be widely distributed in Australia. Chippendale (1960) recorded it from Central Australia on Ayer's Rock and specimens have been

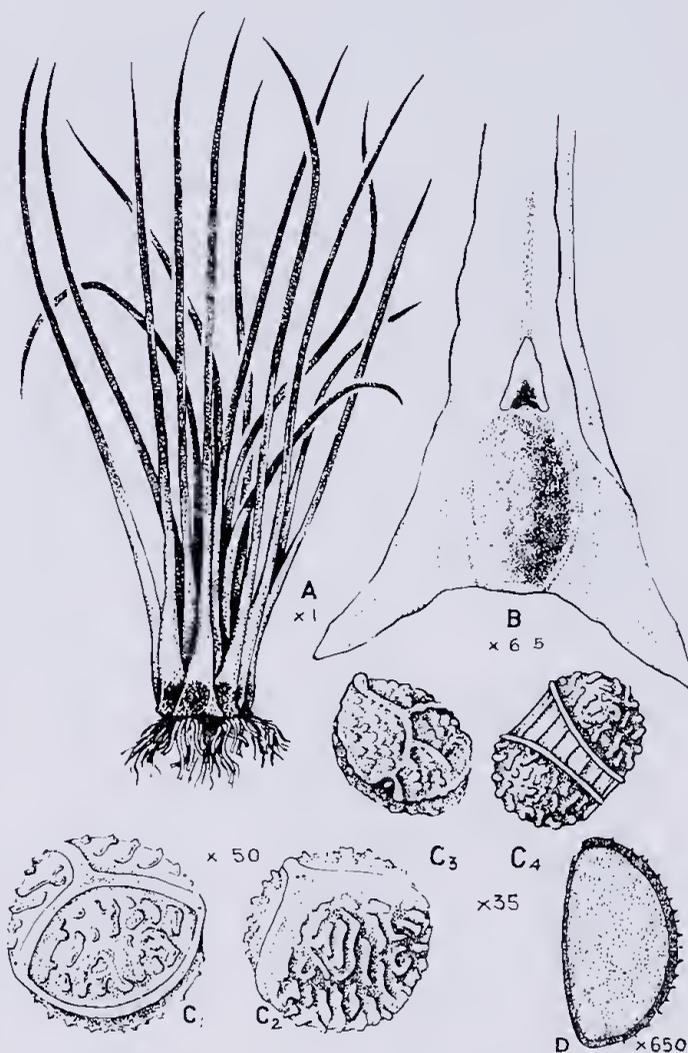


Figure 13.—*I. muelleri*, Glen Cuming. A habit; B base of sporophyll with complete velum; C₁C₂ megaspore proximal and distal faces, C₃C₄ two abnormal spores; D microspore.

examined from the Northern Territory (PERTH), southeast South Australia (AD), Victoria (AD, B, M, MEL, MO, P, W) and New South Wales (SYD). No specimens have been seen from Tasmania.

Specimens examined (only W.A. specimens listed): Western Australia: Glen Cuming, Rawlinson Range; 21.vii.1967; *A. S. George* 8840 (PERTH).—Glen Cuming, Rawlinson Range; 6.viii.1967; *R. C. Carolin* 6128 (SYD).—9.6 km west of Morgans; 29.viii.1962; *A. S. George* 4117 (PERTH).—Mingenew; 16.x.1959; *J. C. Knight* (UWA 484).—Durgacutting Rock, ca 6.4 km north of Merredin; 13.ix.1970; *N. Marchant* 323 (PERTH#).

Observations: Grows submerged in shallow granite rock pools at Glen Cuming (Fig. 3) and in 30 cm water in sandy soil in a large dam near Merredin. Other habitats were in swampy soil at Mingenew and in red loam near a creek near Morgans. Immature megaspores, but no microspores, were on plants collected in late winter and spring at Glen Cuming, Morgans and Merredin. Mature megaspores were obtained in washings from the old roots. Microsporangia only occurred on some plants from Mingenew and on a few were also small megasporangia with immature spores.

Microspores are described for the first time here as Braun did not find mature microspores on his specimens. The velum, a characteristic feature of this species, is usually complete. It was narrow on the Mingenew plants and on a single plant from Morgans it varied from narrow to up to three-quarters the length of the sporangium.

Dimorphic megaspores were present in all collections and were often found in almost equal numbers in the same sporangium. They also occurred among the roots. They appear to be a characteristic feature of this species as they are present on the type from Rockhampton and specimens from other Australian States. Joined megasporites were frequent on the Morgans and Durgacutting Rock plants. Their proximal faces were joined by one or more fine tubules which easily broke off and left a scar on the spore wall. Single large almost oblong spores with abnormal development of their proximal faces and ridges occurred (Fig. 13 C₃C₄).

Distinguished from other species by the pale firm velum, the predominance of sharp crests on the distal faces of the megaspores, a small trilobed stock and rather lax slender tapering leaves.

8. *Isoetes tripus*. A. Braun, Monatsber. K. Akad. Wiss. Berlin 7 Dec 1863: 559, 566, 567, 573, 574, 582, 591, 593, 594 (1864); 13 Aug 1868: 528-530, 535, 544-545 (1868); Baker, J. Bot. 18:66, 109 (1880); Mot. & Venor., Actes Linn. Soc. Bordeaux 36: 361-362 (1882); Baker, Handb. Fern-Allies: 132 (1887); F. Muell., Sec. Syst. Census Austral. Pl. 1:228 (1889); Sadeb. in Engler & Prantl, Nat. Pflanzenfam. 1/4: 778 (1902); Pfeiffer, Ann. Missouri Bot. Gard. 9: 176 (1922); Reed, Bol. Soc. Brot., II, 27:50 (1953).—*Calamaria tripus* (A. Braun) Kuntze. Revis. Gen. Pl. 2:828 (1891).—*Typus*: “. . . in herb. Vindob. et Hook. 1863. Ad flumen Swan River

detexit Drummond 1843 (no. 990).” Nouvelle Hollande occidentale R. des cygnes; c1844; Drummond 990. (W lecto, AD photo; B, K, P). (See note on lectotypification below.)—Figs. 11 and 14.

I. phaeospora Durieu, Bull. Soc. Bot. France 11: 103 (1864); F. Muell., Fragm. 5: 140 (1866); Reed, Bol. Soc. Brot. II, 27: 44 (1953).—*Typus*: “. . . Drummond dans la Nouvelle-Hollande, en 1842 et 1843 . . . L'étiquette de Drummond porte pour toute indication de localité: “Swan River.”” (P n. v., herb. Delessert n.v.) (See note on lectotypification below.)

Plants (Fig. 14) to 7 cm tall, leaves slender forming a tuft invested at base parts of stock. Stock 3-lobed, dark, firm, abscission on caps persistent, projecting horizontally or slightly upwards, sometimes horny. Leaves up to 11, 4-7 cm long, some shorter, ca. 0.5-1 mm broad, semi-terete, attenuate, apex often obtuse, green except near base; wings slightly fleshy, long, gradually narrowing above the level of the ligule; ligule often triangular, apex acute or obtuse, base cordate, sometimes short almost reniform; labium short; velum absent, edge of fovea sometimes acute, extending shortly over sporangium; stomata numerous; peripheral strands absent; median horizontal grooves on the lower dorsal surface of mature leaves. Megasporangia almost circular or oval, 2 mm long × 1.5-2 mm broad, or 3.5-6 mm long × 1.5-3 mm broad, mature flat adaxially, margin slight, wall with small dark brown flecks rarely dark brown all over; megaspores immature 350-500 μm, immature wet dark, dry whitish, mature dry dull brown; proximal faces few tubercles, crests numerous, short, long, branched, distal face crests numerous, rather sharp, branched, often confluent forming few or many reticulations, commissural ridges low ± rounded, equatorial ridge thin. Microsporangia similar in size, shape and

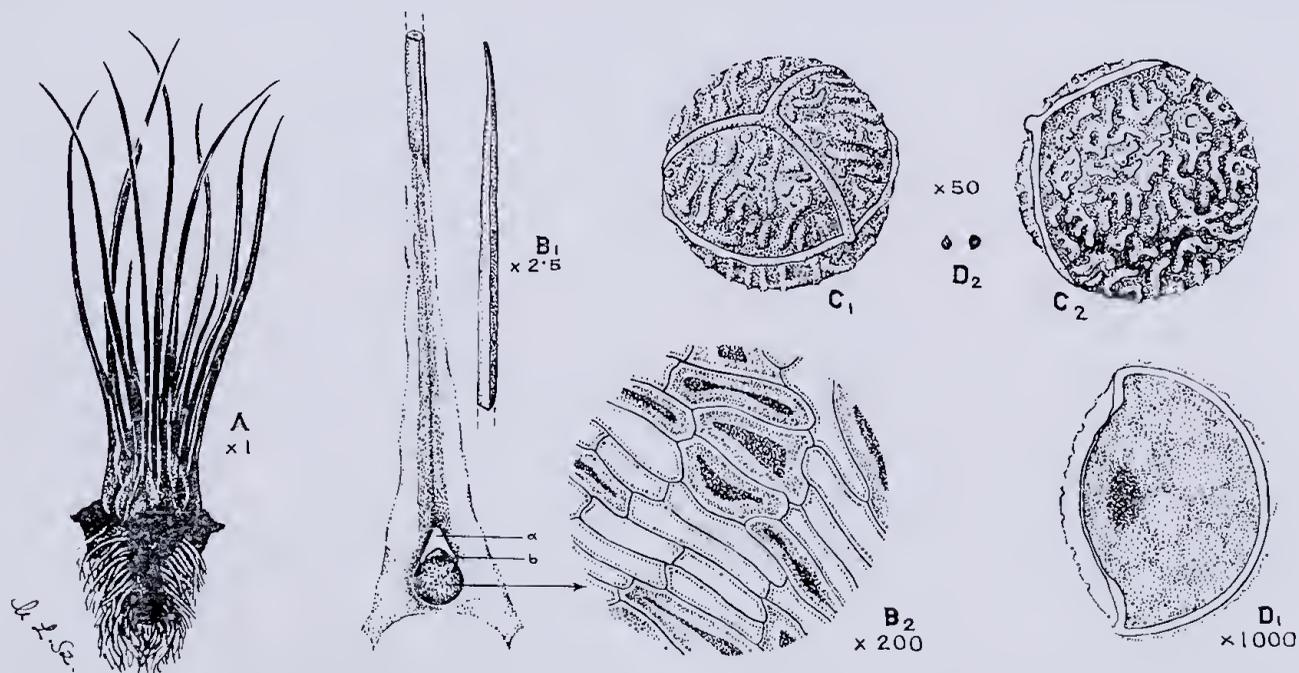


Figure 14.—*I. tripus*, Lake Monger. A habit; B₁ sporophyll, a ligule, b labium, wall of sporangium flecked, B₂ thick and thin walled cells of sporangial wall; C₁C₂ megaspores proximal and distal faces; D₁ microspore with crest and thin envelope, D₂ microspore × 50.

structure to megasporangia; microspores immature fawn in mass, mature dark brown, in lateral view 30-36 μm long \times 18-24 μm deep, wall smooth or almost so with outer thin hyaline envelope, crest present variable in depth.

Distribution (Fig. 11): *I. tripus* is endemic to Western Australia where it occurs mainly in the South Western Province north of lat. 33°S and in the Eremean Province near Mongers Lake. A single collection, considered to be a form of *I. tripus*, was made at Pine Hill an isolated locality east of Esperance. The location at the Swan River where Drummond collected the type is not known.

Specimens examined (selection only): Western Australia: 270 mile peg Mullewa-Morawa road; August 1964; G. G. Smith (UWA 376).—Petruador Rock, east of Pithara; 23.v.i.1971; N. Marchant 71/310 (PERTH*).—Toodyay road, between Toodyay and Clackline; October 1964; G. G. Smith (UWA 454).—Mundaring-Beraking road; 17.ix.1962; G. G. Smith (UWA 331).—11 km north of Tinkurrin; 10.xi.1960; G. G. Smith (UWA 482).—Pine Hill, 57.6 km north-west of Israelite Bay; 15.ix.1971; N. Marchant 71/437 (PERTH*).

Observations: Plants are usually on or near granite outcrops, in shallow rock pools, in adjacent soakage areas with shallow soil or in moss sward on granite. Plants are not submerged and grow and perennate under similar conditions to those described for *I. drummondii*.

In most collections plants were immature. Megaspores were whitish and mature ones, obtained from among the old roots, were dull brown.

Variations occurred in the shape of the ligule, the number and size of the flecks on the sporangial walls and the development of reticulate sculpturing on the megaspores. Ligules were short \pm triangular on the Swan River plants. On some from Mongers Lake and Toodyay (UWA 454) the base was broad and cordate and apex obtuse, on others it was almost reniform. The sporangial wall appeared uniformly brown, and not flecked, in collections from Toodyay (UWA 454), Pine Hill (PERTH) and Goebel's specimen from Perth (M). Complete reticulate sculpturing of the distal faces of the megaspores was rare. Plants were heterosporous. Some plants in a collection made in November at the end of the growing season near Tinkurrin bore only megasporangia.

Plants of this species can be recognized by their fine leaves, firm 3-lobed stock with prominent often horny and slightly upturned abscission caps, dark brown flecks on the sporangial walls and dull brown mature megaspores.

Note on lectotypification: No type was indicated by A. Braun in the first valid publication (1864) of *Isoetes tripus*. In his second paper (1868) he lists "Ad flumen Swan River detexit Drummond 1843 (No. 990)" and the location as "herb. Vindob. et Hook." (= W and K). I have seen both these specimens and designate the W sheet as lectotype and the collection on the K sheet as isolectotype. Both collections are annotated by A. Braun and of equal quality. The W sheet bears *I. tripus* (Drummond 990) only, while on the K sheet is mounted also a collection of *I. drummondii*. Further isolectotypes I saw from P, W and B. A. Braun annotated the B sheet "*Isoetes*

tripus Mihi" and on its label is "Swan River Drummond 1843 No. 990". It bore five packets, three labelled *I. tripus* and two *I. drummondii*, each in A. Braun's handwriting. Collections on the other sheet from W and that from P were not annotated by Braun. The W sheet had "Swan River Drummond 990" on it without date and the P sheet "Nouvelle Hollande occidentale R. des cygnes (Swan River) Drummond 1843" without number. On a second P sheet bearing two plants under Drummond's 989—*I. drummondii*, the right-hand one was found to be *I. tripus*.

I have not seen a specimen collected by Drummond from "Swan River" which was annotated by Durieu as *I. phaeospora*, but it can be safely assumed that it belongs to *Drummond No. 990*, the type collection of *I. tripus*, as this is the only one collected by Drummond with brown megaspores, a feature described by Durieu as diagnostic for his species. As *I. tripus* was almost certainly published early in 1864 and *I. phaeospora* later in the same year, and both names are based on the same collection, I have no hesitation to follow A. Braun in placing the latter as a synonym under *I. tripus*.

Typification of names of Australian *Isoetes* species not known to occur in Western Australia

In the course of this revision of Western Australian species of *Isoetes* a knowledge of the other species of the genus known to occur in Australia had to be gained and the application of their names examined. As no definite holotypes were published, it was indicated to designate lectotypes where appropriate for the names listed below, which were selected from specimens examined, and to publish these here as follows:

I. elatior F. Muell. ex A. Braun, Linnaea 25:722 (1853); Monatsber. K. Akad. Wiss. Berlin 13 Aug 1868:536.—*Typus*: "In Tasmania legit Stuart." (A. Braun 1853); "*I. elatior* Ferd. Müll. in herb. Sonder ... In fluvio South Esk River Tasmaniae 1. Stuart 1849 (No. 461) ..." (A. Braun 1868). From the protologue with the emendation of 1868 it is reasonable to designate the relevant specimen at MEL (sheet No. 1002781) as lectotype of *I. elatior*; the duplicate material at B is to be regarded as an isolectotype.

I. gunnii A. Braun, Monatsber. K. Akad. Wiss. Berlin 13 Aug 1868:535 (1868).—*Typus*: "*I. Gunnii* A. Br. in herb. Hook. 1866 ... In lacubus montanis Tasmaniae, fundum longe lateque obducens. R. Gunn 1841 (No. 1563) ... Die ... Exemplare sind aus dem Lake St Clair." From this protologue it is evident that the relevant specimen at K (herb. Hooker) is to be regarded as the holotype of *I. gunnii*.

I. hookeri A. Braun, Monatsber. K. Akad. Wiss. Berlin 13 Aug 1868:538 (1868), *nom. illeg.*—Because *I. humilior* F. Muell. ex A. Braun (1853) is quoted as a synonym and its type not excluded, and it thus is the type of both names, *I. hookeri* A. Braun is illegitimate. For typification see under *I. humilior*.

I. humilior F. Muell. ex A. Braun, Linnaea 25:722 (1853).—*Typus*: "In fluvio South Esk River Tasmaniae, Aprili 1849, legit Stuart." A. Braun

(1868) changed the name for this species to *I. hookeri* stating that F. Mueller included (in sched.) two species under the name *I. humilior* (v.z. *I. hookeri* and *I. stuartii*). A. Braun then quoted for *I. hookeri*, to which he referred *I. humilior* as a synonym, "*I. Hookeri*. A.Br. in herb.Melbourn. 1866 *Stuart 1849 (no. 579)*". From this emended protologue it is reasonable to designate MEL 1002782 as the lectotype of *I. humilior*. It is automatically the lectotype of the illegitimate name *I. hookeri* although this name does not appear in A. Braun's handwriting on the MEL sheet. A. Braun annotated a fragment of the same collection in B with the name *I. hookeri*.

I. stuartii A. Braun, Monatsber.K.Akad.Wiss. Berlin 13 Aug 1868:539(1868).—*Typus*: "*I. Stuarti*. A.Br. in herb.Melbourn. 1866 In fluvio South Esk River Tasmania inter precedentes [*I. elatior* and *I. hookeri* Ξ *I. humilior*] *I. Stuarti*." A. Braun (1868) says that he has seen only one specimen of this species which belongs to the Melbourne Herbarium. Accordingly the relevant sheet at MEL (no. 1002783) must be regarded as the holotype of *I. stuartii* A. Braun; an isotype is in B.

I. tasmanica F. Muell. ex Durieu, Bull.Soc.bot. France 11:104(1864), *nom. illeg.*—Durieu (1864) had examined specimens from Tasmania collected by W. Archer and R. Gunn and concluded that "*Is. elatior et humilior sont spécifiquement identiques*". He united the two species described by A. Braun (1853) under the name *I. tasmanica* which he attributed to F. Mueller. Therefore, the name is illegitimate under the International Code of Botanical Nomenclature and a lectotypification is unnecessary.

Acknowledgments.—The author is grateful to Dr Hj.Eichler, Keeper, State Herbarium of South Australia (AD), and his staff for providing working space and facilities, including the arrangements for loans from other institutions, to carry out this study in her retirement from the Department of Botany, University of Western Australia. She is particularly grateful for stimulating and encouraging discussions during the course of this work and valuable advice on typification and other nomenclatorial matters. To the following institutions she is indebted for the loan of specimens including types: AD, ADW, B, CHR, K, M, MEL, MO, NY, OXF, P, PERTH, SYD, US, UWA, W and WELT. Special thanks are due to Alex S. George (PERTH), Kevin F. Kenneally (UWA) and Gordon G. Smith (UWA) for their efforts to collect fresh material and specimens preserved in formalin or FAA. Mrs M. L. Szent-Ivany illustrated this paper with line drawings and maps; her contribution is thankfully acknowledged. Photographs of habitats were provided by A. S. George and K. F. Kenneally. Gratitude is expressed to the CSIRO Science and Industry Endowment Fund for providing a stereomicroscope and financial support mainly towards the illustrations.

Editorial Note.—The largest part of the manuscript had been written up by hand by Mrs Johnson when she died on 11 August 1972, including the abstract, introduction, keys to the species, texts to most of the species, and the bibliographic references. Those parts missing (i.e. on *Isoetes caroli*, *I. inflata*, the Latin diagnoses of the new species, and the note on typification of the names of some other Australian species) were compiled by Hj.Eichler from the description of individual specimens Mrs Johnson left in her card index and other scattered handwritten notes. He attempted to conform with the style of presentation used by Mrs Johnson in the parts of the manuscript she had completed and prepared the paper for publication.

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Royal Society Medallist, 1983

J. S. P. Beard

John Stanley Percy Beard M.A. B.Sc., D. Phil. (Oxon.) Educated Marlborough College, Wiltshire, and Pembroke College, Oxford. Forest Service West Indies 1937-1947. Research Officer Natal Tanning Extract Co. Ltd 1947-1961. Director Kings Park and Botanic Garden 1961-1970. Director and Chief Botanist Royal Botanic Gardens and National Herbarium, New South Wales, 1970-1972. Consultant Ecologist—*hodie*.

Shortly after taking up residence in Western Australia Dr. John Beard commenced the analysis of the State's vegetation leading to its classification and eventual mapping, the Vegetation Survey of Western Australia being established in association with Prof. M. J. Webb in 1964. Fifteen years later when Western Australia celebrated its 150th Anniversary the survey, analysis, classification and mapping had been completed. The whole State was covered in seven sheets at scale of 1:1 000 000 and in a single map

at 1:10 000 000. The South West was covered in greater detail by 27 sheets at the scale of 1:250 000. This was achieved through a prodigious programme of fieldwork often over difficult terrain and under rigorous conditions. The subsequent analyses, research, mapping and preparation of the explanatory memoirs accompanying each sheet represent an outstanding contribution by one author.

Dr. Beard derived a new Phytogeographic Map of Western Australia from the vegetation maps. The Phytogeographic Map, available at scales of 1:1 000 000; 1:2 500 000 and approximately 1:10 000 000, being based on natural vegetation is an integration of climatic, geological, edaphic, historic and floristic components. It is a valuable synthesis leading to new understanding of the evolution of the unique flora of Western Australia and a significant contribution to land use planning and management in the State.

Obituary

Kenneth C. C. Tiller 1900-1983, B.A. (Hons.)
U.W.A.; M.A. (Cantab.).

Ken ("KC") Tiller entered Teacher Training College in February, 1919 and, on graduation, took up his first appointment as Head Teacher at Dale Hall, near Beverley. After several other appointments he was a teacher at the Newcastle Street Junior Technical School and then went to Kurrawang and Lakewood Schools, both in the Kalgoorlie area.

After studying in Britain, he was appointed as Lecturer in Geology and Geography at the Perth Technical College (P.T.C.), where he remained until his retirement in 1966. During this time he was also guest lecturer in the Geology and Geography departments at U.W.A. He was also involved in setting up the Applied Geology course in what later became W.A.I.T.

My personal acquaintance with Ken Tiller goes back to 1941 when I was both his student and laboratory assistant. In the late 1960s I became his successor at P.T.C.

At P.T.C., he was the last of a legendary trio of geology lecturers. Messrs. Spencer-Compton, Cecil and Tiller ran geology and mining related courses at a time when P.T.C. had strong links with the Kalgoorlie School of Mines and started many students in mining based careers. He also lectured in geography and may have regarded himself more of a geographer than geologist.

The comment on his record when leaving training colleges was, in part, "... a very earnest and conscientious man..." and this perceptive comment accurately summed up "KC" as a lecturer. His teaching material was meticulously prepared, illustrated with lucid diagrams, and presented in an anecdotal manner that reinforced the learning process. As a lecturer, he was an acknowledged master of the art and outstanding even in the first class P.T.C. staff of the time.

But, most of all, he was able to enthuse his students with the joy of learning and mastering the subject, the feeling that students not doing the subject were somehow lesser mortals. To a young teacher he was a model to follow and the writer learnt much from his example and freely given advice.

Since Ken retired, the writer has met many of his ex-students who proudly proclaimed that they did geology with "KC", how they enjoyed the subject, and, as a lecturer, how easy "KC" made the subject appear.

Surely, there is no better epitaph for a teacher than to be remembered with such affection by his ex-students; including the writer.

W. J. L.

INSTRUCTIONS TO AUTHORS

Contributions to this Journal should be sent to *The Honorary Editor, Royal Society of Western Australia, Western Australian Museum, Francis Street, Perth, Western Australia 6000*. Publication in the Society's Journal is available to all categories of members and to non-members residing outside Western Australia. Where all authors of a paper live in Western Australia at least one author must be a member of the Society. Papers by non-members living outside the State must be communicated through an Ordinary or an Honorary Member. Council decides whether any contribution will be accepted for publication. All papers accepted must be read either in full or in abstract or be tabled at an ordinary meeting before publication.

Papers should be accompanied by a table of contents, on a separate sheet, showing clearly the status of all headings; this will not necessarily be published. Authors should maintain a proper balance between length and substance, and papers longer than 10 000 words would need to be of exceptional importance to be considered for publication. The Abstract (which will probably be read more than any other part of the paper) should not be an expanded title, but should include the main substance of the paper in a condensed form.

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Contents

	Page
Observations on regeneration after fire in the Yule Brook Reserve near Perth, Western Australia. By A. M. Baird	1
Basins and barrels: the geological background to the search for fossil fuels in Western Australia. Presidential address—1983. By A. E. Cockbain	14
Chromosome numbers in Western Australia plants, II. By G. J. Keighery	26
Taxonomic revision of <i>Isoetes</i> L. in Western Australia. By E. R. L. Johnson	28
Royal Society Medallist, 1983: J. S. P. Beard	44
Obituary: Kenneth C. C. Tiller	44

Editor: B. Dell

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The flora and vegetation of Mt Lesueur, Western Australia

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Abstract

This paper details the results of a comprehensive survey of Mt. Lesueur, an important botanical locality in south-western Australia. Both the laterite cap of the mesa and the steep slopes support the complex kwongan (sclerophyllous shrub) vegetation which typifies much of this region. The total of 287 vascular plant species encountered in an area of less than 0.5 km² suggests exceptional richness for this site. Almost 25% of species were either rare, had restricted distributions, or were at the northern limits of generally more mesic distributions. Some of these species were only found in the most favourable sites on the hill. These patterns suggest a refugial role for Mt. Lesueur and may imply a particular sequence of climatic events during the Holocene. A number of species which frequently occur on lateritic uplands in the region were either absent from, or rare on, the top of Mt. Lesueur. One possible explanation for these anomalous distributions is that the habitat already has a stable complement of species.

Introduction

Mt. Lesueur, a laterite capped mesa situated in a deeply dissected part of the northern kwongan or sandplain region of Western Australia, has long been considered a site of special botanical significance. It has been recognised as being central to a node of high angiosperm species richness, particularly of the Proteaceae (Speck 1958, George *et al.* 1979) and as having populations of a number of rare or geographically-restricted species (Gardner 1947, CTRC 1975). Further, the hill and nearby areas are thought to support northern outlying populations of species with more generally southern distributions (CTRC 1975).

The first collection of plants from Mt. Lesueur was made by James Drummond in *c.* 1851. His glowing reports of the area and mention of new, unusual species from there encouraged C. A. Gardner to attempt, during the period 1931-1946, to retrace Drummond's steps, and to recollect the species. This he accomplished with some success. Gardner also discovered two new species on Mt. Lesueur and subsequently published a note extolling the botanical values of the area (Gardner 1947). The vegetation was first described in detail by Speck (1958) who also enumerated 88 species for the hill top. The area has received little detailed botanical attention since that time: the recommendations for the inclusion of Mt. Lesueur in a conservation reserve (CTRC 1975) were justified on the basis of existing lore. The implementation of these recommendations was delayed because some major land-use conflicts were subsequently identified. It seemed appropriate, therefore, to further document the botanical features of the area to assist with resolution of these conflicts.

In addition to describing the flora and vegetation of the hill itself, we have attempted to provide a context for these results through the study of much of the surrounding area. The particular combination of topographic and geological features around Mt. Lesueur has, in fact, provided a unique opportunity for the study of an array of features of complex kwongan vegetation. The results of these studies will be detailed in a series of publications. This first

paper provides an account of the flora and vegetation of the plateau top and the slopes of Mt. Lesueur. Subsequent papers will report on matters such as regional variation in floristic composition, patterns of diversity, and influence of soils, geology and aspect on floristic patterns.

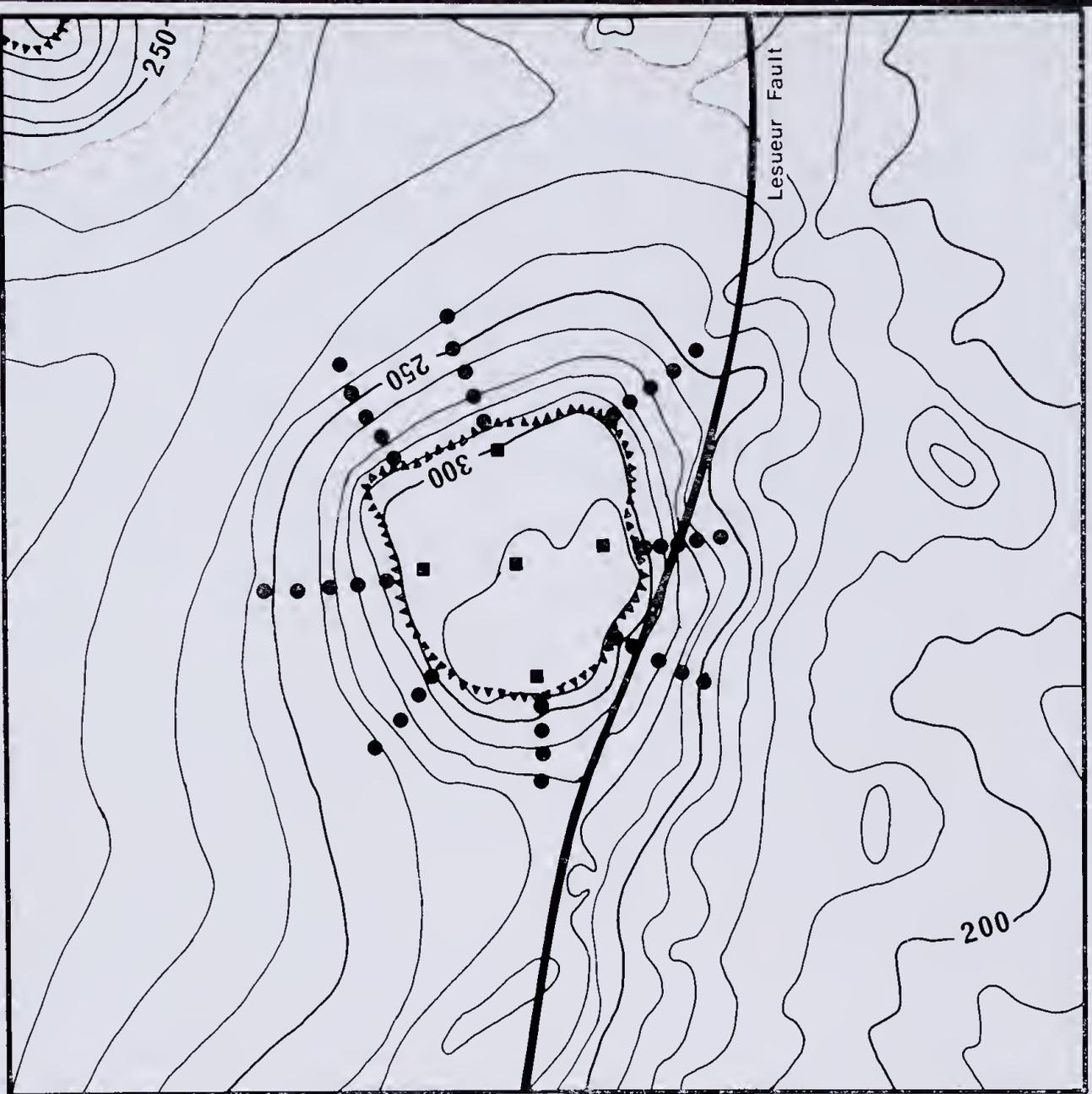
The Study Area

Mt. Lesueur (30°11'S, 115°12'E) is about 22 km NE of Jurien and about 115 km N of Perth (Fig. 1). It is within a small reserve for Educational Purposes (Class C Reserve No. 24275) which is itself set within a larger reserve for Horse Breeding (C 15018). The whole area supports indigenous vegetation; limited horse-grazing in the past has apparently exerted a relatively minor influence.

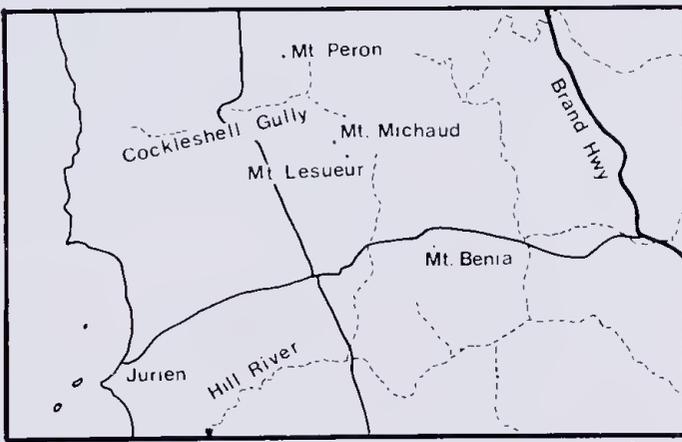
Physiography and Soils

In the setting of the generally subdued topography which characterises much of south-western Australia, Mt Lesueur is a prominent landscape feature. It was named by the early French navigator Hamelin as he sailed up the coast in 1801 and now has a trigonometric station (313 m) near its southern edge. However, it barely exceeds the height of the surrounding uplands; its visual prominence is largely attributable to its mesa form which has resulted from the dissection of a near-horizontal Tertiary landscape and its separation from the surrounding uplands by valleys over 100 m deep.

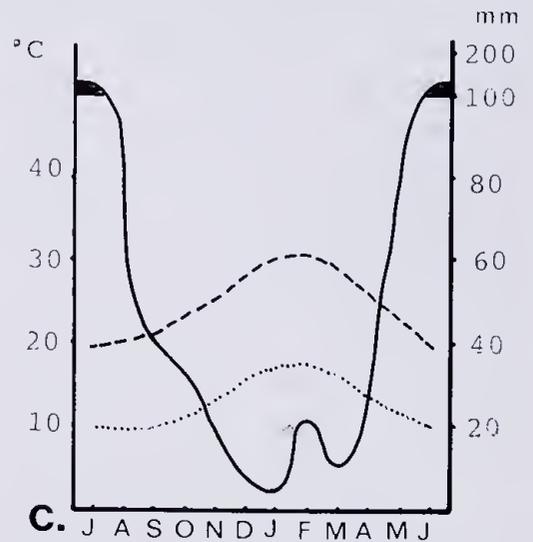
The study area is in the northern part of the Perth Sedimentary Basin. The N-S trending Lesueur Fault on the eastern slopes of Mt Lesueur separates the Triassic Lesueur Sandstone (in the west) from the Jurassic Cockleshell Gully Formation (sandstone, siltstone and shale) (in the east) (Lowry 1974, Playford *et al.* 1979). Deflation during the period of tectonic stability which followed the lower Cretaceous phase of block faulting permitted the development of a gently undulating landscape. A lateritic soil profile developed from the mid-Tertiary onwards. This landscape was dissected by a series of E-W drainage lines which have subsequently been disrupted (interpreted from unpublished maps, W.A. Dept. of Lands and



a.



b.



c. J A S O N D J F M A M J

Figure 1.—Physical features of the study area:

- a) topographic map compiled from W.A. Department of Lands and Surveys unpublished maps showing sample quadrats (■) and slope relevés (•) and the Lesueur Fault. The approximate limits of the plateau are also indicated;
- b) location map of Mt Lesueur in relation to the town of Jurien (c. 200 km N of Perth) and major roads, drainage lines and other hills; and
- c) ombrothermic diagram for Jurien (unpublished data for 1968-1981 from the Bureau of Meteorology).

Surveys). Marine incursions during the Pleistocene involving a maximum relative increase in sea level of about 100 m (Lissiman and Oxenford 1973) have not directly influenced that area of this study.

Present soil patterns generally reflect the landscape stability and general aridity of the period during and since the Pleistocene, which relatively localised deposition of erosional products derived from the old, deep, lateritic soil profile. However, no detailed soil mapping or pedogenetic studies have been conducted in the study area. The following description of Mt Lesueur is based on our own observations and some generalizations extrapolated from a site *c.* 50 km to the south east which has been described by Churchward (1970).

The plateau top of Mt Lesueur is a *c.* 10 ha remnant of the upper part of the lateritic soil profile developed from the Lesueur Sandstone. The typical, massive, duricrust (cemented laterite) which covers most of the top is the result of exposure and subsequent hardening of a ferruginous B soil horizon after removal of the sandy A horizon. Minor subsidence of the duricrust layer is suggested by its roughened and broken nature. Only a few, small, shallow pockets of grey sand are present although this sand is also in cracks in the duricrust. In some areas the sand has a well developed organic layer. What little gravel is present appears to be mainly angular fragments of duricrust rather than discrete pisolites.

At the margins of the plateau, the duricrust is generally broken into large boulders of up to 0.5-1 m diameter. Very little sand occurs. On the north-eastern part of the rim there is a small quantity of coarse, pisolitic gravel.

The slopes of Mt Lesueur are steep ranging from about 30° close to the plateau to about 5° at the foot of the hill, with most of the mid-slope region being in the order of 20°. The duricrust rim provides an occasional vertical drop of up to 3 m. At the foot of the southern, western and northern slopes there is an accumulation of erosional material. The eastern slopes are generally more steep (to 45° in the upper slope) perhaps reflecting the proximity of the Lesueur fault.

The soils generally reflect the steepness and probably the relative stability of the slopes. There is little soil present on the upper portions of the eastern slopes: these surfaces are mainly weathered Lesueur Sandstone which is pale grey, coarse grained and highly siliceous. The southern, western and northern slopes have shallow soils composed of grey sand and gravel with some clay material present. The gravel is most abundant on the mid slopes whereas sand predominates at the foot. Duricrust boulders up to 1 m in diameter litter the upper third of the slopes. Generally the southern and western slopes have more duricrust boulders than the northern slopes where pisolitic gravel is more abundant. As a consequence of this, the northern slopes have a smoother surface than those of the southern and western aspects.

The Lesueur fault is evidenced about half way down the eastern slope by outcroppings of a ferruginous, partially metamorphosed sandstone accompanied by changes in soil type. Small near-vertical cliffs up to 3 m high occur along the faultline and

boulders up to 20 m diameter are also present immediately downslope from it. Shallow grey sands and gravel occur on the steeper slopes above the fault zone, whereas below it there are deeper, red-brown sandy-clay soils often with substantial amounts of gravel.

Climate

No detailed climatic information is available for the immediate vicinity of Mt Lesueur: the closest weather station is at Jurien (14 years records). The area experiences a Thermomediterranean accentuated climate (UNESCO—FAO 1963) with interpolated values of average annual rainfall, mean summer temperature and potential evaporation (from Bureau of Meteorology 1968) being 625 mm, 23°C and 1770 mm respectively. The ombrothermic diagram for Jurien is given in Fig. 2. Winds in mid-summer are predominantly dry and easterly with some afternoon sea breezes (from the SW) where as mid-winter winds are moisture bearing and westerly (N-SW). Estimates of solar radiation for 20° slopes at the latitude of Mt Lesueur show that N-facing slopes receive approximately twice that of S-facing slopes in mid winter but values for mid-summer differ only slightly (G. Roy pers. comm. 1982, see also Roy and Miller 1980). Other effects of landscape on local climate patterns are unknown.

Fire history

The last known fire around Mt Lesueur occurred in March 1967 (J. Grigson pers. comm. 1982). There is no obvious indication on the 1969 aerial photos that this fire missed our study area although there may be remnants of older vegetation in the valleys to the east of Mt Lesueur. The two extensive fires in areas of native vegetation to the NE and NW of Mt Lesueur in early 1983 were both brought under control outside our study area. The major wildfire of January 1984 was confined to the coastal areas of the proposed nature reserve.

Previous descriptions of the vegetation

In his early delineation of vegetation and phytogeographic units in the west-coastal of the South-West Botanical Province, Speck (1958) included Mt Lesueur within his Lesueur Vegetation System, a sub-unit of his Lesueur Botanical District. He described the vegetation as lateritic heath on the lateritic plateau area; sandplain heath, mallee heath and sandplain scrub heath on the sandy lateritic soils of the hill slopes; and low scrub forest and woodlands on the deeper sands, clays and clay loams in the valley bottoms. These vegetation and phytogeographic units were subsequently revised by Beard (1979, 1980) who took two hilly areas (the Gairdner Range, including Mt Lesueur, and the Herschel Range) out of the Lesueur System and placed them in a separate unit, the Gairdner Vegetation System. This distinction was based on the importance of eucalypt woodlands in the valleys of these hilly areas; the uplands of Beard's (1979) Gairdner and Lesueur Systems both support similar heath and scrub-heath vegetation. These two Vegetation Systems represent the southern-most part of the Irwin Botanical District as redefined by Beard (1980).

Methods

Detailed sampling of the Mt Lesueur-Cockleshell Gully area was conducted between July and November 1979. This involved sampling the vegetation on numerous lateritic upland areas, as well as some pediment slopes below escarpments (breakaways) and the recent, rejuvenated valleys. Although this paper only presents results from the Mt Lesueur sites, sampling techniques consistent with those outlined in detail here have been used throughout.

Five 10 m x 10 m quadrats were located on the top of Mt Lesueur: one in the approximate centre of the plateau and one each to the north, east, south and west near to the edge. These four cardinal quadrats were centred a minimum of 20 m from the plateau edge to avoid some obvious effects of the edges on species composition. Cover-abundance values (Domin Krajinna scale, Mueller-Dombois and Ellenberg 1974, p. 62) were recorded for each vascular plant species present in each quadrat. The remainder of the plateau was searched thoroughly for species other than those found in the quadrats. Species found only on the rim (within 5 m of the edge of the plateau) were noted separately.

The slopes were sampled along 8 transects running N, NE, E, SE, S, SW, W and NW from the approximate centre of the plateau (Fig. 1). Use of quadrats was impracticable on the steep slopes so we recorded species present in subjectively defined relevés of about 200 m², centred at 50 m intervals from the rim down the slope, commencing 15 m below the rim. A total of 38 relevés were sampled: 5 along each transect except those of the S and SW slopes where the deep, valley sands were encountered after 4 relevés.

Studies of species-area relationships in kwongan vegetation (George *et al.* 1979) and specifically at this site (our unpublished data) indicated that the difference in species richness due to differences in areas between the quadrats and the relevés is of the order of 3-5% of the total species present at a site. Thus for the purposes of this study we consider these plateau quadrat and slope relevé samples to be comparable.

Observations on soils were recorded at all sites: these have provided the basis for the comprehensive site description already given. Also noted were vegetation structure (according to Specht in Aplin 1979), percentage bare ground and growth habits of species.

Plant specimens were determined at the Western Australian Herbarium (PERTH) where voucher specimens labelled "EAG Latrite Survey 1978/79" are now lodged. Unnamed species are referred to in the text by collector and collection number (e.g. EAG 2575). Aerial photographs from the W.A. Department of Lands and Survycys (1969) were examined for soils—vegetation unit interpretation as well as for the fire history details already given.

In order to compare our list of species with that of Speck (1958), it was necessary to refer back to Speck's original specimens. A thorough search was made of collections in the herbarium of the

Botany Department, University of Western Australia. Where original specimens could be located, these were redetermined in the light of present day taxonomic knowledge. For names used by Speck but not represented by a specimen, appropriate species' distributions were checked at the Western Australian Herbarium. If it was found that Mt Lesueur was within the known distribution of a species reported by Speck (1958), then that species name was accepted. If Mt Lesueur could not be considered to reasonably fit the known distribution of a species reported, even acknowledging the possibility of a disjunction, then a species known to occur in the area with which it might have been confused was proposed.

Results

Floristics.

A total of 287 vascular plant species were found on Mt. Lesueur; these are listed with summaries of occurrence in Appendix I. These species represented 43 families and 131 genera and included 3 indeterminate species and 20 apparently undescribed taxa. Seventy-eight genera and 15 families were represented by only one species each. The four families with the greatest numbers of species recorded, Proteaceae (46 spp.), Leguminosae (39 spp.), Myrtaceae (33 spp.) and Liliaceae (20 spp.) together accounted for almost half the species. Nine genera had 6 or more species present: *Hakea* (15), *Acacia* (12), *Stylidium* (10), *Eucalyptus* (9), *Daviesia* (7), *Hibbertia* (7), *Conostylis* (6), *Petrophile* and *Thysanotus* (6).

The distribution of these plant species was not uniform over the mesa: 14 species were found only on the plateau top well away from the rim, 14 were confined to the rim and 123 species were confined to the slopes (Table 1). Thus there were clear floristic differences between the plateau top and the slopes and this will be developed in a subsequent paper. The rim appeared to be a transition zone between the two habitats but had greater floristic affinities with the slopes than with the remaining plateau area. It was common for species that were abundant on the slopes to have a

Table 1.

Numbers of species occurring on and around Mt Lesueur.

Locality	No.	% of Total
Total species on Mt Lesueur	287	100
Species recorded on plateau* quadrats	109	38.1
Species occurring on plateau top	137	47.7
Species only on plateau top	14	5.0
Species occurring on hill slopes plus rim	273	95.1
Species only on hill slopes plus rim	150	52.6
Species only on hill slopes	123	43.0
Species only on rim	14	5.0
Species in common with other lateritic uplands of the region†	242	84.6
Species in common with other lateritic uplands but not on plateau top (i.e. only on slopes and rim)	109	38.1

* rim excluded from the plateau top.

† Griffin and Hopkins unpublished data.

few individuals on the rim. Structurally, however, the vegetation of the rim differed little from the plateau top, with much of the area being dominated by *Dryandra sessilis*.

Reconciliation with earlier collections.

N. H. Speck (1948) had previously listed 88 plant species for the top of Mt. Lesueur. We investigated this collection in detail; the results are detailed in Appendix II, copies of which are lodged with the Editor and the Librarian, Western Australian Herbarium. In summary, we consider that 23 of Speck's names are now incorrect and we have provided alternatives. Sixty of the 86 species were also found by us to occur on the plateau top. A further two of the species were found on the rim. We recorded 12 more on the slopes. We did not locate specimens of the remaining 12 species on Mt. Lesueur. In fact, for three of the species, *Conospermum densiflorum*, *Dryandra earlinoides* and *Grevillea rudis*, we have not found populations within 2 km of Mt. Lesueur, despite extensive searches. For a further three species (*Conospermum erassinervium*, *Daviesia quadrilatera* and *Lechenaultia hirsuta*) we have not found any populations associated with lateritic soils in the Mt. Lesueur-Cockleshell Gully area.

Rare and geographically restricted species.

Nine species occurring on Mt Lesueur have been reported as being rare (Table 2). Three of these (*Banksia tricuspis*, *Hakea megalosperma* and *Urocarpus phebaloides*) have been gazetted rare under the provisions of the Wildlife Conservation Act 1950-1979 (Rye and Hopper 1981).

Table 2.

Geographically restricted and rare species (presently named species only) found on Mt Lesueur. Data are from (1) CTCRC 1975, (2) Griffin (unpublished data), (3) Marchant and Keighery (1979), (4) Rye (1982) and (5) Rye and Hopper (1981).

Species	Geographic Range (km) (1, 4)	Species reported as being rare and source of classification
<i>Acacia epacantha</i>	<150	
<i>Acacia retrorsa</i>	<50	2, 3
<i>Banksia grossa</i>	<150	
<i>Banksia micrantha</i>	<150	
<i>Banksia tricuspis</i>	<50	1, 2, 3, 5
<i>Casuarina grevilleoides</i>	<150	
<i>Comesperma acerosum</i>	<150	
<i>Conospermum nervosum</i>	<150	
<i>Conostylis crassinervia</i>	<150	
<i>Darwinia helichrysoidea</i>	<50	1
<i>Darwinia neildiana</i>	<150	
<i>Darwinia sanguinea</i>	<150	
<i>Dryandra sclerophylla</i>	<150	
<i>Gasrolobium bidens</i>	<150	
<i>Hakea flabellifolia</i>	<150	
<i>Urocarpus megalosperma</i>	<50	1, 2, 3, 5
<i>Urocarpus neurophylla</i>	<50	1, 2
<i>Isopogon plumuliflorus</i>	<50	1
<i>Petrophile chrysantha</i>	<150	
<i>Petrophile inconspicua</i>	<150	
<i>Tetratheca remota</i> *	<50	2
<i>Urocarpus phebaloides</i>	<50	2, 5
<i>Xanthosia tomentosa</i>	<50	1

* Species reported for Mt Lesueur by Thompson (1976) but not found in the present study.

Twenty-three of the species found on Mt Lesueur have known population ranges of less than 150 km; of these, all 9 species already listed as rare have known ranges of < 50 km (Table 2) (Griffin, unpublished data). In addition, most of the 20 undescribed species (see Appendix I) are probably geographically restricted.

None of the restricted or rare species occurs only on Mt Lesueur. *Banksia tricuspis* occurs on the top and slopes of Mt Lesueur and other hills in the Gairdner Range. *Hakea megalosperma* occurs on the top of some lateritic uplands near and including Mt Lesueur. *Hakea neurophylla* is mainly on some of the breakaway slopes in the Mt Lesueur-Cockleshell Gully area. *Urocarpus phebaloides* is known only a few breakaway slopes in the same area. *Tetratheca remota* is known from the Type specimen from Mt Lesueur, three other collections by Drummond for which no precise localities were given (Thompson 1976) and one more recent collection from just east of Mt Lesueur (R. J. Hnatiuk pers. comm. 1982). *Acacia retrorsa* occurs on some slopes and clay soils of the Cockleshell Gully area.

The 23 restricted, named species include both recently derived species (with close relatives nearby, e.g. *Acacia epacantha*, *Banksia grossa*, *B. micrantha*, *Darwinia helichrysoidea*, *D. neildiana*, *Hakea auriculata* var. *spathulata*, *Petrophile chrysantha*, *Styidium pyenostaehyum*) and species which may be described as probably relictual, having no close taxonomic relatives in the area (e.g. *Darwinia sanguinea*, *Hakea marginata*, *H. megalosperma*, *H. neurophylla*, *Isopogon sphaerocephalus*, *I. linearis*) (G. J. Keighery, B. B. Lamont, B. R. Maslin pers. comm. 1982, Hopper 1983). There are no restricted monospecific genera on Mt Lesueur. Of the 20 undescribed species, all but one belong to genera represented by other species on Mt Lesueur.

Species with outlying populations

Twenty-six of the species found in this survey have distributions for which Mt Lesueur represents an outlying or extreme northern occurrence (Table 3). *Acacia teretifolia*, *Billardiera coeruleso-punctata*, *Boronia crassifolia*, *Isopogon sphaerocephalus*, *Styidium carnosum* and *Thysanotus anceps* are examples of species with their main populations no closer than 150 km to the south. Species at the northern limits of more continuous distributions include *Anarthria graeilis*, *Chorizema ilicifolium*, *Eucalyptus ealophylla*, *E. marginata*, *Isopogon asper*, *Kingia australis*, *Patersonia serieea* var. *rudis* and *Trymalium floribundum*. Some of these continuously distributed species may actually have disjunctions near their range limits which are not revealed by the sparse herbarium data. *Eucalyptus marginata*, for example, has a probable gap in its distribution of c. 120 km between Mt Lesueur and the next population to the south (Lange 1960, Churchill 1968, Hopkins *et al.* 1983). This species is confined to the plateau top and the south-facing slopes of the mesa; both these sites are likely to have most favourable moisture balances when compared with other sites in the study area.

Species absent from the plateau top.

A number of species which were often found on the laterite of uplands in the Mt Lesueur area were not found on the lateritic plateau of Mt Lesueur itself. We therefore compared the species list for Mt Lesueur with that resulting from a survey of nearby lateritic uplands (our unpublished data) and another survey of lateritic uplands from Jurien to Three Springs (Griffin *et al.*, 1983). The results of this comparison are reported in columns L and M of Appendix I. Some 85% (242 species) of the total Mt Lesueur flora had been found on lateritic uplands in the Mt Lesueur-Cockleshell Gully area. Of these, 109 species occurred on the slopes but not in the seemingly equivalent lateritic habitat on the top of Mt

Table 3.

Species at the limit of geographic range or with apparently disjunct distributions.

Species	Nearest Collections
<i>Acacia obovata</i>	Perth Metropolitan Area
<i>Acacia teretifolia</i>	Perth M.A.
<i>Anarthria gracilis</i>	Hill River
<i>Astroloma ciliatum</i>	Gingin
<i>Billardiera coeruleso-punctata</i>	Perth M.A.
<i>Boronia crassifolia</i>	Tutanning Nature Reserve
<i>Chorizema ilicifolium</i>	Regans Ford
<i>Eucalyptus calophylla</i>	Northern limit
<i>Eucalyptus marginata</i>	Northern limit
<i>Eucalyptus wandoo</i> *	Northern limit
<i>Gastrolobium ilicifolium</i>	Mogumber
<i>Grevillea synapheae</i>	Northern limit
<i>Hakea auriculata</i> var. <i>sphatululata</i>	Northern limit
<i>Hakea marginata</i>	New Norcia
<i>Hibbertia montana</i>	Bindoon
<i>Isopogon asper</i>	Cataby
<i>Isopogon sphaerocephalus</i>	Perth M.A.
<i>Kingia australis</i>	Northern limit
<i>Lasiopetalum floribundum</i>	Perth M.A.
<i>Lepidosperma viscidum</i>	Wheatbelt
<i>Patersonia sericea</i> var. <i>rudis</i>	Wannamal
<i>Prasophyllum parvifolium</i>	Northern limit
<i>Pultenaea ericifolia</i>	Perth M.A.
<i>Stylidium carnosum</i>	Perth M.A.
<i>Stylidium pycnostachyum</i>	Perth M.A.
<i>Thysanotus anceps</i>	Perth M.A.

* One further species, *Eucalyptus haematocylon*, has recently been collected nearby. This species is generally confined to the wetter, forested region well to the south.

Lesueur. These included *Anhipogon strictus*, *Caustis dioica*, *Daviesia decurrens*, *D. pedunculata*, *D. preissii*, *Hakea auriculata*, *H. stenocarpa*, *Pileanthus filifolius* and *Synaphea polymorpha*. A number of other species that were characteristic of lateritic uplands in the area were very poorly represented on the top of Mt Lesueur. For example, we found only a few individuals of each of *Allocasuarina humilis* and *Eremaea violaceae* on the plateau.

The Vegetation of the Plateau top and rim

The vegetation of the upland area of Mt Lesueur is composed of three distinct strata, of which only the third (and lowest) was continuous over the plateau top:

(i) A tall shrub stratum composed principally of *Banksia tricuspis* to 3.5 m tall with occasional *Nuytsia floribunda* (to 4 m). Formations with tall shrubs present (high shrublands to high open-shrublands) covered about 25% of the surface of the plateau.

(ii) A shrub stratum (1-2 m tall) was present over about 30% of the surface. This stratum was dominated by *Dryandra sessilis* with occasional *Hakea trifurcata* and *H. undulata*, but mallec-form *Eucalyptus marginata*, *E. sp.* (EAG 2575) and *E. sp.* (S. D. Hopper 2231) also occurred in patches on the more gravelly soils of the north-east. *Dryandra sessilis* dominated formations (open to closed heath) were most common in areas where the surface was rough, with abundant broken duricrust present. These situations were most prevalent on the northern and north-western portions of the plateau and around much of the rim.

(iii) A low shrub stratum (< 1 m tall) was the most important and abundant stratum: it occurred under all other strata and was of diminished importance only where *D. sessilis* formed a closed-heath. The relatively closed low shrub canopy was rather uneven in height, ranging from 30 to 90 cm tall. This stratum was rich in angiosperm species, particularly woody perennial shrub species, but with a number of sedges and restiads (e.g. *Mesomelaena tetragona*, *Restio sphacelatus*, *Tetraria octandra*) and geophytes (e.g. *Drosera macrantha*, *Elythralthera brunonis*, *Thysanotus thyrsoideus*) present. Only one therophyte species (*Hypochoeris glabra*) was located on the top, but a further three species (*Dauthonia caespitosa*, *Trachymeue pilosa*, *Waitsia paniculata*) were common in the cracks of the rim zone. The larger of the low shrubs were usually 50-90 cm tall but occasionally exceeded 1 m. Larger shrub spec.cs included *Calothamnus sanguineus*, *Daviesia* sp. aff. *striata* (EAG 1822), *D. longifolia*, *Dryandra armata*, *Hakea megalosperma* and *Lambertia multiflora*. The arborescent monocots, *Kingia australis* and *Xanthorrhoea reflexa*, were conspicuous in this low shrub layer, frequently emerged from it and reached 1.5 m in height. Amongst the more abundant low shrubs and herbs (20-25 cm tall) were *Actinostrobilus acuminatus*, *Astroloma* sp. (EAG 1022), *Banksia micrantha*, *Conothamnus triuervis*, *Darwinia helichrysoides*, *Dryandra uivea*, *Grevillea synapheae*, *Hakea conchifolia*, *H. incrassata*, *Hibbertia acerosa*, *Hypocalymma xanthopetalum*, *Isopogon asper*, *Lysiuema ciliatum*, *Macropidia fuliginosa*, *Melaleuca* sp. aff. *megacephala* (EAG 2359), *Petrophile striata*, *Sphaerolobium macranthum* and *Synaphea petiolaris*. Few species dominated the cover of this low shrub stratum with only *Banksia micrantha*, *Calothamnus sanguineus*, *Dryandra armata*, *Lambertia multiflora* and *Petrophile striata* exceeding 5% within quadrats.

In the occasional small pockets of sand, each of which may occupy up to 0.1 ha, species more common on sandy soils, rather than laterite, were found (e.g. *Adenanthos cygnorum*, *Bossiaea eriocarpa*, *Hakea ruscifolia* and *Lomandra hastilis*).

The vegetation of the slopes

The tall shrub species which were prominent on the plateau top (*Banksia tricuspis* and *Dryandra sessilis*) were much less abundant on the slopes but, apart from this feature the slope vegetation was similar in appearance to that of the plateau. *B. tri-*

cuspis occurred occasionally on the western and southern slopes, mainly at middle to high elevations. *Dryandra sessilis* was abundant in only a few places, mainly on the northern and eastern slopes within 20 m of the top. Dense clumps of multi-stemmed *Eucalyptus uarginata* (less than 2 m tall but up to 15 m crown diameter) were common on the southern slopes. *Xanthorrhoea reflexa* was generally less than 1 m tall on the slopes and therefore not visually dominant whereas *Kingia australia* was commonly >1 m tall and therefore more conspicuous. *Kingia* up to 2.5 m tall were present at the base of the northern slopes.

At the base of the southern, western and northern slopes on sandy soils, *Bauksia attenuata* and *Eucalyptus tottiana* formed high shrublands and low open-woodlands. This vegetation formation was typical of the sandy valleys of this area. The vegetation of the eastern (and steepest) slopes changed in response to change in soil types. In the heavier soils of the lower slopes there were small patches of low woodland to low open-woodland with *Eucalyptus calophylla*, *E. uarginata*, *E. waudoo* and *E. accedens*.

The shrub stratum of the slopes varied in structure from very sparse low open-shrublands on the steeper parts of the eastern slopes to low open-heath on the northern slopes, low open and low closed heath on the southern and western slopes and open and closed heath on part of the eastern slopes. Many of the major shrub species of the plateau were also abundant on the slopes. A notable absence was *Hakea megalosperma* (the Lesueur Hakea). *Banksia uicrantha* was much less abundant on the slopes. However the slopes supported a great number of species which were either absent from, or rare on, the plateau. For example, *Hakea neurophylla* was abundant on the higher north-eastern slopes, *Allocasuarina humilis*, *Daviesia decurrens*, *Eremaea violacea*, *Leucopogon plumiflorus* and *Melaleuca tricophylla* were abundant on the southern, western and northern slopes, and *Gastrolobium spinosum* and *Petrophile chrysantha* were abundant on the lower eastern slopes, but all were poorly represented on the plateau top. *Cryptandra arbutiflora*, *Hakea auriculata* var. *auriculata*, *Labichea punctuata*, *Neuraclne alopecuroidea*, *Petrophile chrysantha* and *Pultenaea ericifolia* were prominent on the slopes but we did not locate any individuals on the plateau top.

Discussion

We have recorded 287 vascular plant species growing on Mt Lesueur. The study site is small, being less than 0.5 km², yet it includes a variety of habitat types. Kwongan, which is the predominant vegetation of the site, is generally regarded as a floristically rich vegetation type when compared with other types around the world (George *et al.* 1979, Lamont *et al.* 1984). But Mt Lesueur seems to be exceptional. By comparison, for example, 429 species were recorded for a site about 100 km north, but that site encompassed an area of 20 km² and included six units of vegetation that could be distinguished on air photos (Hopkins and Hnatiuk

1981). At Tutanning Nature Reserve, 350 km south-east of Mt Lesueur, 11 discrete patches of kwongan on 4 distinct soil types totalling 0.6 km² but dispersed throughout the 20 km² reserve contained 315 species (Brown and Hopkins 1983).

For almost 25% of the species encountered on Mt Lesueur, the locality is of special significance. Some species (the restricted relicts and those with disjunct distributions) have persisted there while populations at a distance have become extinct; another suite of species (the recently derived, restricted species) may have evolved around Mt Lesueur and not migrated to any extent. For the persistent species, the Mt Lesueur area is a refugium (cf. George *et al.* 1979, Hopkins *et al.* 1983). The evidence suggests that climatic factors/moisture balance are more favourable in this area than in adjacent areas since the general soil types of the mesa are widely distributed elsewhere in south-western Australia (Northcote *et al.* 1967, Churchward 1970, Mulcahy 1973, Lowry 1974). Further, many of the species now showing disjunctions in distribution are likely to have had continuous distributions to Mt Lesueur in the wet, early Holocene (Lange 1960, Churchill 1968, Hopkins *et al.* 1983).

At least some of these persistent species are confined to sites of probable, most favourable moisture relations on the mesa: the S-facing slope and the plateau top. Included are both relict species (e.g. *Hakea megalosperma*) and species with major distribution disjunctions (e.g. *Eucalyptus uarginata*). We interpret these local distribution patterns and, in some cases, growth habits, (e.g. mallee *Eucalyptus marginata*; to the south this species develops as single stemmed trees to c. 40 m tall) to indicate the species are close to their environmental limits under present climatic conditions. We suggest that even slightly more arid conditions, say a 10-15% long-term decrease in annual rainfall, could cause extinctions of Mt Lesueur populations (see Hnatiuk and Hopkins 1980 for an account of effects of drought on kwongan). For the restricted relict species this would mean total extinction. For the disjunct species, recolonization from the south would probably be contingent upon a return of climatic conditions similar to those of the early Holocene.

This contention, if correct, implies that the climate of south-western Australia has not been substantially more arid than it now is, at least through the Holocene and perhaps since a much earlier time. Bowler (1981) derived a similar conclusion from a study of salt lakes in south-eastern Australia. Lundelius (1960), who examined cave faunal deposits from a site near to Mt Lesueur, asserted that the present climate was the result of gradual drying since the early Holocene. While there is now reasonable evidence of mid to late Holocene climate fluctuations (e.g. Churchill 1968, Bowler 1981, Singh 1981) the severity of the arid phases as encapsulated in the concept of a "Great Australian Arid Period" (Crocker and Wood 1947) seems inconsistent with our observations.

A large number of typical lateritic upland species was either totally absent from, or represented by only one or two individuals on, the plateau top of Mt Lesueur. Many of these occurred on the slopes and some were abundant on the rim within 5 m of the plateau edge. Whilst this demonstrates that few species appear to show a distinct and consistent preference for laterite as a soil type, a number of other points may be made about these anomalous absences:

- (i) they may indicate that the laterite of Mt Lesueur is different from that of nearby lateritic areas. The sedimentary rock type from which the lateritic soil profile of the mesa developed is well represented on other lateritic uplands nearby, so this explanation seems unlikely.
- (ii) they merely reflect the extreme heterogeneity of the species-rich kwongan vegetation. The low homogeneity, of high beta diversity, of this vegetation and some possible factors contributing to it have been discussed by Griffin *et al.* (1983), and Hopkins and Griffin (1984).
- (iii) some species may have become extinct on Mt Lesueur and, because of the nature of the site and the generally low vagility of propagules of many of the species (*cf.* Clifford and Drake 1981) there has been no recolonization. Some of the missing species are obligate seed regenerators with seed storage in the foliage in bradyspores): these species are particularly sensitive to disturbances such as recurrent fire (Gill and Groves 1981, Griffin and Hopkins 1981, Hopkins and Griffin 1984). However, the absent species include a number of resprouters, as well as species which are present on the rim of the plateau.
- (iv) some typical laterite species may have been precluded from successfully colonizing the plateau top of Mt Lesueur by the presence of species for which the site is a refugium. Niche pre-emption or competitive exclusion hypotheses could be evoked to explain the mechanism of preclusion but we have no data to test such hypotheses. However, we note that the plateau top has probably provided a very stable habitat for plant species throughout the Quaternary whereas the slopes that are constantly eroding and producing gaps of bare ground do support many of these typical laterite species. Irrespective of the mechanism, the concept implies that the top of Mt Lesueur may be close to a maximum of species-richness for this habitat type.

We have attempted to reconcile our list of plant species from Mt Lesueur with that given by Speck (1958) for the top of the mesa. Twenty-four of his species were not located on the plateau top or rim area during the present survey but half of these did occur on the slopes while the others were found on a variety of soils in the general Mt Lesueur-Cockleshell Gully region. It is difficult to

believe that as many as 24 species have become extinct on the top of Mt Lesueur in the past 25 years. Rather we believe that Speck's concept of the top was more general than the one we have used. However, given the thorough nature of our survey it will be possible for future workers to study immigration and extinction rates. It is relevant to note that only three introduced species, *Hypochoeris glabra*, *Pentasthitis airoides* and *Ursinia anthemoides*, were found on Mt Lesueur during this study; the last two of these occurred in sheltered sites amongst the lateritic rubble of the plateau rim.

A variety of structural vegetation types has been described for the plateau and the slopes of Mt Lesueur, all of which consist predominantly of sclerophyllous, perennial shrub species. The distribution of the structural types is strongly influenced by the distribution of a few tall species; in some cases these dominants actually indicate important ecological features but this need not be the case (*cf.* Hnatiuk and Hopkins 1981). The most important component of the vegetation is the low shrub stratum which is rich in species and complex in pattern. This stratum may be overlooked in the Specht (1970) vegetation classification which is based on the physiognomic dominants. However, with the Beard and Webb (1974) scheme, vegetation is classified by the stratum contributing the most biomass. The vegetation is correctly described by the latter scheme as heath (Beard 1979). The general term kwongan (Beard 1976) also adequately describes this physiognomically heterogeneous vegetation.

Conservation

Mt Lesueur is a place of historical interest and botanical importance. In this paper we have described in detail the botanical values of the mesa and discussed the likely significance of some of them. Results of our studies have confirmed the pressing need for the area to be given adequate conservation status as previously recommended. But reservation alone is not sufficient: appropriate management, particularly in relation to fire, is also of critical importance for the long-term maintenance of the biological values of the area. We note the announcement by Government, in May 1983, of its intention to create a large Nature Reserve in the area of Mt Lesueur. We urge that this be implemented expeditiously and that a management programme be established as soon as practicable.

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- Postscript. A severe wildfire was reported for the proposed reserve on 10-12 May 1985. At the time of going to press the effect of this fire on Mt Lesueur had not been assessed.

Appendix I.

Species present on Mt. Lesueur on the plateau top, rim and along the 8 slope transects, together with some comparative data on species occurrences on other lateritic uplands in the Mt. Lesueur-Cockleshell Gully region (Griffin *et. al.* 1983, Griffin and Hopkins unpublished data). For species of uncertain identity, specimen collection numbers are given in brackets.

Species	Top				Slopes								
	A	B	C	D	E	F	G	H	I	J	K	L	M
<i>Acacia alata</i>	3	+	...	+	+	2	...
<i>Acacia avonitens</i>	+	+	+	+	3	7
<i>Acacia epacantha</i>	+	+	2	...
<i>Acacia incrassata</i>	+	0	...
<i>Acacia lasiocarpa</i> var. <i>lasiocarpa</i>	+	...	3	7
<i>Acacia obovata</i>	1	+	+	+	+	...	1	...
<i>Acacia pulchella</i> var. <i>glaberrima</i>	+	+	1	...
<i>Acacia retrorsa</i>	+	+	...	0	...
<i>Acacia stenoptera</i>	+	3	7
<i>Acacia tamminensis</i>	+	+	3	7
<i>Acacia teretifolia</i>	+	+	+	+	+	...	+	+	1	...
<i>Acacia</i> sp. aff. <i>celestifolia</i> (EAG 2219)	1	+	+	1	...
<i>Actinostrobos acuminatus</i>	4	+	+	+	+	+	+	+	+	4	...
<i>Adenanthos cygnorum</i>	+	0	...
<i>Allocasuarina grevilleoides</i>	+	...	1	...
<i>Allocasuarina humilis</i>	+	...	+	+	+	+	+	+	+	+	4	4
<i>Allocasuarina microstachya</i>	+	2	...
<i>Amphipogon strictus</i>	+	+	+	+	+	+	+	+	4	8
<i>Anathria gracilis</i>	+	+	+	+	+	+	+	+	3	7
<i>Andersonia lehmanniana</i>	+	+	3	7
<i>Anigozanthos humilis</i>	+	+	+	+	2	...
<i>Astroloma ciliatum</i>	+	+	...	0	...
<i>Astroloma microdonta</i>	+	+	3	5
<i>Astroloma serratifolium</i>	+	+	...	+	+	+	2	...
<i>Astroloma stomarrhena</i>	+	2	...
<i>Astroloma</i> sp. (EAG 1022)	5	+	+	+	+	+	+	+	+	4	...
<i>Baeckea crispiflora</i>	+	+	0	...
<i>Baeckea grandiflora</i>	5	+	+	+	+	+	+	+	+	4	...
<i>Banksia attenuata</i>	+	0	...
<i>Banksia grossa</i>	0	1	...
<i>Banksia micrantha</i>	4	+	+	+	+	4	...
<i>Banksia tricaspis</i>	3	+	+	+	+	+	+	2	...
<i>Billardiera bicolor</i>	+	+	0	...
<i>Billardiera coeruleo-punctata</i>	+	+	...	1	...
<i>Boronia crassifolia</i>	2	+	+	+	+	...	1	...
<i>Boronia ramosa</i>	2	2	...
<i>Borya nitida</i>	+	+	1	...
<i>Bossiaea eriocarpa</i>	+	1	...
<i>Burchardia umbellata</i>	2	+	+	+	+	+	+	+	+	4	...
<i>Caladenia patersonii</i>	+	0	...
<i>Calandrinia</i> sp. indet.	0	...
<i>Calectasia cyanca</i>	2	+	+	+	+	+	+	+	+	4	...
<i>Calothamnus quadrifidus</i>	+	+	+	+	2	...
<i>Calothamnus sanguineus</i>	5	+	+	+	+	+	+	+	+	4	...
<i>Calothamnus torulosus</i>	3	+	+	+	+	+	+	+	+	4	...
<i>Calytrix flavescens</i>	+	+	+	+	+	+	2	...
<i>Cassylia glabella</i>	1	+	+	+	+	+	+	+	+	4	2
<i>Cassylia pomiformis</i>	5	+	+	+	+	+	+	+	+	4	...
<i>Caastis dioica</i>	+	4	8
<i>Centrolepis drummondii</i>	+	1	...
<i>Chamaescilla corymbosa</i>	+	+	+	...	1	...
<i>Chorizema ilicifolium</i>	+	+	0	...
<i>Comesperma acerosum</i>	+	...	+	+	+	+	+	+	4	4
<i>Comesperma volubile</i>	+	+	+	1	...
<i>Conospermum uervosum</i>	2	+	+	+	2	...
<i>Conospermum triplinervium</i>	+	+	+	...	+	1	...
<i>Conostephanum pendulum</i>	2	+	...	+	1	...
<i>Conostylis aculeata</i>	+	0	...
<i>Conostylis androstemma</i>	+	...	+	+	+	+	+	...	+	+	4	4
<i>Conostylis aurea</i>	+	+	+	+	+	+	+	...	3	7
<i>Conostylis crassinervia</i>	5	+	+	...	+	+	+	+	+	3	...
<i>Conostylis teretifolia</i>	+	+	+	+	3	7
<i>Conostylis teretiasecula</i>	+	4	...
<i>Conothamnus trinervis</i>	5	+	+	+	+	+	+	+	+	4	...
<i>Crassula ? colorata</i>	+	1	...
<i>Cryptandra arbatiflora</i>	+	+	+	+	+	+	+	+	4	8
<i>Cryptandra leucophracta</i>	+	...	+	+	+	+	...	+	2	...
<i>Cryptandra pungens</i>	+	...	+	+	+	+	+	3	3
<i>Dampiera lavendulacea</i>	+	...	0	...
<i>Dampiera lindleyi</i>	+	+	2	...
<i>Dampiera spicigera</i>	+	+	+	+	2	...
<i>Danthonia caespitosa</i>	+	1	...
<i>Darwinia helichrysoides</i>	5	+	+	+	+	+	+	+	+	3	...
<i>Darwinia neildiana</i>	+	+	2	...
<i>Darwinia sanguinea</i>	+	+	+	3	7
<i>Dasyopogon browniiifolius</i>	+	+	+	+	0	...
<i>Daviesia decurrens</i>	+	...	+	+	+	+	+	+	+	4	6
<i>Daviesia incrassata</i>	+	0	...
<i>Daviesia jancea</i>	+	...	+	...	+	0	...
<i>Daviesia longifolia</i>	4	+	+	+	+	+	+	+	1	...
<i>Daviesia pedunculata</i>	+	+	+	+	+	+	+	...	4	8
<i>Daviesia preissii</i>	+	+	+	+	+	+	+	...	4	8
<i>Daviesia</i> sp. aff. <i>striata</i> (EAG 1822)	5	+	+	+	+	+	+	3	...

Species	Top					Slopes							
	A	B	C	D	E	F	G	H	I	J	K	L	M
<i>Dianella revoluta</i>
<i>Diplolaena ferruginea</i>
<i>Diplopeltis huegelii</i>
<i>Dodonaea ericoides</i>
<i>Drosera erythrorrhiza</i>	1
<i>Drosera heterophylla</i>
<i>Drosera leucoblasta</i>	4
<i>Drosera macrantha</i>	5
<i>Drosera stolonifera</i>	1
<i>Dryandra armata</i>	5
<i>Dryandra bipinnatifida</i>	5
<i>Dryandra nivea</i>	5
<i>Dryandra sclerophylla</i>	4
<i>Dryandra sessilis</i>	5
<i>Elythranthera brunonis</i>	5
<i>Eremaea acutifolia</i>
<i>Eremaea violacea</i>
<i>Eremaea</i> sp. (EAG)
<i>Eriostemon spicatus</i>	5
<i>Eucalyptus accedens</i>
<i>Eucalyptus calophylla</i>
<i>Eucalyptus drumnoudii</i>
<i>Eucalyptus gittinsii</i>
<i>Eucalyptus marginata</i>
<i>Eucalyptus todtiana</i>
<i>Eucalyptus wandoo</i>
<i>Eucalyptus</i> sp. (snberea) (EAG 2575)
<i>Eucalyptus</i> sp. (S. D. Hopper 2231)
<i>Gastrolobium bidens</i>
<i>Gastrolobium ilicifolium</i>
<i>Gastrolobium oxylobioides</i>
<i>Gastrolobium pauciflorum</i>
<i>Gastrolobium spinosum</i>
<i>Glichrocaryon aureum</i>
<i>Gompholobium aristatum</i>
<i>Gompholobium knightianum</i>	4
<i>Gompholobium preissii</i>	5
<i>Gompholobium</i> sp. (EAG 2306)
<i>Goodenia caerulea</i>	1
<i>Goodenia filiformis</i>
<i>Goodenia hassallii</i>
<i>Grevillea synapheae</i>	5
<i>Haemodorum</i> sp. indet (EAG 1616)
<i>Haemodorum</i> sp. (EAG 1296)
<i>Haemodorum</i> sp. (EAG 1564)	5
<i>Hakea auriculata</i> var. <i>auriculata</i>
<i>Hakea auriculata</i> var. <i>spatulata</i>
<i>Hakea conchifolia</i>	5
<i>Hakea costata</i>
<i>Hakea erinacea</i> (form)
<i>Hakea flabellifolia</i>
<i>Hakea incrassata</i>	5
<i>Hakea lissocarpa</i>	1
<i>Hakea marginata</i>
<i>Hakea megalosperma</i>	2
<i>Hakea neurophylla</i>
<i>Hakea ruscifolia</i>
<i>Hakea stenocarpa</i>
<i>Hakea trifurcata</i>	1
<i>Hakea undulata</i>
<i>Heurigenia curvifolia</i>
<i>Hibbertia acerosa</i>	5
<i>Hibbertia aurea</i>	5
<i>Hibbertia huegelii</i>	4
<i>Hibbertia</i> ? <i>hypericoides</i>	4
<i>Hibbertia montana</i>
<i>Hibbertia pachyrrhiza</i>
<i>Hibbertia</i> sp. (EAG 2711)	4
<i>Hovea stricta</i>	5
<i>Hovea trisperma</i>	3
<i>Hybanthus floribundus</i>
<i>Hypocalymna xanthopetalum</i>	5
<i>Hypochoeris glabra</i>	4
<i>Isopogon asper</i>	5
<i>Isopogon divergens</i>
<i>Isopogon linearis</i>	5
<i>Isopogon sphaerocephalus</i>	5
<i>Isotropis cuneifolia</i>
<i>Jacksonia floribunda</i>
<i>Jacksonia restioides</i>
<i>Kingia australis</i>	5
<i>Labichea punctata</i>
<i>Lambertia multiflora</i>	5
<i>Lasiopetalum floribundum</i>
<i>Laxmannia squarrosa</i>
<i>Lechenaultia biloba</i>

Species	Top				Slopes								
	A	B	C	D	E	F	G	H	I	J	K	L	M
<i>Lepidobolus chaetocephalus</i>	+	+	+	2
<i>Lepidobolus</i> sp. (EAG 2093)	+	+	+	+	2
<i>Lepidosperma angustatum</i>	5	+	+	+	+	+	+	+	+	4
<i>Lepidosperma striatum</i>	+	+	+	1
<i>Lepidosperma tenue</i>	1	+	+	+	+	+	+	+	+	4	2
<i>Lepidosperma viscidum</i>	+	+	0
<i>Leptomeria empetriformis</i>	4	+	+	+	4
<i>Leptospermum spinescens</i>	1	+	+	4	2
<i>Lepyrodia</i> sp. (EAG 2535)	+	1
<i>Leucopogon plumuliflorus</i>	2	+	+	+	+	+	+	+	+	1
<i>Leucopogon</i> sp. (EAG 1031)	4	+	+	+	+	+	+	+	+	3
<i>Leucopogon</i> sp. (EAG 1645)	2	+	4
<i>Levenhookia dubia</i>	+	+	2
<i>Logania spermacoea</i>	1	+	+	+	+	+	+	3	1
<i>Lomandra cuespitosa</i>	4	+	+	+	+	3
<i>Lomandra hastilis</i>	+	+	0
<i>Lomandra preissii</i>	3	+	+	+	+	+	+	+	4
<i>Lomandra sericea</i>	5	+	+	+	+	+	+	+	+	4
<i>Loxocarya cinerea</i>	5	+	+	+	+	+	+	+	+	4
<i>Loxocarya fasciculata</i>	5	+	+	+	+	4
<i>Lyginia barbata</i>	+	+	0
<i>Lysinema ciliatum</i>	5	+	+	+	+	+	+	+	+	4
<i>Macropidia fuliginosa</i>	5	+	+	+	+	3
<i>Macrozamia reidleyi</i>	0	0
<i>Melaleuca acerosa</i>	+	3	3
<i>Melaleuca radula</i>	+	+	1
<i>Melaleuca ? scabra</i>	+	+	+	+	+	+	3	7
<i>Melaleuca trichophylla</i>	+	+	+	+	+	+	+	+	+	4	4
<i>Melaleuca</i> sp. aff. <i>megacephala</i> (EAG 2359)	4	+	+	+	+	+	+	+	+	4
<i>Melaleuca ? hybrids</i>	+	2
<i>Mesomeluena stygia</i>	1	+	+	+	+	+	+	+	+	4	2
<i>Mesomeluena tetragona</i>	4	+	+	+	+	+	+	+	4
<i>Mesomelaena</i> sp. (EAG 1842)	5	+	+	+	+	+	+	+	3
<i>Neurachne alopecuroidea</i>	+	+	+	3	7
<i>Nuytsia floribunda</i>	+	2
<i>Olxax benthamianu</i>	+	1
<i>Olxax</i> sp. aff. <i>phyllanthi</i> (RJH 771499)	5	+	+	+	+	+	+	+	4
<i>Opercularia spermacoea</i>	+	+	+	8
<i>Oxylobium capitatum</i>	0
<i>Oxylobium reticulatum</i> var. <i>gracile</i>	+	3	7
<i>Purietaria debilis</i>	+	0
<i>Patersonia drummondii</i>	4	+	3
<i>Patersonia occidentalis</i>	5	+	+	+	+	+	+	+	4
<i>Patersonia sericea</i> var. <i>rudis</i>	3	7
<i>Pentaschlistis airoides</i>	1
<i>Persoonia uicularis</i>	0
<i>Persoonia comuta</i>	1	2
<i>Persoonia rudis</i>	+	3	3
<i>Persoonia</i> sp. aff. <i>sulcata</i> (EAG 795)	3	7
<i>Petrophile chrysantha</i>	2
<i>Petrophile inconspicua</i>	3	7
<i>Petrophile linearis</i>	1
<i>Petrophile macrostachya</i>	1
<i>Petrophile brevifolia</i>	2	4
<i>Petrophile striata</i>	5	4
<i>Phlebocarya filifolia</i>	1
<i>Pileanthus filifolius</i>	3	7
<i>Pimelea angustifolia</i>	1
<i>Pimelea inbricata</i>	1
<i>Pimelea sulphurea</i>	1	4	2
<i>Pithocarpa corymbulosa</i>	5	4
<i>Pityrodiu bartlingii</i>	0
<i>Platysace ? teres</i>	3	7
<i>Platysuce xerophila</i>	4	3
<i>Prasophyllum purvifolium</i>	+	3
<i>Prasophyllum</i> sp. <i>indet</i>	1	3	1
<i>Pterostylis nanu</i>	1
<i>Pultenaea ericifolia</i>	0
<i>Restio sphacelatus</i>	1	4	2
<i>Scaevola canescens</i>	+	3	3
<i>Scuevolu paludosa</i>	5	4
<i>Schoenus globifer</i>	2
<i>Schoenus subflavus</i>	3	4
<i>Schoenus unispiculatus</i>	4	8
<i>Schoenus</i> sp. (EAG 1528)	+	+	4	4
<i>Schoenus</i> sp. (EAG 2541)	1	1
<i>Sphaerolobium macranthum</i>	5	4
<i>Spyridium tridentatum</i>	1
<i>Stackhousia brunonis</i>	1	3	1
<i>Stirlingia latifolia</i>	0
<i>Stylidium adpressum</i>	3	7
<i>Stylidium breviscupum</i>	0
<i>Stylidium carnosum</i>	+	2
<i>Stylidium diuroides</i>	2	4

Species	Top					Slopes							
	A	B	C	D	E	F	G	H	I	J	K	L	M
<i>Stylidium junceum</i>	4	+	...	+	+	+	2	...
<i>Stylidium leptocalyx</i>	+	1	...
<i>Stylidium piliferum</i>	4	+	+	+	+	+	+	...	+	4	...
<i>Stylidium pycnostachyum</i>	+	...	+	+	+	+	+	+	2	...
<i>Stylidium repens</i>	1	2	...
<i>Stylidium schoenoides</i>	5	+	1	...
<i>Synaphea petiolaris</i>	5	+	+	+	+	+	+	+	+	3	...
<i>Synaphea polymorpha</i>	+	4	8
<i>Templetonia biloba</i>	+	+	+	2	...
<i>Tetradlea octandra</i>	5	+	+	+	+	+	+	+	+	4	...
<i>Tetradlea confertifolia</i>	...	+	...	+	+	+	+	+	+	+	+	4	4
<i>Tetradlea pauciflora</i>	+	+	+	0	...
<i>Thelymitra antennifera</i>	+	0	...
<i>Thelymitra villosa</i>	1	+	...	+	+	2	...
<i>Thomasia grandiflora</i>	+	+	2	...
<i>Thysanotus anceps</i>	+	...	+	+	+	...	+	...	3	7
<i>Thysanotus patersonii</i>	4	+	+	+	+	+	+	+	+	4	...
<i>Thysanotus sparteus</i>	+	+	4	8
<i>Thysanotus thyrsoideus</i>	3	2	...
<i>Thysanotus triandrus</i>	2	+	+	+	3	...
<i>Thysanotus</i> sp. (EAG 2511)	+	+	+	3	7
<i>Trachymene pilosa</i>	+	1	...
<i>Tricoryne elatior</i>	+	...	+	+	+	+	+	+	+	4	6
<i>Trymalium ledifolium</i>	1	+	...	+	+	+	+	+	+	1	...
<i>Urocarpus phebalioides</i>	+	0	...
<i>Ursinia anthemoides</i>	+	1	...
<i>Velleia trinervis</i>	+	1	...
<i>Verticordia chrysantha</i>	+	...	2	...
<i>Verticordia densiflora</i>	+	3	7
<i>Wahlenbergia gracilentia</i>	+	0	...
<i>Waitzia paniculata</i>	+	1	...
<i>Xanthorrhoea reflexa</i>	5	+	+	+	+	+	+	+	+	4	...
<i>Xanthosia huegelii</i>	4	+	...	+	+	2	...
<i>Xanthosia tomentosa</i>	3	+	+	+	+	+	+	+	+	4	...

Column codings

- A Number of quadrats on top in which species found (max = 5).
- B For species not in A, + = presence on top > 5 m from edge.
- C For species not in A or B, + = presence on rim < 5 m from edge.
- D North-eastern transect (5 relevés) + = in relevé, 0 = nearby
- E Northern transect (5 relevés) + = in relevé, 0 = nearby
- F North-western transect (5 relevés) + = in relevé, 0 = nearby
- G Western transect (5 relevés) + = in relevé, 0 = nearby
- H South-western transect (4 relevés) + = in relevé, 0 = nearby
- I Southern transect (4 relevés) + = in relevé, 0 = nearby
- J South-eastern transect (5 relevés) + = in relevé, 0 = nearby
- K Eastern transect (5 relevés) + = in relevé, 0 = nearby
- L Relative frequency of species occurrence on lateritic uplands in region (our unpublished data)
Code
0 — not found
1 — very low
2 — low
3 — medium
4 — high

- M Coding of species which occur on lateritic uplands of the region and occur on the slopes of Mt Lesueur but are absent from or are infrequent occurrences on the top.
Code
8 — High frequency on uplands (Code 4 in column L) but absent from top,
7 — Medium frequency on uplands (3) but absent from top,
6 — High frequency on uplands (4) and only on rim of top,
5 — Medium frequency on uplands (3) and only on rim of top,
4 — High frequency on uplands (4) and occurring outside the quadrats on top.
3 — Medium frequency on uplands (3) and occurring outside of quadrats on top,
2 — High frequency on uplands (4) and occurring in only 1 quadrat on top.
1 — Medium frequency on uplands (3) and occurring in only 1 quadrat on top.
Other species uncoded.

Acacia cyclops G. Don (Leguminosae-Mimosaceae) in Australia: Distribution and Dispersal

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Abstract

Acacia cyclops is a shrub found along the coast of southwestern Australia and of mediterranean-climate South Australia. Within its natural distribution, *A. cyclops* was associated with naturally- and artificially-disturbed habitats. Reproduction occurred only by seed. Regionally, human dispersal for horticulture and revegetation projects has occurred across thousands of kilometres. Locally, birds have distributed the seed in regurgitated pellets or in faeces. Pellets were usually associated with feeding sites while faeces were common under perches and near watering points. Seed moved in these ways was found less than 200 m from the nearest mature bush. Secondary dispersal of seeds by six ant species was observed. Ants left seeds on the surface or took it into their nests: dispersal distances were less than 2 m. Seed-feeding bugs were common in the litter beneath bushes but absent from bare ground. Higher temperatures experienced by seeds on bare ground are likely to enhance germination. Dispersal away from canopies onto bare ground may allow successful establishment because of reduced predation and enhanced chances of germination and establishment.

Introduction

Like many species which have become pests in alien lands, *Acacia cyclops* A. Cunn. ex G. Don, a native of Australia, has been studied more in South Africa than in its homeland. This shrub was introduced into South Africa in the 1850s as a sand binder (among a number of purposes) but was so successful it became a pest in the fynbos vegetation of the Cape (Roux 1961, Shaughnessy 1980). The present study began in order to compare and contrast the ecology of *Acacia cyclops* in the two countries where seed dormancy and behaviour appear to differ (Gill 1981). This report attempts to provide an ecological perspective of the species within Australia. Specifically, it is concerned with the distribution and dispersal of the species, both locally and regionally.

Distribution

Acacia cyclops is usually found as a spreading shrub up to 4 m in height. It may also occur as a low-profile shrub in exposed locations along the coast or as a small tree up to 6 m tall. Its distribution has been gleaned from records of herbaria in Perth, Adelaide and Canberra as well as by personal observation. Typically, the species is found in coastal localities but has been recorded up to 60 km from the sea at Jerramungup (between Albany and Esperance) in southwestern Australia. It is known from localities just north of Jurien Bay on the Indian Ocean, and at many coastal localities to the south and east through to Kangaroo Island in South Australia (S.A.) on the Southern Ocean.

The entire range of the species is in the winter rainfall zone where frosts are rare and summers are warm and dry. Much of the climatic range of the species is encompassed by the "mediterranean" designation but *A. cyclops* also occurs in very dry conditions at the head of the Great Australian Bight. Average annual rainfall at Eyre over a three year period was less than 300 mm (Congreve 1982) while

at William Bay near Denmark, Western Australia (W.A.), the mean annual rainfall is between 1150 and 1270 mm (Commonwealth of Australia 1962).

Calcareous sands are a feature of the occurrence of *A. cyclops* in the Perth area where some aspects of zonation have been mentioned by Seddon (1972), Smith (1973) and Powell and Emberson (1981). The species is not confined to calcareous substrates, however. It occurs on siliceous sands at Point Culver, W.A. (Nelson 1974), on ironstone gravel near middle Mt. Barren, W.A. (annotation on Perth specimen collected by R. A. Saffrey October 1970), in heavy red clay near Jerramungup (annotation on Perth specimen collected by Tindale and Maslin, March 1970) and in cracks between granite boulders outcropping from the sea at Two Peoples Bay Nature Reserve, W.A.

These broad features of distribution represent only part of the framework of this species' tolerance: an important missing local element is the positive effect of certain levels of disturbance on distribution. Mapping the appropriate types and levels of disturbance across the present distributional range is not yet possible but the common occurrence of *A. cyclops* on naturally and artificially disturbed ground can be illustrated by the following example.

At remote Eyre on the Great Australian Bight, *A. cyclops* was found on the 300 m wide calcareous erosion pavement inland of the miniature dune at the head of the beach. Frequency of occurrence was greater on the inland side of the pavement and on the more stable of the recently mobile dunes which abutted it. The species was rare on the long-stable dunes supporting mallee eucalypts although one 6 m tall specimen was found on an eroding remnant. The cause(s) of mobility of these dunes and their colonization are not known. Geologically, however, this part of the Roe Plain must have had mobile dunes repeatedly during its formation and as the sea retreated.

Historically, too, mobile dunes have been a feature of the Roe Plain as noted by the explorer Eyre (1845). Whether or not settlement and rabbit invasion exacerbated this situation is unknown. Aerial photos available from 1941 to the present show an increase in the area of mobile dunes over the past 40 years or so.

While *A. cyclops* at Eyre was associated with what appeared, at least in part, to be a natural erosion-sediment cycle, the species in many other localities was commonly associated with human disturbance. At Two Peoples Bay Nature Reserve near Albany, the species was found along the commonly travelled roads, on old vehicle tracks now disused, around the picnic area and close to the most frequently used areas of the bayside beach.

Christensen and Kimber (1975) noted that *Acacia cyclops* was "rarely subject to fire". At Eyre there was no evidence of fire at all and on the dunes there was insufficient fuel to carry a fire. Near Perth, however, fires—usually small in area—have occurred in areas of *Acacia cyclops* especially where fuels were influenced by the presence of exotic grasses. Mature *Acacia cyclops* was readily killed by fire.

Dispersal

Natural dispersal of seed of *Acacia cyclops* was studied mainly at Perth and at Two Peoples Bay. A little supplementary data on bird dispersal of seed was collected at Cape le Grand National Park near Esperance, W.A. Because the species has horticultural value in Australia and has been exported, enquiries were made of seed merchants in Perth and of CSIRO Division of Forest Research in Canberra regarding their dispersal of seed. In Perth, one of the major merchants was the Forests Department of the Western Australian Government. Their records showed the sale of seed from W.A. to S.A. and to various plant nurseries in southwestern Australia. Seed from W.A. and S.A. has been sent by CSIRO to a number of countries including Yugoslavia, India, United States of America, Mexico, the Sudan, Egypt, Ajibouti, Iran, Malta, Chile and Madagascar. Historically, the carriage of seed to South Africa has already been mentioned: it is of interest that seed of *A. cyclops* arrived in South Africa via Europe (Shaughnessy 1980).

Natural dispersal of *Acacia cyclops* was strongly influenced by the presence of the bright red aril encircling the shiny black seed. The seed itself had an average dry weight of about 25 mg while the aril weighed about half this. The seed contained an average about 12% oil but the aril contained 40% (O'Dowd and Gill, unpublished) thereby being an excellent nutritional source. When the fruit, a legume, dehisced in late spring or summer the seeds were exposed but held on the plant by the aril—thereby presenting a colourful display of red/black dispersal units. Potentially, the seeds could remain on the plant for long periods because the legumes persisted for a year or two before deteriorating and falling: actually, the seeds may be removed quickly by dispersers or fall of their own accord before most legumes fall.

Five types of post-dispersal units could be distinguished on the ground at Two Peoples Bay Nature Reserve. They were the seed-plus-aril, the seed alone

and three aggregate structures. The last three were cylindrical, of bird origin, and distinguished on the basis of diameter (Fig. 1) viz. 2-3 mm, 4-9 mm and 12-15 mm. The smallest diameter units were bird faeces typically with one seed; the medium diameter units, also faeces, usually contained about 8 seeds;

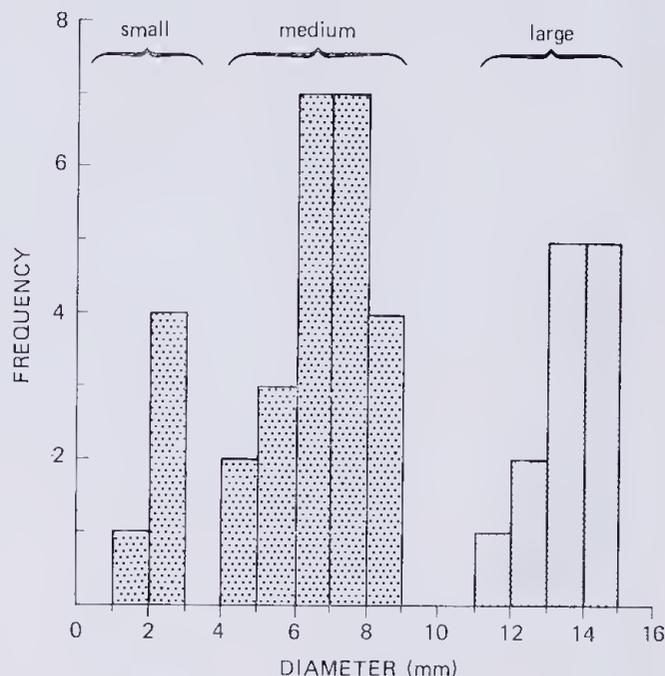


Figure 1.—Frequency distribution of diameters of aggregated dispersal units of *Acacia cyclops* from Western Australia. The largest diameter units were regurgitated pellets, the others faeces.

the largest units were regurgitated pellets and had an average of 38 seeds each (Fig. 2). Each type of aggregate often contained materials unrelated to *Acacia cyclops*: the smallest units had mostly very small seeds as well as the single large *Acacia* seed, while the other units often contained insect remains and some other seeds. The smallest dispersal units were consistent with being the faeces of silvereyes (*Zosterops lateralis*), small birds weighing about 9 g, medium units with faeces of red wattlebirds (*Anthochaera carunculata*) or other medium to large avian dispersers (see below) and the largest with regurgitated pellets of grey currawongs (*Strepera versicolor*)—large birds weighing about 400 g.

At Perth, silvereyes and singing honeyeaters (*Meliphaga virescens*) were netted and excreted intact seed of *A. cyclops*; at Eyre, silvereyes and brush bronzewing pigeons (*Phaps elegans*) have been reported to excrete seeds (Congreve, pers. comm.); and at Two Peoples Bay Nature Reserve, birds taking seed were silvereyes, red wattlebirds, grey currawongs and Australian magpies (*Gymnorhina tibicen*). Birds observed defaecating seed at Two Peoples Bay were the grey currawong (L. D. Gill, pers. comm.) and the magpie. The grey currawong also regurgitated seed-filled pellets (G. Folley, pers. comm.): its close relative, the pied currawong (*Strepera graculina*) in eastern Australia regurgitates pellets too. Currawongs were absent from Perth and singing honeyeaters were absent from Two Peoples Bay.

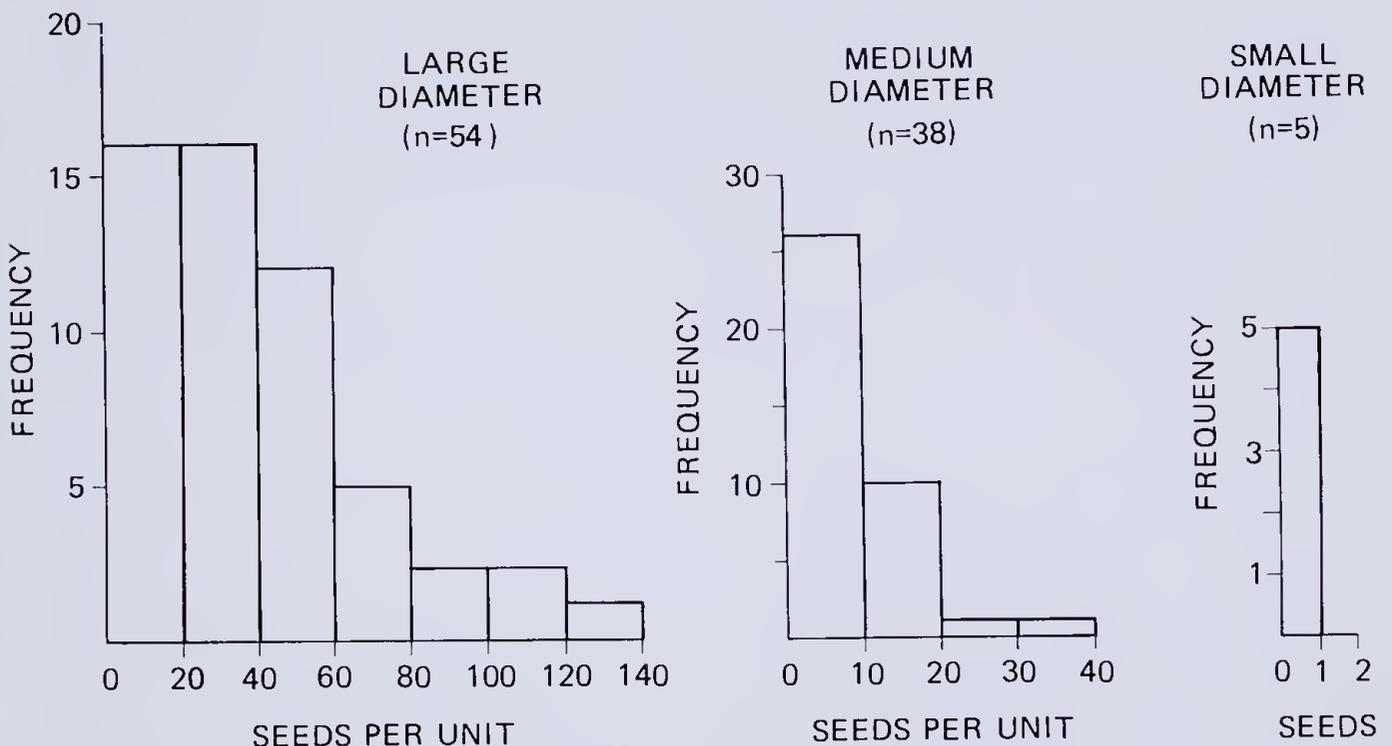


Figure 2.—Numbers of seeds per dispersal unit. The large diameter units were pellets, the others faeces.

The frequency distributions of pellets and faeces in relation to nearest possible source of seed was studied by walking transects along roads and tracks and in the picnic area at Two Peoples Bay i.e. following the distribution of plants (Fig. 3). Supplementary data on faeces came from Cape le Grand National Park. Pellets showed an hyperbolic distribution with distance from the nearest bush while the medium-size faeces, on the other hand, showed a peak associated with perch locations such as rocky outcrops, beneath overhanging branches and close to water points: the peak at 90 m was largely due to a collection made at Cape le Grand National Park. The smallest diameter faeces with single seeds were found only under bushes after intensive searching: the large *Acacia* seed tended to be poorly attached to the faecal unit.

Seed on the ground, whether aggregated or not, may be further transported. Grey currawongs, for example, will take arillate seed from the ground. Lizards (*Tiliqua rugosa*) and small mammals (*Rattus fuscipes*) were other possible dispersal agents. *Tiliqua* took *Acacia cyclops* seed in the laboratory and excreted it up to 2 weeks later (O'Dowd, *pers. comm.*) but a single dissection in the field revealed no seed. Similarly, a single *R. fuscipes* trapped under *Acacia cyclops* had no seed in its alimentary tract although there is circumstantial evidence that this species may take seed in the field (A. Baynes, *pers. comm.* and P. Christensen, *pers. comm.*). More obvious than vertebrate removal of seeds is invertebrate removal.

A number of invertebrates were attracted to seeds and arils of *A. cyclops* including beetles, bugs, grasshoppers and ants. Only ants commonly moved seed.

At Two Peoples Bay, frequent observation of 32 seed placements each of 3 arillate seeds were made during daylight in January 1983 over a period of 4 days. Any seed removed was replaced. Activity of ants around seeds varied widely from place to place and time to time and involved a number of species (Appendix 1). Seed was either left alone, had its aril removed *in situ*, was transported short distances (e.g. a few cm or dm), was dropped in favour of other materials, or was transported into nests up to 2 m from point of collection.

Seed in loose currawong pellets was moved by ants occasionally but seed in cemented faeces seemed immobile. Breaking up dry faeces allowed ants to move this seed, with mostly-destroyed arils, to nests. Artificially supplying 40 fresh arillate seeds to a nest of *Melophorus* sp. in Perth followed by nest excavation the following day showed that seeds were placed at depths from 2 to 20 cm but mainly between 6 and 12 cm. Five excavations 20 cm × 20 cm square and 12 to 20 cm deep under bushes of *Acacia cyclops* at Swanbourne, Perth, showed seeds in the profile but no obvious preferred depth: seeds below the surface lacked arils. Fresh seeds placed on small wooden trays, 10 seeds per tray, replicated 5 times at 3 sites with and without arils were all removed from the Swanbourne site within a week in November 1982.

At Two Peoples Bay, the fate of seed on the soil surface was studied on a poorly vegetated firebreak about 5 m from, and parallel to, a gravel road lined with bushes of *Acacia cyclops*. Seeds were placed on small wooden trays (63 mm square and 6 mm thick with a central circular depression 2 mm deep and 38 mm diameter) either under wire mesh cages (ca 130 mm square and 70 mm deep of mesh size

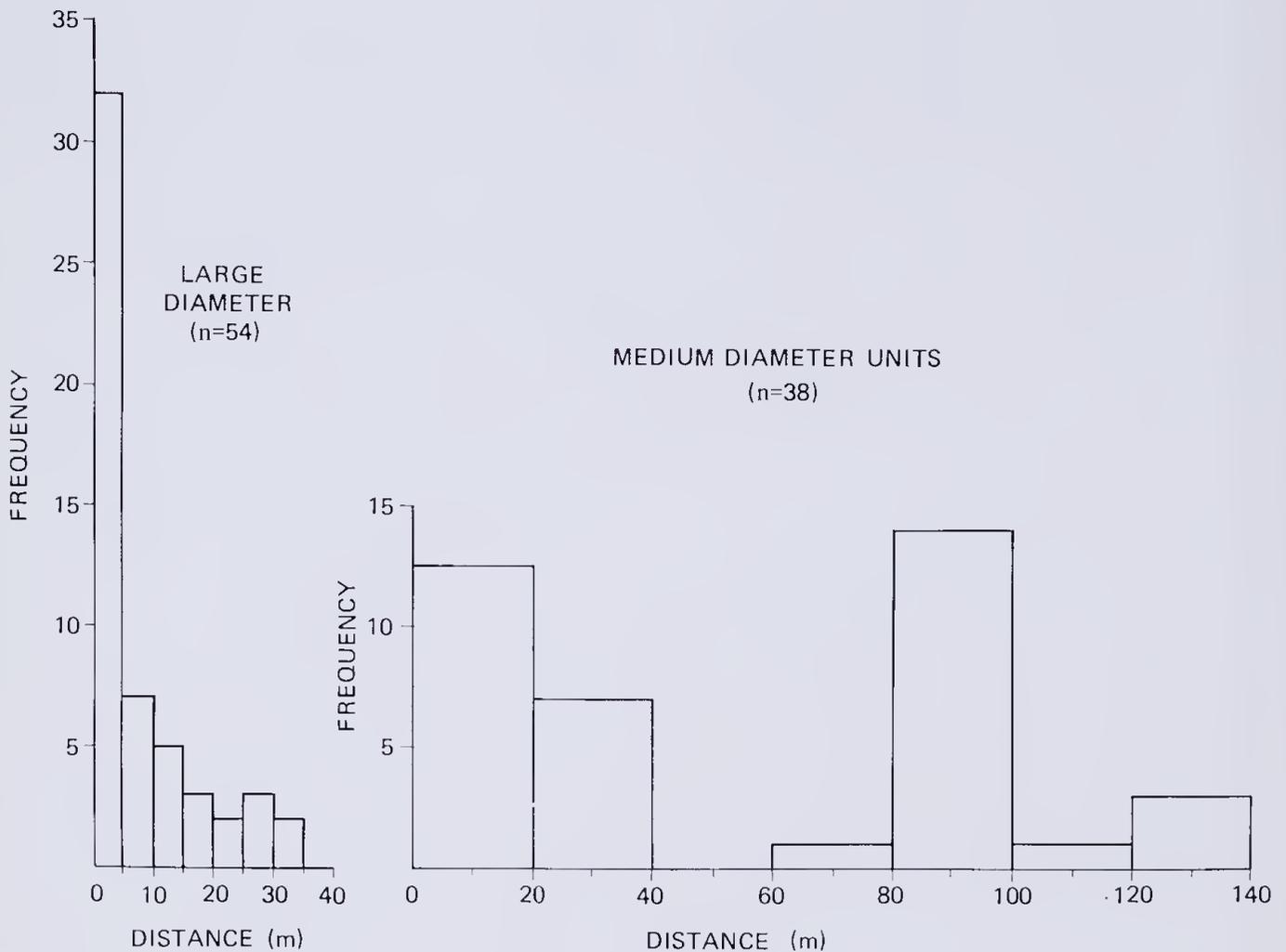


Figure 3.—Distances of dispersal from the nearest source of seed.

about 14-18 mm)—to deter birds and other vertebrates—or in the open, and either surrounded by a ring of sticky gel on the border of the wooden tray—to deter ants particularly—or left clean. On each tray were placed 10 seeds with arils or 10 seeds which had had most of the aril removed by ingestion and regurgitation by currawongs. The treatments were replicated 5 times at 5 locations about 10 m apart.

Ants were observed removing seed from trays, and bird tracks and a pellet consistent with currawong presence was seen next to affected trays. Uncaged arillate seed protected by gel tended to be lost all at once from any one replicate: at the same time all remaining arillate seed from other uncaged treatments also disappeared in four of the five replicates—consistent with removal by birds.

At the end of this three day experiment, 60% of the arillate seed had been removed but only 16% of the seed without arils had gone. The gel inhibited removal as only 23% of seed was removed from these treatments whereas 55% of seed on "clean" trays had been taken. The smallest difference between contrasting treatments was between caged and free seed: only 27% seed was removed from caged treatments and 50% from free. When combinations of treatments were compared the largest

contrast was between the arillate seeds without gel protection (91% removal) and non arillate seed with gel (4% removal). Caged seeds with gel protection also lost 4% of seed (total), this loss being the seed removed by wind or by ants crossing the gel barrier after "bridges" of leaves and wind-blown sand had formed.

Three other experiments of this type showed similar removal rates by ants but presumed bird-removal rates were rather erratic depending on foraging success. Despite these results showing rapid removal of seed from trays, bushes with abundant arillate seed beneath them were easy to find. In these cases, one can infer the operation of one or more processes such as local exclusion of efficient dispersers by aggressive but less active foragers of *Acacia* seed (such as magpies), frequent disturbance of birds by motor vehicles, satiation of foragers or the absence of granivorous ants.

Seed dispersal and predation

Seed dispersal may enhance chances of seed survival in the presence of seed predators. A dispersal agent may remove the seed from the predator's habitat before predator attack or kill any predators in seeds before seed damage was lethal (as in the case of bruchid-attacked *Acacia* seed when dispersed

by mammals in Africa—Lamprey *et al.* 1974). Predation of seeds was studied largely at Swanbourne (Perth) and Two Peoples Bay but observations were also made at Eyre.

Predispersal seed predation

Birds were major predators of immature seed at Eyre but not at the other study sites. Large pink cockatoos (*Cacatua leadbeateri*) virtually destroyed seed crops of individual bushes at Eyre in spring 1982. However, this damage was not severe enough on a population basis to prevent a prolific set of seed by many individual *A. cyclops* (P. Congreve, *pers. comm.*).

Insect predators of rapidly developing seed in spring were abundant at Swanbourne. In particular, bugs, weevils and moths were noticeable. The green hemipteran shield bug, *Coleotichus* sp. (prob. *C. costatus*, family Scutelleridae), and the brown, and much more streamlined Alydid bug *Riportus* sp. (Van den Berg 1980 *b*) were common and fed on seeds within legumes (before dehiscence) and on seeds still in their legumes directly following legume dehiscence. Local swarms of the red and khaki nymphs of Pentatomid bugs, probably *Dictyotus* spp. (Van den Berg 1980 *b*) had a similar feeding behaviour. Evidence of attack of all these bugs was obtained by direct observation or from the small translucent "turrets" left upon withdrawal of their feeding tubes from the seed. "Turrets" were truncated cones of material with a cylindrical hole passing through their centres into the seed (or legume). They were *ca* 0.3 mm tall for the adult bugs and had a hole of about 0.03 mm which passed through the seed coat. Usually 1 to 7 "turrets" were found on affected seeds but up to 19 were observed. Holes through immature (green) testas tended to close but those in drier mature (black) testas tended to persist.

Larvae of weevils and moths affected dispersal by attaching seed to the pod wall or by binding the pod walls together thereby preventing dehiscence. Weevil larvae (*Melanterius* spp.) hatched from eggs inserted onto the surfaces of developing seeds within pods in spring. Eggs were abundant but not all hatched to larvae. Larvae fed on single seeds and completely consumed them. Their life cycle seemed short as the larvae fell to the ground and pupated before active dispersal of seed occurred (Van den Berg 1980 *a*). By contrast, larvae of the seed-feeding lepidopteran *Xerometra crocina* were found in the legumes of the previous seasons crop even while the present season's legumes were maturing rapidly in spring.

Post dispersal seed predation

Seed on the ground beneath bushes was not immune from attack. Bugs were particularly common. Of major importance was the shield-type bug *Adrisa* sp. (Cydnidae), a chocolate brown to black insect (when mature) found in the litter and upper soil layers under *A. cyclops* bushes at Eyre, Albany and Perth. Small sleek *Riportus* sp. (Alydidae) seen feeding on seeds at Two Peoples Bay were also pitfall-trapped at Swanbourne. Bugs were not found in 15 soil excavations (20 cm × 20 cm × 20 cm) at 5 m from bushes of *A. cyclops* in open ground at Two Peoples Bay but 12 of 15 samples from under 15 bushes had *Adrisa* in litter or soil with an average of 3 insects per sample.

Dispersal and germination

Dispersal of seed may cause it to be exposed to summer soil temperatures commonly of 60°C although these may only persist for short periods each day (Taylor 1981). In litter under bushes, this peak is unlikely to be reached and temperature fluctuations would be expected to be moderate. The large fluctuations and high temperatures of open ground may be expected to improve germination rate by analogy with behaviour of *Trifolium subterraneum* in the same region (Taylor 1981). Passage through birds and predation by bugs could also enhance germination through damage of the seed coat. Two germination experiments assessed these possibilities for *A. cyclops*.

Temperature treatments were applied to dry seed with and without arils using 50 seeds per Petri dish and 3 replicates of each treatment. For 8 days the seeds were exposed to a constant temperature of either 15°C or 60°C or given repeated half day exposures of 15°C followed by 60°C. After treatment the seeds were placed on moist filter papers in the laboratory and observed for 4 weeks. Of the 900 seeds used, 208 had germinated after 4 weeks: 49% of these had arils, 51% did not. Replicate results for any one temperature treatment did not overlap those for any other treatment. Means were 6% for 15°C treatment, 21% for 60/15°C and 42% for the 60°C treatment, thereby indicating a close correlation between time of exposure to 60°C and germination percentage and no effect of fluctuating temperatures.

Limited supplies of seeds were available from faeces, pellets and from fresh seed with evidence of feeding by bugs (*viz.* "turrets"). Three replicates of 50 seeds from faeces and the same numbers affected by bugs or unaffected—all from Perth—were placed in Petri dishes on moist filter paper at 20°C in a constant-temperature room. Similarly, seeds from droppings and pellets were compared with seeds taken directly from bushes at the Two Peoples Bay site. All of these comparisons continued for 120 days. Seeds from faeces at the Perth site germinated similarly to the control—near 60%—while seeds with "turrets" showed about 20% germination only. Seeds from faeces and regurgitated pellets from Two Peoples Bay showed about 80% germination while the controls gave about 15% only.

Discussion and conclusions

The weedy nature of *Acacia cyclops* which has become so evident in South Africa is apparent in its native land as well. In Australia it is often a species of disturbed areas, has abundant seed production, is quick growing and has effective dispersal mechanisms. Human dispersal and human disturbance as well as deliberate cultivation have expanded the distribution of the species and in some localities it is difficult to decide whether or not the species is a local escape from cultivation, is a chance introduction, or is indigenous to the area. With overseas interest in the species as a firewood crop (Ayensu *et al.* 1980), its possible use in Australia as a sand binder, and with further human disturbance in its natural area of occurrence, *Acacia cyclops* is likely to become even more prominent than at present.

Weeds tend to have generalist dispersers and this is true of *A. cyclops*. The avian dispersers identified in this study are all very widespread birds with opportunistic diets of various seeds and insects (for most) and nectar (for a few). Even the peripheral vertebrate possibilities—*Rattus fuscipes* and *Tiliqua rugosa*—are very widespread. Distributions of all these vertebrates extend well beyond the range of *Acacia cyclops*.

This study has suggested that regurgitation of seeds by currawongs is an important aspect of dispersal that differs in its pattern from that of avian faeces. Dispersal by regurgitation seemed to be associated with feeding patterns while dispersal in faeces had a strong component associated with perching behaviour. Scattered pellet material has been found near artificial watering points, however. In South Africa, the regurgitation mechanism has not been identified but patterns of seedling distribution have been interpreted in terms of perching behaviour of birds and distance from the presumed source (Glyphis *et al.* 1981) as in this study with seeds.

Seeds that have passed through birds have been found previously to germinate more rapidly than controls in South Africa (Glyphis *et al.* 1981) although present results were variable. This variability may deserve closer scrutiny and may be associated more with time exposed to the sun in the field than actual passage through the bird. Higher temperatures of seed dispersed onto open ground may increase rate of germination so that the response observed may depend on the time the seeds are left in the open before collection. Another factor may be the rate of passage through the bird. For pellets from currawongs, the seeds in some cases were associated with macerated arils while in others the arils were largely unaffected. Effects of passage through the complete digestive

system may also vary according to speed—affected by type and amount of food ingested—and the nature of the gizzard. Birds which are usually predators of ripe seed (with strong gizzards) may pass only a few or no intact seed while seed dispersers (with softer gizzards) may pass a greater proportion. The boundary between predators and dispersers of ripe seed may not be clear cut. The same may be true for ants.

Ants showed varying interest in the seed-plus-aril combination and seemed much more concerned with the latter rather than the former part of this dispersal combination. Their activity served to bury the seed in some cases and scatter it in others. Distances of dispersal were small but position of dispersal could be significant. Burial in the nest may protect it from predators and even provide a more nutrient-rich environment in which to grow.

The heterogeneity in the distribution and abundance of predators and dispersers was marked. Predation of unripe seed by cockatoos was prevalent at Eyre but absent at other study sites; canopy feeding by bugs was more common at Swanbourne (Perth) than at Two Peoples Bay; currawongs were present at Eyre and Two Peoples Bay but absent from Perth; and, at a local level, the dispersion and types of seed-collecting ants varied widely. Ants were slower but more consistent in removal of seed from the ground than birds which were erratic in their discovery and ingestion of seed.

Three scales of dispersal distance were detected in this study. People moved seeds locally but also up to thousands of kilometres. Birds moved seeds distances of the order of hundreds of metres from the nearest possible sources; and ants moved seed up to 2 m (Fig. 4). Each level may be important to the spread and establishment of *Acacia cyclops*: people allowed the species to spread beyond Australia, birds have dispersed the seeds to newly-disturbed sites and ants have buried seeds. The details of dispersal are numerous and concern many species across the range of *Acacia cyclops*: a simplified view of this process is depicted in Fig. 4.

Optimum chances of germination and seedling establishment seem to be associated with bird dispersal to bare unshaded soil in the dispersal season. If the seed was dispersed early it had a greater chance of avoiding predation by hemipteran predators. Populations of predatory bugs seemed to increase through spring and summer thus predisposing late maturing seeds to greater attack. Their feeding reduced viability of seed. Early in the season, the supply of mature seeds to bird dispersers was limited and eagerly sought; later, the crop was abundant and the chances of quick dispersal seemed diminished. If deposited after passage through a bird, germination of seed could be enhanced; when food was abundant the time spent internally was likely to be minimal. Deposition in full sun may have enhanced germination. If the seed was dispersed away from the host plants of predatory *Adrisa*, the chances of establishment were again likely to be improved. Evidence for these conclusions has sometimes been indirect but the stage is now set for the direct test of these ideas.

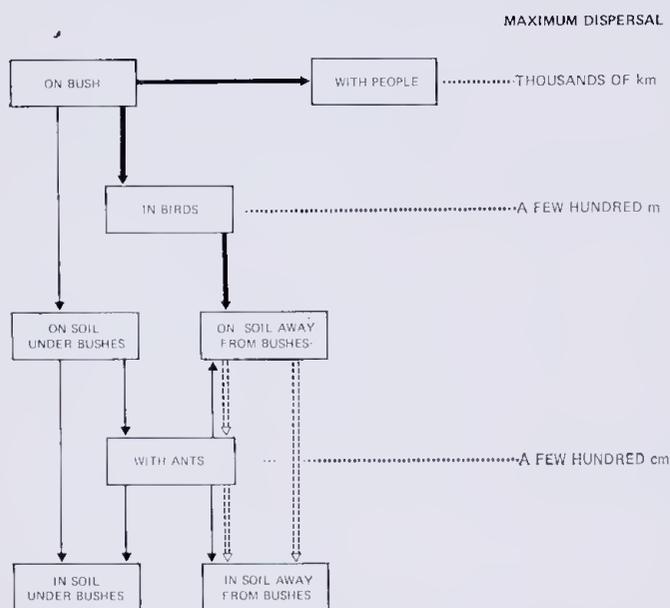


Figure 4.—A simplified summary of the processes of dispersal of *Acacia cyclops* in Australia. The thicker arrows represent what appear to be major paths for dispersal and successful establishment. The importance of burial at sites away from bushes is not known (dotted lines).

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Appendix

Ants observed in association with seeds of *Acacia cyclops* in Western Australia.

Dolichoderinae

Iridomyrmex sp.^{1,2} (carried seed-plus-aril).

Formicinae

Camponotus sp.² (carried seed-plus-aril).

Melophorus spp.^{1,2} (two species either removing arils from seeds or carrying the seed-plus-aril combination).

Myrmicinae

Monomorium sp.¹ (tiny ants which cut arils into tiny pieces for transport and only inadvertently moved seeds a few cm at most).

Pheidole sp.^{1,2} (removed arils and carried them away or moved whole seed-plus-aril unit).

Ponerinae

Rhytidoponera spp.^{1,2} (two species carrying seed-plus-aril units).

¹ See also Berg (1975); Berg classified his *Camponotus* spp. as non-collectors.

² See also Majer (1982).

Guide to the termites (Isoptera) from the extreme south-west of Western Australia

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Abstract

Keys to genera are provided for soldiers and alates of the species of termite known from the jarrah forest of south-western Australia, and areas west and south of it, with notes on their identification, distribution and biology.

Introduction

Termites comprise a substantial component of the Australian soil fauna, and make a major contribution to the turnover of organic materials in soils (Lee and Wood 1971). They are, in addition, an important part of the diets of many animals and their diversity, distribution and abundance are becoming recognised as useful indicators in the formulation of management strategies in environmental conservation (cf. Braithwaite and Dudzinski 1982; Bunn 1983).

Silvestri (1909) published the first substantial account of Western Australian termites, an account extended by Mjöberg (1920) (Watson and Gay 1983). The most recent detailed statement of our knowledge was that of Hill (1942). However, several substantial papers dealing with particular groups have been published since then (Calaby and Gay 1956, Gay 1968, 1971, Watson and Perry 1981, Gay and Watson 1982) and, although summaries have appeared (Gay 1970, Gay and Calaby 1970, Gay and

Watson 1974), they are of little help in ascertaining which species occur in the south-west, let alone in determining their identities.

During the last few years, Perry and Watson have received increasing numbers of requests for help in identifying termites collected during ecological surveys, many linked to conservation projects affecting the jarrah forest and areas south and west of it, and the need has become apparent for a guide to the termite fauna of that part of south-western Australia.

Use of the keys

Tabular keys to termites from the extreme south-west, here defined as the region of jarrah forest and the areas between it and the coast from Yancheep in the north to east of Albany (Fig. 1), are given in Tables 1-4; the numbers in the keys refer to the relevant figures. The morphological features mentioned in the tables and text are depicted in Fig. 2, on the following illustrations:

antenna	a,g	: marginal tooth	d,i
arolium	h	: tooth	e
eye	g	maxilla	d
femur	h	maxillary palp	g
fontanelle	a,g	nasus	b
frontal tubercle	c	ocellus	g
gula	d	pronotum	f
head width	b,g	tarsal claw	h
mandible	a,g	tarsus	h
		tibia	h
	: apical tooth	i	
	: cutting edge	i	: apical spur
	: distal part	e	wing scale
	: length	e	: length
	: lower condyle	d,e	f

Table 1, to genera (and to species, for those with only one extreme south-western representative), is based on the soldier caste, the diagnostic caste most often encountered, and the character states used can be observed with a 10x hand lens. With the aid of the additional information given in the text and in Figs. 3-6, species of all genera except *Amitermes* and those of the *Termes* complex can readily be identified from the soldiers, but the identification may require a good stereomicroscope fitted with an ocular micrometer. Tables 2 and 3 deal respectively with species of *Amitermes* and the *Termes* complex (Figs. 3b-h, 4a-e). These are difficult termites to identify, and recourse should be made to the text and, in uncertain cases, to the references cited.

A further key to genera (Table 4) is based on winged adults (alates). As with the soldiers of *Amitermes* and the *Termes* complex, the identification of alates is not necessarily easy, and calls for a stereomicroscope and micrometer. To examine the mandibular dentition, it is usually necessary to

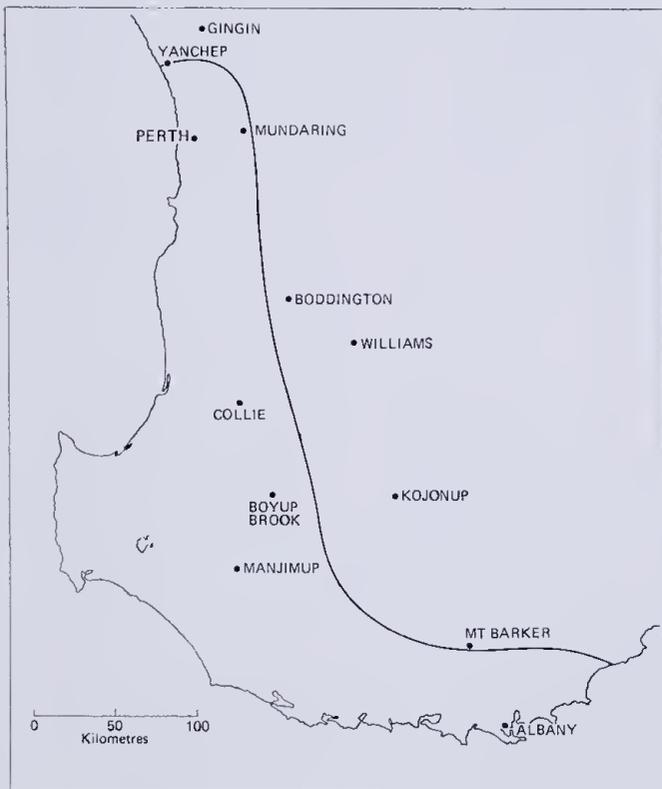


Figure 1.—The extreme south-west of Western Australia.

dissect out the mandibles, which requires fine watchmaker's forceps and mounted needles. The terminology is that of Ahmad (1950) (see also Gay 1970). Further information is given in the text; colour and flight time are often useful characters.

No key is given for workers; although they can usually be identified to genus by their mandibular dentition, which resembles that of the alate (*cf.* Ahmad 1950, Gay 1970, Campbell and Watson 1975), they can rarely be identified to species.

The tabular keys should be read from left to right. The specimen is allocated to one or other of the character states in the first column, then to a character state in the relevant section of the second column, and so on until it is allocated to a genus or species. Once the genus has been determined, guidance to specific identity can be obtained from the notes on each genus, given in the subsequent section of the paper.

Fauna

The following checklist includes the 32 species of termite of which we have records from the extreme south-west (Fig. 1). The records are those of material held in the Australian National Insect Collection, Canberra, and the D. H. Perry collection, which is to be lodged in the Western Australian Museum; a few are added from the literature. Further details are given in later sections of this paper.

Family Kalotermitidae

- Bifiditermes improbus* (Hagen 1858)
- Cryptotermes austrinus* Gay and Watson 1982
- Kalotermes aemulus* Sewell and Gay 1978
- Kalotermes hilli* Emerson 1949

Family Rhinotermitidae

- Coptotermes acinaciformis raffrayi* Wasmann 1900
- Coptotermes michaelsoni* Silvestri 1909
- Coptotermes* sp. indet.

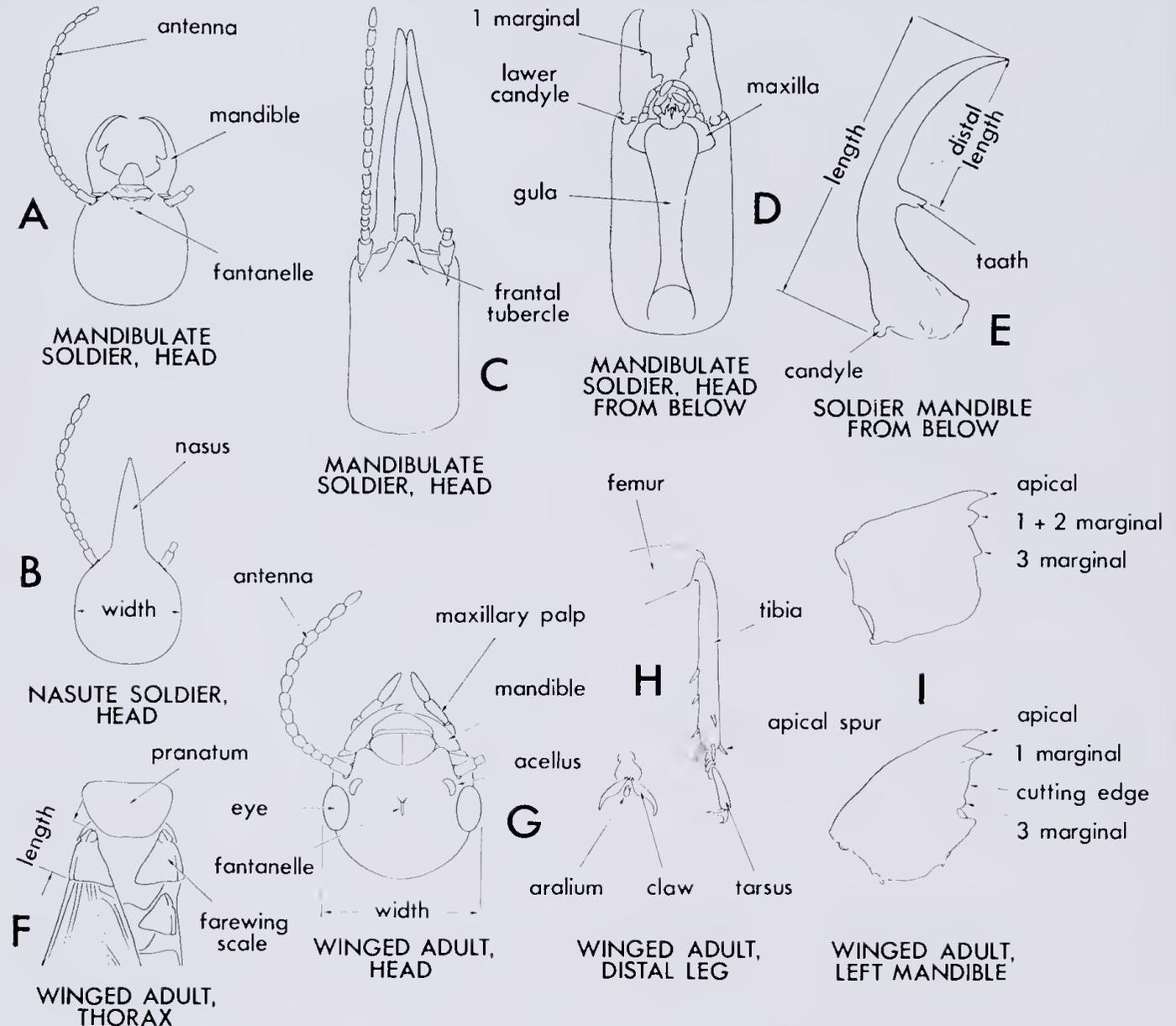


Figure 2.—Morphological features and measurements of termite soldiers and alates (not to scale).

Table 1

Tabular key to termite genera from south-western Australia, based on the soldier caste (for terminology, see figs 2a-e).

Head:	<i>L. mandible:</i> more than one tooth on blade (3, 4a)	<i>Fontanelle:</i> absent (3)	<i>3rd antennal segment:</i> elongate, swollen (3a)	<i>Bifiditermes improbus</i>		
			neither elongate nor swollen (3b)	<i>Head shape:</i> squarish, armoured (3b)	<i>Cryptotermes austrinus</i>	
	present (4a)				<i>Head shape:</i> elongate, smooth (3c, d)	<i>Kaloterme</i> spp.
			<i>Schedorhinotermes reticulatus</i>			
	mandibulate (3-5, 6a-d)	one tooth on blade (4b-h)			<i>Amitermes</i> spp. (Table 2)	
		no prominent teeth on blade, or serrated (5, 6a-d)	<i>Frontal tubercle:</i> present (5a-e)		<i>Termes</i> complex (Table 3)	
absent (5f-h, 6a-d)			<i>Head shape:</i> oval or tapered (5f-h)	<i>Aperture of fontanelle:</i> concealed from above (5f)	<i>Ahamitermes hillii</i>	
				parallel-sided (6a-d)	<i>Aperture of fontanelle:</i> prominent from above (5g,h)	<i>Coptotermes</i> spp.
		<i>Mandibles:</i> upcurved in profile (6a, b)	<i>Heterotermes</i> spp.			
			straight in profile (6c, d)	<i>Microcerotermes</i> spp.		
nasute (6e-h)	<i>Head and abdomen:</i> yellowish brown			<i>Occasitermes occasus</i>		
	pale reddish brown to dark brown	<i>Head, excluding nasus:</i> oval, or tapered to front (6f, g)		<i>Tumulitermes</i> spp.		
		almost circular from above (6h)		<i>Nasutitermes exitiosus</i>		

Table 2

Tabular key to the extreme south-western Australian species of *Amitermes*, based on the soldier caste (for terminology, see figs 2b, e).

<i>Mandibular tooth:</i> hatchet-shaped (4c)		<i>A. heterognathus</i> (4c)		
barb-shaped (4b, d-h)	<i>Head width:</i> < 0.80 mm	<i>A. insolitus</i> (4d)		
	> 0.90 mm	<i>Mandible length:</i> ≥ 1.00 mm	<i>Amitermes</i> sp. near <i>A. neogermanus</i> (4f)	
		0.80-1.00 mm	<i>Head width:</i> < 1.10 mm	<i>A. pallidiceps</i> (4h)
			≥ 1.10 mm	<i>A. obeuntis</i> (4g)
		< 0.80 mm	<i>Distal part of mandible:</i> 0.34-0.40 mm	<i>A. conformis</i> (4b)
0.30-0.36 mm	<i>A. modicus</i> (4e)			

Table 3

Tabular key to the extreme south-western Australian species in the *Termes* complex, based on the soldier caste (for terminology, see figs 2c, d, h).

<i>Frontal tubercle:</i> reduced (5a)		<i>Hesperotermes infrequens</i> (5a)		
prominent (5b-e)	<i>Mandibles:</i> asymmetrical (5b)	<i>Paracapritermes kraepelinii</i> (5b)		
	symmetrical (5c-e)	<i>Gula:</i> sharply angled posteriorly (5c)	<i>Termes argutus</i> (5c)	
		evenly rounded (5d, e)	<i>Hind tibia:</i> < 1.0 mm long	<i>Termes occidualis</i> (5d)
			> 1.0 mm long	<i>Termes tomentosus</i> (5e)

Table 4

Tabular key to termite genera from south-western Australia, based on the alate caste.

Forewing scale length (2f): > 2x hindwing scale	Arolium (2h): absent					<i>Bifiditermes improbus</i>	
	present	Anterior margin L 3rd marginal tooth (2i): > posterior margin L 1+2nd marginal				<i>Cryptotermes austrinus</i>	
		= posterior margin L 1+2nd marginal				<i>Kalotermes</i> spp.	
< 2x hindwing scale	L mandibular teeth (2i): apical + 3 evident marginal	Head, from above: elongate oval			<i>Heterotermes</i> spp.		
			semicircular behind eyes	Head colour: golden brown	<i>Schedorhinotermes reticulatus</i>		
		reddish brown to very dark brown		<i>Coptotermes</i> spp.			
	apical + 2 evident marginal	Fore tibia (2h): 3 apical spurs	Antennal segments (2g): 13-14	<i>Microcerotermes</i> spp.			
				15	Cutting edge L mandible (2i): notched before 3rd marginal	<i>Termes</i> complex	
		2 apical spurs	Cutting edge L mandible (2i): notched before 3rd marginal		Head width (2g): < 1.15 mm	sinuously curved to 3rd marginal	Apical segment maxillary palp (2g): inflated
						not inflated	<i>Anitermes</i> spp.
				> 1.15 mm	<i>Tumulitermes</i> spp.		
			evenly curved to 3rd marginal		<i>Occasitermes occasus</i>		
				<i>Nasutitermes exitiosus</i>			

Heterotermes occiduus (Hill 1927)
Heterotermes platycephalus Froggatt 1896
Schedorhinotermes reticulatus (Froggatt 1896)

Family Termitidae

Ahamitermes hillii Nicholls 1929
Anitermes conformis Gay 1968
Anitermes heterognathus Silvestri 1909
Anitermes insolitus Gay 1968
Anitermes modicus Hill 1942
Anitermes obeuntis Silvestri 1909
Anitermes obtusidens Mjöberg 1920
Anitermes pallidiceps Gay 1969
Anitermes sp. near *A. neogermanus* Hill 1942
Hesperotermes infrequens (Hill 1927)
Microcerotermes distinctus Silvestri 1909
Microcerotermes newmani Hill 1927
Microcerotermes serratus (Froggatt 1898)
Nasutitermes coalescens (Mjöberg 1920)
Nasutitermes exitiosus (Hill 1925)
Occasitermes occasus (Silvestri 1909)
Paracapritermes kraepelinii (Silvestri 1909)
Termes argutus (Hill 1929)
Termes occidualis Gay 1971
Termes tomentosus Gay 1971
Tumulitermes apiocephalus (Silvestri 1909)
Tumulitermes westraliensis (Hill 1921)

Genera allied to *Termes* Linnaeus are not necessarily easy to distinguish so, in the keys and the discussions that follow them, *Termes*, *Hesperotermes* Gay and *Paracapritermes* Hill are referred to collectively as the *Termes* complex.

Notes on south-western termite genera and species

The names of genera are listed in the same order as in the checklist, i.e., alphabetically within family.

Family Kalotermitidae

Genus *Bifiditermes* Krishna

Only a single Australian species of *Bifiditermes* is recognised, *B. improbus* (Hill 1942, Krishna 1961, Watson *et al.* 1984) (Fig. 3a). It is morphologically a very variable species that has a wide range in Australia, including Tasmania, but we have only a few records from the extreme south-west.

In common with other kalotermitids, *B. improbus* excavates a series of galleries and chambers in trees, usually eucalypts; there is no connection with the ground. The nest is centred in dead wood, but galleries extend into the live tissue. Some of the chambers contain masses of dry, sand-like faecal pellets, which can be voided through short galleries leading to the outside.

The alates of *B. improbus* are pale brown and very variable in size (Hill 1942). In the extreme south-west, they have been recorded only in January and March, although in south-eastern Australia they can occur between October and April (Hill 1942).

Genus *Cryptotermes* Banks

Gay and Watson (1982) have revised the genus *Cryptotermes* in Australia. Only one species, *C. austrinus*, has so far been found in Western Australia. Although widely distributed and, in places, abundant in central and south-eastern Australia, it

has been recorded from only one locality (Pemberton) within the extreme south-west. It has also been found not far outside the area, between Quindanning and Williams (Gay and Watson 1982). The ridging and rugosity of the soldier head, which acts as a plug to seal galleries under attack from predators, make *C. austrinus* unmistakable [Fig. 3b, and Figs. 7-12 in Gay and Watson (1982)].

As is common in species of *Cryptotermes*, the nests of *C. austrinus* occur in dead stumps, branch stubs and scar tissue, and have no connection with the ground.

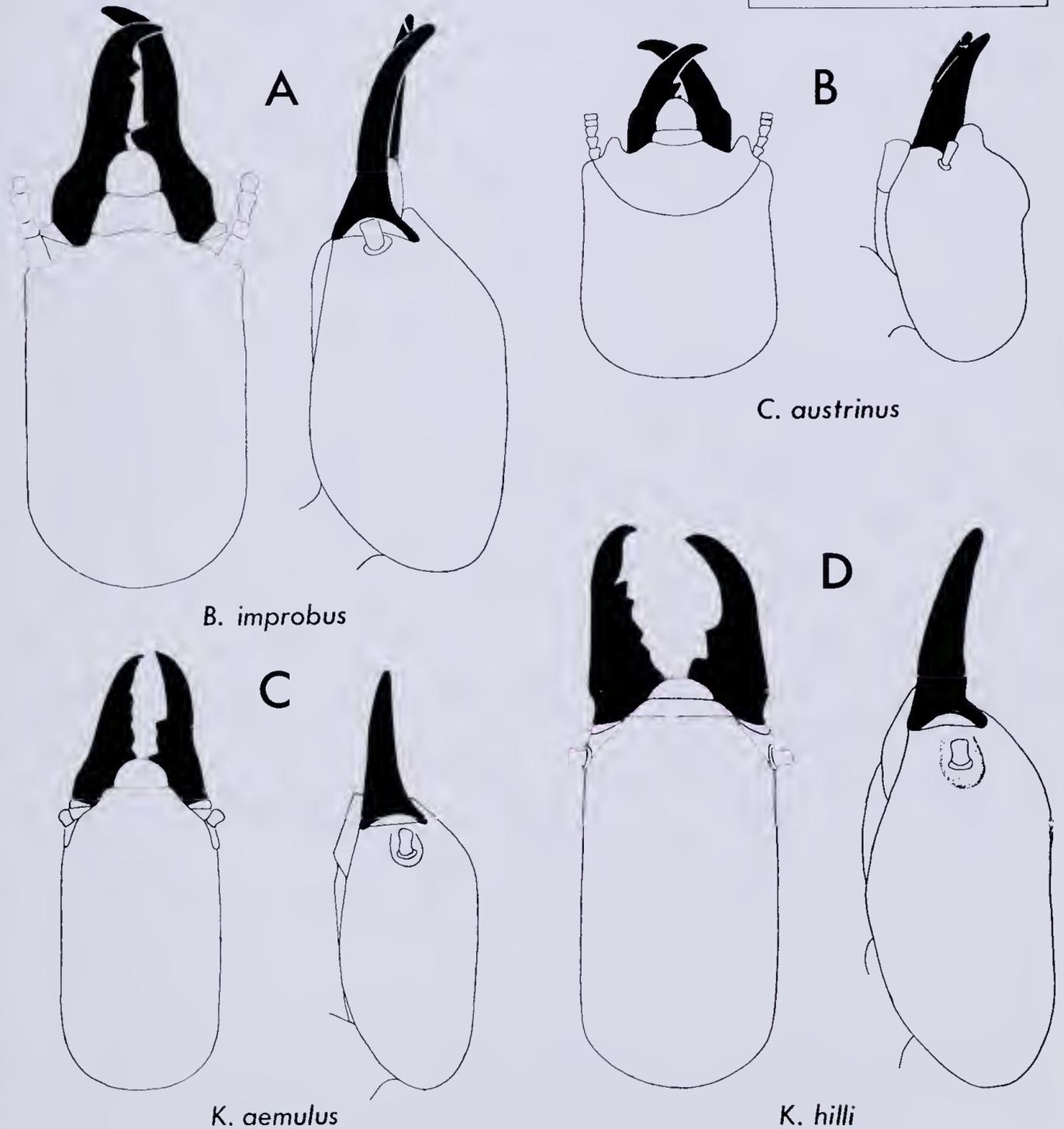


Figure 3.—Dorsal and left lateral views of kalotermitid soldier heads. Scale = 2.0 mm.

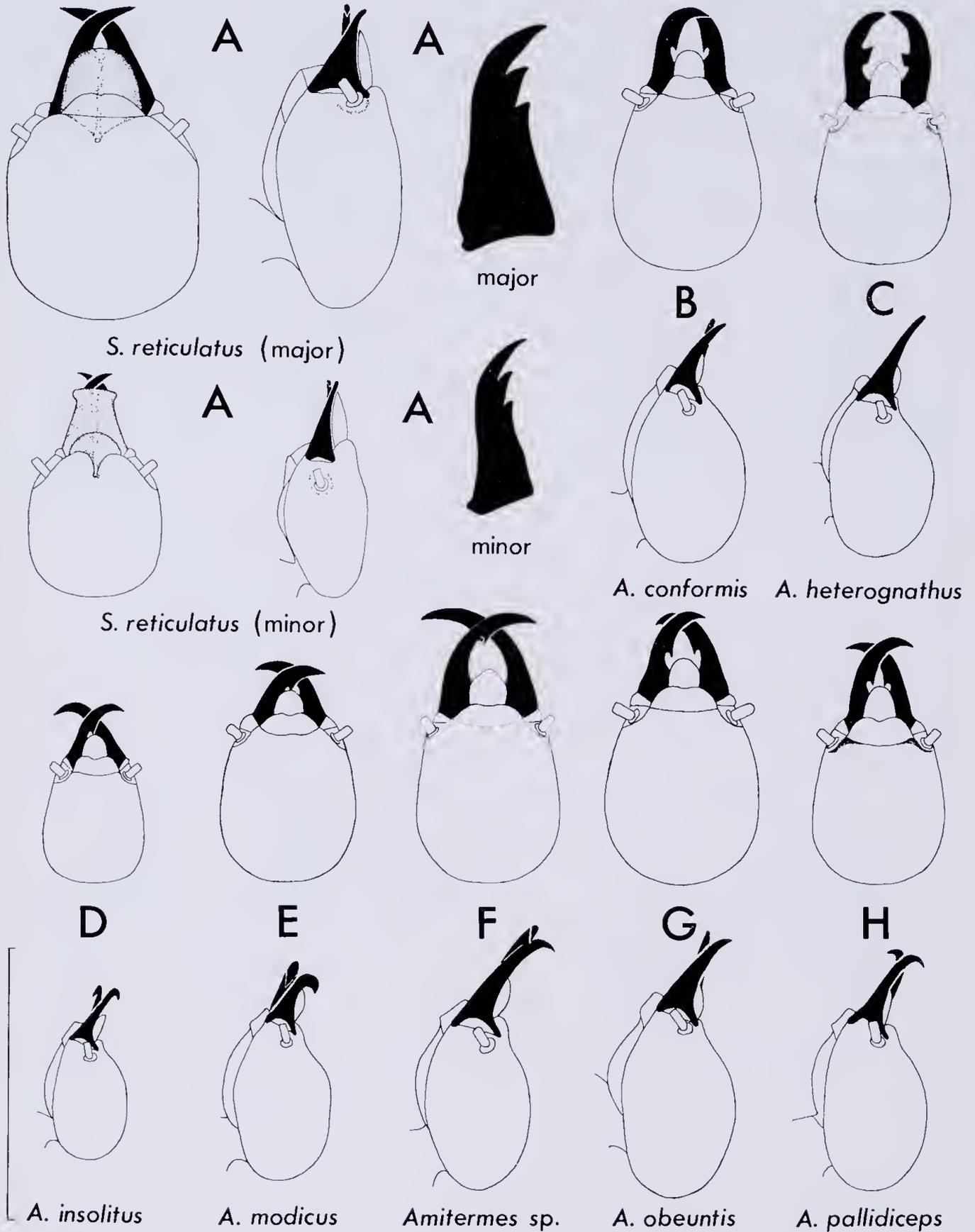


Figure 4.—Dorsal and left lateral views of heads of *Schedorhinotermes* and *Amitermes* soldiers, and left mandibles of *Schedorhinotermes* soldiers. Scale = 2.0 mm (heads) or 1.25 mm (mandibles).

In Western Australia nests have been recorded from several species of eucalypts, and comprise diffuse systems of galleries and chambers which may extend from the dead wood to living sapwood and heartwood (Gay and Watson 1982). The chambers commonly contain large quantities of dry faecal pellets, which are periodically jettisoned through small galleries cut through the outer face of the wood; normally these are plugged when not in use.

Although alates have been collected only in January in Western Australia, they have also been recorded in autumn and spring elsewhere in Australia (Gay and Watson 1982). They are mid-brown to dark chestnut in colour, with faintly brown-tinged wings.

Genus *Kaloterмес* Hagen

Two endemic species of *Kaloterмес* occur in the south-west, *K. aemulus* and *K. lilli*. Sewell and Gay (1978) gave keys for the identification of soldiers and alates. The most useful character for distinguishing soldiers is the ratio between the length of the right mandible (measured from the tip to the end of the lower condyle) and the length of its apical tooth (measured from the tip of the mandible to the tip of the first marginal tooth). This ratio is 2.55-3.13 in *K. aemulus* and 2.10-2.60 in *K. lilli* (Sewell and Gay 1978) (Figs. 3c, d).

The distributions of the two species also differ; *K. aemulus* occurs throughout the extreme south-west, whereas *K. lilli* is southern, extending from Ludlow through Bridgetown to the vicinity of Mt Barker (Sewell and Gay 1978). Both species nest in moist dead wood (on living trees, as well as logs and stumps) in which they cut diffuse systems of galleries and chambers; the nest of *K. aemulus* may extend into the root system. Faecal pellets tend to be damper and to cohere more than those of *Bifiditerмес* or *Cryptoterмес*. Major host plants for both include species of *Banksia* and *Eucalyptus*, and *K. aemulus* has been taken in *Leptospermum* (Sewell and Gay 1978).

Alates of *K. aemulus* have been found in nests from March to May, and of *K. lilli* in January (Sewell and Gay 1978).

Family **Rhinotermitidae**

Genus *Coptoterмес* Wasmann

In economic terms, species of *Coptoterмес* are our most important termites. Three occur in the extreme south-west, the endemic subspecies *raffrayi* of the widespread *C. acinaciformis* (Froggatt), *C. michaelsoni*, and an undescribed species so far known only from alates collected near Jandakot (Calaby and Gay 1956, F. J. Gay unpubl. data). Soldiers of *C.a. raffrayi* and *C. michaelsoni* are readily separable by size; those of *C.a. raffrayi* usually exceed 5 mm in overall length, with heads more than 1.2 mm wide, whereas *C. michaelsoni* soldiers are less than 4.5 mm long and have head widths of 1.0 mm or less (Hill 1942, Calaby and Gay 1956) (Figs. 5g, h). To judge from its alates (see below), the undescribed species from Jandakot is likely to have soldiers similar in size to those of *C. michaelsoni*.

Coptoterмес a. raffrayi occurs throughout the south-west, north at least as far as Northampton, and intergrading with typical *C. acinaciformis* from about Cunderdin and Lake King in the west eastwards to the vicinity of Kalgoorlie and Norseman (Calaby and Gay 1956). *C. michaelsoni*, on the other hand, has a restricted range, extending perhaps 100 km south and east from Perth, and 75 km north (Calaby and Gay 1956). The two coexist on the Swan Coastal Plain, where both can be abundant. Both species damage sound timber in service, *C.a. raffrayi* severely so.

Coptoterмес a. raffrayi builds large nests of clay and carton (*i.e.*, faecal material) in or under living or dead eucalypt trunks or stumps, and occasionally takes over mounds of *Nasutiterмес exitiosus* (Calaby and Gay 1956, J. A. L. Watson unpubl. data). It often feeds on fungus-affected heartwood of living trees (Perry *et al.* 1985), filling the resulting hollows with brown "mud gut", composed largely of faecal material, and sealing cracks in the trunk with clay. The nests of *C. michaelsoni* are unknown, but are not associated with trees (Calaby and Gay 1956); unlike *C.a. raffrayi*, *C. michaelsoni* can occur away from eucalypts. At feeding sites in dead wood, both species build a network of patchy brown carton (*cf.* Watson and Barrett 1981).

The alates of *C. michaelsoni*, and of the undescribed species, are relatively small, with heads between 1.0 and 1.2 mm wide. *C. michaelsoni* has a dark brown head, but the head of the undescribed species is pale reddish brown. *C.a. raffrayi* alates have dark chestnut-brown heads and are larger, with head widths greater than 1.2 mm, sometimes up to 1.4 mm. *C. michaelsoni* flies from August to November, and the undescribed species was recorded in August; *C.a. raffrayi* flies later, from October to early January, the main flights being in the first half of November (Hill 1942, Calaby and Gay 1956, F. J. Gay unpubl. data).

Genus *Heteroterмес* Froggatt

The two south-western species of *Heteroterмес*, *H. occiduus* and *H. platycephalus*, differ in size; the soldiers of *H. occiduus* are less than 5 mm long, with a head width of up to 0.9 mm, whereas those of *H. platycephalus* exceed 5 mm in length, and their heads are more than 1.1 mm wide (Hill 1942) (Figs. 6a, b). Both species are primarily Western Australian, although both have been recorded in South or central Australia. *H. occiduus* is closely related to the widely distributed south-eastern species *H. ferox* (Froggatt) (*cf.* Hill 1942, F. J. Gay unpubl. data), and ranges north to the north-west coast and Barrow Island, east through the Western Australian border and south to the Manjimup area, Denmark and Esperance. *H. platycephalus* is more southern, being known from Northampton and Mileura Station, in the Upper Murchison, to the south coast from Augusta to the Madura Pass.

The two species have similar habits. The nest is subterranean, apparently consisting of a rambling system of chambers and galleries, sometimes built in the nests of other species of termite. The workers feed on the sapwood or fungus-affected heartwood of a wide range of species, usually on or in the soil. Established galleries are lined with a mottled layer of faecal material, pale brown to grey, sometimes almost white.

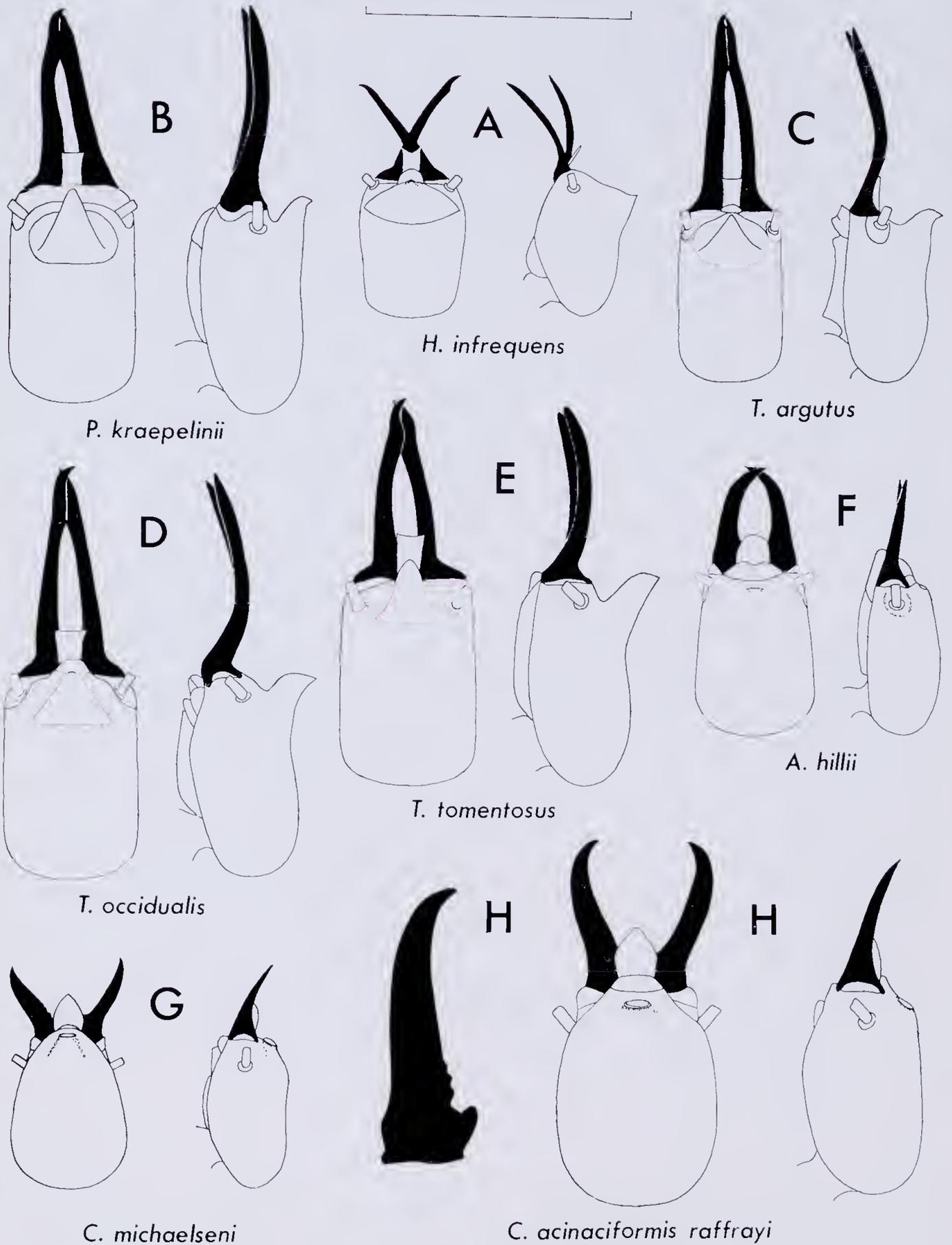


Figure 5.—Dorsal and left lateral views of soldier heads of the *Termes* complex, *Ahamitermes* and *Coptotermes*, and left mandible of *Coptotermes* soldier. Scale = 2.0 mm (heads) or 1.25 mm (mandible).

Alates of *H. occiduus* are dark brown with brown-tinged wings, whereas winged *H. platycephalus* are pale brown with wings of similar hue. Both species produce their alates in summer to autumn, *H. occiduus* in February to June and *H. platycephalus* from January to April.

Genus *Schedorhinotermes* Silvestri

Schedorhinotermes reticulatus is the only south-western species of termite that regularly has markedly dimorphic soldiers, large major soldiers and small minors (Fig. 4a). Although widely distributed in southern Australia (cf. Hill 1942), *S. reticulatus* does not extend far into the extreme south-west, being known only from Wanneroo northwards.

The nest of *S. reticulatus* has not been described, but it probably resembles the nests of other species of *Schedorhinotermes*, i.e., a small aggregation of chambers, with or without a defined nursery region, in the base of a stump or post, in logs or derelict termite mounds or, perhaps, in the soil (Hill 1942, Miller 1981). Like species of *Coptotermes*, *S. reticulatus* can damage sound timber, but it also feeds on weathered or rotted wood, and materials such as particle board (Hill 1942, Ratcliffe *et al.* 1952, J. A. L. Watson unpubl. data), lining its galleries with mottled brown faecal deposits. It sometimes ensheaths exposed surfaces with fragile earthen walling (Gay and Calaby 1970).

The alates are golden brown (Hill 1942), but their flight time in the extreme south-west has not been recorded. Elsewhere in Western Australia alates have been collected in April and May, and in south-eastern Australia, as early as January.

Family Termitidae

Genus *Ahamitermes* Mjöberg

Ahamitermes contains only one south-western species, *A. hillii* (Fig. 5f), which is known from as far east as Zanthus and Mt. Ragged and north to the lower Murchison. A related species, *Ahamitermes inchus* Gay, has been recorded north and east of Geraldton and Northampton (Gay 1955).

Species of *Ahamitermes* are inquiline in the fabric of live *Coptotermes* nests, in trees and in mounds. The gallery systems of the inquiline and its host are separate. *A. hillii* lives in the nests of *C. acinaciformis*, of both subspecies, forming its nest just above the nursery of its host (Gay 1955). As far as known, *A. hillii* subsists on carton, i.e., those parts of the host's nest built predominantly of faecal material.

Alates of *A. hillii* are released in February to April, from small domes, 5-10 cm high on the foot of the host mound, or near the base of the tree in which the host is living. They are predominantly dark brown above, with paler brown wings (Hill 1942).

Genus *Amitermes* Silvestri

Amitermes is the largest of the termite genera recorded from Australia, with upwards of 100 Australian species known (Gay 1968, F. J. Gay and J. A. L. Watson unpubl. data). Eight species have been recorded from the extreme south-west, but the status of one of these, *Amitermes obtusidens*, is uncertain (see below). A key to soldiers of the

remaining seven is given in Table 3, and Gay (1968) has provided a key to the alates of the then-known Australian species.

Amitermes conformis (Fig. 4b).—*A. conformis* is known only from the south-west, east to Hyden and Kirwan and north to Yuna; it extends to the south coast. It is closely related to *A. modicus*. Its workings are typical of *Amitermes*, the galleries and chambers having dark brownish, woody walls. It may occur in mounds of other species of termite and, near Denmark, has been collected from mounds, apparently self-built, approximately 20 cm in diameter and 5-10 cm high. It feeds on sapwood and decay-affected heartwood of a range of tree species.

Alates have been taken on the wing in February to May (Gay 1968).

Amitermes heterognathus (Fig. 4c).—*A. heterognathus* is also endemic to south-western Australia. It has been recorded as far north as Northampton, and east to Corrigin and Gnowangerup. In the extreme south-west, *A. heterognathus* extends to the south coast. Its galleries and chambers have grey-brown, woody linings, and it may ensheath its food (fungus-affected wood, cow dung and other plant debris) with fragile earthen walling. It also invades the fabric of termite mounds.

Alates have been collected from mid-February until early April (Gay 1968).

Amitermes insolitus (Fig. 4d).—There is very little information on *A. insolitus*. Although the first series known was collected from the gut of a frog, *Myobatrachus gouldi* (Gray) (Gay 1968), labelled as having been collected in Perth, subsequent searches on the Swan Coastal Plain have failed to uncover further material. *A. insolitus* is, however, present at eneabba, where it constructs fragile chambers and galleries in the soil. It apparently feeds on vegetable debris.

Alates have been collected in April (Gay 1968).

Amitermes modicus (Fig. 4e).—*A. modicus* is closely similar to *A. conformis* but has a wide distribution in southern Australia, occurring in all the southern mainland states. In Western Australia it has been recorded north to Three Springs, east to the South Australian border, and south to the coast at Israelite Bay. In the extreme south-west, it is known as far south as the Manjimup area and Denmark. It is common on the Swan Coastal Plain.

The biology of *A. modicus* in the south-west is much like that of *A. heterognathus*. *A. modicus* feeds primarily on weathered or rotted wood, but has also been collected from dry cow dung and plant debris (Ferrar and Watson 1970). It also invades the mounds of other termites.

South-western records of alates have been made in February to April (Gay 1968).

Amitermes obeuntis (Fig. 4g).—Widespread in the southern part of Western Australia, *A. obeuntis* is also known from a few localities in South Australia (F. J. Gay unpubl. data). In the west it has been taken as far north as Yuna, east to Karonie and Balladonia and, in the extreme south-west, along the entire south coast where soils are suitable. It is extremely abundant in many areas.

Amitermes obeuntis is usually a mound-builder. The mounds are of clay, which restricts the species to soils where clay is accessible, and are commonly 5-10 cm high and 30 cm or more wide, although some mounds are 60-90 cm high. They are often irregular in shape, unlike the mounds of *Nasutitermes exitiosus* (see below), and their central region is made up of broad, transversely oriented chambers. The mounds provide housing for many other species of termite, and is not uncommon to find several species of invaders in a single mound. Conversely, *A. obeuntis* may be found in nests of other termites, and in chambers in the soil. Its diet apparently consists of weathered wood, but there are a few records of finely comminuted forage stored in its mounds.

Alates can be found in the nests from late February until June (Hill 1942, D. H. Perry unpubl. data).

Amitermes obtusideus.—Hill (1942) recorded *A. obtusideus* from the extreme south-west. A well-known eastern, northern and central Australian species, it has not been found in Western Australia again, and its status as a south-western termite must be regarded as very doubtful. It has, therefore, been omitted from the key. The soldier has blunt, peg-like mandibular teeth, unlike those of any other extreme south-western termite (cf. Hill 1942).

Amitermes pallidiceps (Fig. 4h).—Originally described as *A. pallidus*, *A. pallidiceps* is poorly known (Gay 1968, 1969). It has been collected only from Upper Swan and near Bindoon, from galleries in the soil and what might have been a nest in an old mound of *Nasutitermes exitiosus*. Its diet is unknown.

Alates have been recorded in April (Gay 1968).

Amitermes sp. near *A. neogermanus* (Fig. 4f).—As with some other south-western *Amitermes*, this undescribed species is little known. It has been recorded only from siliceous sands between Eneabba and Gnangara, but it could well extend farther south. All the known specimens were collected from brown, woody-walled chambers and galleries in the soil. Presumably, this *Amitermes* does not feed on wood but, perhaps, on other buried plant material. The alate is unknown.

Genus *Hesperotermes* Gay

See below, under *Termites* complex.

Genus *Microcerotermes* Silvestri

The Australian species of *Microcerotermes* are much in need of revision. The status of the south-western species is poorly understood. Three have been recorded, *M. distinctus*, *M. newmani* and *M. serratus*, but south-western material attributed to *M. distinctus* and *M. serratus* is very limited. Furthermore, *M. serratus* is a very variable species (Hill 1942), and may constitute a species-complex; its occurrence in the extreme south-west is open to doubt (D. H. Perry unpubl. data). We therefore confine our comments to *M. distinctus* and *M. newmani*.

Microcerotermes distinctus and *M. newmani* can readily be identified by differences in size; *M. distinctus* soldiers have a body length usually exceeding

6 mm and a head width of 0.87-0.98 mm, whereas *M. newmani* is smaller, the soldier being 4.2 to 5.3 mm long with a head 0.74-0.82 mm wide (Hill 1942) (Figs. 6c, d). *M. distinctus* is widely distributed in inland Australia, including the Western Australian wheat belt, but has been recorded from the extreme south-west only in and north of the Perth metropolitan area, including Mundaring, and south on the Darling Scarp at Wagerup. *M. newmani*, in contrast, is confined to Western and South Australia and, in W.A., extends north at least to Barrow Island and Jigalong Mission, east to Warburton Mission, and south to the coast.

Little is known of the nests of *Microcerotermes* in the south-west (cf. Hill 1942). Both south-western species inhabit galleries and chambers in the soil, in wood, and in the nests of other species of termite. Reproductives and young have been found in brown woody cells in clumps some 10 cm in diameter, and in old mounds. Both species commonly feed on fungus-affected wood, usually on or near the ground, plant debris and dung (cf. Ferrar and Watson 1970), although *M. serratus* has recently caused extensive damage to railway sleepers in the Pilbara region (J. E. Barnacle pers. comm.). The galleries of *Microcerotermes* are built of pale to, more commonly, dark brown carton.

Alates of *M. distinctus* are predominantly dark brown, with smoky brown wings, whereas *M. newmani* has reddish brown alates (Hill 1942). In the extreme south-west, *M. distinctus* alates have been collected in February and March, and those of *M. newmani* in December to February. Farther inland, alates of *M. distinctus* have been recorded from August to May, but only in January and February in the case of *M. newmani*.

Genus *Nasutitermes* Dudley

Although two species of *Nasutitermes* have been recorded from the extreme south-west, it seems likely that only one occurs there. *Nasutitermes coalescens*, originally described from Mundaring (Mjöberg 1920), has not been recorded from the south-west since (Hill 1942), and our more recent data indicate that it is a north-western species. We have, therefore, disregarded it in constructing the key. *Nasutitermes exitiosus*, on the other hand, occurs virtually throughout southern mainland Australia, and is of some economic importance (Hill 1942; Watson and Barrett 1981) (Fig. 6h). The subject of many studies, it is better known than any other Australian species of termite (Watson and Gay 1981).

Throughout the extreme south-west, but not necessarily in the inland, *N. exitiosus* builds uniformly domed mounds, commonly up to 1 m in diameter and approximately half that in height. The outer casing of the mound is usually friable, but the inner material is tough and woody carton, enclosing a central nursery with thin, fragile walls (cf. Hill 1942; Watson and Barrett 1981). Subterranean galleries radiate out to about 50 m from the mound, to feeding sites in dead standing or fallen timber, or in litter; both sound and fungus-affected wood are eaten.

There are a few records of *N. exitiosus* hollowing-out living trees (J. A. L. Watson and H. M. Abbey unpubl. data), and many of it attacking timber in service, including buildings (Watson and Barrett 1981). Gallery work, and the material used to fill hollowed timber, are dark brown.

Alates of *N. exitiosus* have reddish brown to dark brown bodies and yellowish brown, translucent wings (Hill 1942). The main flight is in spring, commonly October, but a second flight of alates may be produced, coinciding with late summer or autumn rains (Watson and Abbey 1985).

Genus *Occasitermes* Holmgren

Two species of *Occasitermes* are known, one, *O. occasus*, being widely distributed in south-western Australia, with an outlier on the Eyre Peninsula in South Australia (Calaby 1956, Gay 1974). *O. occasus* is abundant in the extreme south-west, where it is the only nasute termite with yellowish-headed soldiers (Fig. 6e).

The nest of *O. occasus* apparently consists of widely-spaced galleries and chambers in the soil; no compact nest has been discovered. It also commonly occurs in mounds of *Amitermes obeuntis*. *O. occasus* feeds on sapwood and weathered, fungus-affected heartwood from a range of trees (Gay 1974), and its galleries have pale brown walls.

The alates are pale reddish to tawny brown, and have been collected throughout the year (Hill 1942, Gay and Calaby 1970, Gay 1974).

Genus *Paracapritermes* Hill

See below, under *Termes* complex.

Generic complex *Termes* Linnaeus

Genera of the *Termes* complex all have soldiers with long mandibles, often comparable in length with the head capsule (Figs. 5a-e); the soldier can forcibly click them into a crossed position. The taxonomy of the Australian members of the complex is at present under study (L. R. Miller unpubl. data), and the southern Australian members, including those from the south-west, were reviewed by Gay (1971). The five south-western species are allocated to three genera but, as is common in the complex, neither genera nor species are necessarily easy to identify. It is, therefore, best to treat them together.

Soldiers of the five species are keyed in Table 3.

Hesperotermes infrequens, the only species of its genus, is entirely south-western, extending north to Eneabba, east to Woorooloo and to near Williams, and south to the coast. The soldier is distinguished not only by its reduced frontal tubercle (Fig. 5a), but also by its reddish brown head capsule.

The only south-western species of *Paracapritermes*, *P. kraepeliii*, has asymmetrically swollen mandibles in the soldier, the left mandible being markedly more irregular in width than the right (cf. Gay 1971) (Fig. 5b). However, when the mandibles are crossed,

their asymmetry may be difficult to recognise unless they are dissected out and placed in an uncrossed alignment. *P. kraepeliii* is endemic to Western Australia but is more widespread than *H. infrequens*, with many records from the wheat belt and a few as far east as Leonora, but none in the extreme south.

Of the three species of *Termes* one, *T. argutus*, occurs widely in southern and central Australia. The southernmost record in the extreme south-west is from Hamel, but *T. argutus* is, apparently, common in the Kojonup-Tambellup-Gnowangerup area, and north and east of it. The other two species, *T. occidualis* and *T. tomentosus*, are both endemic and have ranges closely overlapping that of *H. infrequens*.

All south-western members of the complex inhabit galleries and chambers in the soil or in the nests of other species of termite. However, in the southern part of the extreme south-west, *T. occidualis* builds low, blackish, woody carton and soil mounds. All species feed on rotted wood and plant debris, and their galleries are dark-walled.

Gay (1971) included a key to the alates. They have been recorded during the following months: *H. infrequens*, March-April; *P. kraepeliii*, February-March; *T. argutus*, February (in W.A.); *T. occidualis*, January-April; and *T. tomentosus*, April.

Genus *Tumulitermes* Holmgren

Of the two south-western species of *Tumulitermes* one, *T. apiocephalus*, has also been recorded from the western slopes of New South Wales, whereas *T. westraliensis* is endemic. Both occur throughout much, if not all, of the extreme south-west. *T. apiocephalus* ranges north at least as far as Shark Bay and east, within the State, to Paynes Find and Salmon Gums, but *T. westraliensis* has a slightly more southern range, north to Three Springs and east to Esperance. There is also a single series from Giles.

Tumulitermes apiocephalus is a small species, the soldier being less than 4 mm long, with a pale, reddish brown head, whereas the soldier of *T. westraliensis* is larger, usually much longer than 4 mm, with a very dark brown, almost black, head (Figs. 6f, g). There is occasional soldier dimorphism in both species.

Tumulitermes apiocephalus lives in galleries and chambers, lined with dark brown carton, in the soil and in mounds of other species of termite. It feeds on plant debris and rotted wood, and may store finely comminuted forage. *T. westraliensis*, however, builds low, irregular, clay mounds and, hence, is not found on deep sand. It eats grasses, forbs and dry plant litter, which it gathers in the open at night and stores in its mounds. It is the only harvester termite in the extreme south-west, for the most highly specialised of the Australian harvester termites, of the genus *Drepanotermes* Silvestri, narrowly fail to extend into the region (cf. Watson and Perry 1981).

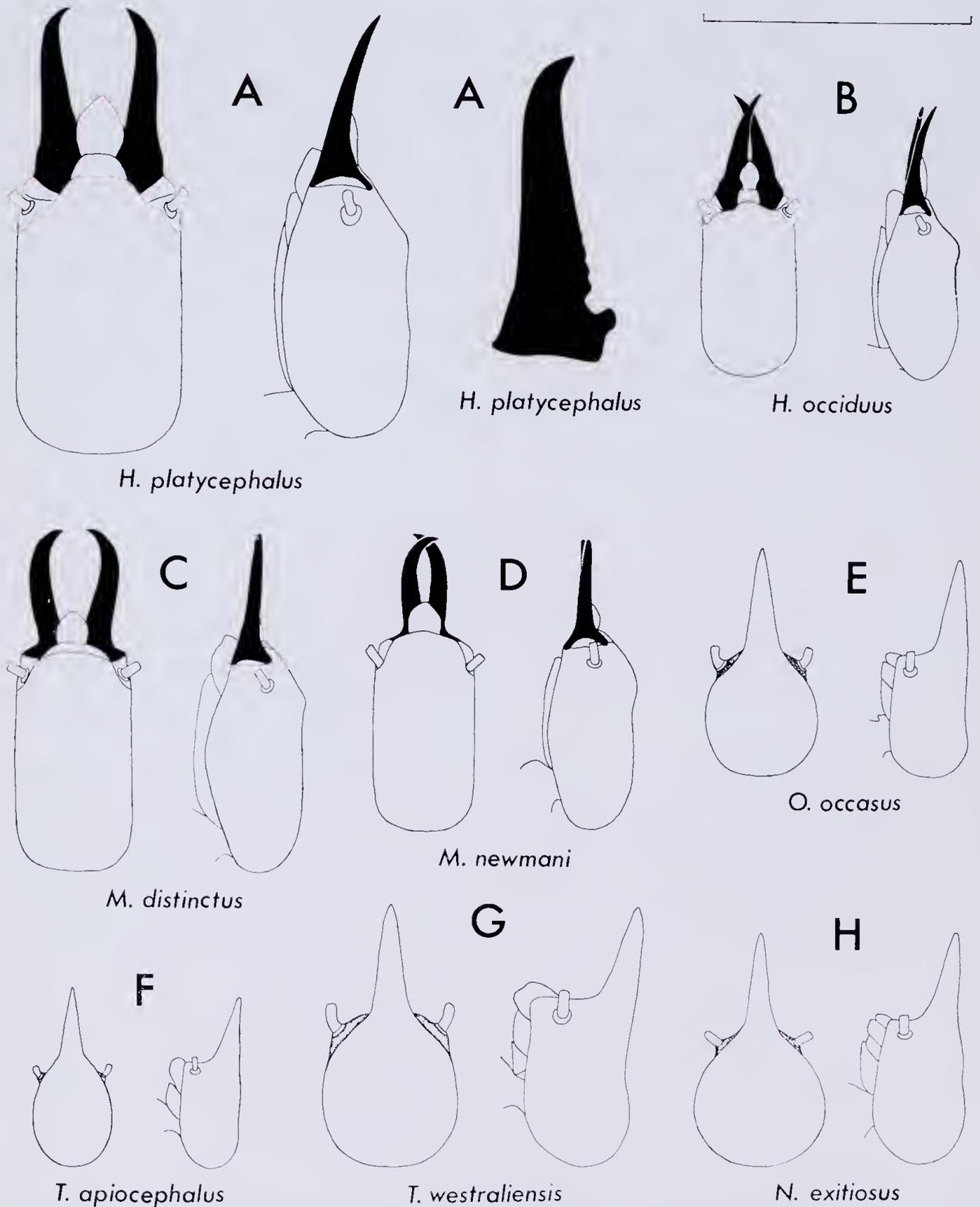


Figure 6.—Dorsal and left lateral views of soldier heads of *Heterotermes*, *Microcerotermes* and nasute genera, and left mandible of *Heterotermes* Soldiers. Scale = 2.0 mm (heads) or 1.25 mm (mandible).

The alates of both species are very dark brown, almost black, with brown wings (Hill 1942). Alates of *T. apiocephalus* have been collected in the south-west from October to February, and of *T. westraliensis* in September to July, perhaps occurring throughout the year (cf. Gay and Calaby 1970).

A third species, *T. comatus* (Hill), has been recorded slightly north of Yanchep. It is widespread elsewhere in Australia, including the Western Australian wheat belt, and may occur within the extreme south-west. The soldier has an orange-brown head, paler than that of *T. apiocephalus*, and colonies near Yanchep are housed in small, dark brown woody nests, approximately 30 cm in diameter, the tops of which just subtend the soil surface. *T. comatus* feeds under earthen sheathing, on weathered wood and plant debris.

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CORRIGENDUM

Volume 67, Part 1.

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Page headings should read as follows:

Page 1—Journal of the Royal Society of Western Australia, Vol. 67, Part 1, 1984, p. 1-13.

Page 14—Journal of the Royal Society of Western Australia, Vol. 67, Part 1, 1984, p. 14-25.

Page 26—Journal of the Royal Society of Western Australia, Vol. 67, Part 1, 1984, p. 26-27.

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Journal
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Volume 67

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PART 2

Contents

	Page
The flora and vegetation of Mt. Lesueur, Western Australia, By E. A. Griffin and A. J. M. Hopkins	45
<i>Acacia cyclops</i> G. Don (Leguminosae-Mimosaceae) in Australia: distribution and dispersal. By A. Malcolm Gill	59
Guide to the termites (Isoptera) from the extreme south-west of Western Australia. By D. H. Perry, J. A. L. Watson, S. E. Bunn and R. Black	66
Corrigendum	79

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Mangrove environments of Port Darwin, Northern Territory: the physical framework and habitats

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Abstract

Port Darwin, with its mangrove-vegetated tidal flats, is a ria coast formed by the post-glacial marine flooding of a dissected plateau. The major ancestral riverine courses and the local terrestrial geomorphology have pre-determined the structure of the coast. The large-scale coastal units recognised in this study are: (1) narrow embayments; (2) broad embayments; (3) embayments with spits/cheniers; (4) islands; (5) riverine channels; and (6) open oceanic coast. Subsequently, depending on the interplay of sand/mud tidal sedimentation, terrestrial sedimentation, tidal creek erosion, wave erosion or equilibrium conditions, there have been developed a wide range of medium-scale geomorphic units: (1) tidal flat/hinterland contact, (2) high tidal alluvial fans, (3) the main tidal flat, (4) tidal creeks, (5) spits/cheniers, and (6) rocky shores. Each of these units have their own suite of substrate types.

Stratigraphic analyses show that much of the tidal lands are infilled terrestrial lowlands. The main tidal flat accumulation has resulted in a wedge of mud which interdigitates with gravel/sand deposits developed along the hinterland edge, and with sand deposits of the spits/cheniers. On the sandy coasts the stratigraphic interval is composed of sand overlying bedrock. Sediment discharge from the hinterland and fluvial sources continue to accrete sediment along the tidal flat edges. The stratigraphy also shows that muddy tidal flat coasts, spit/chenier coasts and rocky shores are long-term stable features.

The stratigraphic/lithologic system forms the framework for both the tidal flat hydrologic system and the tidal flat/hinterland hydrologic exchanges. Soilwater and groundwater regimes are linked closely to stratigraphy, substrate, recharge mechanisms and evapotranspiration. The salinity of groundwater and soilwater on tidal flats shows a graded increase in value from seaward mangrove environments through to salt flats, with a decrease in values along the freshwater-influenced hinterland margin and alluvial fans.

The interplay of substrate type, salinity and tidal level results in a proliferation of habitat types which have distinct mangrove assemblages. These habitat types correspond to geomorphic unit types. Eight broad mangrove assemblages have been recognised in the Port Darwin region; these are: (1) hinterland fringe assemblage inhabiting the tidal flat/hinterland contact; (2) alluvial fan mangrove assemblage, inhabiting high tidal alluvial fans; (3) main tidal flat mangrove assemblage; (4) creek bank assemblage; (5) creek shoal assemblage; (6) creek mouth assemblage; (7) spit/chenier assemblage, inhabiting margins of spits/cheniers; and (8) rocky shore assemblage. Within the habitats there are local small scale gradients in salinity, soil types and frequency-of-inundation which result in zonation within any given assemblage.

Introduction

This paper reports on studies conducted over several years on the tidal flats and mangroves of Port Darwin (Fig. 1). The first most comprehensive published work on the Darwin area dealt with the hinterland and described landforms, soils, geology, vegetation and land use of the Katherine-Darwin region with brief description of the littoral vegetation (Christian and Stewart 1953). Subsequently publications have dealt with regional geology (Bureau of Mineral Resources 1961), regional bathymetry (Hydrographic Service, RAN 1973) and climate (Bureau of Meteorology 1976), but there are no published detailed studies on the coastal sector. The flora and fauna, both marine and terrestrial, have been described in Christian and Stewart (1953), Blackburn (1975), Gow (1977) and Fogarty *et al.* (1979).

Mangrove species and the various fauna in mangals of Darwin have been listed by Saenger *et al.* (1977) and Wells (1982) as part of their regional studies of Northern Australian mangroves. Some data on mangrove environments of Port Darwin also are scattered in numerous unpublished reports which are

retained by various government, industrial or private organisations. Such studies, however, were initiated *ad hoc* to gather data relevant for a particular project and the results have limitations in that they do not provide an overview (framework) of the environment for the Port Darwin mangroves because they are oriented toward specific problems.

The objectives of this paper are to provide:

- firstly, a description of the Port Darwin area in terms of its morphology, stratigraphy, substrates and hydrology, all of which are useful in understanding the basis of the mangrove systems;
- secondly, a classification of mangrove habitats and assemblages of Port Darwin; and
- finally, a brief description of the mangrove assemblages in terms of distribution and composition.

A second paper describing in more detail the structure, composition and zonation of the mangrove assemblages and their relationship to habitats of Port Darwin is in preparation.

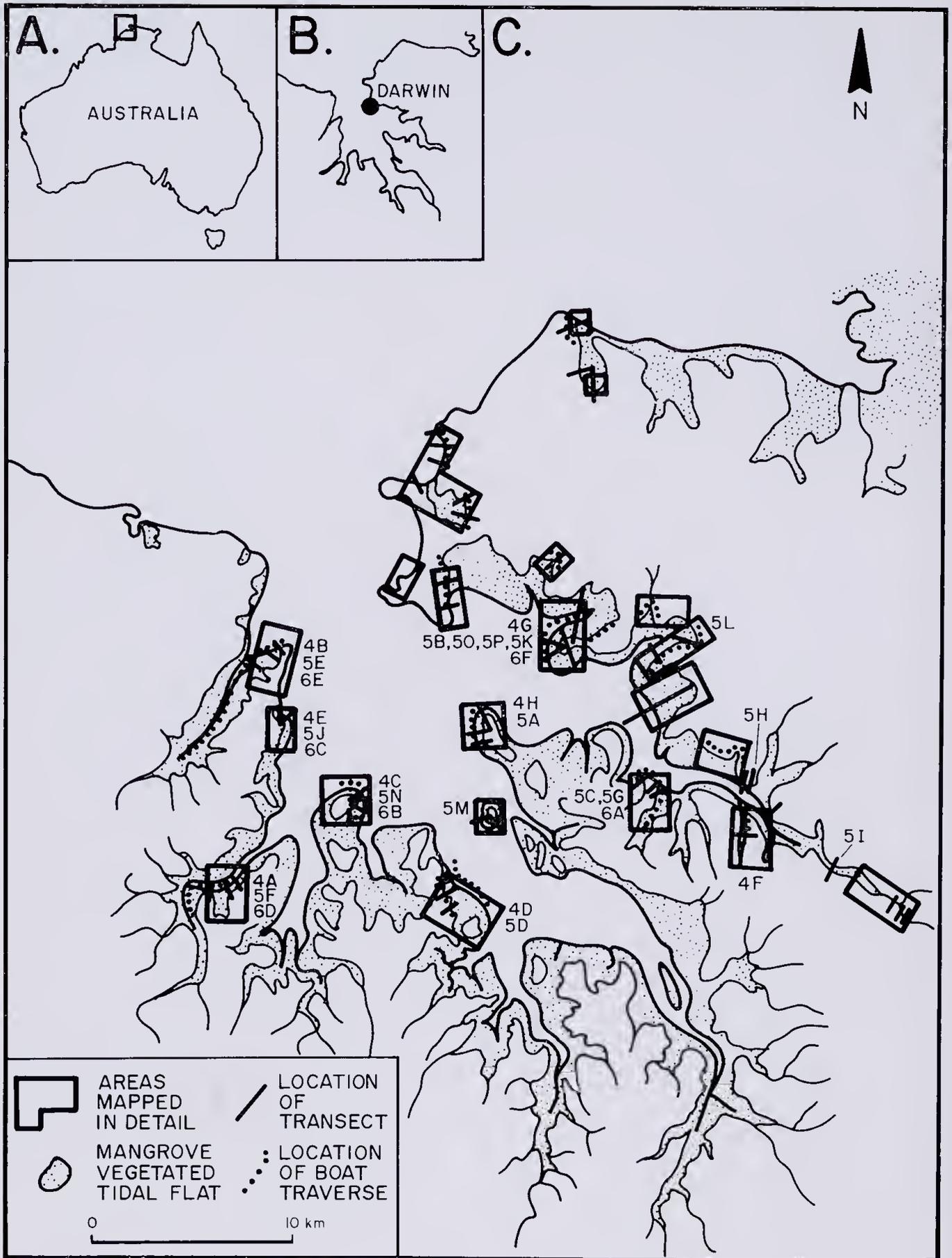


Figure 1.—Maps showing study area and location of study sites (mapped area) transects, boat traverses. Numbers alongside designated mapped areas refer to Figure numbers wherein maps and profiles are illustrated in more detail.

Methods

Mangrove-vegetated tidal flats are a complex product of natural physico-chemical and biological interactions. Accordingly, in documenting these systems, it is necessary to use an interdisciplinary approach, utilising data on regional setting and processes with that of the local environment, and integrating data on physiography, oceanography, hydrology, chemistry, sedimentology, stratigraphy, and biology.

A three-phased approach was used in the documentation of mangrove environments of Port Darwin. Firstly, with coloured aerial photographs the main large-scale coastal types were identified (Table 1): (1) narrow embayments, (2) broad embayments, (3) spit/chenier-lined embayments (4) islands with spits and connecting tidal-lands, (5) riverine embayments, (6) oceanic rocky shores, and (7) oceanic sandy shores. Secondly, the various phototones within a mangrove-lined coastal type were checked by transects through mangrove zones, by lengthy boat traverses along the seaward mangrove fringe and creek banks, aided by spot checks (by vehicle, boat or helicopter). The main phototones investigated were: (1) mangroves on high-tidal alluvial fans, (2) mangroves fringing the hinterland, (3) high-tidal mangroves fringing spit/cheniers, (4) stands of *Ceriops*, (5) stands of *Rhizophora*, (6) stands of *Sonneratia*, (7) stands of *Avicennia* (mixed with other species), (8) stands of *Rhizophora/Campostemon*, (9) salt flats, (10) cyclone-destroyed (vegetation-

clear) patches within *Rhizophora* stands, (11) cyclone-cleared patches within *Ceriops* stands, (12) terrestrial parts of spits/cheniers, (13) rocky shores, (14) mid-low tidal flats, (15) small-scale (*ca* 1 m) cliffs, (16) terrestrial freshwater drainage/vegetation units and (17) the terrestrial hinterland and its vegetation.

Thirdly, selected areas were investigated in more detail along (some 36) transects to study geomorphology, substrate, stratigraphy, soil/groundwater salinity, fauna and flora (Fig. 1C). Sampling of flora/fauna generally was not extended to below MSL because the study concentrated mainly on mangrove environments. Mangrove vegetation composition, height, canopy structure and distribution was documented by continuous belt transect to verify disposition of zones and their phototones. At selected intervals, usually in the middle of a zone or phototone, the composition and density of the vegetation was quantified within five replicate 5 m x 5 m quadrats. In many locations ten, fifteen or twenty replicates were used because of low numbers of individuals or variability of composition. In total some 3 000 quadrats were counted.

Substrate and groundwater/soilwater were sampled at the same sites as vegetation. Soil, excavated to 30 cm, was described in terms of: colour, structure, fabric, texture and composition. The surface soil, the soil at 25-30 cm depth and the groundwater table were sampled for salinity analyses. Soil samples were hermetically sealed and frozen, and thawed only when ready for laboratory analysis. Groundwater samples, and water extracted from soil samples, were analysed for total dissolved solids by evaporation technique.

The stratigraphy of sites was investigated by pits (0.3-1.2 m deep), auger (0.3-4 m deep), and by probing with an extendable rod to 8 m deep. With probing the following rock/sediment types could be differentiated in the subsurface: (1) mud, (2) sand, (3) rock, (4) gravelly sediment, (5) muddy sand, (6) interlayered sandy and muddy sediment.

At all sampling sites along the transects note was made of processes that were important to the tidal flat system. In many instances the processes could be directly observed, otherwise it was necessary to document the products and hence infer the processes. Some of the main processes and products noted were as follows: (1) *physical*: wave reworking of substrates producing cleanly washed sand/gravel; fluvial sheetwash from the hinterland during the wet season, producing aprons of sand along the hinterland edge; tidal current/wave action erosion of mud, producing small steep cliffs; seepage of freshwater, diluting the normal tidal flat water; seepage of marine water from slope of sand bar beaches; (2) *chemical*: alternating oxidation/reduction of substrates at groundwater table, producing Fe colour mottles in substrates; precipitation of CaCO₃ and ironstone, producing illuvial hardpans; precipitation of halite from soilwater, producing a surface efflorescent on the salt flat; (3) *biological*: burrowing by fauna, producing bioturbation structures, open burrows and burrow excavations; predation by fish, producing fragmented shells; binding of substrates by vegetation pneumatophores and other roots.

Table 1

Distribution and relative abundance of medium-scale geomorphic tidal units within large-scale morphologic units

MAJOR UNIT	MEDIUM-SCALE GEOMORPHIC UNIT
Narrow embayments	tidal flats > hinterland margins > tidal creeks > alluvial fans ≥ rocky shores
Broad embayments and spit/chenier-lined embayments	tidal flats > hinterland margins > tidal creeks spits/cheniers > alluvial fans ≥ rocky shores
Islands	tidal flats > spits/cheniers ≥ rocky shores
† Riverine embayments	steep banks, cliffs, shoals, narrow tidal flats, hinterland margins, alluvial fans
* Exposed cliff rocky shores	rocky pavements, rocky slopes, cliffs
* Exposed sandy shores	sand beaches, beach ridges and coastal dunes

† not considered further in this paper because this unit is assigned to the Riverine Zone of the regional system.

* not considered further in this paper because these units generally do not support mangals; they are included only for completeness.

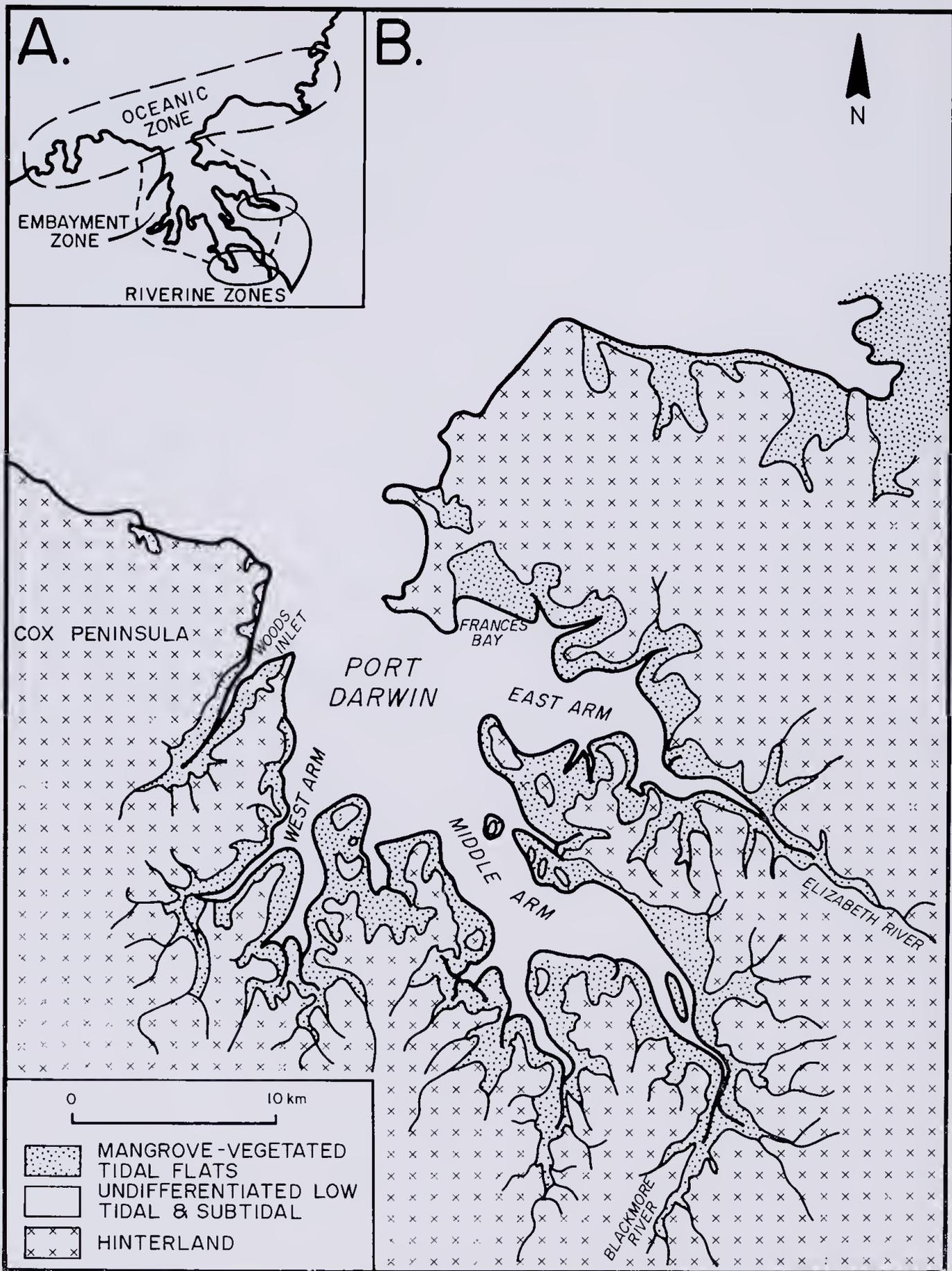


Figure 2.—A. Map showing regional characterisation of Port Darwin area into Oceanic, Riverine and Port Darwin Embayment zones. B. Map of Port Darwin showing distribution of mangrove-vegetated tidal flats.

Results

Description of Port Darwin Environment: Regional Setting

Climate

Darwin has a tropical humid climate (Aw of Köppen 1936) with two major seasons: a summer wet season which may be classed as monsoon, and a winter dry warm/hot season. Bureau of Meteorology (1976) data show that Darwin has some 97 rainy days per year with about 1,500 mm of precipitation. Mean maximum summer temperature in January is 32.2°C; mean minimum summer temperature is 25.0°C. Mean maximum and mean minimum temperatures in winter in July are 30.4°C and 19.6°C, respectively. Evaporation is 2,773 mm per year with a monthly minimum of 187 mm during February, and a monthly maximum of 285 mm during October.

Wind originates from various sectors dependent on the time of day and season (Bureau of Meteorology 1973). In winter it originates from southeast (and in addition south and east) sectors in the morning and may shift to east, southeast (and north) sectors in the afternoon with average speeds of 2.5-2.8 m/sec.; in summer, it originates from a variety of sectors but mainly from west, northwest and south in the morning and shifts to west, northwest and north sectors in the afternoon with average speeds of 2.6-3 m/sec. Storms in the summer generally approach from the west, north and northwest. Periodically tropical cyclones impinge on the coast. These are associated with destructive winds, substantial rainfall and storm surges.

Oceanography/Riverine Hydrology

Port Darwin tides are macrotidal; the maximum range is 7.8 m; the mean spring range is 5.5 m and the mean neap range is 1.9 m (Australian Tide Tables, 1983). Tidal currents measured near the main jetty are 0.25-1.4 m/sec. Landbreeze/seabreeze systems and thunderstorms generate local waves which are an important prevailing feature in the coastal zones in that they develop spits, sand bars and cheniers on the exposed portions of the coastline.

Port Darwin functions seasonally as a large estuary because, during the monsoon and shortly afterwards, the main rivers discharge substantial quantities of freshwater into the marine system. There is also a substantial input of freshwater from the surrounding hinterland by sheet flooding and by the numerous small creeks and streams. Subterranean freshwater seepage from the hinterland also continues as an important phenomenon well into the dry season.

Regional Coastal Morphology (Large Scale Units)

The Port Darwin area is a large indented embayment some 450 km² in area (Fig. 1). The hinterland is a dissected plateau underlain by Precambrian rocks with a variable cover of Cainozoic laterites and weathering products (Christian & Stewart 1953). The hinterland landforms have determined to a large extent the disposition of coastal and marine landforms and environments within Port Darwin.

Two major rivers, the Elizabeth and the Darwin River/Berry River drain into Port Darwin. The disposition of these rivers and their distributaries has controlled the *regional scale structure and shape of Port Darwin*. The (post-glacial) marine flooding of

the Elizabeth River has developed East Arm; flooding of the Darwin and Berry Rivers has developed Haycock Reach, and flooding of various tributaries has developed West Arm and Woods Inlet.

The regional large-scale morphology in this study area can be categorised as (Fig. 2):

- (1) *Riverine channels*, which constitute the headwaters of the main rivers/creeks that drain into Port Darwin; Holocene riverine processes are dominant in shaping both the medium scale geomorphology and sedimentation patterns; there are steep tidal river banks, riverine shoals and channels, and freshwater flow that seeps into and interacts with the marine environment.
- (2) *Open oceanic coastline*, comprised of rocky and sandy shores that front the open Timor Sea; locally there are small embayments.
- (3) *The Port Darwin Embayment*, formed by the marine flooding of the dissected Pleistocene terrain.

Embayment-dominant environments of Port Darwin form the main emphasis of study for this paper. Riverine and oceanic environments are not discussed further.

Physical Features of the Port Darwin Embayment

Geomorphology

Prior to the post-glacial transgression, Port Darwin was a dissected terrain which had a subdued drainage, scattered subplanar lowland plains and wetlands, scattered hillocks, knolls and hills, and riverine courses. Marine flooding and sedimentary infill of this terrain has resulted in a development of narrow embayments, broad embayments, islands and tidal land connections between these islands. At the large scale the shoreline of this embayment-dominated system can be subdivided into the following *intergradational* units (Fig. 3):

- (1) *Narrow embayments*, where relatively narrow riverine courses have been flooded by the post-glacial transgression and infilled with tidal deposits (mud).
- (2) *Broad embayments*, where open undulating terrain has been flooded by post-glacial transgression and filled with tidal deposits.
- (3) *Embayments with spits/cheniers*, as for (2) above but with more exposure to waves such that reworking of sediments develops spits/cheniers.
- (4) *Islands*, where hills of the original terrain have been isolated by marine flooding and tidal deposits; these islands, where exposed to wave action, have *bordering spits/cheniers*, and where protected, have muddy *tidal-land connections* with the mainland or other islands. The islands are gradational from large-scale features such as Quarantine and Channel Islands to small hillocks on the tidal flat.

The medium-scale coastal geomorphology of the Port Darwin embayment, has been determined by the finer-scale geomorphology of the hinterland and by processes of marine sedimentation and erosion. Thus, protected embayments have accumulated a mud wedge (tidal flat) which is locally dissected by tidal creeks. Semi-protected embayments have accumulated mud wedges (tidal flats) with encroaching sand spits and cheniers formed by wave rework-

ing and tidal dispersion. Exposed localities either have rocky shores swept clear of major sedimentary accumulations or have spits which develop muddy accumulations on their protected side.

Subsequently, depending on the result and interplay of mud sedimentation, sand sedimentation, tidal creek erosion, wave erosion, or equilibrium condi-

The disposition of these medium-scale geomorphic units are shown for selected small areas in Fig. 4. All these units except subtidal channels and bays support mangroves to some extent.

- (1) *Hinterland margin*: these units (10-50 m wide) form the junction of the hinterland and tidal flat; they are inundated only on the highest

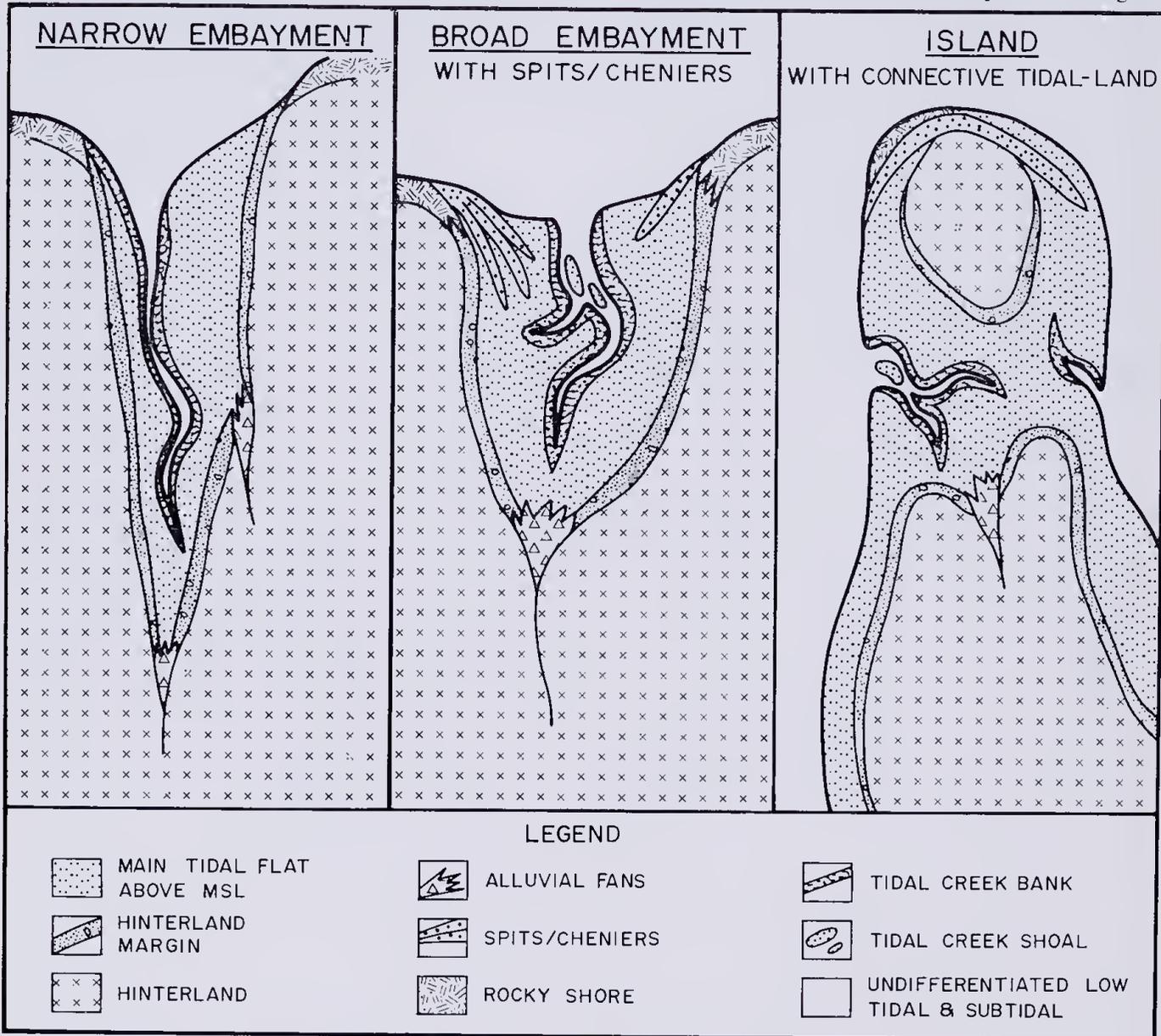


Figure 3.—Schematic diagram showing three types of coasts in Port Darwin. Within each coastal type there is a similar range of medium-scale tidal-zone geomorphic units.

tions, there have been a wide range of medium scale tidal and subtidal zone geomorphic units that generally are either peripheral to the main Port Darwin embayment shoreline, or circumferential to islands. The units are (Fig. 3):

- (1) Hinterland margin
- (2) Alluvial fans
- (3) Tidal flats
- (4) Tidal creeks
- (5) Spits/cheniers
- (6) Rocky shores
- (7) Subtidal channels and bays

tide and are underlain by reworked colluvium or muddy sand washed off the hinterland; the unit is subject to freshwater seepage.

- (2) *Alluvial fan*: these alluvial accumulations, fan to deltoid in shape, form in high tidal environments where creeks and streams debouch onto tidal flats; substrates are sandy/gravelly and mixed with mud; the fans are subject to freshwater seepage.
- (3) *Tidal flats*: These are broad (100 m to more than 1 km) gently inclined surfaces underlain by sand in low tidal levels and mud or muddy sand/sand in mid-high tidal levels; generally mud is the more common substrate in mid-

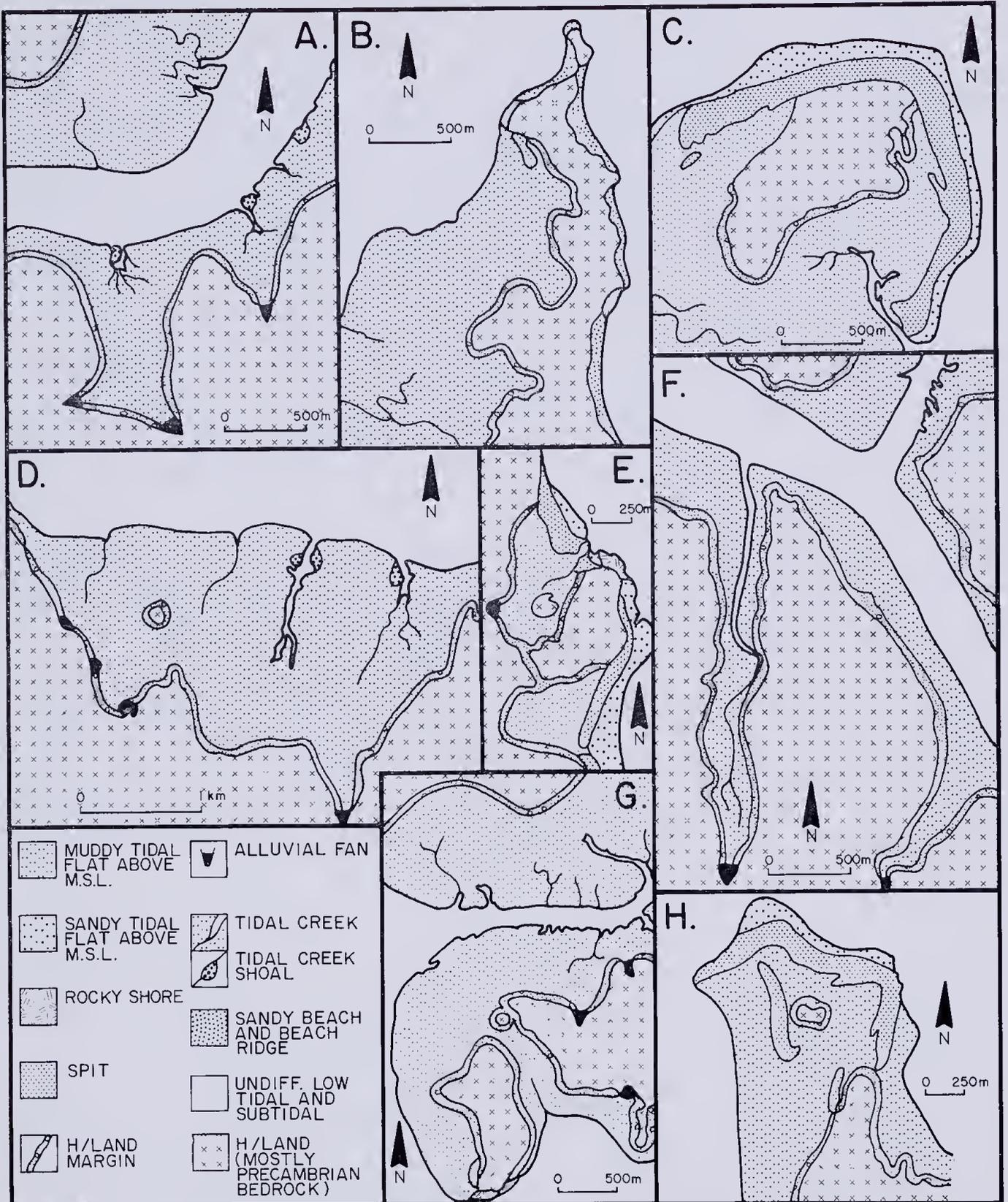


Figure 4.—Maps of selected small areas in Port Darwin to illustrate the distribution and interrelationship of medium-scale geomorphic units. The location of the areas is shown in Fig. 1. These maps also show: the various stages of island development and isolation (compare A, E, G and C); the intergradation of embayment shapes (compare B, D, A and E); the range of geomorphic units within any area; the various sizes of islands that are isolated by tidal-lands (compare C, D, E, G and H).

high tidal levels but sand is common where tidal flats front a spit/chenier system; mid-high tidal flats are vegetated by mangroves. A *salt flat* is developed at high tidal levels where mangroves have died back due to the development of a highly hypersaline groundwater/soilwater field. Locally the mangrove-vegetated tidal flat is truncated at its seaward margin by a small (1-2 m) cliff cut into tidal-flat muds.

- (4) *Tidal creeks*: these are erosional channels (3 m-100 m wide, and approximately 2 m-10 m deep) that meander and bifurcate across tidal flats; creeks may be clogged with shoals.
- (5) *Spits/cheniers*: these are elongate, narrow (10-50 m wide) sand/gravel deposits which are wave-developed features; spits typically

The distribution and relative abundance of these medium-scale units in relationship to the large-scale geomorphology is summarised in Table 1. Origin of the units is summarised in Table 2. Typical distribution of the units is shown in Figures 3 and 4.

Substrates (Soils)

There are a wide variety of substrates in this study area, however, all can be related to geomorphology and associated processes. In the Port Darwin area there are four major settings for substrates and each have generated distinctive suites of substrates. The settings are ordered below in decreasing wave exposure.

- (1) exposed rocky shores
- (2) exposed sandy shores
- (3) semi-protected embayments with spit/cheniers
- (4) sheltered muddy shores
- (5) terrestrial/tidal flat junction

Table 2

Origin of geomorphic units

GEOMORPHIC UNIT	ORIGIN	
	MAIN PROCESSES	DETAILS OF PROCESSES
Hinterland	ancestral topography	current processes of terrestrial pedogenesis, erosion, transport and sedimentation
Hinterland/tidal flat margin	marine reworking and terrestrial sedimentation	marine reworking of colluvial deposits; zone of mixing between muddy tidal flat sediments and hinterland; later, on-going sedimentation (sheet-wash off terrestrial environments) contributes to this unit
High tidal alluvial fan	terrestrial sedimentation and marine reworking	fluvial discharges of sediment from creeks onto high-tidal flats; sedimentation keeping pace with tidal flat accretion develops an interdigitating stratigraphic relationship between alluvial gravel/sand and tidal flat muddy sediments. Further sedimentation builds the alluvial fan up above the level of the tidal flat (salt flat)
Main tidal flat	tidal flat sedimentation	sedimentary progradation develops a tidal flat wedge, the upper surface of which is the low-inclined tidal surface which is colonised by mangroves between MSL and MHWS; evolution of a high-tidal hypersaline groundwater/soilwater causes mangroves to die back and there is patchy development of a salt flat
Tidal creek	marine erosion marine sedimentation	marine erosion of the tidal flat by drainage incisions accumulation of sediments develops local shoals
Spits/cheniers	marine sedimentation	wave processes acting on rocky headlands at high tidal level cause the migration and progradation of linear shell grit and sand deposits
Bouldery and rocky intertidal shore	marine erosion and marine reworking	formed by marine erosion of spurs of a rocky terrain and marine reworking of their colluvial or soil-covered slopes

emanate from exposed to semi-exposed headlands; cheniers are detached from headlands.

- (6) *Rocky shores*: these are steeply inclined to cliffed, fissured to bouldery shores comprised of rock or rock boulders; these shores generally are wave-exposed environments.
- (7) *Subtidal channels and bays*: these are the permanently-inundated environments that adjoin the tidal zone units listed above; the units are underlain by rock, sand or mud depending upon which tidal zone unit is adjoining. These units are not discussed further in this paper.

The processes significant for the generation of the suites of sedimentary (substrate) products are: 1) sediment supply, which determines whether the shores are rocky or covered with sediment; 2) wave and tidal energy, which determine whether the shores are winnowed free of sediment or are covered by winnowed sand; 3) wave exposure, storm action, and frequency of flooding, which determine that the shores are underlain by sand in low tidal zones and by mud in progressively high tidal zones, and 4) fluvial input, which determines the amount of coarse sediment (sand and gravel) that is discharged along the hinterland edge and high tidal alluvial fans.

Table 3
Substrate/soil types *

GEOMORPHIC UNITS	SOIL DESCRIPTION					
	TYPES OF SOILS	STRUCTURE	FABRIC AND TEXTURE	COLOUR	WATERLOGGING	SOIL SALINITY
Hinterland/ tidal flat contact	rock gravel sheets boulder deposits interlayered mud/sand,	structureless varying to mottled	gravel or sand framework with interstitial mud	grey to brown	waterlogged during wet season and after (infre- quent) tidal flooding	depending on freshwater seepage there may be a gradient of $\sim 14^{\circ}/_{00}$ up to $48^{\circ}/_{00}$
High tidal alluvial fan	rock gravel sheets bioturbated and root- structured mud, mud/ sand and sand	layered, varying to burrow-mottled and root- structured	a grain framework of fine, medium and coarse sand varying to gravel, locally with interstitial mud	mainly brown, grey at depth	waterlogged during wet season, otherwise satu- rated in phreatic zone (usually 50 cm deep)	gradient $< 1^{\circ}/_{00}$ to $39^{\circ}/_{00}$
Tidal flat	bioturbated and root- structured mud, homog- enous mud, texture- mottled mud and sand, muddy sand, and sand	homogenous, mottled to root- structured	mainly mud with less amounts of sand	grey to brown	waterlogged most of the time	gradient MSL $\sim 33^{\circ}/_{00}$ up to $196^{\circ}/_{00}$ at salt flat
Spits/ cheniers	homogeneous sand, laminated sand, inter- layered sand/mud	layered	a grain framework of medium to coarse sand and shell gravel	cream to buff	waterlogged during high tide; well- drained during ebb tide	gradient of $42^{\circ}/_{00}$ - $73^{\circ}/_{00}$
Bouldery or rocky head- land shore	rocky gravel sheets, boulder deposits	structureless to imbricated	boulder or pebble framework with patchy interstitial mud; rock crevices with infiltrated (geopetal) sand/mud	interstitial mud is grey	waterlogged during high tide; well- drained during ebb tide	gradient of $\sim 30^{\circ}/_{00}$ at MSL to $> 46^{\circ}/_{00}$ above HWN

* soils developed on the supratidal/terrestrial hinterland are not described since they do not support mangroves.

The main materials composing substrates are mud, sand, shell, rock gravel and bedrock. Mud is clay minerals and quartz silt, and is mainly fluvial; sand is quartz, rock fragments, or comminuted shell; shell is the accumulated tests of the marine benthos; rock gravel is eroded hinterland rocks, or is marine-reworked colluvium; bedrock is the metamorphic rock of the hinterland. The components of mud, sand, shell and rock gravel when accumulated and/or mixed develop a wide variety of substrate types. The effect of burrowing biota such as crabs serves to further mix the sediments and produce homogeneous and bioturbated or burrow-structured substrates. Vegetation contributes to substrate variability by input of detritus and by bioturbation (root structuring).

The main substrates encountered in this study in order of abundance include:

- (1) bioturbated and root-structured *mud*
- (2) homogenous *mud*
- (3) textured mottled *mud* and *sand*
- (4) homogenous *muddy sand*
- (5) root-structured *muddy sand*
- (6) homogenous *sand*
- (7) laminated *sand*
- (8) rock *gravel sheets*
- (9) *boulder* deposits
- (10) interlayered *mud* and *sand*

A summary description of substrate types occurring in each setting is presented in Table 3. The occurrence of these substrate types are noted on most profiles (Figs 5 and 6). These units are also encountered in the stratigraphic profiles.

Stratigraphy

The Quaternary stratigraphy of coastal areas such as Port Darwin is important for several reasons. Firstly, it provides an historical context for the origin and distribution of habitats since the stratigraphy can preserve the short-term to long-term Holocene history of the coast. Consequently it also can provide information on the longevity and maintenance of (mangrove-vegetated) tidal flats and other tidal environments since sedimentary/biotic lithotopes are distinctive stratigraphic units. Finally, the stratigraphy forms the basic framework of both the tidal flat hydrologic system and the tidal flat/hinterland hydrologic exchanges. Since groundwater salinity, recharge and mixing are important elements of mangrove ecosystems, it follows that the stratigraphic array of aquifers and aquatards is an essential part of these systems.

The distinction between Holocene and Pleistocene stratigraphic units was not warranted for purposes of this study. Nevertheless comments as to the age of most of Quaternary sections are presented here: (1) much of the upper parts of the sedimentary accumulations (as illustrated in Fig. 5) are interpreted as Holocene, since the bulk of the deposits appear largely uncemented/unweathered as compared to other Pleistocene tidal flat units described elsewhere (see Semeniuk 1980); in addition, there is a lack of discrete pedogenic horizons such as harpans and nodular soils at depth to indicate weathering periods; (2) the profiles of stratigraphy (Fig. 5) illustrate sediment bodies mostly in their correct stratigraphic-topographic positions relative to present sea-level; and (3) many of the stratigraphic units are still depositional at the modern surface. There is a

possibility, however, that some of the stratigraphic units at depth (say 4 m below MSL) are of Pleistocene age.

The stratigraphic profile under the sediment-accreted tidal flats has the following components:

- (1) *mud wedge*: thick wedge of bioturbated and root-structured mud (some formed under mangrove cover); it is at least 3-4 m thick at its seaward edge and pinches out to landward; this deposit occupies the major portion of an embayment. The wedge interdigitates with gravel/sand deposits developed along the hinterland edge, and with sand deposits of the spits/cheniers.
- (2) *mud/sand lens*: hummocky, lensoid shoal deposits (up to 3 m thick) of layered mud and sand formed within channels of tidal creeks.
- (3) *muddy sand/gravel sheet*: a sheet (=1 m thick) of muddy sand or gravel sandwiched between the main tidal wedge and the hinterland; this deposit is buried and/or reworked soil/colluvium mixed with tidal mud, and has developed where the tidal flat sediments overlapped the hinterland.
- (4) *sand/gravel fan*: a fan-shaped (to deltoid-wedge) deposit of sand, muddy sand or gravel formed where terrestrial drainage has discharged sediment onto the high tidal flats; the alluvial fan interdigitates with the muddy tidal flat wedge.
- (5) *sand bar*: a shoe-string or ribbon-shaped sand/shelly sand, up to 500 m wide, 3 000 long and 3-4 m thick, formed as a (mid-) high-tidal to supratidal spit or chenier; it interdigitates with and progrades over mud wedges; these deposits commonly are located at headland entrances to embayments or along wave-exposed portions of islands.

Stratigraphic profiles show that much of the tidal lands are infilled terrestrial lowlands; the stratigraphy records a gradual infilling by one or more of the lithologic/stratigraphic units described above (Fig. 5). On the main tidal flat the sedimentary accumulation has resulted in a wedge of mud, while on sandy coasts the entire stratigraphic interval is composed of sand overlying bedrock. The consistent internal lithology and structure of muddy tidal flat coasts and spit/chenier coasts show that these shore types are long-term stable features which, during the latter Holocene, do not appear to alternate between environmental extremes. For instance, on the spit-lined islands the stratigraphic sections frequently show that a sandy (or muddy sand) spit has interdigitated with tidal flat muds as the shoreline accreted; the wave-exposed parts of islands have consistently acted as loci for spits. On the other hand, some spit/chenier sections indicate a much more recent incursion of a sand bar into the muddy tidal flat environment. Alluvial and colluvial discharge onto tidal zones from fluvial and hinterland sources continue to accrete sediment and thus maintain the geomorphic units/habitats associated with them.

Groundwater/Soilwater

The salinity of the groundwater and soilwater systems on tidal flats and adjoining hinterland is an important mechanism which regulates mangrove

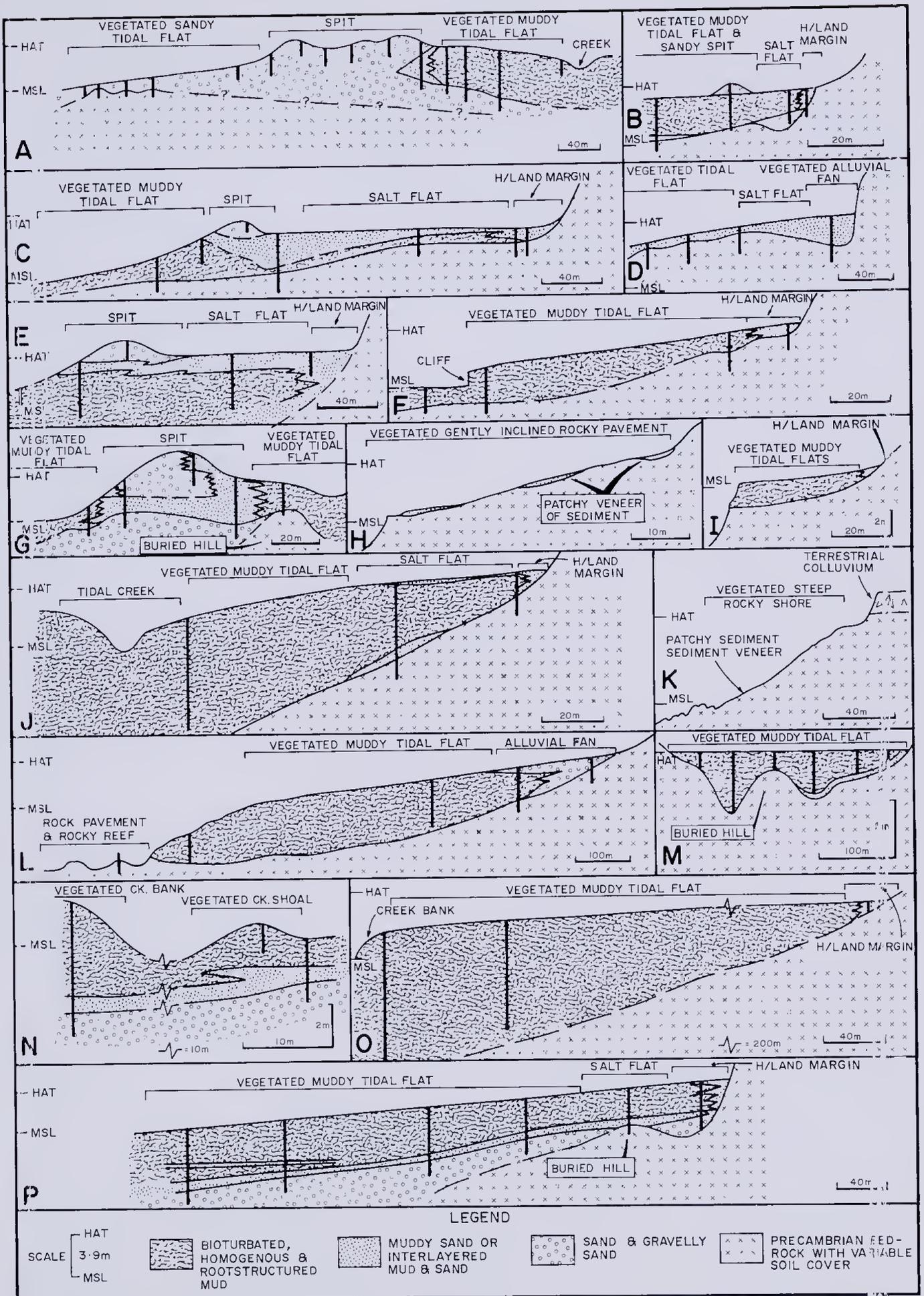


Figure 5.—Stratigraphic profiles across selected tidal areas chosen to illustrate a wide variety of coastal settings. The locations of these profiles are shown on Fig. 1. The profiles illustrate: hinterland bedrock and tidal flat mud relationships (B, C, F, I, J, L); buried hills (A, G, M, P); alluvial fan and hinterland margin relationships with the tidal flat muds (B, C, D, E, F, I, J, L, O); inter relationships between spits and tidal flat muds (A, B, C, E, G); rocky shore stratigraphy (H, K); creek bank and creek shoal relationships (N); island and spit relationships (A); the stratigraphy incised by rivertine processes (I); differentiation of the tidal zone lithofacies into upper-tidal mud, lower tidal/subtidal sand (M, N, P).

Table 4
Main aquifers: properties and groundwater IDS

GROUNDWATER			
AQUIFER	TYPE OF WATER	SALINITY OF WATER	RECHARGE MECHANISM
Hinterland		fresh water	rainfall
Hinterland/ tidal flat colluvium	contains water developed by mixing of hyper-saline seawater and freshwater seepage from hinterland	up to 130‰ where there is no freshwater seepage; otherwise with freshwater seepage 15-54 ($\bar{x}31 \pm 13$)‰	recharged infrequently with seawater by highest tides; recharged perennially or annually by freshwater seepage which precludes any potential extreme hypersalinity
High tidal alluvial fan	contains water developed by mixing of hyper-saline seawater and freshwater seepage from hinterland	1-90‰ dependent on amount of freshwater seepage	recharged infrequently with seawater by highest tides; recharged perennially or annually by freshwater seepage which precludes any potential extreme hypersalinity
Tidal flat mud wedge	contains water approximating to seawater at seaward portion, grades up to very hypersaline at landward portion	gradient: 33-40‰ at MSL, 41 \pm 4‰ mid Rhizophora zone, 89 \pm 24‰ at landward edge of mangal grading up to 132‰ across salt flats	recharged daily to fortnightly at levels up to MHWN and MHWS respectively; evapo-transpiration and evaporation combine to develop a gradient of increasing hypersalinity
Spits/ cheniers	contains water approximating normal seawater grading up to hypersaline seawater	22-112 ($\bar{x} 46 \pm 28$)‰	depending on tidal level, recharged daily to fortnightly by seawater, and seasonally by meteoric water

populations (MacNae 1968, Chapman 1976, Cintron *et al.* 1978, Semeniuk 1983). Soilwater and groundwater salinity are linked closely to stratigraphy, substrate, recharge mechanisms and evapo-transpiration. There are five main bodies of groundwater (Semeniuk in prep.); there are:

- hinterland groundwater (freshwater)
- hinterland margin groundwater (saline/mixed)
- alluvial fan groundwater (saline/mixed)
- tidal flat groundwater (saline)
- spit/chenier groundwater (saline/mixed)

Each has its own range of salinity as well as its own internal gradients of salinity and chemical composition due to (1) seawater recharge, (2) freshwater recharge, (3) mixing and (4) evaporation. Ultimately there are only two prevailing sources of groundwater: freshwater (discharged from the hinterland), and marine water (recharged daily, fortnightly, varying to half-yearly). The disposition of aquifers and aquatards/aquaculdes, and the processes of recharge, groundwater migration, evaporation/transpiration results in a gradient of increasing hypersalinity across tidal flats complicated by a zone of mixing between freshwater (seepage) and tidal flat (hypersaline) groundwater. There is

also mixing between seawater (seeping from spits/cheniers) and tidal flat groundwater. The resulting groundwater bodies have various salinities as shown in Table 4 and Figs 6 and 7. Soilwater frequently mirrors the salinity gradients of groundwater because there is mixing vertically due to recharge by tidal waters and to bioturbation by fauna. The essential aspects of soilwater salinity are summarised in Table 3 and Figs 6 and 7).

Hinterland groundwater—The groundwater under the hinterland is freshwater. This seeps to seaward along soil, colluvium and rock interfaces along the hinterland margin and discharges onto the tidal flats in the subsurface. Where it infiltrates the tidal flat it mixes with and dilutes tidal groundwater hypersalinity. The hinterland groundwater is recharged seasonally by meteoric water.

Hinterland margin groundwater/soilwater—This groundwater/soilwater system resides in the muddy colluvial/soil sheet and forms a zone of mixture between tidal flat hypersaline groundwater and freshwater seepage from the hinterland. As a result there is a gradient from brackish water (15‰ or less) at landward margins to hypersaline (54‰) where the system adjoins the main tidal flat. Recharge by seawater is infrequent (varying from monthly to twice-yearly); recharge by freshwater runoff and seepage is marked in the wet season and less pronounced, but perennial, in the dry season. The water table is elevated relative to the adjoining high tidal flat system.

Alluvial fan groundwater/soilwater—The water table of the alluvial fans is elevated by freshwater discharge particularly during the wet season where there is combined surface runoff and subsurface seepage. During the dry season there is ongoing subsurface seepage and the water table is still elevated (0.5 m below the ground) relative to the adjoining high tidal flat. The salinity of groundwater and soilwater is freshwater (less than 1‰) at landward parts of the system and grades (via mixing with hypersaline water) up to values of 16-90‰.

Tidal flat groundwater-soilwater—On the main tidal flat groundwater generally occurs about 10 cm below the surface at seaward mangrove locations during low tide periods. Depending on substrate and tides (neap vs spring), it is found progressively deeper until it may be > 1 m deep under salt flats. Groundwater salinity is 38-40‰ at seaward locations where it is recharged daily, and progressively increases up to highly hypersaline values greater than 100‰ above MHWS where it is recharged fortnightly (Table 4). Groundwater salinity values decrease along the freshwater-influenced hinterland margin and alluvial fans.

Soilwater salinity shows a graded increase in the salinity from 33‰ to 190‰ across the tidal flat, with a decrease in values along the freshwater-influenced hinterland edge and alluvial fans (Table influenced hinterland edge and alluvial fans (Table 3). *Spit/chenier groundwater/soilwater*—The spit/chenier groundwater resides within the sand bar stratigraphic unit. The sand is well drained and the water table lies generally more than 0.5 m below the surface. The groundwater salinity where there is daily recharge at seaward parts of the spits/chenier approximates

seawater; salinity grades up to values greater than 100‰ at levels of HWS where recharge is fortnightly. On the wider emergent terrestrial spits/cheniers there may be a thin freshwater lens. Soilwater salinity gradients generally follow that of groundwater.

Habitats

The term 'habitat' refers to the area which abiotic factors determine as suitable for colonisation by biota. The important abiotic factors for mangroves include: (1) tidal levels, which determine the frequency of inundation; (2) salinity; (3) substrate types (which are a function of geomorphic setting, tidal exposure and exposure to waves); (4) wave exposure, which determine the amount of reworking of substrates; and (5) terrestrial effects (such as freshwater seepage). These factors are frequently inter-related. For example, salinity gradients in tidal flat soilwater/groundwater are related to frequency of inundation (i.e. tidal levels) and salinity regimes along the hinterland edge are related to terrestrial effects such as freshwater seepage and alluvial input.

Habitat Types

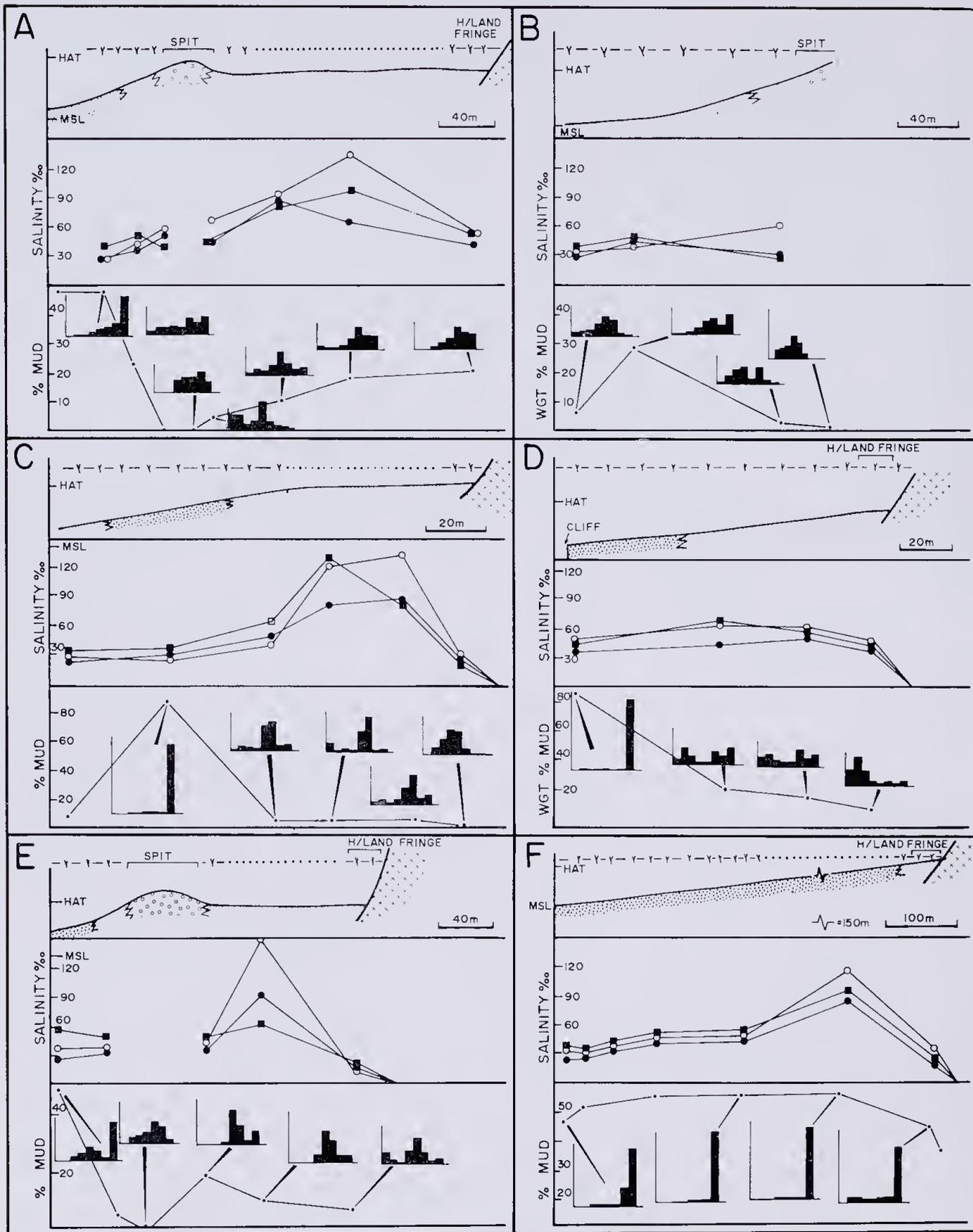
The interplay of tidal level, salinity and substrate type results in a proliferation of tidal zone habitats which, as will be shown later, have distinct biotic assemblages. Habitat types are aggregated for convenience into groups related to geomorphic units and are listed below; the specific habitats which support mangroves are in italics:

- *hinterland fringe*;
- *alluvial fans*;
- *tidal flats* (which may be subdivided on tidal level, substrates and salinity into low tidal flats, *mid to high tidal (mud) flats*, *mid to high tidal (muddy sand/sand flats)* and salt flats);
- *tidal creeks* (which are comprised of *creek banks*, *shoal* and *eroded creek mouth* habitats);
- *spits/cheniers* (which may be further subdivided into *mid to high tidal*, *high tidal* and *supratidal/terrestrial* parts);
- *rocky shore* (which similarly may be subdivided on tidal levels into *subtidal*, *mid to low tidal*, *mid to high tidal*, *high tidal* and *supratidal*);

All habitat types are widespread but there may be variation in their distribution at the local scale. In addition, there are other tidal zone and subtidal habitats that do not support mangroves but nevertheless comprise part of the Port Darwin tidal-marine system. These include tidal beaches, low tidal sand shoals/sand flats, rocky reefs, rocky pavements and deep water channels. Table 5 summarises data on the essential elements of the main tidal habitats of Port Darwin. Fig. 7 summarises the main salinity and tide-levels gradients that occur within habitats (viz. main tidal flat, hinterland fringe, spit/chenier and alluvial fan).

Mangrove Assemblages According to Habitat

Given that there is a range of habitat types and also a variation of physico-chemical conditions within these habitats, there is therefore a wide range of distinct mangrove assemblages (and zones) that inhabit the coastal environments of Port Darwin. The mangrove assemblages that are recognised are



LEGEND

- BEDROCK & SOILS OF HINTERLAND
- MUDDY SAND
- MUD
- SAND & GRAVELLY SAND

- SALINITY:**
- SALINITY OF SOIL AT SURFACE
 - SALINITY OF SOIL AT 25-30cm DEPTH
 - SALINITY OF GROUNDWATER

- DISTRIBUTION OF MANGROVE:**
- Y-Y- MANGROVE VEGETATED TIDAL FLAT
 - SALT FLAT

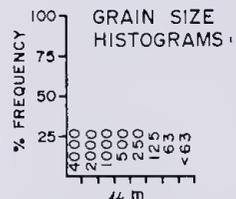


Figure 6.—Profiles showing the distribution of substrates, gradients of soilwater/groundwater salinity, gradients of grain size and the distribution of mangroves. Profiles across a spit are shown in A, B and E; the tidal flat-hinterland margin relationships are shown in A, C, D, E and F; the gradients across broad tidal flats are shown in C, D and F.

Table 5
Summary of characteristics of the mangrove habitats

HABITAT	DESCRIPTION	MAIN GRADIENTS IMPORTANT FOR MANGROVE ZONATION	COMMENTS ON UNIQUENESS AND THE MAIN FEATURES THAT MAINTAIN HABITATS AND GRADIENTS
Hinterland fringe	moderately steep to gently inclined surface underlain by muddy sand/gravel	salinity; substrate grainsize	habitat is developed and maintained by freshwater seepage and sediment sheet-wash off the hinterland
Alluvial fan	gently inclined surface underlain by muddy sand/gravel sand, and gravel	salinity; substrate grainsize	habitat is developed and maintained by extensive freshwater seepage, and sediment input along stream/creek channel
Main tidal flat	gently inclined surface between MSL and HAT, underlain mainly by mud but depending on relationship to spit, may be underlain by sand	frequency of inundation; salinity	habitat surface is maintained by sedimentation/erosion; salinity regimes are maintained by marine water recharge, evaporation and seasonal meteoric water recharge
Creek bank	steep to moderately inclined muddy surface between MSL and HWN	frequency of inundation; salinity; drainage	habitat surface is maintained by erosion; steep banks and bioexcavation/burrows ensure rapid drainage
Creek shoal and eroded creek mouth	hummocky muddy surface MSL	distinct gradients not evident	habitat surface is maintained by sedimentation alternating with erosion
Spit/chenier	steep to moderately inclined surface underlain by sand, gravelly sand and muddy sand	frequency of inundation; salinity; substrate grainsize; drainage	habitat surface is maintained by sedimentation/erosion; salinity regimes maintained by marine water recharge, evaporation and periodic freshwater seepage
Rocky shore	steep to moderately inclined surface underlain by bedrock or boulder/pebble sheet	frequency of inundation; salinity	habitat surface is maintained by erosion/sedimentation; very shallow soil or no soil; marked surface water runoff, salinity regimes maintained by marine water recharge

restricted to the medium-scale habitat type so that maps of habitat distribution virtually represent areas of these assemblages (Figs 3 and 4). These assemblages are termed as follows:

- (1) "hinterland fringe" assemblage
- (2) "alluvial fan" assemblage
- (3) "main tidal flat" assemblage
- (4) "creek bank" assemblage
- (5) "creek shoal" assemblage
- (6) "creek mouth" assemblage
- (7) "spit/chenier fringe" assemblage
- (8) "rocky shore" assemblage.

The occurrence of these assemblages according to habitat, and the components of these assemblages are summarised in Table 6. The detailed description of the zones within the assemblage forms the subject of another paper in preparation.

Synthesis

There are a number of aspects of the Port Darwin environment that are useful to understanding mangrove distribution, mangrove assemblage variation

and population maintenance. Firstly, at the large scale, there are a wide range of mangrove settings developed as a result of geomorphic history. Thus riverine, narrow-embayment, broad-embayment, spit/chenier lined-embayment and island environments are developed in response to variable interaction of (1) oceanic processes, (of sedimentation, erosion, wave action), and (2) riverine processes (of sedimentation, erosion), and (3) terrestrial processes (of weathering, erosion, transport).

Secondly, within a given (large-scale) setting there is a variable but recurring array of geomorphic units and habitats which determine the distribution of broad mangrove assemblages; these units reflect (medium-scale) geomorphology and its history. The resulting units are a product of marine (tidal-flat) sedimentation; tidal erosion, wave action, terrestrial transport/sedimentation and freshwater/marine interactions.

Finally, there is variation within habitats since there are a range of small-scale physico-chemical gradients within geomorphic/habitat units; these gradients

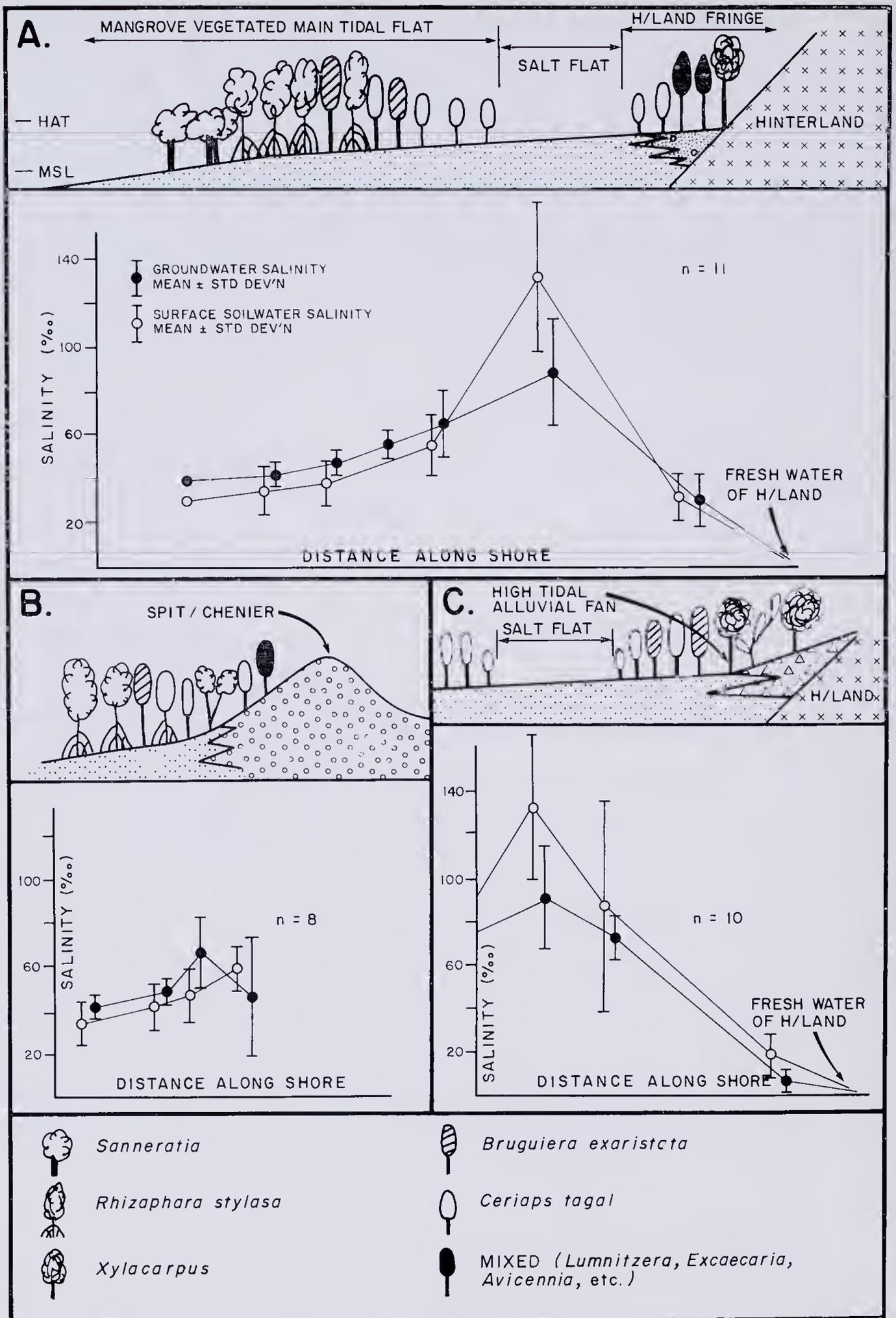


Figure 7.—Summary diagram showing gradients in tidal level and soilwater/groundwater salinity across four main habitats (viz main tidal flat, hinterland margin, alluvial fan and spit/chenier). The number 'n' refers to the number of transects used to compile this summary information and to derive the mean ± SD value for the salinity.

Table 6

Main components of the biotic assemblages and their occurrence according to habitat

HABITAT		ASSEMBLAGE	MAIN COMPONENTS
HINTERLAND/ TIDAL FLAT MARGIN		"Hinterland fringe"	Lumnitzera racemosa, Ceriops tagal, Excoecaria agallocha, Xylocarpus sp., Avicennia marina
HIGH TIDAL ALLUVIAL FAN		"Alluvial fan" mangal	Ceriops tagal, Bruguiera exaristata, Lumnitzera racemosa, Excoecaria agallocha, Xylocarpus sp., Scyphiphora hydrophyllacea, Diospyros ferrea and Rhizophora stylosa
MAIN TIDAL FLAT		"Main tidal flat mangal"	seaward Sonneratia zone with Aegiceras and Avicennia, followed by Rhizophora zone, followed by a zone of mixed Rhizophora, Bruguiera, Ceriops, Avicennia and Aegialitis, followed by Ceriops zone
TIDAL CREEKS	banks	"Creek bank"	Rhizophora stylosa, Campostemon schultzei, Bruguiera parviflora Ceriops decandra, Ceriops tagal, Aegiceras corniculatum, Avicennia marina
	shoals	"Creek shoal"	Aegiceras corniculatum, Aegialitis annulata
	mouths	"Creek mouth"	Sonneratia alba, Aegiceras corniculatum, Aegialitis annulata
SPITS/ CHENIERS		"Spit/ chenier fringe"	below HWS: Ceriops tagal, Bruguiera exaristata, Rhizophora stylosa, Xylocarpus sp., Osbornia octodonta, Avicennia marina followed by Hibiscus tiliaceus, Lumnitzera racemosa, Excoecaria agallocha, Pemphis acidula above HWS
ROCKY HEADLANDS		"Rocky shore"	Sonneratia followed by mixed zone Rhizophora, Campostemon, Aegiceras, Avicennia, followed by mixed zone of Ceriops, Osbornia, Excoecaria, Xylocarpus, Hibiscus, Pemphis.

(grain size, variability of soils, inundation frequency and salinity) are responsible for a profusion of internal zonation in mangrove assemblages. The key factors for developing gradients therefore are: (1) tidal level (hence inundation frequency), (2) the interplay between marine water recharge, freshwater recharge, and evaporation, which result in salinity regimes and salinity gradients, and (3) the interplay between tidal level and wave action which result in substrate variability. The key geomorphic and physico-chemical processes that maintain the various mangrove habitats are presented in Table 5.

In summary, in Port Darwin the interplay of various physico-chemical processes at various scales has resulted in a range of mangrove settings, mangrove habitats and various types of gradients within habitats. The resultant mosaic of mangrove assemblages and zones essentially reflect the variation in these physico-chemical processes and products.

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The relationship of fire and soil type to floristic patterns within heathland vegetation near Badgingarra, Western Australia

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Abstract

Land management in the heath vegetation near Badgingarra, Western Australia, must involve a controlled burning regime which insures sufficient winter-flowering shrub communities for apicultural needs while providing protection of life and property for the adjacent agricultural and pastoral farmland. This study documents the major vegetation and habitat patterns in the region.

Species cover data were recorded from eight permanent plots representative of major topographical features and fire history. Ordination by principal components analysis and a hierarchical polythetic agglomerative classification revealed that the major habitat variables determining the diverse floristic composition of the plots were soil depth and time-since-the-last fire. Implications of imposing a controlled burning regime on these highly diverse plant communities are considered.

Introduction

Coastal areas of south-west Western Australia are dominated by extensive stands of heath vegetation (Beard 1984). These heathlands are considered to be among the most species-rich vegetation communities of the world and are further characterized by high levels of species endemism (Lamont *et al.* 1984). Ecologically complex, the heathlands have apparently developed as a result of habitat continuity over a long geological period, regional isolation, prolific speciation and adaptive radiation of certain groups, and the recurrent stress of a transitional climatic zone (Hopper 1979).

Although some of these heathlands are being preserved in National Parks and Nature Reserves, extensive areas have been cleared for agricultural, pastoral and mining land uses. The remaining native plant communities serve a number of economic purposes including tourism, the wildflower seed industry, the cut-flower trade and, in the northern regions (Fig. 1), as winter-season "honey bee pastures". The apicultural industry utilizes these plant communities, and especially the pollen they produce, to build bee numbers and hive vigour in anticipation of the spring and summer honey production seasons in the *Eucalyptus diversicolor*, *E. calophylla* and *E. marginata* dominated forests in the lower south-west of the state.

Amongst apiarists it is commonly believed that extended periods of many years free from fire are required for heath vegetation to achieve maximum pollen and nectar production. This need for fire protection is therefore, in apparent conflict with the far more frequent burning regime desired by agriculturalists and pastoralists for protection against wildfires which start in the native vegetation and spread into developed land. The Western Australian Bush Fires Board is charged with the management of non-vested vacant Crown land and with the establishment of a land management plan incorporating a fuel reduction burning regime to rationalize these, apparently, conflicting requirements.

Effective multiple-land use management requires both detailed knowledge of the biology of individual species and functional aspects of community ecology. Relevant information for the northern heath

vegetation is however, presently limited. The objectives of the research described here were exploratory in nature and included (1) the establishment of a collection and listing of the flora from a small area within the region, (2) a determination of the relationships between plant species and specific soil types and (3) establishing whether differences in species composition could be documented for sites where the date of the most recent fire was known.

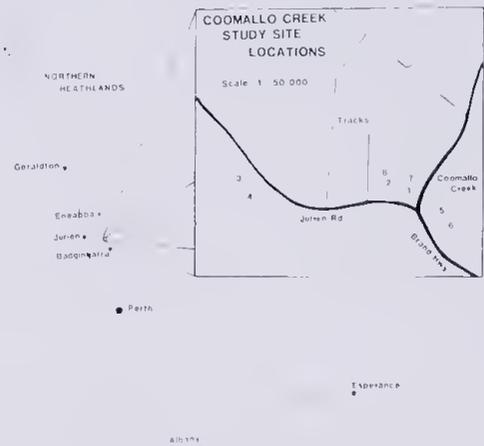


Figure 1.—Study site location in the northern heathlands of Western Australia between Badgingarra and Jurien.

Study Area

The major study area was sited within the northern heath vegetation in the vicinity of Coomallo Creek and approximately 20 km north of Badgingarra at the junction of the Brand Highway and the Jurien Road (30° 13'S 115° 23'E) (Fig. 1). Badgingarra has a typical Mediterranean type climate with cool, wet winters and hot, dry summers. The average rainfall, recorded at the Badgingarra Agriculture Research Station, is 633 mm with June having the highest monthly total. February is the warmest month with a mean monthly maximum of 34.8°C, and August is the coolest with a mean monthly minimum of 6.3°C. Geologically, the area is part of the Arrowsmith Region which comprises remnant laterized strata of Mesozoic age subsequently dissected by drainage channels (Lowry 1974). The present

topography consists of lateritic plateau crests with gently sloping valley margins and sandy swales between the ridges. The colluvial slope and valley material is of local origin derived largely from the original laterites (Mulcahy 1973). The soils of the region are similar to those described immediately to the east of Badgingarra (Churchward 1970), predominantly a mosaic of yellow sands with ironstone and lateritic gravels outcropping on the ridges and appearing at varying depths below the sand on the valley sides. In the swales when associated with a watercourse the soils can be high in clay content.

The natural vegetation of the upper slopes and duricrust outcrops of the study area consists of low shrubs, 0.5-1.0 m in height, with scattered emergent individuals of *Xanthorrhoea reflexa* and *Kingia australis* (Beard 1979). Dense stands of *Hakea* spp., *Banksia* spp., *Adenanthos cygnorum* and *Jacksonia floribunda* attaining height of 2 to 3 m occur on the deep sands. Woodlands of *Eucalyptus wandoo* and *E. accedens* occur along the larger watercourses.

Several fires have burned through the study area in the recent past leaving patches of vegetation of varying age-since-last-burn.

Methods

Selection of Study Sites

Eight permanently marked study sites were established in the mosaic of soil and fire history types (Fig. 1):

- Site 1. (Plots 1-5). Midslope, deep, yellowish sand burnt 9 years previously; located 220 m NW of the junction of the Brand Highway and Jurien Road.
- Site 2. (Plots 6-10). Upper slope, laterite outcrop burnt 9 years, previously; located 1 km W of Site 1.
- Site 3. (Plots 11-15). Upper slope, deep, yellowish sand burnt 2.5 years previously; located approx. 4 km WSW of Site 2.
- Site 4. (Plots 16-20). Upper slope, laterite outcrop burnt 2.5 years previously; located 200 m SE of Site 3.
- Site 5. (Plots 21-25). Midslope, deep, yellowish sand burnt 1.5 years previously; located 100 m E of the Coomallo Creek Campground.
- Site 6. (Plots 26-30). Midslope, laterite outcrop burnt 1.5 years previously; located 200 m SE of Site 5.
- Site 7. (Plots 31-35). Midslope, deep, yellowish sand burnt 10 years previously; located 100 m N of Site 1.
- Site 8. (Plots 36-40). Upper slope, laterite outcrop burnt 10 years previously; located 100 m ENE of Site 2.

Although chosen to be represented of the more common plant communities in the area, the study sites represent a very small percentage of the geographic coverage of the vegetation types. The sites were generally believed to lie on a gradient of topographically related soil depths ranging between the very shallow sands over laterite of the old plateau surfaces to the deeper sands of the mid-

slopes. Samples of this soil depth range included sites known from W.A. Bush Fires Board records to have been last burnt 1.5, 2.5, 9, and 10 years ago. For discussion purposes, sites burnt <3 years previously are designated to 'burnt', those >8 years as 'unburnt'.

Data Collection

Initial reconnaissance of the site involved collection of both vegetative and flowering material of the plants of the region. Subsequent identification revealed a total 212 recognizable taxa. Specimens are held in the herbarium of the Department of Botany, University of Western Australia. Nomenclature follows Green (1981).

Within each study site, five rectangular plots consisting of 10 contiguous replicate 1 m² quadrats were established at 5 m intervals. This sampling area of 50 m² per site based on spaced plots was regarded as appropriate to the preliminary nature of the investigation. The species within each quadrat were identified and cover values for each species recorded. Average cover per m² for each plot was determined and resulting data were key punched for storage and statistical manipulation on the Western Australia Regional Computing Centre's CDC-CYBER 170-720 computer.

Sites 1-4 were sampled in October 1979 and Sites 5-8 in October 1980.

Data Analysis

Due to computer storage limitations, the floristic data matrix was reduced to the 60 highest 'eident values' species by means of the matrix reduction system of Dale and Williams (1978). Analyses included both ordination and classification procedures.

Ordination was by centred and non-centred principal components analysis (PCA) utilizing the ORDIFLEX package of Gauch (1977). Separate computer runs for each form of PCA were performed in which species were, respectively, represented by presence/absence values and their cover values. The relative success with which centred and non-centred PCA may identify patterns amongst species associations is influenced by the number and complexity of discontinuities in the species distributions (Noy-Meir 1973). In this instance because the patterns were similar only those for the centred (presence/absence data) PCA are considered further.

Classification involved the hierarchical polythetic agglomerative procedures based on minimum dispersion (MDISP) and mutual information (MINFO) programmes of Orloci (1967, 1969). The data used were the species cover values. The results of the MINFO classification have been chosen for presentation as both algorithms produced similar patterns.

Results

A total of 212 taxa (γ -diversity) were recorded in the vicinity of the eight sites with 162 of these occurring at least once within the 40 sampled plots (Appendix 1). The general floristic richness of the region is indicated by the distribution of the taxa among families, genera and species (Table 1).

Table 1

Distribution of taxa within the study region.

	Families	Genera	Species
Gymnospermae	1	1	1
Monocotyledonae	8	36	50
Dicotyledonae	28	73	161
Total	37	110	212

Major families from the Monocotyledonae included Haemodoraceae (6 genera, 10 species), Lilaceae (6 genera, 7 species) and Restionaceae (7 genera, 9 species) while Epacridaceae (5 genera, 13 species), Leguminosae subfamily Papilionoideae (11 genera, 23 species), Myrtaceae (13 genera, 24 species) and Proteaceae (11 genera, 39 species) were predominant in the Dicotyledonae.

Given the relatively small plot area (50 m²) examined at each site, species richness levels were high and α -diversity varied between 90 (Site 4) and 62 (Site 5). Average species richness levels for the individual plots were around half the appropriate site value (Table 2). An ANOVA of the species richness values across the eight sites showed no significant differences ($F_{7, 32} = 1.42; 0.3 > p > 0.2$).

Species occurrences ranged from single plants in single quadrats to *Hibbertia crassifolia* which occurred in 37 of the 40 plots. As many as 41 of the 162 encountered species exhibited some degree of restriction within the sand/laterite and burnt/unburnt environmental dichotomy (Table 3, Appendix 1). Given that the 'eident value' approach of Dale and Williams (1978) identifies those species contributing most to any patterning amongst species/plot occurrences, it could be expected that the 60 species selected for the analyses would include some *potentially* indifferent to either soil type or burning (generalists), those with preference for one or other soil types (edaphic indicators), and those responsive to the fire history of the plots (pyric indicators). Examination of the simplest of the PCA ordinations, that using species presence/absence data, would appear to confirm this assumption (Figs. 2 and 3).

Table 2

Levels of species richness amongst sampled plots and sites.

Site	Ecological Category		Overall Site Species Richness*	Mean number of species per plot	Range in species richness amongst plots
	Edaphic	Pyric			
1	Sand	Burnt >8yrs	74	33.2	28 - 37
2	Laterite	Burnt >8yrs	79	36.0	26 - 42
3	Sand	Burnt <3yrs	71	35.6	31 - 42
4	Laterite	Burnt <3yrs	90	37.0	32 - 45
5	Sand	Burnt <3yrs	62	35.6	34 - 38
6	Laterite	Burnt <3yrs	72	32.0	29 - 36
7	Sand	Burnt >8yrs	72	36.4	33 - 41
8	Laterite	Burnt >8yrs	77	39.0	34 - 44

* Study Region: Average 74.6

Table 3

Distribution of species amongst ecological site categories.

Pyric ^(a) Distribution	Edaphic Distribution ^(b)			Totals
	Sand	Non-edaphic specific	Laterite	
Burnt < 3 yrs	13	5	13	31
Non-pyric specific	7	76 ^(c)	24	107
Unburnt > 8 yrs	7	9	8	24
Totals	27	90	45	162

(a) Species restricted to either 'burnt' (<3 years) or 'unburnt' (>8 years) sites (pyric indicators)

(b) Species restricted to either sand or lateritic sites (edaphic indicators)

(c) Species with no evident site preferences, occurred in 3 of the 4 main ecological categories (generalists)

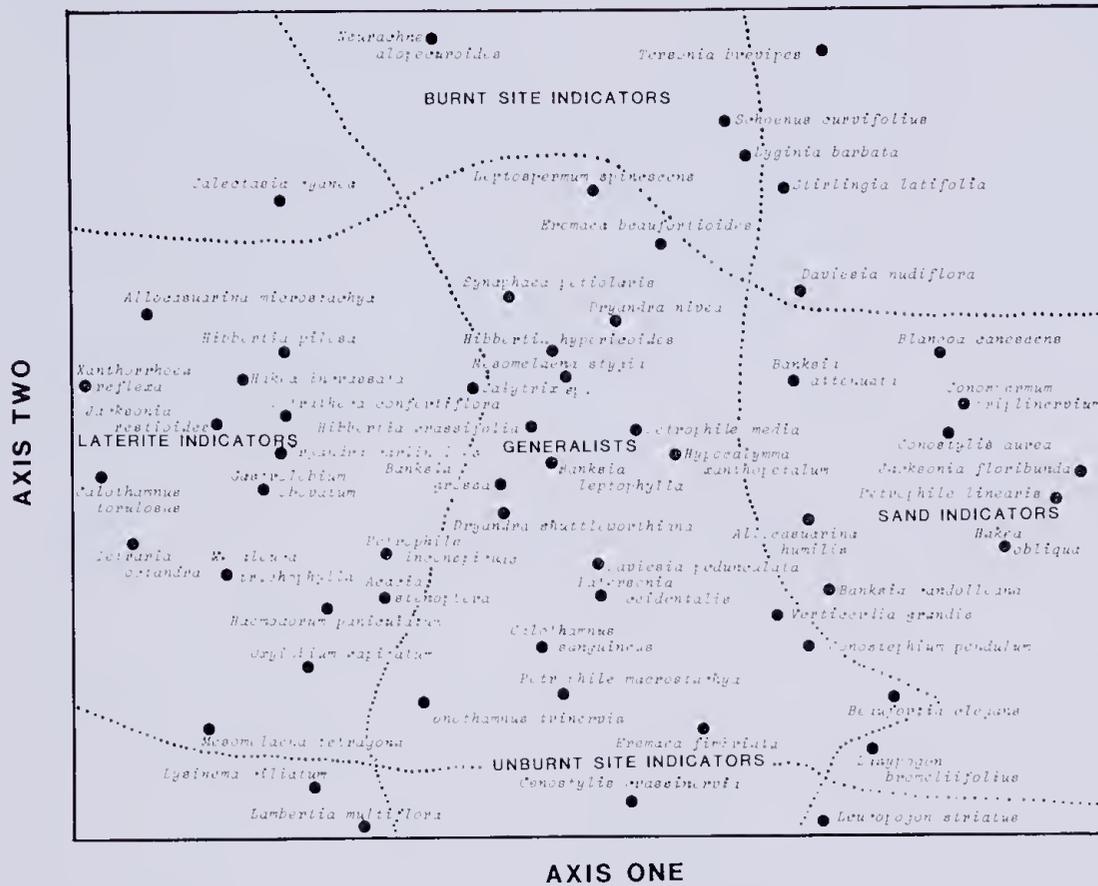


Figure 2.—Species ordination for centred PCA ordination on presence/absence data for the 60 highest eident value species. Soil type and fire category designation subjectively established from site preference data.

On the basis of their ecological distribution (Appendix 1), species can be segregated along the first axis into three subjective groups (Fig. 2). Species to the left end of the axis are those largely restricted to the laterite outcrop areas (e.g. *Xanthorrhoea reflexa*, *Calothamnus torulosus* and *Allocasuarina microstachya*). In the central region are species found both on laterite and deep sand plots (e.g. *Hibbertia hypericoides*, *H. crassifolia* and

Dryandra shuttleworthiana). Towards the right end of the axis are those species largely restricted to sand (e.g. *Hakea obliqua*, *Jacksonia floribunda* and *Petrophila linearis*). The second axis differentiated in the upper half of the ordination those species occurring predominantly in recently burnt plots (e.g. *Tersonia brevipes* and *Neurachne alopecuroides*) and, in the lower portion, those species most often restricted to successional older unburnt plots. Species restricted to sites in the deep sands where fires occurred more than 8 years prior to sampling included *Leucopogon striatus* and *Dasyogon bromeliifolius*. Species restricted to the unburnt laterite sites were *Lambertia multiflora* and *Lysinoma ciliatum*. Other species with tendencies toward edaphic or fire history responses were subjectively categorised based on their location in the ordination space and the constancy of their presence in specific habitat types (see also Appendix 1).

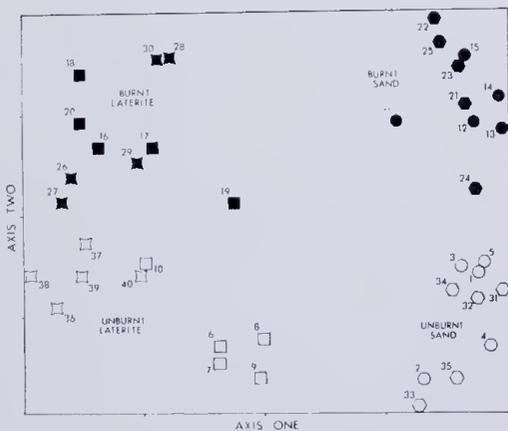


Figure 3.—Plot ordination for the centred PCA ordination on presence/absence data for the 60 highest eident value species. Location numbers appear for each of the 40 plots. Plots of each site appear as different symbols. The recently burnt sites are the darkened symbols; those more than 8 years since burnt appear as open symbols.

The combined effects of these edaphic and pyric indicator species resulted in a plot ordination which separated the sites according to their soil and fire date differences (Fig. 3). The separation of plots along the first PCA axis (accountable variance 23%) indicated that edaphic conditions were the most important parameters controlling community variation within the environmental domain sampled. The second axis (accountable variance 9%) showed a segregation of the burnt plots from the unburnt plots. Species responses to fire, therefore, appear also to be a factor in determining the composition of the habitats in the region. The absence of plot separation within

the major fire history groups (i.e. between the 1.5 and 2.5 years-since-burnt plots or between the 9 and 10 years-since-last-burnt plots) is an indication that maturation of the communities following fire is gradual requiring several seasons for any changes in species composition to become obvious. The third PCA axis was found to be a reflection of the second axis and further axes (each with accountable variation <7%) could not be interpreted in ecological terms.

While the present levels of floristic variation attributable to the first two axes might seem meagre, interpretability of PCA ordination is not always simply related to accountable variation (Whittaker and Gauch 1973) and has not affected resolution in this study. Inclusion of quantitative cover data in

Initial fusions amongst laterite sites grouped related plots from a single site, plot 10 (Site 2) being an exception but one in accord with its 'displaced' location within the ordination (Fig 3). Subsequent re-examination of the area has revealed the existence of laterite close to the surface in the vicinity of plot 10. This plot therefore, is more appropriately aligned with plots from Site 8 than its spatial location would otherwise suggest. Although the fire interval pattern is evident (mutual information level of 200), the fusion sequence indicates that Site 8 (unburnt) is more closely related to Sites 4 and 6 (burnt) than to Site 2 (unburnt).

Plot affiliations amongst the deep sand sites appear less precise than those for laterite, principally because of the diverse allocation of plots from Site 1 in the

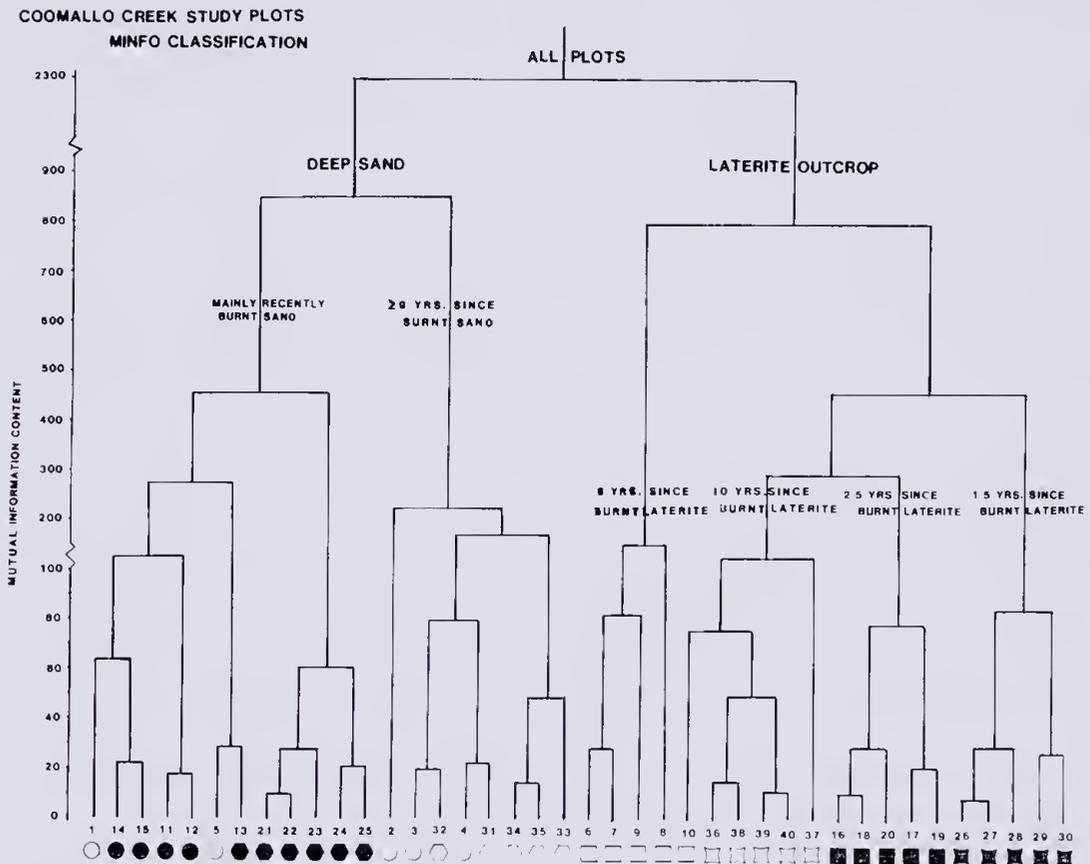


Figure 4.—Mutual Information Analysis (MINFO) plot classification of Badgingarra study area average cover value data. Location numbers and symbols appear as described on Figure 3.

the ordination made little difference to the overall interpretation. Those differences observed reflected the effects of a particular species present with locally high abundance (e.g. spreading shrubs such as *Banksia candolleana*). Most species had only low values when averaged across a plot and, therefore, were not greatly different from the 1's and 0's of presence/absence data.

Classification using the quantitative data supported the importance of edaphic variables as the major parameters defining the vegetation pattern (Fig. 4). The MINFO classification (as well as the MDISP classification) ultimately fused all plots from the deep sand areas into one group and the plots from the laterite outcrop areas into a second group.

early stages of the agglomeration process. In this respect the classification and ordination results are most at variance. The difference would relate to the use of cover values by the classification and only presence/absence data in the ordination, for example, *Banksia candolleana* had very high cover in Sites 5 and 13 while *B. attenuata* was an important species in Sites 1, 14 and 15, being absent elsewhere. Apart from the inclusion of Sites 1 and 5 with the recently burnt group, the fire pattern of the sand sites is recovered by the classification in a consistent sequence.

Discussion

Because of the distribution of sites across a distance of some 6 km and the spacing of plots within sites, the effective area covered by this study was

considerably larger than the overall quadrat area (400 m²) actually examined would imply. The total of 212 species encountered and average site richness of 75 species/site represents levels of τ - and α -diversity respectively which are comparable with those reported from elsewhere in the northern heathlands (Table 4). As these figures also indicate, a larger plot size could be expected to result in a higher α -diversity while increased sampling intensity, inclusion of major drainage channel areas and seasonal collections would further increase γ -diversity. These levels of species richness highlight the botanical importance of the region and the need for more specific information of species behavioural patterns if future management is not to adversely affect the area's floristic composition.

Separation of the vegetation into areas represented by the laterite outcrops and the deep sandy sites is undoubtedly overemphasized by the choice of the site locations. Indeed, Hnatiuk and Hopkins (1981), who also found a similar division in areas away from winter-wet depressions in their Eneabba study, reported that although there were separate groups of species characterizing a lateritic soils unit and a deep sands unit, there was also a large degree of continuity between these two major units as nearly half of the species were found in both. The choice of study sites at the extremes of the topographically related soil depth gradient has perhaps maximised the polarization of species response patterns though even in this study, some 77 of the 162 species could be regarded as wide ranging.

Table 4

Summary of α - and γ -diversity levels for selected studies in northern heathland vegetation.

Location	Soils	α -diversity		γ -diversity		Reference
		Area (m ²)	Number of Species	Area (km ²)	Number of Species	
Eneabba Res. 31030	Sand over clay, deep sand, sand over laterite			6	239	A
Eneabba Res. 31030	Deep, white sand, Sand over laterite	50	65			B
		500	77			B
		500	71			B
Eneabba Location 10413	Grey yellow sand or laterite	50	92			B
		500	70			B
Eneabba	Clay, deep sand, laterite	1 000	91	20	429	C
Eneabba	Deep sand, laterite	16	54	ca 15	148	D
Mt. Lesueur Res. 15018	Clayey sand over laterite	50	60			B
		500	67			B
Mt. Lesueur Res. 15018	Sand over laterite, laterite			0.5	286	E
Badgingarra Nat. Park 31809	Deep sand over laterite	50	59			B
		500	71			B
Badgingarra-Coomalloo Ck.	Deep sand, laterite	50	75	ca 6	212	F

A Lamont (1976)

B George *et al.* (1979)

C Hnatiuk and Hopkins (1981)

D Griffin and Hopkins (1981)

E Griffin and Hopkins (In press, cited in Lamont *et al.* 1984)

F Current study

The analysis of the floristic data by classification and ordination indicates that patterns related to the obvious geologic/edaphic features and most recent year of burning could be recovered. Additionally, these patterns were evident using either simple presence/absence records (in ordination) or species cover values (in classification). Given the nature of the expected patterns it must also be concluded that the 'eident value' reduction system has effectively reduced the large data set by maintaining the relative proportions of potential indicator species from the major ecological groups (Table 3).

While polarization of the sites into 'burnt' and 'unburnt' categories is similarly evident, the degrees to which this pattern is also indicative of site fire-history is more questionable. Records relating to fire intensity, seasonality, frequency and periodicity, those factors impinging upon the 'vital attributes' of species (*sensu* Noble and Slatyer 1979, 1981) and hence of importance in determining the pathway of post-fire succession, were unavailable. The slightly greater separation in the ordination between the burnt and unburnt sand sites when compared to the burnt and unburnt laterite sites may indicate that

the sand regions are more affected by fires or that recovery from fire is more rapid in the laterite zones. A broader floristic survey is needed to substantiate the existence of any greater floristic dispersion between recently burned sites and sites older than 8 years on the deep sands than between sites on laterite.

Evidence is accumulating (see Baird 1977, Bell and Koch 1980, Bell *et al.* 1984) that many heathland species are either long-lived resprouters, (e.g. *Hibbertia hypericoides*, *Jacksonia floribunda*) or potentially long-lived seeders (e.g. *Hakea obliqua*, *Leucopogon striatus*) with relatively few species being short-lived perennials germinating from seed immediately following fire (e.g. *Tersonia brevipes*). Thus, a community should recover its original pre-fire composition and structure quickly and alter little over time. If the vegetation recovery pattern of these heathlands follows this initial floristic composition model (*sensu* Egler 1954), the pyric pattern identified here owes its origin to the floristic heterogeneity of the region as much as to any previous fire-history. Sites of known fire frequency etc. are required to establish this point.

Notwithstanding the exact source of the observed pyric pattern, if the fire frequency in managed heathlands is shorter than the time required by obligate seedling species to flower and successfully set seed, some species could be eliminated from a particular area. For example, the winter flowering species of *Leucopogon* are particularly favoured in apiculture (Smith 1969). If *L. striatus* proves to be an important species because of its pollen production, its apparent restriction to unburnt sites on deep sands could be a reason to restrict the burning of these habitats or increase the length of time between control burns. Elimination of a species by fire would not only be a potential loss to apiarists but also in an area which has a high degree of endemism, the loss could lead to eventual extinction. The enlightened use of fire in land management depends strongly on appropriate ecological information (Naveh 1974). Further data are required on the ecology of the species and communities in the Badgingarra region before a management policy incorporating all interests can be determined.

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Appendix 1

Coomallo Creek Study Area Species List. * denotes species not in transect sites. C denotes species used in computer analysis.

	Sand		Laterite		In Computer Analysis
	<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt	
GYMNOSPERMAE					
Cupressaceae					
<i>Actinostrobus acuminatus</i>			+	+	
ANGIOSPERMAE					
MONOCOTYLEDONAE					
Cyperaceae					
<i>Caustis dioica</i>			+	+	
<i>Lepidosperma</i> sp.	+	+	+	+	
<i>Mesomelaena stygia</i>	+	+	+	+	C
<i>Mesomelaena tetragona</i>	+	+	+	+	C
<i>Schoenus curvifolius</i>	+	+	+	+	C
<i>Schoenus</i> sp.	+	+	+	+	
<i>Tetraria octandra</i>			+	+	C
Haemodoraceae					
<i>Anigozanthos humilis</i>	+	+	+		
<i>Blancoa canescens</i>	+	+		+	C
<i>Conostylis aurea</i>	+	+	+	+	C
<i>Conostylis crassinervia</i>		+		+	C
* <i>Conostylis preissii</i>					
<i>Conostylis teretifolia</i>	+	+	+	+	
<i>Haemodorum paniculatum</i>	+	+	+	+	C
<i>Haemodorum spicatum</i>	+		+	+	
<i>Macropidia fuliginosa</i>			+	+	
* <i>Phlebocarya ciliata</i>					
Iridaceae					
<i>Patersonia occidentalis</i>	+	+	+	+	C
Liliaceae					
<i>Burchardia umbellata</i>	+				
<i>Johnsonia pubescens</i>	+	+			
<i>Laxmannia grandiflora</i>	+		+		
<i>Stawellia dimorphantha</i>			+		
<i>Thysanotus multiflora</i>	+	+			
<i>Thysanotus patersonii</i>		+	+		
<i>Tricoryne elatior</i>			+		

Appendix 1—continued

	Sand		Laterite		In Computer Analysis
	<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt	
Orchidaceae					
* <i>Caladenia flava</i>					
* <i>Caladenia gemmata</i>					
* <i>Caladenia hirta</i>					
* <i>Drakaea glyptodon</i>					
* <i>Elythranthera brunonis</i>					
* <i>Prasophyllum australe</i>					
* <i>Thelymitra campanulata</i>					
Poaceae					
<i>Amphipogon turbinatus</i>		+			
<i>Neurachne alopecuroides</i>	+	+	+	+	C
<i>Stipa variabilis</i>	+				
Restionaceae					
<i>Alexgeorgia</i> sp.	+	+	+	+	
<i>Ecdiocolea monostachya</i>	+	+	+	+	
<i>Hypolaena</i> sp.				+	
<i>Loxocarya fasciculata</i>				+	
<i>Loxocarya</i> sp.	+	+	+		
<i>Lyginia barbata</i>	+	+	+	+	C
<i>Restio megalotheca</i>				+	
<i>Restio sphaelatus</i>	+	+	+	+	
Xanthorrhoeaceae					
<i>Calectasia cyanea</i>	+		+	+	C
<i>Dasyopogon bromeliifolius</i>	+	+			C
<i>Lomandra hermaphrodita</i>	+		+		
<i>Lomandra sericea</i>	+		+	+	
<i>Lomandra</i> sp. 1	+	+	+	+	
<i>Lomandra</i> sp. 2				+	
<i>Xanthorrhoea reflexa</i>	+	+	+	+	C
DICOTYLEDONAE					
Amaranthaceae					
* <i>Ptilopus alopecuroides</i>					
Apiaceae					
<i>Xanthosia huegeli</i>	+	+		+	
Asteraceae					
* <i>Angianthus tomentosus</i>					
* <i>Podotheca gnaphalioides</i>					
Caesalpiniaceae					
<i>Labichea punctata</i>			+	+	

Appendix 1—continued

Appendix 1—continued

	Sand		Laterite		In Computer Analysis		Sand		Laterite		In Analysis Computer
	<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt			<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt	
Casuarinaceae						Goodeniaceae					
<i>Allocasuarina humilis</i>	+	+		+	C	<i>Dampiera layandulacea</i>	+		+		
<i>Allocasuarina microstachya</i>			+	+	C	* <i>Dampiera lindleyi</i>					
Dicrastylidiaceae = (Verbenaceae)						* <i>Goodenia pulchella</i>					
* <i>Lachnostachys verbascifolia</i>						* <i>Lechenaultia biloba</i>					
<i>Pityrodia bartlingii</i>	+	+				* <i>Lechenaultia linearoides</i>					
Dilleniaceae						<i>Scaevola caescaens</i>	+	+	+		
<i>Hibbertia crassifolia</i>	+	+	+	+	C	<i>Scaevola paludosa</i>	+		+		
<i>Hibbertia glaberrima</i>	+					* <i>Velleia pilosella</i>					
<i>Hibbertia hypericoides</i>	+	+	+	+	C	Haloragaceae					
<i>Hibbertia pilosa</i>			+	+	C	* <i>Glischrocaryon aureum</i>					
* <i>Hibbertia stricta</i>						Lauraceae					
Droseraceae						<i>Cassytha glabella</i>					+
<i>Drosera drummondii</i>	+			+		* <i>Cassytha pubescens</i>					
<i>Drosera erythrorrhiza</i>	+					Leguminosae subfamily Mimosoideae					
* <i>Drosera heterophylla</i>						<i>Acacia anroniteus</i>	+				
<i>Drosera menziesii</i>	+	+	+	+		* <i>Acacia lasiocarpa</i>					
* <i>Drosera nitidula</i>						<i>Acacia pulchella</i>	+				
<i>Drosera paleacea</i>	+	+	+			<i>Acacia stenoptera</i>	+		+	+	C
* <i>Drosera pallida</i>						Leguminosae subfamily Papilionoideae					
* <i>Drosera sewelliae</i>						<i>Daviesia divaricata</i>		+		+	
<i>Drosera stolonifera</i>		+		+		* <i>Daviesia epiphylla</i>					
Epacridaceae						<i>Daviesia nudiflora</i>	+	+	+		C
<i>Andersonia heterophylla</i>		+				<i>Daviesia pectinata</i>			+	+	
<i>Andersonia lehmanniana</i>	+	+	+	+		<i>Daviesia pedunculata</i>		+	+	+	C
<i>Astroloma microdonta</i>				+		<i>Daviesia quadrilatera</i>	+				
<i>Astroloma serratifolium</i>	+	+	+			* <i>Daviesia striata</i>					
<i>Astroloma stonarrhena</i>		+				* <i>Dillwynia uncinata (patula)</i>					
<i>Astroloma xerophyllum</i>		+				<i>Gastrolobium bidens</i>			+	+	
<i>Astroloma sp.</i>	+	+	+	+		<i>Gastrolobium obovatum</i>			+	+	C
<i>Conostephium pendulum</i>	+	+	+	+	C	<i>Gastrolobium pauciflorum</i>			+		
<i>Leucopogon conostephioides</i>	+	+	+	+		* <i>Gastrolobium spinosum</i>					
<i>Leucopogon polymorphus</i>		+				<i>Gompholobium knightianum</i>				+	
<i>Leucopogon striatus</i>	+	+		+	C	<i>Hovea stricta</i>		+	+		
<i>Leucopogon sp. 1</i>	+	+		+		<i>Isotropis cuneifolia</i>	+				
<i>Lysinema ciliatum</i>		+	+	+	C	* <i>Jacksonia aphylla</i>					
Euphorbiaceae											
<i>Monotaxis grandiflora</i>	+	+	+								

Appendix 1—continued

	Sand		Laterite		In Computer Analysis
	<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt	
<i>Jacksonia floribunda</i>	+	+		+	C
<i>Jacksonia restioides</i>		+	+	+	C
* <i>Kennedia prostrata</i>					
<i>Oxylobium capitatum</i>			+	+	C
<i>Oxylobium</i> sp.			+		
* <i>Pultenaea ericifolia</i>					
* <i>Sphaerolobium macranthum</i>					
Loganiaceae					
<i>Logania</i> sp.			+		
Myrtaceae					
<i>Baeckea camphorosmae</i>			+	+	
<i>Baeckea grandiflora</i>			+	+	
<i>Baeckea</i> sp.	+		+		
<i>Beaufortia elegans</i>	+	+	+	+	C
* <i>Calothamnus hirsutus</i> (villosus)					
<i>Calothamnus sanguineus</i>	+	+	+	+	C
<i>Calothamnus torulosus</i>		+	+	+	C
<i>Calytrix brachyphylla</i>	+				
<i>Calytrix stowardii</i>			+		
<i>Calytrix unguolata</i>		+		+	
<i>Calytrix</i> sp.			+	+	C
<i>Conothamnus trinervis</i>	+	+	+	+	C
<i>Darwinia speciosa</i>	+	+	+	+	
<i>Eremaea beaufortiioides</i>	+	+	+	+	C
<i>Eremaea fimbriata</i>	+	+	+	+	C
<i>Eremaea pauciflora</i>		+		+	
* <i>Eucalyptus todtiana</i>					
<i>Hypocalymma xanthopetalum</i>	+	+	+	+	C
<i>Leptospermum spinescens</i>	+	+	+	+	C
<i>Melaleuca trichophylla</i>	+	+	+	+	C
* <i>Pileanthus filifolius</i>					
<i>Verticordia grandiflora</i>			+		
<i>Verticordia grandis</i>	+	+	+	+	C
<i>Verticordia ovalifolia</i>		+		+	
Gyrostemonaceae					
<i>Tersonia brevipes</i>	+				C
Polygalaceae					
<i>Comesperma</i> sp.	+		+	+	

Appendix 1—continued

	Sand		Laterite		In Computer Analysis
	<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt	
Proteaceae					
<i>Adenanthos</i> sp.	+				
<i>Banksia attenuata</i>	+	+			C
<i>Banksia candolleana</i>	+	+	+		C
* <i>Banksia chamcephyton</i>					
<i>Banksia leptophylla</i>	+	+	+		C
<i>Banksia grossa</i>				+	C
* <i>Conospermum incurvum</i>					
* <i>Conospermum nervosum</i>					
<i>Conospermum triplinervium</i>	+	+			
<i>Dryandra</i> aff. <i>falcata</i>				+	
<i>Dryandra bipinnatifida</i>				+	
<i>Dryandra carlinioides</i>		+	+	+	C
<i>Dryandra nana</i>	+		+	+	
<i>Dryandra nivea</i>	+	+	+	+	C
<i>Dryandra shuttleworthiana</i>	+	+	+	+	C
<i>Dryandra tridentata</i>		+		+	
<i>Grevillea pilulifera</i>		+			
* <i>Grevillea shuttleworthiana</i>					
<i>Grevillea synapheae</i>				+	
<i>Hakea conchifolia</i>				+	
<i>Hakea corymbosa</i>		+			
<i>Hakea cristata</i>				+	
<i>Hakea flabellifolia</i>		+			
<i>Hakea incrassata</i>	+	+	+	+	C
* <i>Hakea linearis</i>					
<i>Hakea obliqua</i>	+	+			C
* <i>Hakea prostrata</i>					
<i>Isopogon asper</i>				+	
<i>Isopogon linearis</i>				+	
<i>Lambertia multiflora</i>		+	+	+	C
<i>Petrophile inconspicua</i>				+	
<i>Petrophile linearis</i>	+	+	+	+	C
<i>Petrophile macrostachya</i>	+	+	+	+	C
<i>Petrophile media</i>	+	+	+		C
<i>Petrophile striata</i>				+	
<i>Stirlingia latifolia</i>	+	+	+		C
* <i>Stirlingia simplex</i>					
<i>Synaphaea petiolaris</i>	+	+	+	+	C
<i>Synaphaea polymorpha</i>		+		+	

Appendix 1—continued

	Sand		Laterite		In Computer Analysis
	<3yrs burnt	>8yrs burnt	<3yrs burnt	>8yrs burnt	
Rhamnaceae					
* <i>Cryptandra</i> <i>pungens</i>					
Rutaceae					
<i>Boronia</i> sp.				+	
<i>Eriostemou</i> <i>spicatus</i>	+			+	
Stackhousiaceae					
<i>Stackhousia</i> <i>brunonis</i>			+		
<i>Stackhousia</i> <i>pubescens</i>			+		
Sterculiaceae					
<i>Lasiopetalum</i> <i>drummondii</i>		+		+	
<i>Thomasia</i> <i>grandiflora</i>				+	
Stylidiaceae					
* <i>Levenhookia</i> <i>pauciflora</i>					
<i>Stylidium</i> <i>bulbiferum</i>			+	+	
<i>Stylidium</i> <i>rosso-</i> <i>cephalum</i>	+	+			
* <i>Stylidium</i> <i>hispidum</i>					
<i>Stylidium</i> <i>piluliferum</i>	+				
* <i>Stylidium</i> <i>pubigerum</i>					
<i>Stylidium</i> <i>repens</i>	+		+	+	
<i>Stylidium</i> sp.			+		
Thymelaeaceae					
* <i>Pimelea</i> <i>floribunda</i>					
<i>Pimelea</i> <i>suaveoleus</i>	+	+	+	+	
<i>Pimelea</i> <i>sulphurea</i>	+		+	+	
Tremandraceae					
<i>Tetralochea</i> <i>confertifolia</i>			+	+	C
Violaceae					
* <i>Hybanthus</i> <i>calycinus</i>					

The Becher Sand, a new stratigraphic unit for the Holocene of the Perth Basin

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Abstract

The term Becher Sand is proposed for the sequence of Holocene sediments comprised predominantly of homogenous to bioturbated sand and muddy sand that occurs along the coastal zone of the Swan Coastal Plain. The sediments are in part contemporary and also occur in subcrop. The sediments have formed mainly as submarine seagrass bank sequences. The Becher Sand was formerly part of the Safety Bay Sand and separation of the new formation will significantly clarify formational relationships and Holocene history in the coastal zone.

Introduction

The coastline of southwestern Australia is comprised of a number of Quaternary lithostratigraphic units of which the Tamala Limestone and Safety Bay Sand are the most widespread. The stratigraphy of coastal areas frequently records a complex coastal history and reflects variation in sedimentation style, supply, climate, tectonism and eustatism. The identification of distinct stratigraphic units therefore is an important prerequisite to describing and unravelling coastal history because it is only with the recognition of lithofacies, unconformity and sealevel markers that a realistic reconstruction of palaeo-environments, sealevel fluctuations and intervals of subaerial exposure can be achieved. To this objective for instance it is important to be able to recognise lithofacies that have environmental significance in terms of

- precise sea level indicators e.g. beach sequences
- occurrence as a lithotope, e.g. seagrass bank sediments
- terrestrial conditions e.g. lacustrine sediments
- subaerial exposure e.g. soils
- water table and vadose conditions e.g. calcrete or sparry calcite cements
- shoreline conditions e.g. rocky shore sequences

To date a number of papers have described and defined Quaternary stratigraphic units and in particular Holocene stratigraphic units in the Perth Basin, that are important to understanding coastal history. These works include: Passmore (1970) who described the "Coastal Limestone" (= Tamala Limestone), Coo loongup Sand and the Safety Bay Sand in the Rockingham district; Fairbridge (1950, 1953) who described the "Coastal Limestone" at Point Peron as well as the Peppermint Grove Limestone and Rottne st Limestone; Playford *et al.* (1976) who reviewed and summarised the stratigraphic information up to 1975; Playford and Leech (1977) who described the Quaternary Stratigraphy of Rottne st Island; France (1978) who described Holocene barrier and fringing seagrass banks of Cockburn Sound; Semeniuk (1983) who described the Eaton Sand, Leschenault Formation and Australind Formation and subdivided the Safety Bay Sand in the Leschenault Peninsula area; Semeniuk and Johnson (1982) who described beach/dune sequences, Woods (1983) and Woods and Searle (1983) who described stratigraphic sequences under

prograded plains; and Semeniuk & Searle (1985) who described Holocene aeolian, beach and sublittoral sands as a framework to studies on calcrete.

In the course of stratigraphic studies along the coastline of southwestern Australia it has become evident that the original concepts of the Safety Bay Sand as defined by Passmore (1970) include two distinct lithologic units that have formed in separate environments and that have distinct palaeo-environmental implications. It is the purpose of this paper therefore to describe these differences between these units and to establish a new formation within Holocene sequences of the Swan Coastal Plain, Perth Basin.

Geological setting

The study area is set along the coastline and nearshore marine environment of the Rottne st shelf (Carrigy & Fairbridge 1954) of southwestern Australia, where contemporary sediments of the modern Perth Basin are accumulating (Fig. 1). This coastal system is composed of Holocene sediments as well as erosional surfaces cut into Pleistocene materials, and is the seaward extremity of the Swan Coastal Plain, a Quaternary sedimentary system of the Phanerozoic Perth Basin (Playford *et al.* 1976). Along this shoreline the Spearwood Dune (= Tamala Limestone) and Quindalup Dune systems constitute the dominant landforms. Localised sediment accretion together with erosion of the partially inundated Pleistocene aeolianite-ridge topography has developed a complex array of coastal components as described in Searle & Semeniuk (1985).

The most important sites of sediment accumulation along the coast occur in the Cape Bouvard-Trigg Island sector. This sector is characterised by a series of parallel offshore and onshore limestone ridges in various stages of erosional degradation. Accumulation of Holocene sediment in this sector has been mainly restricted to loci termed accretionary cells, in zones of wave energy shelter behind prominences (reefs, cays, islands) of the first offshore ridge (Searle 1984, Searle & Semeniuk 1985). Similar accretionary sites occur in discrete coastal cusps in the adjoining coastal sectors to the north from Whitfords Point to Jurien Bay.

Accretion in the loci begins with shoaling and prograding of a submarine bank, in most cases under a cover of seagrasses. Eventually the bank forms a submarine barrier or sill spanning the depression from

the offshore ridge to the shore. This initiates progradation of beach, beachridge, and dune sediments, across the submarine bank top to form a growing cusped promontory. The various banks and

submarine sandy promontories in a given area may represent various stages of development of these accretionary cells (Searle 1984). In the Bouvard-Trigg sector, Rockingham and Becher promontories

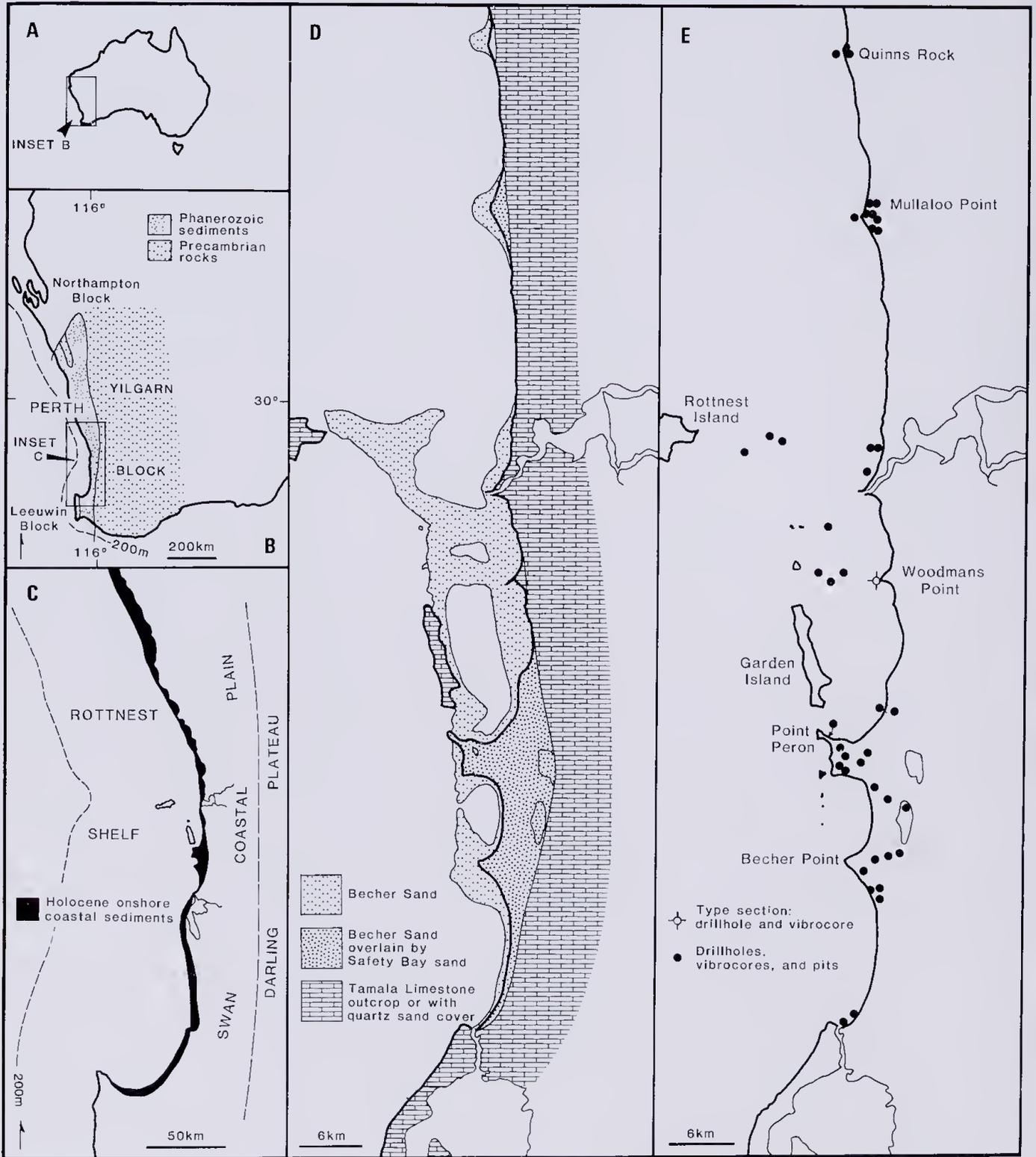


Figure 1.—A and B.—Location of study area within Perth Basin. C.—Distribution of Holocene sands along the coast zone of the Swan Coastal Plain. D.—Contemporary distribution and subcrop distribution of Becher Sand in the Cape Bouvard-Trigg Island sector of the Rottnest Shelf coast. E.—Location of type section and other drill holes that intersect Becher Sand. Drill holes from Passmore (1970), Woods and Searle (1983), Searle (1984) and this paper.

have achieved final stage of accretion (i.e. "island-capture"), *Parmelia* and Success banks have achieved the submarine barrier stage, and Fairway Bank is still in the initial stages of submarine bank growth. The fully developed stratigraphic sequence produced in these loci is:

- top:
 - aeolian sands
 - beach/beach ridge sediments
 - seagrass bank sediments
 - unconformity
- bottom:
 - Pre-Holocene sediments

It is this sequence of Holocene sediments that forms the subject matter of the present paper.

Previous work on Safety Bay Sand

Passmore (1970) defined the Safety Bay Sand as the "fine to coarse grained calcareous sand consisting in most places of more than 50% skeletal fragment of marine organisms and lesser amounts of quartz grains. The upper part is buff-colored beach and dune sand while the lower part is grey marine sand. The formation forms the land surface of almost all of the Rockingham and Cape Peron peninsulas, and includes modern shallow water marine and dune sands of similar composition". This original definition obviously included submarine seagrass bank sand, beach sand and aeolian sand.

At a later stage Playford and Low (1972) in a revision and formal definition of Perth Basin Quaternary units reapplied the term Safety Bay Sand to include dune, beachridge, strand and shallow marine sediments and extended the formation to encompass all similar deposits along the Perth Basin Coastline. The only other stratigraphic work on the Safety Bay Sand was carried out by Semeniuk (1983) who subdivided the formation in the Leschenault Peninsula area into several members based on lithologic and diagenetic criteria and relationship of units to mean sealevel.

Rationale for new stratigraphic unit

Holocene marine and coastal sediments along the nearshore and coastline of southwestern Australia are predominantly of two types—

- a beach-beachridge-dune suite that forms a genetically internally related shoaling package
- a seagrass bank suite

The beach—beachridge—dune suite forms a blanket to prism-like body. The small scale stratigraphic sequence within the suite has been described by Semeniuk & Johnson (1982). This suite of sediment may occur as a capping to submarine sands, or may occur as a shoestring body adjacent to Tamala (Limestone shore/cliff, or may occur as a unit encroaching over varied terrain such as Tamala Limestone ridges, wetlands or lagoons. The sediment types in this suite contain distinct sedimentary structures, which are formed by wave action, aeolian and pedogenic processes, and sedimentary textures (Table 1). The sedimentary structures are sufficiently diagnostic to be useful indicators of subaerial conditions, tide levels and mean sealevels (Semeniuk & Johnson 1982).

On the other hand, the sediment comprising the submarine (seagrass) banks generally all form mound-like bodies. The sediments are relatively more homogeneous due to the nearly pervasive imprint of bioturbation and root structuring (Table 1). These sediment bodies overlie submarine unconformities or overlie submerged terrestrial unconformities. The sediments may be capped by a beach-dune sequence or they may be still developing and thus are at a contemporary seagrass bank stage.

In terms of sand grain composition the seagrass bank sediments are similar to those of the beach-beachridge-dune suite and in fact they supply such grain types to the strand environment. However, in terms of sedimentary processes and products as expressed in sedimentary structures, grain sorting and range of grain sizes, and in terms of diagenetic processes as expressed in sediment colour, cementation, solution, and humification, the two sedimentary suites are readily and consistently distinguishable. The units thus satisfy the requirements to be viewed as separate formations in that both possess some degree of lithologic homogeneity, particularly in the type of primary sedimentary structures, as well as textural components and colour. These differences are sufficiently distinct to enable the two units to be mapped separately and thus satisfy the requirements for formational status (Hedberg 1976, North American Commission on Stratigraphic Nomenclature 1983).

Clearly therefore there are two obvious mappable Holocene litho-stratigraphic units along southwestern Australia and each unit is indicative of specific environments. If these units are left unidentified within a framework of "Safety Bay Sand" as presently defined, the clarification of Quaternary stratigraphic relationships and coastal history would be diminished.

Description of Becher Sand

The Becher Sand is the name proposed for the sequence of grey structureless to bioturbated, fine and medium quartzo-skeletal sand with lesser muddy sand, layered mud and seagrass peat that underlies modern (contemporary) seagrass bank and prograded coastal plain sequences. Its name is derived from nearby Becher Point, south of Warnbro Sound, where contemporary seagrass mound-like sediment bodies are accumulating (grid reference 370998 Pinjarra 1:250 000 sheet).

Type Section: Core site at Woodmans Point (grid references 374026 Pinjarra 1:250 000 sheet) through the *Parmelia* (Seagrass) Bank is designated as the type section (Fig. 1). Material from the core has been lodged with the Geological Survey of Western Australia. The sequence within the type section is described in Table 2.

Distribution: The Becher Sand has been intersected in numerous cores and its distribution, both currently depositional (contemporary) and subsurface is widespread (Fig. 1).

Table 1

Characteristics of Becher Sand and Safety Bay Sand

Formation and their facies suite	Litho-topo unit	Subdivisions	Lithology	Geometry	Large structures	Small structures	Texture	Colour	
Beach-Ridge-Dune Suite = Safety Bay Sand	Dune	mobile dunes	laminated quartzo calcareous sand with local soil sheets	wedge to prism to blanket to shoe-string	large scale cross layering	cross-layering	fine and medium sand	buff-cream	
		vegetated dunes			large scale cross layers; bioturbated-homogeneous layers	cross-layering	fine and medium sand with humus	buff-cream	
	Beach Ridges	soils	homogeneous		Homogeneous, root structured, bioturbated	fine and medium sand with humus	buff-cream		
		mobile	large scale cross layering		cross layering	fine and medium sand	buff-cream		
		vegetated	large scale cross layers; bioturbated-homogeneous layers		cross layering; root structured; bioturbated at surface	fine and medium sand	buff-cream		
Beaches	Beaches	backshore	laminated quartzo calcareous sand locally shelly	sheet to ribbon	horizontal layering	Cross layering, bioturbated; homogeneous; horizontal layering	medium and coarse sand with shell	buff-cream	
		foreshore			inclined layering	fine lamination and vesicular structure	medium and coarse sand; shell	buff-cream	
		shoreface			horizontal and cross layering	trough cross layering	gravel to coarse to fine sand	buff-cream	
	Sea-grass Bank Suite = Becher Sand	No sub-division	bank crest	structureless quartzo calcareous sand and muddy sand, and mud	prism to wedge	structureless	bioturbated to homogeneous to root structured	fine, medium and coarse sand, locally muddy, locally shelly	grey to cream
			bank slope			structureless to crudely layered	bioturbated to layered		grey to

Table 2

Description of type section at Woodman's Point*

top:	Safety Bay Sand	laminated buff medium, coarse and fine carbonate/quartz sand, very shelly	2 m
			water table
		bioturbated to structureless fine to medium grey carbonate/quartz sand, very shelly with seagrass rhizomes and roots locally with muddy sand layers	1 m
		bioturbated to crudely layered fine to coarse grey carbonate/quartz sand, very shelly	2 m
	Becher Sand	bioturbated to structureless fine to medium grey carbonate/quartz sand few shells; some coarse sand layers	3 m
		bioturbated to structureless fine to coarse grey carbonate/quartz sand, shelly with seagrass fibre	3 m
		fine to very coarse grey carbonate/quartz sand, shelly	1.5 m
		fawn coloured mud with seagrass fibre	0.5 m
	Unnamed Unit	peat and wood	0.5 m
base:	Tamala Limestone	calcreted aeolianite limestone	0.5 m and end of hole

* Based on vibrocore for upper 12 m and reverse circulation air-core for remainder of section.

Geometry and Thickness: The formation is over 20 m thick under the coastal plain in the Rockingham area; elsewhere the formation is generally 10-15 m thick. In localities where it is a contemporary and depositional the unit forms mound-like bodies standing with up to 10-22 m in relief above the adjoining basin depression floors. Where it has prograded and shoaled, as in the Becher Point—Rockingham Plain area, it forms a seaward thickening wedge body, triangular to rectangular in plan.

Lithology (Fig. 2): The dominant sediment type in the formation is a grey, structureless to bioturbated, medium and fine sand composed of quartz and skeletal grains. Locally there are shell gravel layers, coarse sand layers, calcareous muddy sand (pack-stone), calcareous mud layers that may be laminated, seagrass rhizome horizons, seagrass peat and laminated sand.

Stratigraphic relationships (Fig. 2): The formation overlies the following units:

1. Tamala Limestone (sharp unconformable contact)
2. Cooloongup Sand (bioturbated to gradational unconformable contact)
3. Calcareous muds of deeper water submarine depressions (conformable contact)
4. Calcareous/terrigenous muds of the Leschenault Formation (conformable contact)

The formation may be overlain by the laminated sediments of the Safety Bay Sand and the contact is conformable and mostly sharp. In addition the formation interdigitates with contemporary lateral facies such as deeper water basin muds.

Age and fossils: The Becher Sand is wholly Holocene. Radiocarbon ages from shells within the unit all give ages less than 7 000 years (Searle 1984, Woods & Searle 1983, and this paper). Fossils collected from the formation include:

Foraminifera: *Marginopora vertebralis*, *Discorbis vesicularis*, *Peneroplis planatus*; **Bivalvia:** *Anodontia perplexa*, *Brachidontes ustulatus*, *Callucina lacteola*, *Chioneryx cardioides*, *Divalucina cunningi*, *Donax francisensis*, *Electroma georgiana*, *Eucrassatella* sp., *Glycymeris striatularis*, *Gomphina undulosa*, *Hemidonax chapmani*, *Irus distans*, *Maetra australis*, *Maetra matthewi*, *Mysella* sp., *Saccostrea cucullata*, *Paphies cuneata*, *Pinna* sp., *Tawera coelata*, *Tawera lagopus*, *Tellina tenuilirata*, *Thraciopsis subrecta*, *Wallucina cf jacksoniensis*; **Gastropoda:** *Acteocina* sp., *Amalda monilifera*, *Amblychilepas oblonga*, *Astrarium squamiferum*, *Bedevea paivae*, *Bittium granarium*, *Bulla quoyii*, *Calyptrea calyptraeformis*, *Cantharidus (Phasianotrochus) irisodontes*, *Cantharidus (Phasianotrochus) sp.*, *Clanculus* sp., *Cominella tasmanica*, *Conus anemone*, *Dicathais orbita*, *Drupa* sp., *Ethminolia vitiliginea*, *Gibbula (Notogibbula) lehmanni*, *Gibbula preissiana*, *Haminoea brevis*, *Hipponix conicus*, *Hipponix foliaceus*, *Leiopyrga octona*, *Mangelia* sp., *Mitrella (Dentimitrella) austrialia*, *Mitrella (Dentimitrella) menkeana*, *Naccula punctata*, *Natica* sp., *Collisella onychitis*, *Notozochlis gualteriana*, *Notomella bajula*, *Oliva australis*, *Parcanassa* sp., *Phasianella australis*, *Phasianella solida*, *Phasianella ventricosa*, *Polinices conicus*, *Proterato sulcerato*, *Pyrene scripta*, *Syrnola* sp., *Thalotia (Prothalotia) lehmanni*, *Thalotia (Prothalotia) pulcherrima*, *Thalotia (Odontotrochus) chlorostoma*, *Turbo intercostalis*, *Tanea sagittata*, *Vexillum marrowi*, *Zafra vercoi*; and **Bryozoa:** *Rhynchozoon* sp. (commonly in colony form wrapped around former *Amphibolus* seagrass stems) and other species. In addition there are numerous traces of crustacean burrows, seagrass rhizomes, and, locally, seagrass leaves.

Discussion

The separation of the original Safety Bay Sand into two units, an upper, laminated to cross-laminated unit (related to beach, beachridge and dune systems) and a lower structureless unit (related to seagrass systems) recognises the inherent lithological differences between these two units as reflected by primary sedimentary structures and textures. The Safety Bay Sand thus is retained for the upper unit which crops out and forms the contemporary aeolian,

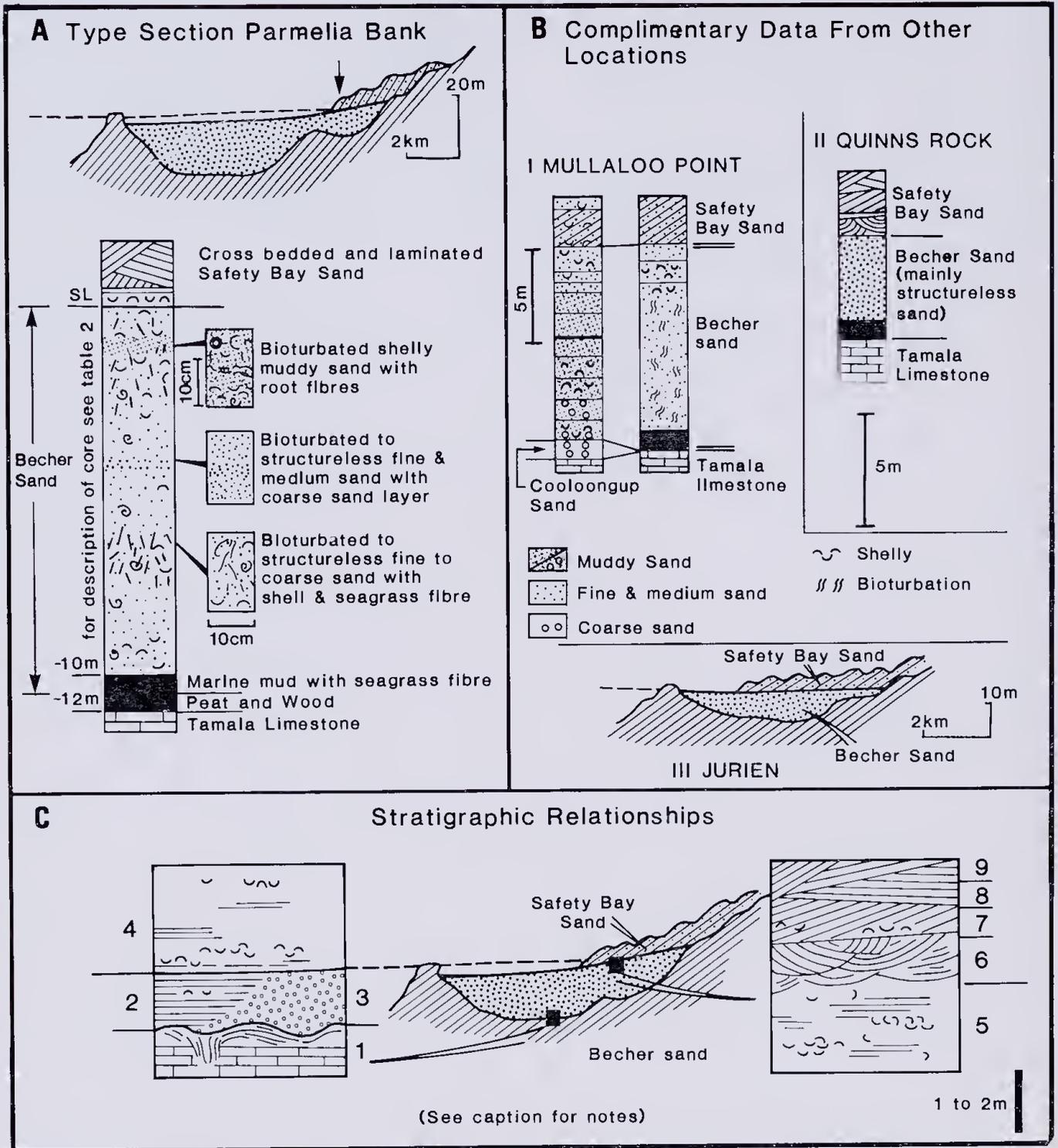


Figure 2.—A.—Details of profile along the type section of Becher Sand at western tip of Woodmans Point. B.—Complementary stratigraphic information on Becher Sand from other localities. C.—Details of stratigraphic geometry, and types of contracts at base and top of Becher Sand.

Key to units is as follows:

- (1) Becher Sand with minor amount of bioturbation mixing with underlying mud and quartz sands.
- (2) Leschenault Formation and/or undifferentiated marine muds grading laterally to (3) quartzose Cooloongup Sand.
- (4) Tamala Limestone with calcareous capstone and calcareous-lined solution pipes
- (5) to (8) Safety Bay Sand showing a well defined sequence of aeolian cross-bedding; shallowly seaward or landward dipping lamination and bedding, more steeply seaward dipping lamination; and complex trough cross-bedding.
- (9) largely structureless Becher Sand with occasional zones of lamination and discontinuous shell lag horizons.

beachridge and beach systems of the coast. In effect the Safety Bay Sand becomes coincident with the Quindalup Dunes of McArthur & Bettenay (1960). The term Becher Sand is given for the lower unit which forms the contemporary submarine sand promontory and seagrass systems of the coast and extends beneath the coastal plain.

As defined herein the formations should clarify studies of stratigraphic relationships and coastal history in that workers in the Holocene can now identify and map out the distinct sediment bodies. Dune fields encroaching shoreward upon subaerial limestone terrain can be viewed as systems where Safety Bay Sand is prograding over Tamala Limestone; beachridge/dune fields prograding seawards over seagrass banks can be viewed as systems where Safety Bay Sand is prograding over Becher Sand. Sand bodies that occur *below* the water table can be assigned either the Becher Sand *or* to the Safety Bay Sand; this will be important distinction (e.g. Semeniuk 1983) and will significantly clarify stratigraphic/history relationships in Holocene sequences.

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The natural sectors of the inner Rottneest Shelf coast adjoining the Swan Coastal Plain

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Abstract

The coastal environment of southwestern Australia encompassing the inner Rottneest Shelf that adjoins the Swan Coastal Plain, can be compartmentalised into five distinct natural sectors. Each sector has its own ancestral geomorphology, processes of sedimentation-erosion-transport, stratigraphic evolution and modern coastal geomorphology. The coastal sectors are: (1) Geographe Bay sector, characterised by a low hinterland and a broad, open, north-facing embayment and simple bathymetry, (2) Leschenault-Preston sector, characterised by a barrier dune-estuarine lagoons system and a simple submarine bathymetry, (3) Cape Bouvard-Trigg Island sector characterised by a complex bathymetry of marine ridge-and-depression morphology developed on Tamala Limestone, and extensive but discrete loci of Holocene sediment accumulation resulting in prograded beachridge and aeolian sand plains, (4) Whitfords-Lancelin sector, characterised by marine ridge-and-depression morphology, limestone rocky shores and isolated accretionary cusps of Holocene sediment, and (5) Wedge Island-Dongara sector characterised by a complex nearshore bathymetry of ridges-and-depressions, limestone rocky shores erosionally scalloped at a large scale, extensive shoreward migrating dune fields and asymmetric accretionary cusps of Holocene sediments.

The dominant stratigraphic units of the coast are: (1) Safety Bay Sand, (2) Becher Sand, (3) Leschenault Formation, (4) deltaic units, (5) Eaton Sand, (6) Cooloongup Sand, and (7) Tamala Limestone, and each of these units either directly influences the development of coastal morphology or is formed as a result of specific coastal environments. The main components of the coastal zone are Safety Bay Sand, Becher Sand and Tamala Limestone, and these have developed a varied range of nearshore, shoreline and onshore components.

The results suggest that the sector approach described herein is important to coastal studies of morphology, dynamics, history and function.

Introduction

The coastal environment of southwestern Australia presents an apparently simple system of rocky shores and sandy beaches. Yet within this system there is a marked compartmentalisation of coastal types, each with its own ancestral geomorphology, processes of sedimentation, erosion and transport, stratigraphic evolution and, as a result of the above, modern coastal geomorphology. This paper describes the results of several years work by the authors on the coast, culminating in the recognition that the modern coastline and inner portion of the Rottneest Shelf, inexorably linked in many ways, can be subdivided into distinct sectors. These sectors form the regional/sub-continental framework to understanding the coastal forms, coastal dynamics and coastal history that are evident at the large, medium and small scale.

The results of this paper have implications in studies on regional sediment transport pathways, coastal history, and coastal management. In coastal management, realistic comparisons can be made between genetically similar segments of coast within a given sector or, in some cases where dynamics/landforms are equivalent, between segments of different sectors. The delineation of natural sectors also allows for workers to determine the regional or local significance of particular tracts of coastline as well as the potential sediment dynamics of any particular location along the coast.

Methods

The results of this paper are based on fieldwork, reconnaissance surveys, aerial photograph studies, low altitude aerial surveys and literature review. Fieldwork involved study of geomorphology, sedimentology and stratigraphy by surface mapping, sample

collection, coring/trenching and low altitude aerial flights. Sites where fieldwork was carried out include (Fig. 1): Geographe Bay, Leschenault Peninsula to Myalup area, Mandurah, Pt Becher to Trigg Island area, Whitfords to Two Rocks area, Lancelin, Jurien Bay, Green Head-Leeman, and Dongara area. Fieldwork was supplemented by reconnaissance surveys and low altitude aerial surveys to numerous other localities including the Cape Naturaliste area, Preston, Dawesville, Madora Bay, Guilderton, Cape Leschenault, Ledge Point, Wedge Island and Cervantes. Examination of aerial photographs, utilising black/white and water-penetrating colour photographs, was also undertaken.

The Rottneest Shelf and coast— Definition : this study

The Rottneest Shelf is defined to encompass the continental shelf between the Abrolhos Islands and Cape Leeuwin (Clarke 1926, Carrigy & Fairbridge 1954). However, this study concentrates only on the Rottneest Shelf adjoining the Swan Coastal Plain and excludes that portion adjoining the uplifted Leeuwin Block (Fig. 1). Specifically, the study area of this paper encompasses only the inner part of the Rottneest Shelf (i.e. landward of the 30 m isobath). This zone incorporates both the bathymetrically complex nearshore shelf with its islands, ridges, reefs, submarine sandy promontories, associated deep-water depressions (as exemplified by the Pt Becher-Garden Island area), and more simple inner continental shelf systems (such as offshore from Geographe Bay-Bunbury). Additionally, the study area encompasses the shoreline and the narrow near-coastal onshore area parallel to the coast. This latter coastal strip is included because landforms here either directly

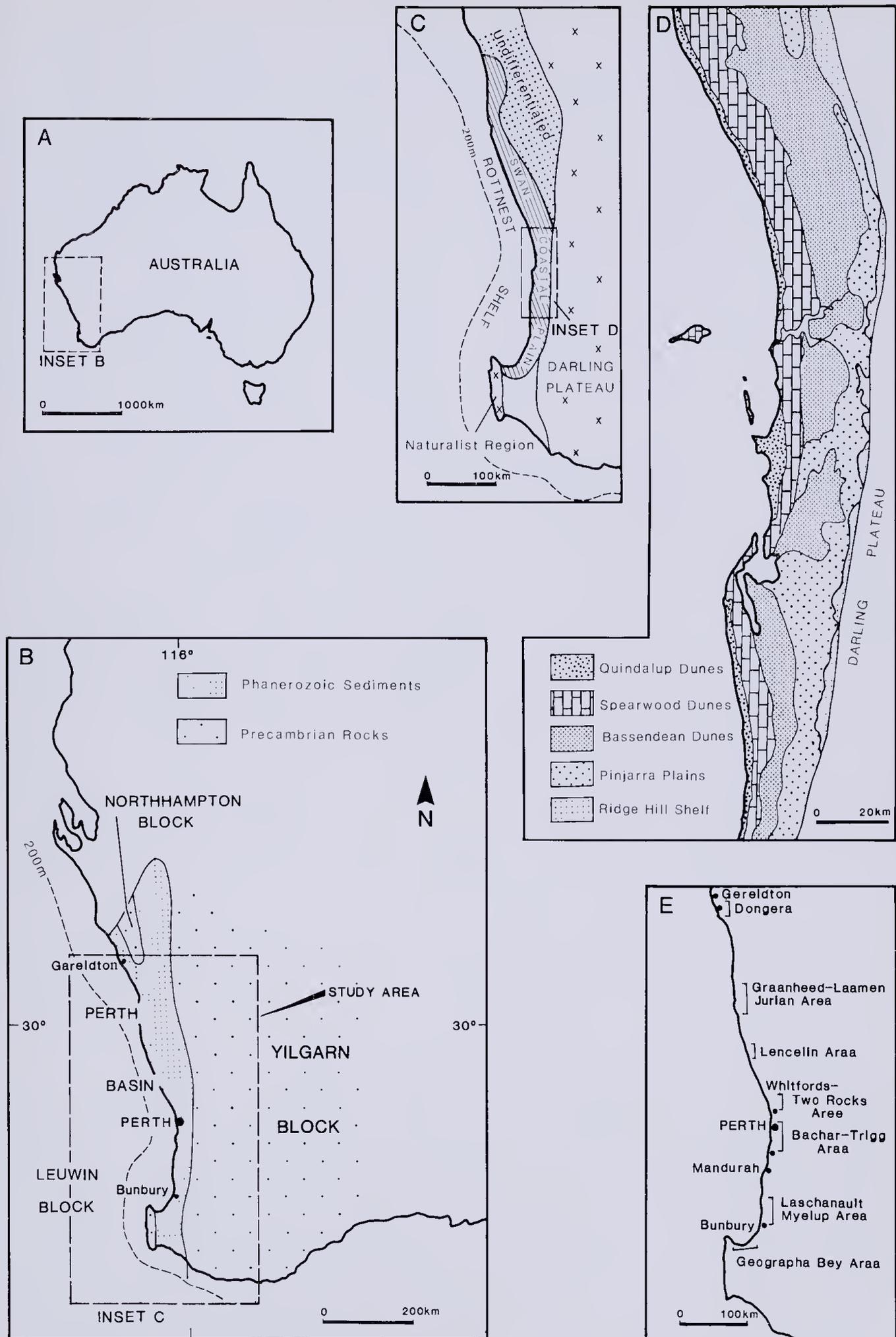


Figure 1.—Location diagrams and geomorphic/geologic setting. A.—Location. B.—Geological setting of study area within Perth Basin. C.—Geomorphic setting of study area along shoreline of the Swan Coastal Plain. D.—Geomorphic units of central portion of Swan Coastal Plain (after McArthur and Bettenay, 1960). E.—Location of study sites.

influence the development of coastal form, or have developed as a result of Holocene coastal evolution, or are stratigraphically related to the modern coast. The northern limit of the study area is delineated at Dongara which forms a natural boundary to the Rottneest Shelf coast of this study. The southern boundary is the Leeuwin block which also forms a natural sharp boundary to the Rottneest Shelf coast of this study.

Previous studies/literature review

There are a number of papers written on the Quaternary geologic/geomorphic features of the Rottneest Shelf coast between Geographe Bay and Dongara. These are discussed below as: regional studies, coastal geomorphology, coastal stratigraphy, coastal processes.

The Rottneest Shelf coast was briefly described regionally by Jutson (1950), Davies (1977), Woods (1980) and Gill (1982). Jutson (1950) and Woods (1980) described the coastline as a single homogenous unit. Davies (1977) similarly treated large sections of the Rottneest Shelf coast as simple units and divided the coast into a "large barrier coast" between Geographe Bay and (approximately) Perth, and a "mainland beach coast" between Perth and Dongara. Gill (1982) classified the coast of this study into one type—the reef and aeolianite coast of Western Australia, which extends from Albany to Exmouth Gulf. All these classifications however are too broad and in many places inaccurate.

Studies in coastal geomorphology have been few in number (Fairbridge 1950, McArthur & Bettenay 1960, Semeniuk & Meagher 1981a, Woods & Searle 1983). Fairbridge (1950) described in some detail the geology and geomorphology of the Point Peron area; McArthur & Bettenay (1960) briefly described coastal dunes as part of their study of the Swan Coastal Plain, and Semeniuk & Meagher (1981 a, b) described the geomorphic processes and products of a barrier dune system in detail. Woods & Searle (1983) documented the prograded sedimentary plain of beach ridges/dunes at Rockingham and calibrated its age structure.

Studies in coastal stratigraphy are more numerous. Searle (1977) described the Quaternary stratigraphy of the Geographe Bay area. Semeniuk & Meagher (1981a,b) and Semeniuk (1983) described the stratigraphy and history of the Leschenault Inlet-Australind area. Searle & Logan (1979) reported briefly on the coastal stratigraphy near Mandurah. Passmore (1970), France (1978), Woods & Searle (1983), and Searle (1984) described the stratigraphy under prograded coasts in the Pt Becher, Rockingham, Cockburn Sound and Trigg Island area. Arakel (1980) described the physiographic setting, stratigraphy and sediments of a near-coastal lagoon at Lceman. Woods (1983) described the stratigraphy under the prograded plain at Jurien. On a more regional basis, Semeniuk & Johnson (1982) described the detailed stratigraphy under beach/dune coastlines. Semeniuk & Johnson (1985) outlined the stratigraphy of limestone rocky shores, and Semeniuk & Searle (1985 a) documented the gross stratigraphic settings of prograded coasts as a framework to studies on Holocene calcrete.

Numerous scattered works dealing with coastal processes also have been published. In addition to those papers cited above which in part also may describe coastal processes of sedimentation, erosion and transport, there are the works of Kempin (1953), Silvester (1957, 1959, 1961, 1963, 1974) Welch (1964), Ruck (1974), Searle & Logan (1978, 1979), Eliot *et al.* (1982), Clarke & Eliot (1983) and Semeniuk & Searle (1985 c). These authors described seasonal or long term fluctuations along sand shorelines or develop models for sediment transport. Studies in coastal oceanography in this region of the Rottneest Shelf include those by Silvester (1957, 1963, 1974), Easton (1970), Department of Construction (1977), Paul & Seale (1978) and Steedman & Craig (1979, 1983). However, there is also a large amount of unpublished data in numerous reports commissioned by and submitted to government agencies, local shires and private organisations.

It is evident from this literature review that no works to date have adequately described or classified the full length of the coastline of the Rottneest Shelf to the detail presented here. Rather, individual studies have concentrated on the details of local areas. Where authors have attempted more regional/subcontinental classifications, the results are either inaccurate or too broad.

Regional geological/geomorphic setting

The coastal lowlands of southwestern Australia comprised of Holocene sediments and/or Pleistocene materials is the seaward portion of the Swan Coastal Plain (McArthur & Bettenay 1960). This plain is composed of Quaternary sedimentary materials which are part of the Phanerozoic Perth Basin (Playford *et al.* 1976). The Swan Coastal Plain is comprised of several geomorphic systems which, from east to west, are (Fig. 1):

- Ridge Hill Shelf—a unit of Pleistocene laterite and sand
- Pinjarra Plain—a unit of Pleistocene to recent alluvial landforms and sediments
- Bassendean Dunes—a unit of degraded Pleistocene aeolian landforms and quartz sand
- Spearwood Dunes—a unit of Pleistocene limestone ridges with intervening swales (= depressions)
- Quindalup Dunes—a unit of Holocene dunes and beaches forming along the modern coast.

To the north of the study area additional units make appearances, e.g. Eneabba Plain (Lowry 1974, Playford *et al.* 1976).

The Spearwood Dunes and Quindalup Dunes are the dominant landforms along the modern coastline of southwestern Australia and most coastal features are a direct result of the disposition and inter-relationships of these units. For instance, limestone rocky shores result where the Spearwood system occurs at the coast, and nearshore island systems such as the Garden Island-Carnac Island chain result where ridges of Spearwood Dunes were incompletely inundated by the last postglacial transgression. The occurrence/disposition of Spearwood Dune ridges also has a direct influence on the development of local Holocene sediment buildups (= the Quindalup Dunes).

Table 1
Description of coastal Quaternary formations, Swan Coastal Plain

	Description	Stratigraphic relationships	Age	Coastal landforms	Occurrence	Author(s)
Safety Bay Sand	buff to cream laminated and cross-shelly sand and shelly sand; soil horizons	overlaps Tamala Limestone and overlies Becher Sand or Leschenault Formation	Holocene	beaches, beachridges and various types of dunes	throughout study area	Passmore (1970)
Becher Sand	grey bioturbated to structureless sand and shelly sand with seagrass biota assemblage	overlies Tamala Limestone or Cooloongup Sand; overlain by Safety Bay Sand	Holocene	seagrass banks and submarine sandy promontories	mainly developed in Cape Bouvard-Trigg Is. sector and Geographie Bay sector; patchy development elsewhere	Semeniuk & Searle (1985b)
Leschenault Formation	bioturbated and inter-layered grey sand, muddy sand and mud with estuarine biota	overlies Eaton Sand; overlain by or interfingers with Safety Bay Sand	Holocene	estuarine lagoons	mainly developed in Leschenault Preston sector and locally in Geographie Bay sector	Semeniuk (1983)
Deltaic units	complexly interlayered and interdispersed sand, muddy sand and mud, locally shelly	overlies Tamala Limestone, Eaton Sand, Cooloongup Sand or even older units; interfingers with estuarine deposits	Holocene	deltaic landforms	mainly developed in Leschenault-Preston sector	not defined
Eaton Sand	yellow-orange quartzose sand (locally with shell layers and limestone)	overlies Tamala Limestone; overlain by Leschenault Formation	Pleistocene	linear, shore-parallel ridges and elevated sand plains	developed in Leschenault-Preston sector	Semeniuk (1983)
Cooloongup Sand	yellow-orange quartzose sand	overlies Tamala Limestone; overlain by Becher Sand	Pleistocene	mainly subsurface	developed in Cape Bouvard-Trigg and Whitford-Lancelin sectors	Passmore (1970)
Tamala Limestone	quartzo-calcareous sand variably cemented into limestone, friable limestone and calcareous capstone	unconformably overlain by combinations of all younger formations, depending on location	Pleistocene	linear, shore-parallel onshore ridge and wetland system, and nearshore/offshore submarine ridge-and-depression systems	throughout the study area	Logan <i>et al.</i> (1970) Playford & Low (1972)

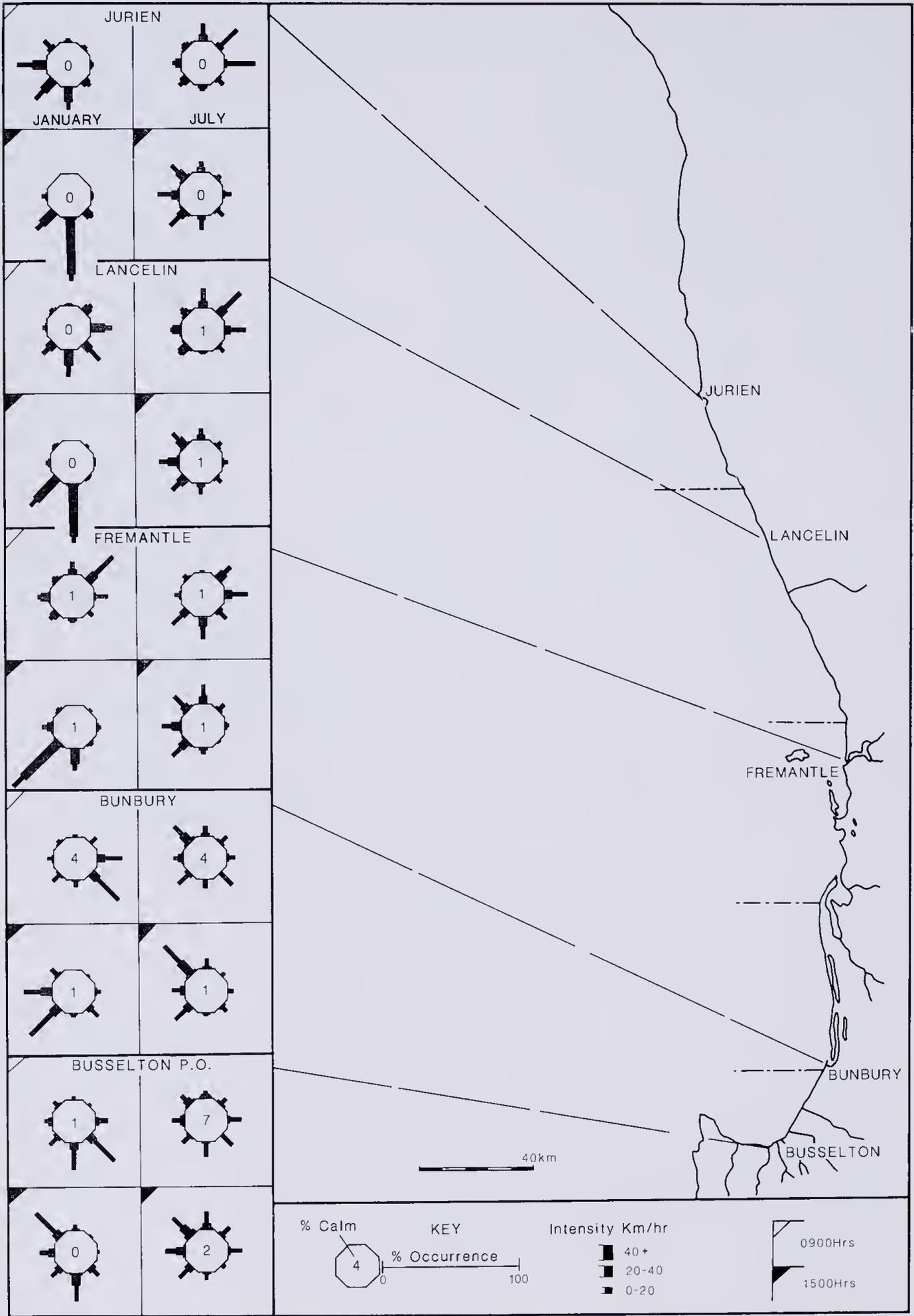


Figure 2.—Wind rose diagrams for selected localities along the southwestern coast. Each locality is typical of a given coastal sector.

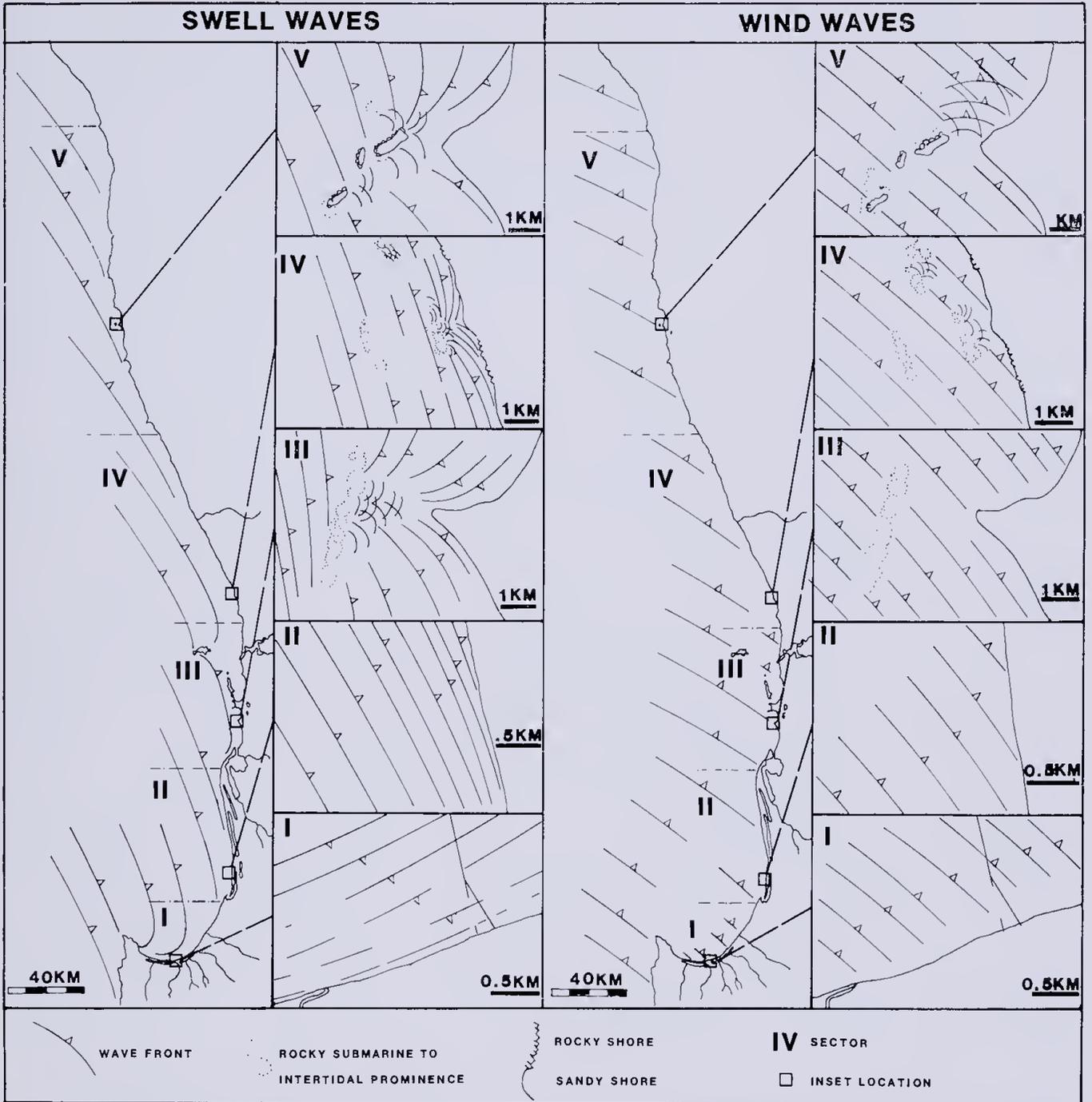


Figure 3.—Diagram to illustrate the pattern of swell waves and wind waves along the southwestern coast of the study area. The overall regional swell and wind wave pattern is shown on the left; the variability of wave pattern developed as the waves interact with the various coastal bathymetric types is shown on the right. The diagram is intended to convey the variability and modification of waves that may ensue in the near coastal zone. Wave fronts have been traced off aerial photographs.

Geologically the Spearwood Dunes is referred to the Tamala Limestone which is a ribbon-to wedge-shaped limestone unit that parallels the coast in outcrop on the subaerial parts of the Swan Coastal Plain. It crops out along the shoreline (where not covered by Quindalup Dunes), it comprises the core of nearshore and offshore islands, and submarine ridges, and it dominantly underlies the vast Continental Shelf (Collins, 1983; Searle, 1984). The limestone has been described by various authors including Teichert (1947), Fairbridge (1950),

Seddon (1972), Playford *et al.* (1976), Playford & Leech (1977), Semeniuk (1983) and Semeniuk & Johnson (1985).

The coastal dune and beach sediments of the Quindalup Dunes stratigraphically are termed the Safety Bay Sand (Playford *et al.* 1976). This formation extends discontinuously along the coast and is best developed in embayments, sheltered bays and tombolo settings where it forms prograded sediment bodies within which there is a distinct stratigraphic

sequence of beach sand overlain by dune sand (Searle 1977, 1984; Semeniuk & Johnson 1982; Semeniuk 1983; Woods & Searle 1983)

The sediments of submarine seagrass banks and sandy promontories have recently been assigned formation status and are referred to the Becher Sand (Semeniuk & Searle 1985b). This unit forms under seagrass cover and is composed of structureless to bioturbated quartz and skeletal sand, muddy sand and mud. The unit generally underlies prograded plain systems beneath a cap of Safety Bay Sand beach/dune sequences (Searle 1984).

Stratigraphic Framework

There is a recurring pattern in distribution of the main Quaternary formations throughout the entire study area. The main formations that directly develop coastal morphology and hence are relevant to this paper are: (1) Safety Bay Sand, (2) Becher Sand, (3) Leschenault Formation, (4) deltaic units, (5) Eaton sand, (6) Coo loongup Sand, and (7) Tamala Limestone. These abut or overlie older Quaternary units such as Bassendean Sand or Australind Formation, or may overlie pre-Quaternary materials. Quaternary units relevant to this paper are described in Table 1. The stratigraphy for individual sectors is described later in the relevant sections.

Dynamics of the coast : meteorology/Oceanography

Meteorology

The significant meteorological factor for coastal areas is wind; it generates wind waves and mobilises aeolian sand. The coastal area of the inner Rottneest Shelf spans a climatic range from subtropical humid at Geographe Bay to subtropical arid at Dongara and, as may be expected, there is gradual change in features of the wind system although regionally there is an overall consistency in the wind pattern. For instance, there is a clear division over the entire study area between summer and winter patterns which are related to the position of eastward-travelling high/low pressure systems (Gentilli 1972).

Winter is characterised by storms with intervening calm weather. Storms typically have mean wind speeds of up to 20 m/s for 6-24 hours duration, and prevail from northwest, west and southwest. Two to four (to ten) such storms may be expected each winter with minor storms occurring every two weeks (Steedman & Craig 1979). During summer, seabreeze/landbreeze systems control the winds in the coastal area. Seabreezes blow from west to southwest in southern areas and from southwest to south in northern areas. Speeds are up to 15 m/s in southern areas and *ca* 20 m/s in northern areas. Seabreezes are significant, firstly in that they induce littoral drift along the shore and, secondly they mobilise sand in aeolian drifts onshore. The direction and abundance of dune blowouts reflect the direction and intensity of seabreezes. Landbreezes have no significant part in coastal processes except in two situations: (1) eastward side of islands, and (2) Geographe Bay area.

In summer there is also the possibility of extra-tropical cyclones travelling through the study area. Although weakening, these are still capable of producing extreme wind and waves. Fig. 2 summarises the formation on wind essential to this coastal study area.

Oceanography

The Rottneest Shelf is exposed to the regional wave climate and circulation patterns of the southern Indian Ocean (Department of Construction 1977; Steedman & Craig 1979, 1980, 1983; Steedman & Associates 1981). Coastal areas of the shelf are subject to these regional processes as well as locally-generated wind waves and currents. Tidal ranges in coastal areas of this shelf are small (Hodgkin & DiLollo 1958, Easton 1970), and are not significant in sedimentary processes except in constricted channels/passages.

Wave Climate: Oceanic swells with periods mainly from between 10 and 14 seconds, and deriving from between west and southwest dominate the regional wave climate and impinge year round on the entire Rottneest Shelf coast (Silvester 1963, Commonwealth Depart of Construction 1977). As swell passes over the shelf it is refracted from deepwater paths by 5 to 15° on the outer shelf and by about 5° or less on the lower gradient inner shelf (Collins 1983). The complex bathymetry of the nearshore dampens, refracts and diffracts both swell and locally-generated seas, creating complex convergences and divergences of wave orthogonals (Fig. 3). Swell is also markedly refracted around Cape Naturaliste (Fig. 3).

Locally-generated wind waves also are a significant influence, supplementary to swell, close inshore and during storm events. Wind waves commonly have a period less than 10sec and are generated under the prevailing wind system associated with the easterly-moving pressure cells (Gentilli 1972), and by the summer landbreeze/seabreeze system. Winter storms generate locally significant seas, with 8 to 10 second periods, which approach first from the northwest, then west, before shifting to southwest as the storm passes over the coast.

In summary therefore, depending on the extent that offshore island/ridge barriers are developed, the incident waves approaching the coast may be: (1) swell waves, (2) wind waves, (3) wind waves and swell, or (4) wind waves *with dampened swell*.

Circulation: The regional circulation pattern as described by Andrews (1977), Kitani (1977), Cresswell *et al.* (1978), Golding & Symmonds (1978) for areas of the continental shelf and shelf edge have little influence on nearshore waters, particularly shoreward of the 20 m isobath. Nearshore circulation on the Rottneest Shelf is largely wind driven with regional oceanic circulation exerting only a minor residual effect (Steedman & Craig 1979, 1980; Steedman & Associates 1981). In restricted nearshore environments like Cockburn Sound, wind forcing results in current gyres, with only limited exchange with adjacent shelf waters. Outside these embayments, winds tend to generate transient north-south flows typically in the range of 5 to 20 cm/sec (Steedman & Associates 1981). Summer wind patterns tend to generate northward flows, winter winds generate a southward flow. In addition, regional oceanic circulation involves current drifts of about 5 cm/sec, also directed north in summer, and south in winter.

Geomorphic components of the coast at the large scale to small scale

Localized Holocene sediment accretion together with erosion of the partially-inundated Pleistocene aeolinite topography has developed a complex array

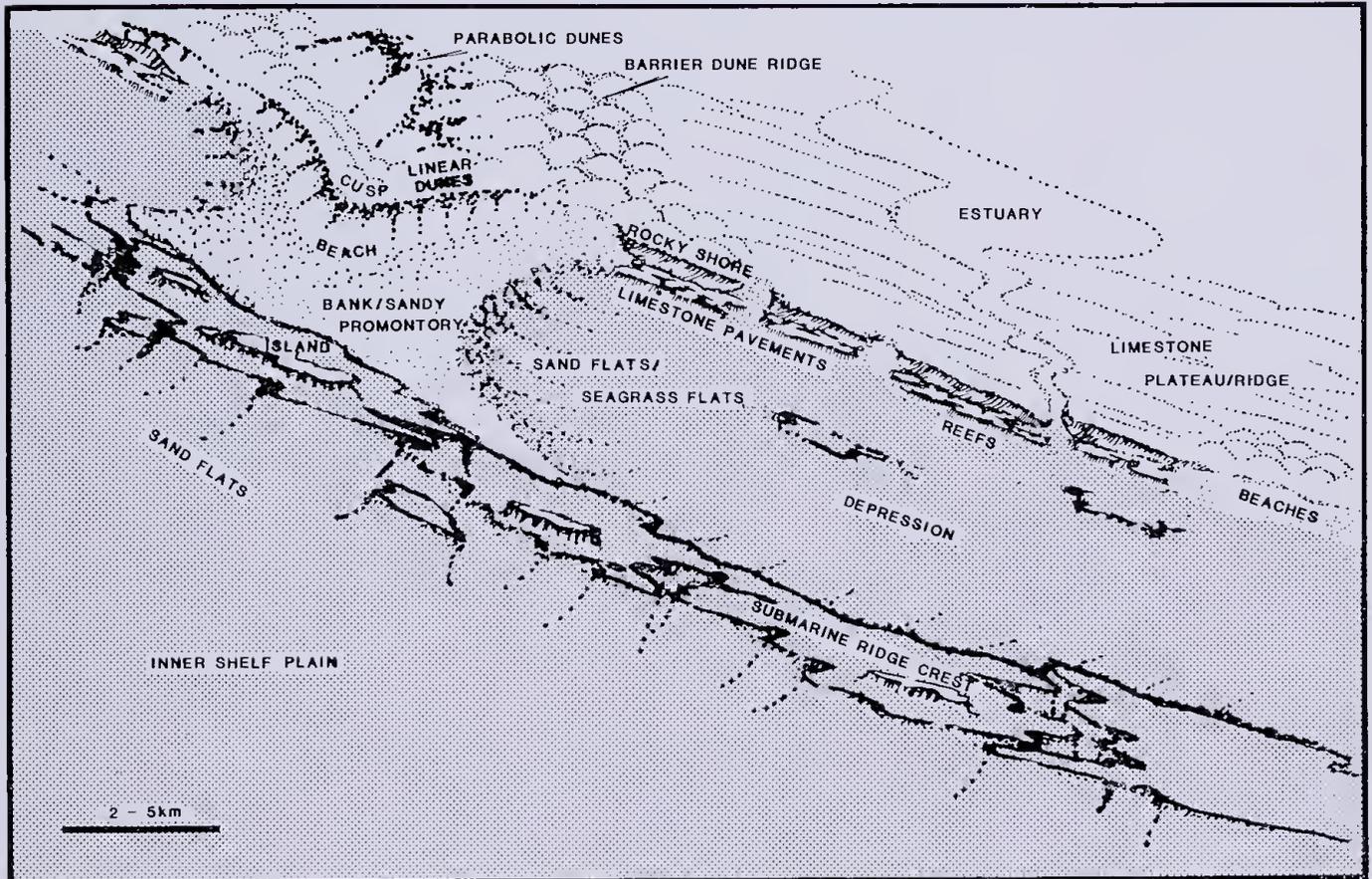


Figure 4.—Schematic diagram illustrating typical components of the coastal zone in southwestern Australia.

of coastal components along the southwestern coast of Australia. The main components of this coastal region evident at the large, medium and small scale, listed within a framework of nearshore-shoreline-onshore units, are as follows (Fig. 4):

Nearshore components

- islands
- submarine ridges and reefs
- depressions
- sand flats and seagrass flats
- limestone pavements
- sand promontories/banks

Shoreline components

- rocky shores
- beaches

Onshore components

- beach ridges and linear dunes
- parabolic dunes (blowouts)
- barrier dune ridges
- limestone plateau /ridges
- lagoons/estuaries/wetlands

Nearshore Components: Islands, submarine ridges and reefs represent various intergradational stages of development and/or breakdown of ridges of Tamala

Limestone inundated by the present sea. Deeper-water depressions in the nearshore environment are inundated inter-ridge swales. Limestone pavements are planed submarine extensions of limestone rocky shores and the nearshore islands, ridges and reefs. Sand flats and seagrass flats are seaward extensions of sandy shorelines or are sand covered submarine plains. Sand promontories/banks are mound-like submarine sediment bodies vegetated by seagrass that

have developed in the inundated inter-ridge depressions during the Holocene; where nearly emergent, the banks can be topped by extensive beach ridge and dune plains that later extend out from the mainland as broad cusped promontories.

Shoreline Components: Shoreline components are rocky shores and beaches. The abundance of these shore types varies according to location: rocky shores are more common north of Perth; sand shores are the more common type south of Perth. The rocky shore environment is complex and varied, with erosional products of cliffs, breccia wedges, shore platforms and breccia pavements predominating (Fairbridge 1950, Semeniuk & Johnson 1985); however there is also local sand accumulation on these shores in pocket beaches and as sheets. Beaches in this region can be subdivided on normal global criteria into shoreface, foreshore, backshore and beachridge/dune environments (Semeniuk & Johnson 1982).

Onshore Components: The narrow subaerial coastal strip parallel to the shoreline is comprised of varied landforms, depending on location. Mostly it is shore-parallel Tamala Limestone ridges. In some localities these ridges separate a lagoon from the Indian Ocean (e.g. Lake Clifton). In other localities a barrier dune of Safety Bay Sand separates an estuary and lagoon (e.g. Leschenault Inlet and Lake Preston) from the Indian Ocean. Locally in the protected lagoons where there is fluvial drainage there are small deltas such as Collie River delta and Harvey River delta. On sediment-accreting (or prograded) coasts, the onshore is composed of

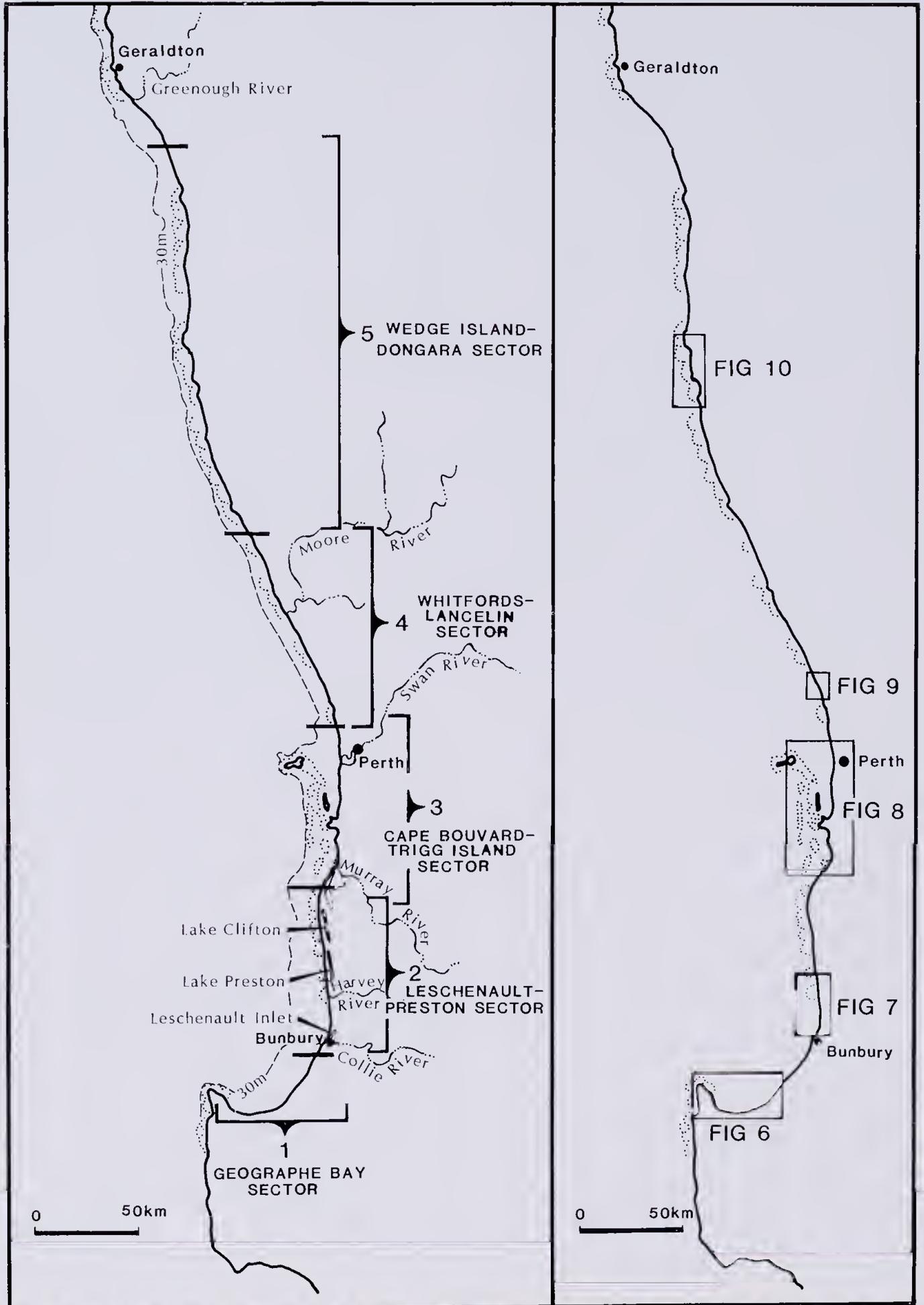


Figure 5.—A.—Map showing the location of the five coastal sectors along the shoreline adjacent to the Swan Coastal Plain in southwestern Australia. B.—Locations of detailed maps shown in Figures 6-10.

beachridges and dunes. Dunes may also comprise the dominant onshore landform along a rocky shoreline where aeolian sand has encroached upon and buried a limestone plateau/ridge hinterland. Dune landforms vary from shore-parallel ridge types to parabolic dune (blowout) types. Dune landforms may form barrier ridge systems, or tombolos or (triangular) cusp systems.

The natural sectors of the Rottneest Shelf coast

The coast of the Rottneest Shelf adjoining the Swan Coastal Plain may be divided into five sectors, each distinguished by a unique combination of modern onshore and offshore geomorphology, coastal processes and Holocene sediment accumulations. The sectors from south to north are: (1) Geographe Bay Sector, (2) Leschenault-Preston Sector, (3) Cape Bouvard-Trigg Island Sector, (4) Whitfords-Lancelin Sector, and (5) Wedge Island-Dongara Sector.

Each of these sectors are described below in terms of (1) bathymetry (= offshore geomorphology) and onshore geomorphology, (2) stratigraphic framework, (3) sedimentation and erosion, and (4) resultant coastal morphology. A summary of the salient features of these sectors is presented in Table 2 and Figs 5 and 6-10.

Geographe Bay Sector

Geographe Bay is a broad, 100 km wide, north-facing embayment at the southern end of the Rottneest Shelf. The western headland is well defined by an upthrust fault block of Precambrian rock. The eastern margin is not well defined and the arcuate shoreline curves into north-south alignment of the main Rottneest Shelf coast at about Casuarina Point. This sector is characterised by a simple

offshore bathymetry, a lowland onshore, and Holocene sedimentation confined to an onshore beachridge/strandplain to nearshore sand sheet deposits.

Bathymetry and Onshore Geomorphology (Fig. 6): The coastal hinterland and seafloor of Geographe Bay slope gently northward to depths of 12 to 15 m where the embayment floor opens out onto the inner Rottneest Shelf. Onshore, undulating hummocks and low discontinuous ridges 1 to 2 m high are shore-parallel bands of Quaternary (Pleistocene-Recent) coastal deposits that generally young towards the present shore. A narrow band (average 500 m wide) of Holocene beachridges is developed behind the contemporary beach shoreline. In swales and inter-beachridge areas there are numerous narrow lagoons and impounded drainage channels. Offshore the gently sloping floor of the bay is a sand sheet, vegetated by dense seagrass meadows. The sand sheet extends from near the beach to about 12 m depth about 4 km offshore. Below this depth the sand sheet thins to expose underlying Pleistocene limestone that locally forms discontinuous 1 to 3 m high shore-parallel ridges. Because of their lack of expression and continuity, submarine limestone ridges have only minimal influence on sedimentation.

An array of sand floored scours aligned transverse to the shore are developed in the meadow cover of the offshore sand sheet. Up to 250 m wide, and incised up to 1.5 m into the sand, the scours extend from near the beach to the thinning northern edge of the sand sheet offshore. Their orientation reflects the orthogonals of the refracted and prevailing westerly swell in the embayment. Towards their landward extremities the scours merge with elongate sand bars

Table 2

Summary of main feature of the coastal sectors

Sector	Description			
	Nearshore bathymetry	Coastal form	Landforms developed by Holocene accretion	Onshore hinterland
Geographe Bay	simple—gently-inclined shelf	even, arcuate low coastal plain	narrow shore-parallel beachridge/dune belt	low surface of limestone and alluvial plain
Leschenault-Preston	simple—gently-inclined shelf	even, linear shore-parallel barrier systems with intervening estuaries and lagoons	linear barrier dune system and protected estuarine deposits	linear ridges of Pleistocene limestone and sand
Cape Bouvard-Trigg Is.	complex—composed of islands, submarine ridges, reefs and intervening depressions	cusped to tombolo coast forming broad accretionary plains prograded from a limestone hinterland	merged cusps and tombolos developing a broad sand plain	linear ridges of Pleistocene limestone
Whitfords-Lancelin	complex—composed of submarine ridges, reefs and intervening depressions	dominantly straight rocky shore with isolated accretionary cusps	isolated cusps and landward migrating dunes	linear ridges and low plateau of Pleistocene limestone
Wedge Is.-Dongara	complex—composed of submarine ridges, reefs and intervening depressions	dominantly scalloped rocky shore with isolated accretionary cusps and landward migrating dune fields	landward migrating dunes and isolated cusps	linear ridges and low plateau of Pleistocene limestone

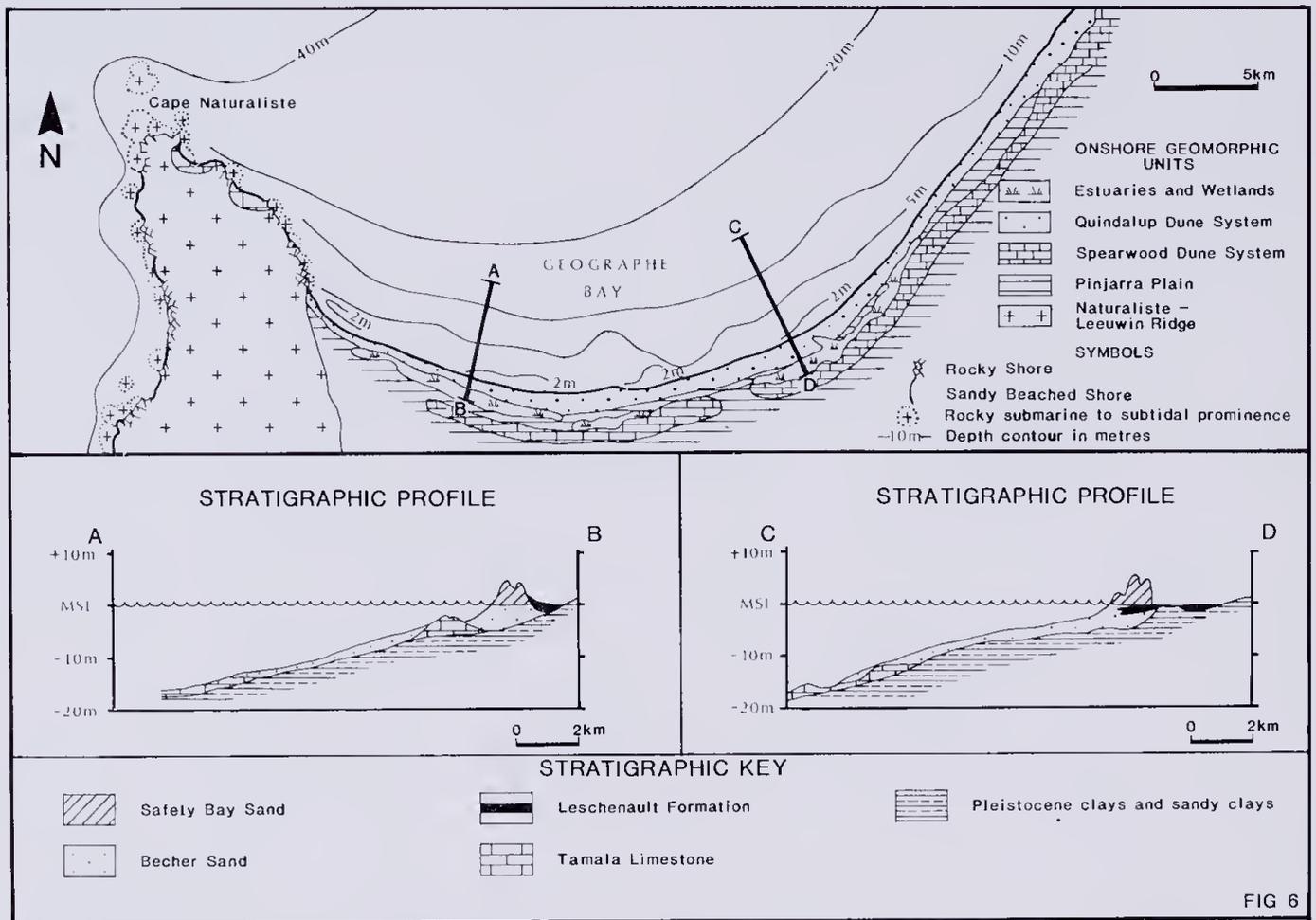


Figure 6.—Portion of coast of the Geographe Bay Sector showing: arcuate Holocene dune system, general coastal form, geomorphic units, simple nearshore bathymetry, and selected stratigraphic profiles.

(up to 3 m relief) oriented at a lesser angle to the shore. The interaction between the shoaling swell, the extensive meadow cover, sand floored scours and bars influences the distribution of wave energy along the coast, and produces a low amplitude sinuosity in coastal alignment. The formation, morphology, and long term dynamics of the scours and bars are discussed by Searle (1977), Paul & Searle (1978) and Searle & Logan (1978).

Stratigraphic Framework (Fig. 6): Holocene sediments form a seaward thinning wedge and reach up to 8 m thick locally beneath the larger beachridges in this area. Offshore Holocene sediments decrease in thickness to an average thickness of about 1.5 m and further offshore become thin and discontinuous, exposing a gently north-sloping unconformity cut mainly on Tamala Limestone, and an underlying semi-lithified green sandy clay. The limestones are aeolian and marine, and form a thin (less than 5 m thick) discontinuous capping on the underlying clay. In the far western part of Geographe Bay adjacent to the Dunsborough Fault and the Leeuwin-Naturaliste Block headland, Holocene sediments also overlie biotite-rich green sands (of indeterminate age) and Precambrian rocks.

The onshore Holocene sediments are mainly Safety Bay Sand, (beach and beachridge sediments), consisting of quartzo-feldspathic, skeletal sand. Lenses and ribbons of estuarine mud (stratigraphically correlated with the Leschenault Formation of Semeniuk, 1983) have been incorporated in the

Holocene sequence due to the impounding of the natural drainage system behind and within the beachridges. The offshore sand sheet is referred to the Becher Sand.

Sedimentation/erosion: In the long term (past 5 000 years) sediment accretion in Geographe Bay has resulted in an average progradation of about 500 m and the development of a thin but extensive sand sheet offshore. Although there has been net accretion, aerial photographs indicate at some time earlier in the Holocene there also were pronounced periods of coastal erosion. Quartzo-feldspathic sands have been reworked from older Pleistocene coastal deposits, probably during the post-glacial marine transgression. The skeletal sediment component has been generated mainly within the embayment by the carbonate-producing organisms of extensive seagrass meadows and, to a lesser extent, by organisms inhabiting adjacent bare sand. Both the rate and extent of sediment accretion have been limited by the lack of a significant post-transgression source of quartzo-feldspathic sand and losses of skeletal sediment from the embayment in the littoral transport system.

In the short term, sedimentation is controlled by the interaction of: (1) the prevailing refracted and shoaling swell regime, (2) locally-generated wind waves, (3) wind-driven nearshore circulation, (4) the extensive seagrass meadow-covered shoreface, (5) the scour/bar systems, and (6) the arcuate north-facing geometry of the embayment. Under prevailing conditions, refracted westerly swell and longer period

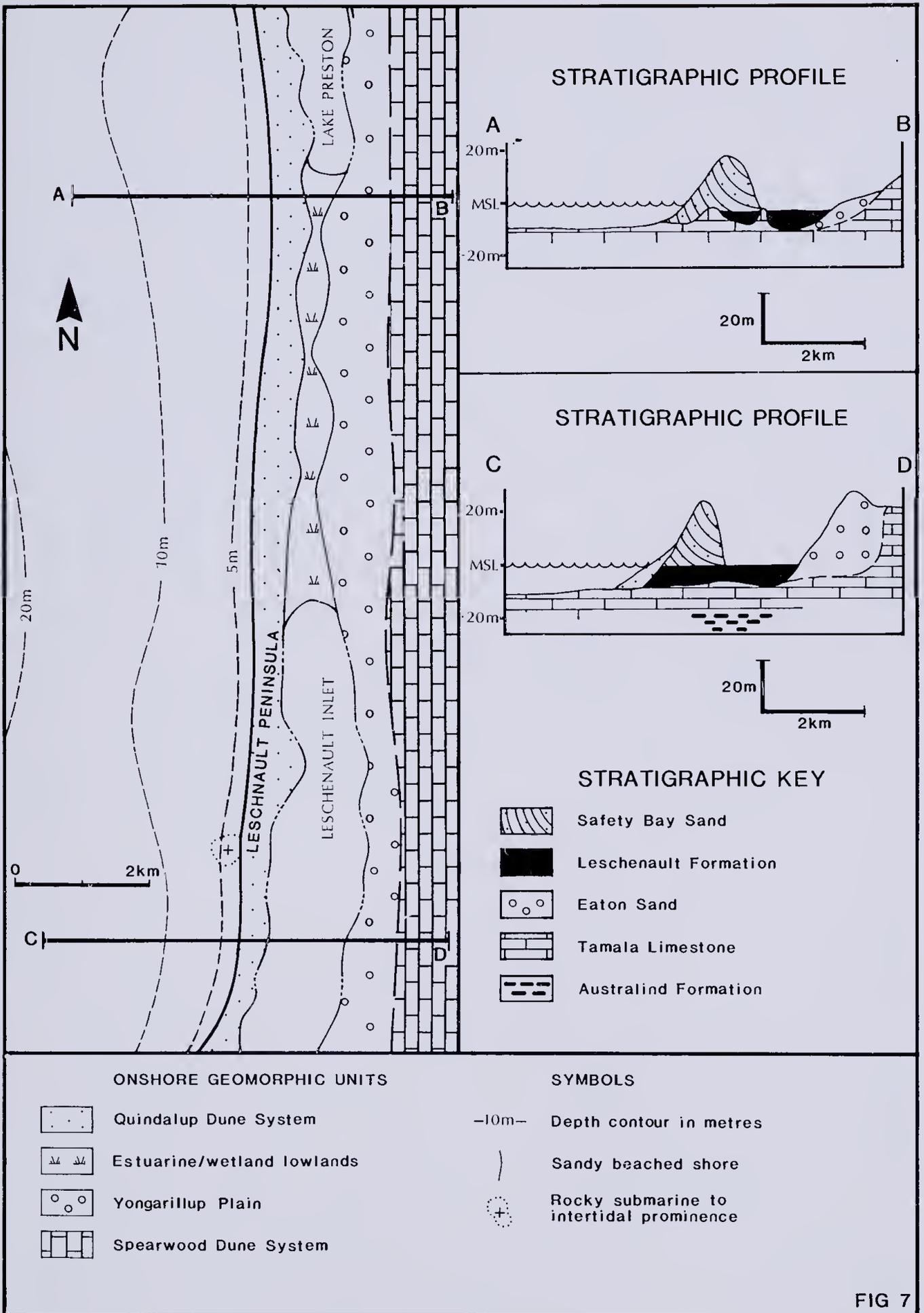


Figure 7.—Portion of coast of the Leschenault-Preston Sector showing: the linear Holocene barrier dune, general coastal form, geomorphic units, simple nearshore bathymetry and selected stratigraphic profiles.

wind waves impinge on almost all the Geographe Bay shoreline. Sediment tends to be transported shoreward from the scours and bars toward the shore. Wave induced and westerly wind generated currents then impel a littoral movement eastward.

In winter months (and rarely in the summer due to cyclones) storm conditions disrupt the prevailing system. Northerly storm waves impinge on the whole shoreline. In the eastern part of the embayment particularly, the storm waves and winds impel a westerly littoral transport. Locally the littoral currents move offshore along the scour/bar systems entraining some of the littoral drift. The sediment supplied in this manner to the scour/bar system is then returned gradually to the shore and nearshore by prevailing conditions. Easterly (landbreeze) winds also generate analogous westward littoral transport and seaward diversions to the scour/bar systems. Diversion of artificial drain mouths and natural river mouths clearly indicates net littoral transport is eastward within the embayment.

Resultant Coastal Morphology: The coastal form of Geographe Bay is largely developed by the configuration of Pleistocene limestone. Holocene sedimentation in Geographe Bay has not substantially altered the ancestral coastal morphology. During the transgression, the low ridges of Pleistocene limestone were probably subject to erosion, resulting in the stratigraphic discontinuity observed at present. Limited sediment accretion along the shore has resulted in a seaward migration of the shoreface along a broad front, grossly maintaining the arcuated bay form and developing a beachridge ribbon peripheral to the bay. The development of successive beach ridges during the coastal progradation also has significantly impeded the natural drainage from the hinterland, resulting in the elongate fresh to brackish lagoons/inlets developed in and behind the ridges.

Leschenault-Preston Sector

The Leschenault-Preston sector of the Rottne Shelf coast extends about 80 km in a northerly alignment. The southern margin is defined by Casuarina Point, the northern margin is defined by Cape Bouvard. This sector is characterised by a simple offshore bathymetry, a series of parallel dune systems onshore and Holocene sedimentation largely confined to a barrier dune system with its accompanying lagoons.

Bathymetry and Onshore Geomorphology (Fig. 7): The onshore area in this sector is dominated by a series of Spearwood and Quindalup dune ridges which form a 45 to 60 m high and 4-6 km wide topographic barrier between the main low-lying Swan Coastal Plain and the inner Rottne Shelf. The ridges trend either parallel or slightly oblique to the coast. The Quindalup Dunes occur at the present coast where they form a separate ridge as a barrier dune system, or flank the seaward face of a larger Spearwood dune ridge. Older, less prominent dune systems form an undulating lower coastal hinterland.

In depressions between major dune ridges there are elongate, shallow (usually less than 2 m deep) water bodies. Harvey estuary, Peel Inlet and Lake Clifton occur in depressions between Spearwood Ridges. Lake Preston and Leschenault Inlet occur between a Quindalup ridge and a Spearwood ridge;

Leschenault Peninsula and the Preston Barrier, both of which are barrier dune systems, separate the lagoons/inlets from the ocean. The main drainage in this sector is either into Leschenault Inlet or Harvey estuary.

The bathymetry of this coastal sector is simple. A coast of beach/beachridge/dune is developed on the seaward flank of the Quindalup barrier dune or a Spearwood ridge. Seaward of the shore, the sand-mantled shoreface slopes seaward to merge with the inner shelf plain about 1-2 km offshore in water depths of 12 to 15 m. Low-lying limestone pavement surfaces and discontinuous limestone ridges (1-2 m high) and relict beach-rock slabs (Semeniuk & Searle, 1985c) are exposed on the inner shelf plain, and protrude through a sand veneer in several locations. These rocky areas are not sufficiently prominent or continuous to influence sedimentation in this sector.

Stratigraphic Framework (Fig. 7): This sector contains a complicated array of stratigraphic units which include Pleistocene units: Tamala Limestone, Eaton Sand and Australind Formation; and two Holocene units: Safety Bay Sand and Leschenault Formation. The Australind Formation is a calcareous estuarine unit; the Tamala Limestone is aeolian and marine sediment; and the Eaton Sand is a shoestring-shaped body of coastal sand which is thickest along the eastern shore of Leschenault Inlet and thins rapidly westward. The Pleistocene units occur in stratigraphic superposition.

Quartzose and calcareous sand of the Safety Bay Sand dominate the shoreline throughout this sector. These sands form the barrier dune system of the Leschenault Peninsula and Preston Barrier, mantle the seaward face of Spearwood ridges, and extend over the shoreface down to depths of 12 to 15 m. Maximum thickness of the Safety Bay Sand is up to 40 m in the Leschenault Peninsula. To the north the Holocene sands may overlie semi-lithified dune sands and limestone of the Tamala Limestone. In the Leschenault Peninsula area and northwards, Safety Bay Sand also overlies and locally interfinger with Holocene estuarine mud and sand (= Leschenault Formation). The Safety Bay Sand passes offshore into sand sheets that variably overlie areas of Leschenault Formation, the Eaton Sand, or the Tamala Limestone.

The Leschenault Formation, up to 6 m thick, extends as a ribbon from the floor of the contemporary estuarine lagoon to underneath the Safety Bay Sand of the barrier dunes. This mud/sand sheet largely overlies the Eaton Sand, but may also directly overlie an irregular Tamala Limestone surface.

Sedimentation/erosion: Throughout the Holocene the west-facing shores of this sector have been fully exposed to the wind, wave and current regime of the Rottne Shelf. As a result, there has been a continuing reworking of the Holocene sediment bodies developed initially during the late stages of the post-glacial transgression. In response to the prevailing onshore nature of the energy regime, erosion of the seaward face of this sandy coast is accompanied by dune migration eastward across the barrier dune system, and up the seaward flank of the Spearwood Dunes of the shoreline to the north. There is also significant longshore transport of material in the littoral and nearshore zones. Under conditions of

combined prevailing wind waves and swell, sediment is impelled northward along the upper shoreface. This pattern is interrupted by northerly storms which impel a reverse transport. However, although dramatic, these interruptions are only interim and net transport year round is northward.

The sediment available to this coast during the Holocene mostly has been quartz sand (except in the sheltered lagoonal environments where calcareous mud and terrigenous mud have accumulated). The source of this sand largely has been the reworking of pre-Holocene materials in the adjacent shelf and coast during the latter stages of the post-glacial transgression. River-transported sand supplements this source only to a very minor degree. Supply of sediment from Geographe Bay to the south has been minimal as indicated by provenance studies (Searle and Semeniuk, in prep.).

Resultant Coastal Morphology: The exposure and continuing reworking of the coastal deposits of this sector throughout the Holocene has produced major changes in the coastal morphology. Some time after the transgression a major shore-parallel, emergent barrier dune system developed several kilometres seaward of the present Leschenault Peninsula. At its southern end the barrier may have joined with Casuarina Point. At its northern end, the barrier may have developed from a shoreline founded on Spearwood Dune ridges located some distance to seaward of the present shore (probably about 3 km). The sheltered waters to landward became an elongate lagoon system, the combined Lake Preston and Leschenault Inlet. Under the effect of the onshore wind and wave system, the barrier retreated and migrated eastwards into the barred lagoon system. Staggered dune advances resulted in an irregular encroachment of the barrier into the barred lagoon, and at one point dune advancement segmented the lagoon into a northern portion (Lake Preston), and a southern portion (Leschenault Inlet). The current coastal landforms of barrier dunes, lagoons and inlets reflect this history with the barrier dune system still slowly advancing landwards.

Cape Bouvard to Trigg Island

The Cape Bouvard to Trigg Island Sector of the Rottneest Shelf coast extends over 100 km in a north to 300° alignment. This sector is characterized by a complex nearshore bathymetry and extensive but discrete cells of Holocene sediment accretion. The southern boundary with the Leschenault-Preston boundary is defined by the abrupt termination of rocky shores south of Halls Head near Cape Bouvard. The northern boundary of the sector is defined by the emergence of a new and discrete, separate set of offshore ridges north of Trigg Island.

Bathymetry and Onshore Geomorphology (Fig. 8): The nearshore-onshore geomorphology and bathymetry is dominated by a series of north to 300°-trending (slightly oblique or parallel to shore) submarine to emergent aeolian ridges, of the Spearwood Dune system. These are termed from west to east: the Five Fathom Bank Ridge, Garden Island Ridge and Spearwood Ridge. The ridges vary in prominence from a few metres to in excess of 60 m, and in continuity from continuous to discontinuous. Onshore the Spearwood Ridge forms the basis of the mainland shore and has developed

topographic barriers up to 60 m high between the inner Rottneest Shelf and the low Swan Coastal Plain further to landward. About 12 km offshore the Garden Island Ridge forms a perforate chain of rocky submarine reefs, pinnacles, and islands with interspersed passages. The Garden Island Ridge rises locally up to 65 m above the surrounding seafloor, and extends from near Cape Bouvard (where it is wholly submarine and discontinuous) to Rottneest Island where it abruptly terminates. The least prominent ridge, the Five Fathom Bank Ridge, is located a further 10 km to seaward where it forms a wholly submarine chain of rocky prominences rising up to 25 m above the surrounding seafloor. This ridge extends south past Cape Bouvard before terminating offshore from Myalup. Northward it merges with the Garden Island Ridge at Rottneest.

Discrete and significant bodies of Holocene sediment have developed across the submarine depression (20-25 m deep) only between the coastal mainland Spearwood Ridge and the offshore Garden Island Ridge, dividing it into a series of marine basins. In contrast, accretion in the depression between the Garden Island and Five Fathom Bank Ridges has been minimal. The Holocene sediment bodies consist of submarine to nearly emergent barrier and fringing sand banks that stand up to 30 m above the central axis of the depression. The bank structures may be capped by extensive terraces of low beachridges formed successively as the mainland shore prograded seaward across the adjacent submarine bank top to form cusps and tombolos. In addition, much of the seaward face of the mainland Spearwood Ridge is flanked by stabilised and mobile Holocene dunes.

The Swan River estuary also occurs within the sector but it is apparent that this fluvial influence has had little impact on the development of the coastal sector either geomorphologically or sedimentologically.

Stratigraphic Framework (Fig. 8): Holocene sediments of this sector overlie an irregular unconformity surface developed mainly on the Tamala Limestone; unconsolidated quartz sand (= Cooloongup Sand) occurs as sheets or wedges on low-lying parts of the unconformity surface. These quartz sands are relict, reworked from soils and other surficial materials during the post-glacial transgression (Passmore 1970), and are in part equivalent to the Eaton Sand of the Leschenault-Preston Sector. The Holocene sediments (up to 30 m thick) consist of shoaling and prograding sequences of quartzo-carbonate sand formed in submarine bank, beach, beachridge and dune environment (i.e. the Becher and Safety Bay formations). Sheets of carbonate muds up to 7 m thick have also developed in the quiescent marine basins formed between the major bank structures in the depression between the Spearwood and Garden Island ridges. Elsewhere in more exposed locations, Holocene carbonate sand veneers the submarine flanks of the mainland and Spearwood Ridges.

Sedimentation/erosion: Holocene sediment accretion in this sector has been largely controlled by (1) the interaction of the shelf wave regime, (2) the complex ridge-and-depression bathymetry, and (3) abundant sources of carbonate sediment. The Garden Island Ridge acts as a perforate barrier allowing a portion

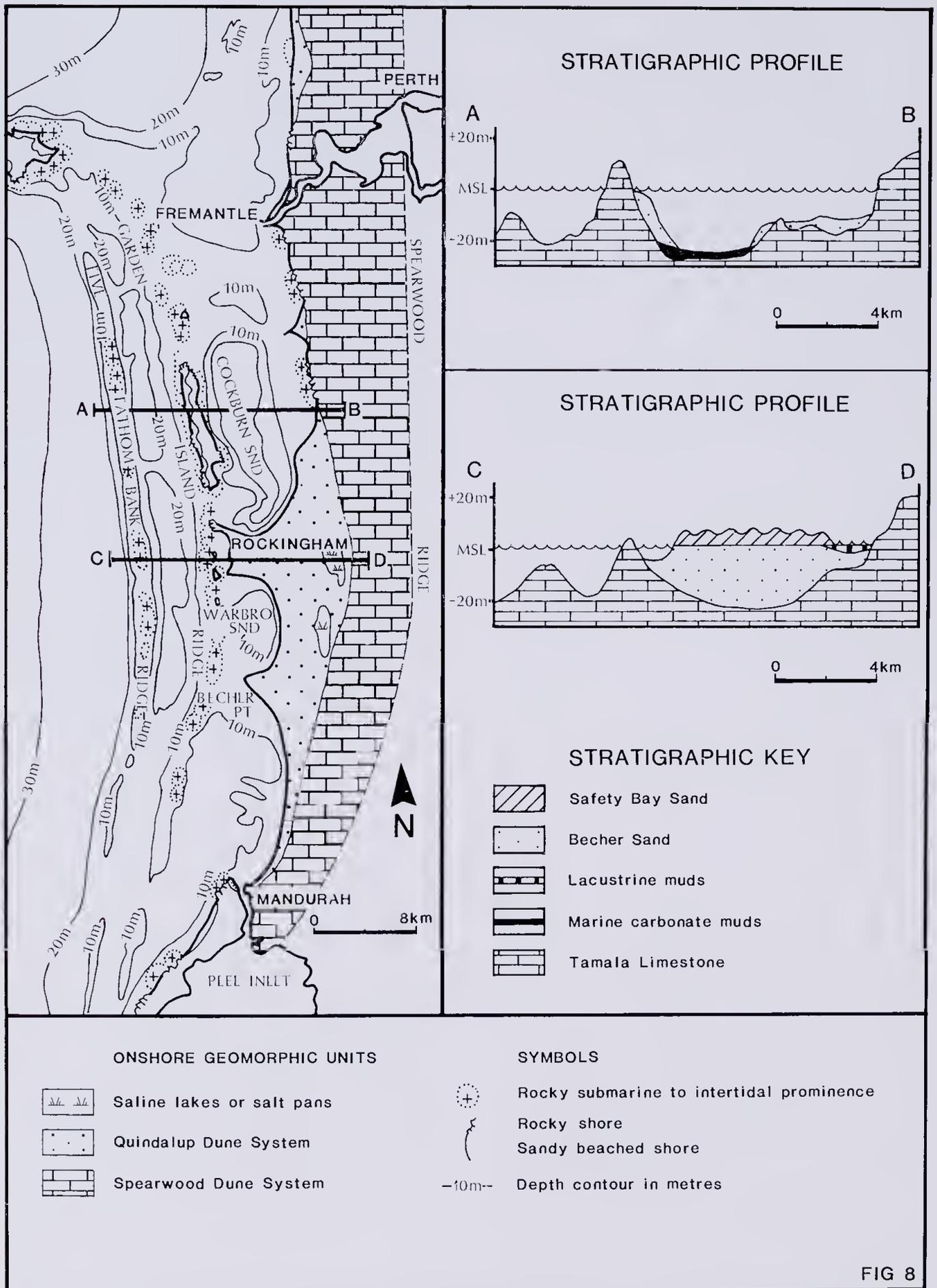


Figure 8.—Portion of coast of the Cape Bouvard-Trigg Island Sector showing: extensive Holocene cusped and tombolo accretionary plains, general coastal form, geomorphic units, complex nearshore bathymetry of ridges and depressions, and selected stratigraphic profiles.

of the incident onshore waves through gaps and passages into adjacent parts of the otherwise sheltered, 20 to 25 m-deep depression to landward. Holocene sediment accretion has been largely restricted to these discrete loci of transmitted wave energy to form well defined submarine barrier and fringing bank structures.

Under the influence of prevailing swell and wind waves, sediment is transported northward along the exposed seaward faces of the Garden Island Ridge and mainland Spearwood Ridge. Where the offshore ridge shelters the shore along the Spearwood Ridge, transport is minimal and localised. Northerly storms impel a reverse transport on these exposed shores. The portion of the onshore waves passing through gaps in the Garden Island Ridge diverts sediment from the transport pathway on the seaward side. This sediment is then transported landward onto the adjacent submarine bank.

Refraction over the bank causes convergence of the wave that passes through the ridge crest toward the central axis of the bank. Sediment thus is impelled shoreward and contained within the bank locus. The convergence of wave energy as it passes shoreward also causes a concentration of littoral transport toward the central axis of the bank on the mainland shore. Progradation of the mainland shore seaward across the submarine bank top is centred on this convergence axis. The form of the prograding shore reflects the refractively-converged wave trains.

Since the end of the post-glacial transgression, sediment supply in this sector has come from two main sources: (1) erosion of the variably lithified Pleistocene aeolianite of the Garden Island Ridge which has supplied abundant carbonate lithoclast sand, and (2) production of skeletal material by the biota of seagrass meadows inhabiting the submarine banks in the system. This latter material is largely accumulated *in situ*. Transport into the system along the coast from the south has been a minor but locally important source of sediment.

In contrast to the carbonate dominated sediment of the bank systems, the mainland coast and adjacent shelf immediately to the north are blanketed by thin sheets of predominantly quartzose sands; this indicates there is no significant loss or supply of sediment to the system to the north.

Resultant Coastal Morphology: The Cape Bouvard-Trigg Island Sector coastal morphology has been extensively modified by both erosion and accretion since the end of the last post-glacial transgression and the coastal geomorphology reflects both these processes. Immediately following the transgression, the crest of the offshore Garden Island ridge was mostly emergent, forming a continuous elongate barrier island. Due to erosion on its seaward side, breaches have progressively developed and widened reducing the ridge crest to its present form. Accretion of sediment in submarine bank complexes in the depression to landward has been controlled by the breaching and subsequent erosion of the ridge crest. Formation of breaches and the activation of bank accretion in the adjacent part of the depression has been sequential rather than synchronous.

Each of the banks evolved in a well defined sequence. The initial stage of bank growth is the formation of a discrete submarine sediment lobe on

the landward flank of the Garden Island Ridge adjacent to an initial breach. This lobe, supplied with eroded ridge material and locally generated skeletal sediment, progrades toward the mainland shore accompanied by continued erosional widening of the adjacent breach which in turn widens the evolving lobate bank. The lobate submarine structure eventually links with the mainland shore and sediment transported shoreward across the bank top then is supplied to the mainland shore where convergent littoral transport ensures it remains in the bank locus. This sediment supply initiates the progradation of the mainland shore seaward across the bank top, forming an extensive, low-lying beach ridge terrain. Ultimately the beach ridge terrain extends seaward, linking with emergent remnants of the Garden Island Ridge crest forming a tombolo. At present, the five major bank structures within the sector represent all stages of this evolutionary process from the submarine lobe to fully emergent stage.

Along more exposed portions of coast in this sector accretion has been restricted to development of thin carbonate and quartz sand sheets in the nearshore, and localised beach/beachridge/dune development on the seaward flanks of the emergent mainland and offshore Pleistocene limestone ridges. Elsewhere, locally, the coast is comprised of eroding, exposed Pleistocene limestone and, as a result, rocky shores with pocket beaches are developed.

Whitfords-Lancelin Sector

The Whitfords-Lancelin Sector extends 100 km in a 330° alignment. The southern limit of the sector is sharply defined by the recurrence of shore-parallel submarine rocky ridges, the Marmion Reef Ridge and the Staggie Reef Ridge, in the vicinity of Trigg Island, which then extend northward throughout the sector. However, the northern limit is gradational and defined by a transition from a wave dominated (this sector) to wind dominated (Wedge Island to Dongara Sector) pattern of Holocene sediment accretion. There is also a gradual change from relatively straight rocky shore (this sector) to deeply scalloped rocky shore.

This coast is characterised by a variety of features. The nearshore bathymetry has well defined, largely submarine, shore-parallel ridges. The coast consists largely of diffuse rocky coasts and pocket beaches interspersed with straight, beached coasts backed by the high dunes; locally, discrete and isolated cusped dune-topped promontories extend up to 800 m seawards.

Bathymetry and Onshore Geomorphology (Fig. 9): A series of shore-parallel (330° trending) limestone ridges form the basis of the bathymetry and onshore geomorphology of this sector. There are four main limestone ridges. One forms the architecture of the shore and together with less prominent ridges immediately to the east this mainland ridge forms a topographic barrier between the low-lying Swan Coastal Plain and the coast. Lithified portions of the limestone ridge are exposed at the shore as diffuse rocky headlands and low (2-5 m high) seacliffs with intervening pocket beaches. Intertidal to submarine platforms and rocky prominences extend up to 150 m seawards of these rocky shores. The mainland limestone ridge may also be mantled by well vegetated, linear and parabolic dune forms. Immediately adjacent to the present coast, dunes on

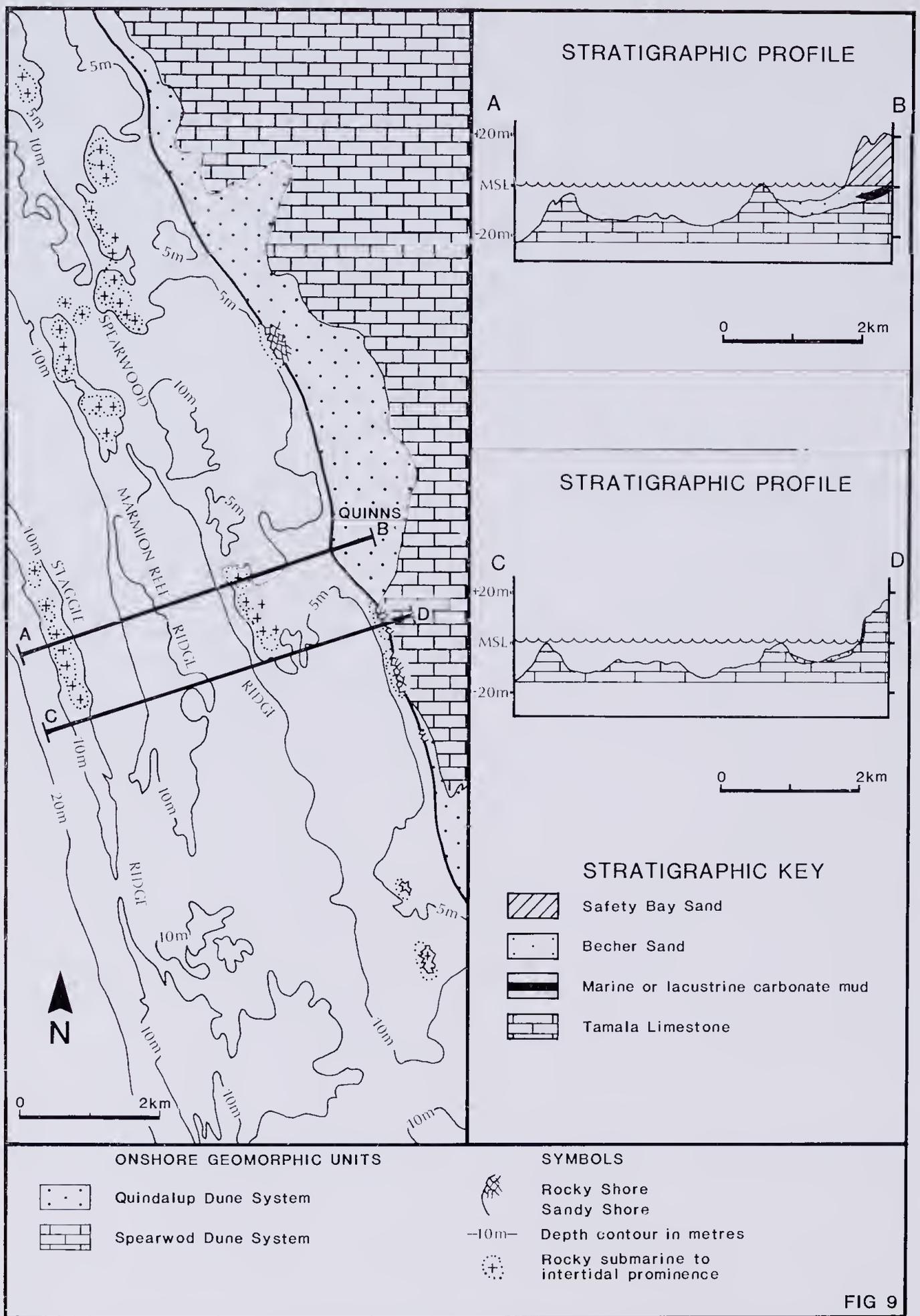


FIG 9

Figure 9.—Portion of coast of the Whitford-Lancelin Sector showing: small isolated Holocene accretionary cusps, general coastal form, geomorphic units, complex nearshore bathymetry of ridges and depressions, and selected stratigraphic profiles.

the ridge flank tend to be linear and parallel to the shore. Inland dunes are either hummocky or parabolic. The parabolic forms are the stabilised remnants of large blowouts and they are uniformly oriented to the prevailing onshore westerly wind regime. Elsewhere, unconsolidated sands mantle the limestone ridge and form sandy beached coasts backed by high, well vegetated dunes. Locally these sandy coasts extend up to 800 m seawards to form discrete cusps. The cusps are also topped by well vegetated dunes. Adjacent to the beaches, parallel sets of beach ridges up to 5 m high are sometimes developed.

The other three limestone ridges, termed Staggy Reef Ridge, Marmion Reef Ridge and Spearwood Ridge are located ca 6, 4 and 2 km offshore. On these, the outer ridge, the Staggy Reef Ridge, is the least prominent, rising about 6 to 8 m above the surrounding seafloor to crest in a perforate chain of wholly submarine rocky prominences. The middle ridge (Marmion Reef Ridge) rises up to 15 m above the surrounding seafloor, and the most prominent parts of the ridge crest form small isolated rocky islets. The Spearwood Ridge appears as an extension of the mainland ridge of the Cape Bouvard-Trigg Island Sector; it occurs here as a discontinuance ridge of shore. Water depths in the depressions between the ridges reach up to 15 m.

In several locations subridges extend obliquely across the trend of the three main ridges. These are oriented mainly between 0° and 010° , but several less prominent cross-trends are oriented at about 320° . The subridges form discontinuous chains of submarine rocky pinnacles and reefs commonly less prominent than the main ridges.

Locally there are small rivers that drain into the coastal areas but these are not significant either geomorphologically or sedimentologically.

Stratigraphic Framework (Fig. 9): Holocene sediment in the offshore and onshore areas varies greatly in distribution and thickness. Offshore, Holocene sands commonly form thin, discontinuous sheets which overlie low-lying portions of an irregular unconformity surface developed on the eroded remnants of the Tamala Limestone ridge-and-depression topography. Onshore Holocene dunes locally mantle the seaward flank of the mainland ridge. These dunes overlie either lithified Tamala Limestone or semi-lithified Pleistocene dune sands and soils. In the cusped promontories the Holocene stratigraphic sequence is analogous to the beach/dune (Safety Bay Sand) and submarine bank (Becher Sand) overlying a Pleistocene unconformity as described for the cusped and tombolo promontories of the Bouvard/Trigg Sector.

Sedimentation and Erosion: Holocene sediment accretion in this sector has been controlled by the interaction of 1) the prevailing onshore wave regime, 2) the nearshore bathymetry, and 3) the onshore wind regime. As in the Bouvard-Trigg Sector, accretion has occurred in loci of wave-energy convergence in the comparatively-sheltered, inter-ridge depression between the shoreline ridge and the adjacent offshore ridge. The accretionary sites, however, are not prominent and have prograded only relatively small distances to seaward. Sediment in these loci has again

been derived from local benthic assemblages (principally the seagrass assemblage) and from the erosion of the Pleistocene ridges. Elsewhere along this sector Holocene accretion has only occurred as ENE to NE migrating dunes. These dune fields can extend up to several kilometres inland. The source of sediment for these dunes has probably been the underlying unconsolidated Pleistocene dune material supplemented at the coast by sediment leaked from the littoral transport regime.

Since the Pleistocene limestone ridge-and-depression topography first began to be inundated by rising post-glacial sea levels, it has been subjected to extensive but selective erosional modification. In general terms the less-lithified aeolianite materials have been removed, leaving the more resistant portions as rocky submarine to emergent platforms, pinnacles and prominences, the processes and products of intertidal erosion of aeolianite limestone/sand (Semeniuk & Johnson 1985).

The erosional retreat of the shoreline however has not been uniform. As mentioned above, the interaction of the onshore wave regime and the nearshore bathymetry creates loci of wave convergence in the depression between the shore and adjacent offshore ridge. Where there has been both a pronounced convergence of wave energy (and hence convergence of littoral and sublittoral transport) and a supply of sediment, significant accretion has occurred. Where either of these factors has been less pronounced a locus of 'delayed' erosion has occurred. Although not accreting, the coast in this locus has not retreated at the same rate as the adjacent coast. Extensive landward migrating dune fields develop in these loci as a result of sediment supply due to diminished littoral transport. In some locations these landward migrating dunes have inundated marine marshes or lakes developed in depressions within the onshore topography. Clearly, the loci of arrested retreat and the loci of accretion are intergradational and, if sediment supply conditions were to change, accretion and progradation could begin in one, and erosional retreat in the other.

Resultant Coastal Morphology: Offshore marine erosion has left the more lithified remnants of the original ridge topography largely as submarine rocky prominences. Retreat of the shoreline has left rocky remnants as platforms and submarine pinnacles in a zone up to 150 m wide in front of the contemporary shoreline. Retreat of the shoreline has in places been accompanied by the ongoing landward migration of Holocene dunes.

The interaction between the prevailing onshore wave regime and the offshore bathymetry has created the longstanding loci of shelter between the shore and the adjacent offshore ridge. Where this effect has been particularly pronounced, the accretion of shoaling and prograding sequences of bank, beach, beachridge and dune sediments has developed isolated cusps. The cusps are analogous to those of the Bouvard-Trigg Sector but are smaller, due to the scale and separation of the Pleistocene ridges. Where the interaction of the wave regime and bathymetry has been less pronounced, erosional retreat of the coast has only been slowed and not wholly offset by accretion, resulting in cusp-shaped limestone residuals.

Wedge Island-Dongara Sector

The northermost sector of the Rottneest Shelf from Wedge Island to about Dongara extends 180 km in a 340° to north alignment. This coastal sector is characterised by a progressive, northwards change in the nearshore bathymetry and the configuration of the shoreline. The regular, shore-parallel submarine ridges become increasingly dissected by oblique sub-ridge trends, before becoming largely discontinuous. Along the shore the cusped promontories become less well defined and more asymmetric before disappearing altogether, and the limestone rocky shore becomes more deeply scalloped due to large-scale erosion. Northwards of Dongara the coast gradually changes in character from a complex nearshore system dominated by Pleistocene ridge-and-depression topography, to a higher cliffed coast developed in much older Phanerozoic rocks which are only locally blanketed by Quaternary coastal deposits.

Bathymetry and Onshore Geomorphology (Fig. 10): Offshore limestone ridges present in the Whitfords-Lancelin Sector extend into the Wedge Island-Dongara Sector but become progressively overprinted and dissected by oblique sub-ridges uniformly trending at about 010° to 015°. Coincident with this, the ridges become more discontinuous. The bathymetric prominence of the main ridges and sub-ridges vary from a few metres to over 12 m above the surrounding seafloor. Occasionally the ridge prominences form small rocky islets.

The coastal geomorphology consists largely of large erosional scallops into the Pleistocene limestone as well as discrete cusped sediment promontories. The rocky coastline contains numerous small pocket beaches and it is interspersed with straight to gently arcuate beached coasts. Northwards the sediment cusps become asymmetric and eventually disappear north of Green Head. The dune terrains adjacent to the coast form a discontinuous and irregular coastal ridge. Mobile dunes and old vegetated dunes exhibit an alignment reflecting directions of blowouts or linear ridges between about 010° and 030°. Elongate, roughly shore-parallel lagoons or saline marshes may be developed in the coastal dune terrain. In places, these have been segmented and/or encroached on by dune migration.

Stratigraphic Framework (Fig. 10): Offshore the stratigraphy consists of discontinuous Holocene sand sheets overlying an irregular unconformity surface developed on Tamala Limestone. Onshore modern mobile dune fields (Safety Bay Sand) overlie Pleistocene and older Holocene dune deposits. Locally in the cusped promontories the Holocene stratigraphic sequences encountered are similar to that in the Whitfords-Lancelin sector with a well defined shoaling and prograding banks (Becher Sand) and beach, beachridge, dune sequences (Safety Bay Sand), as evidenced at Jurien Bay (Woods 1983).

Sedimentation and Erosion: Holocene sediment accretion has occurred in discrete coastal loci and in NNE migrating dune fields. The loci are the product of interaction between the wave regime and the nearshore bathymetry. Northwards in this sector the

accretion of Holocene sediment in dune fields becomes increasingly more important, while the decline in the offshore ridge protection limits the occurrence of accretionary loci.

As in the Whitfords-Lancelin Sector, the erosion of the Pleistocene limestones has been pronounced but not uniform. In the southern parts of the sector the continuity and prominence of the offshore ridges result in variable erosional retreat of the mainland shore. In the north the offshore ridges are discontinuous and less prominent, consequently retreat of the adjacent shore has been more irregular.

Resultant Coastal Morphology: The coastal morphology of this sector reflects the decline in shelter afforded by the offshore bathymetry and the increase in onshore development of NNE migrating dunes. Towards the north some of the erosional scallops and accretionary cusped promontories become asymmetric. Some of the cusps are erosional and the asymmetry reflects active migration of dunes NNE and the effects of an eroding coast with a pronounced NNE trend of relict Pleistocene and Holocene dune forms. The accretionary cusps (like Jurien Bay) tend to be largely symmetric despite periods of differential accretion on the NW and SW shores. In the northern parts of the sector the coast is devoid of prominent cusps which reflects the lack of offshore bathymetric features for protection.

Discussion of significance of results

There are several significant aspects of the classification of coastal sectors presented above. Firstly, it is obvious that the various coastal sectors can be separated in terms of morphology, dynamics, history and function. Secondly, comparisons should only be made between relevant portions of similar coastlines: for instance, the data, erosion rates, coastal dynamics and conclusions of Semeniuk & Meagher (1981) and Semeniuk & Searle (1985c) are not comparable with, and are irrelevant to, sections of the coast at (say) Becher Point or Quinns Beach. On the other hand, similar parts of the coast within or between sectors can be more confidently compared. For instance, the data on the evolution of individual cusps or sandy promontories as described by Woods & Searle (1983), Searle (1984) and Searle & Woods (1984) at Warnbro Sound are applicable to sedimentation sites such as Whitfords Point and Jurien. The sector approach thus allows realistic comparisons and use of coastal dynamic models between similar portions of coastline, but also allows comparison between the similar components of differing sectors of coast because a given section of coast is then viewed in regional perspective. These first two points have important implications for coastal management.

The third aspect is that the categorisation of the coast into sectors provides a regional to subcontinental framework wherein the origin and maintenance of the coast in a geological time scale can be more readily understood.

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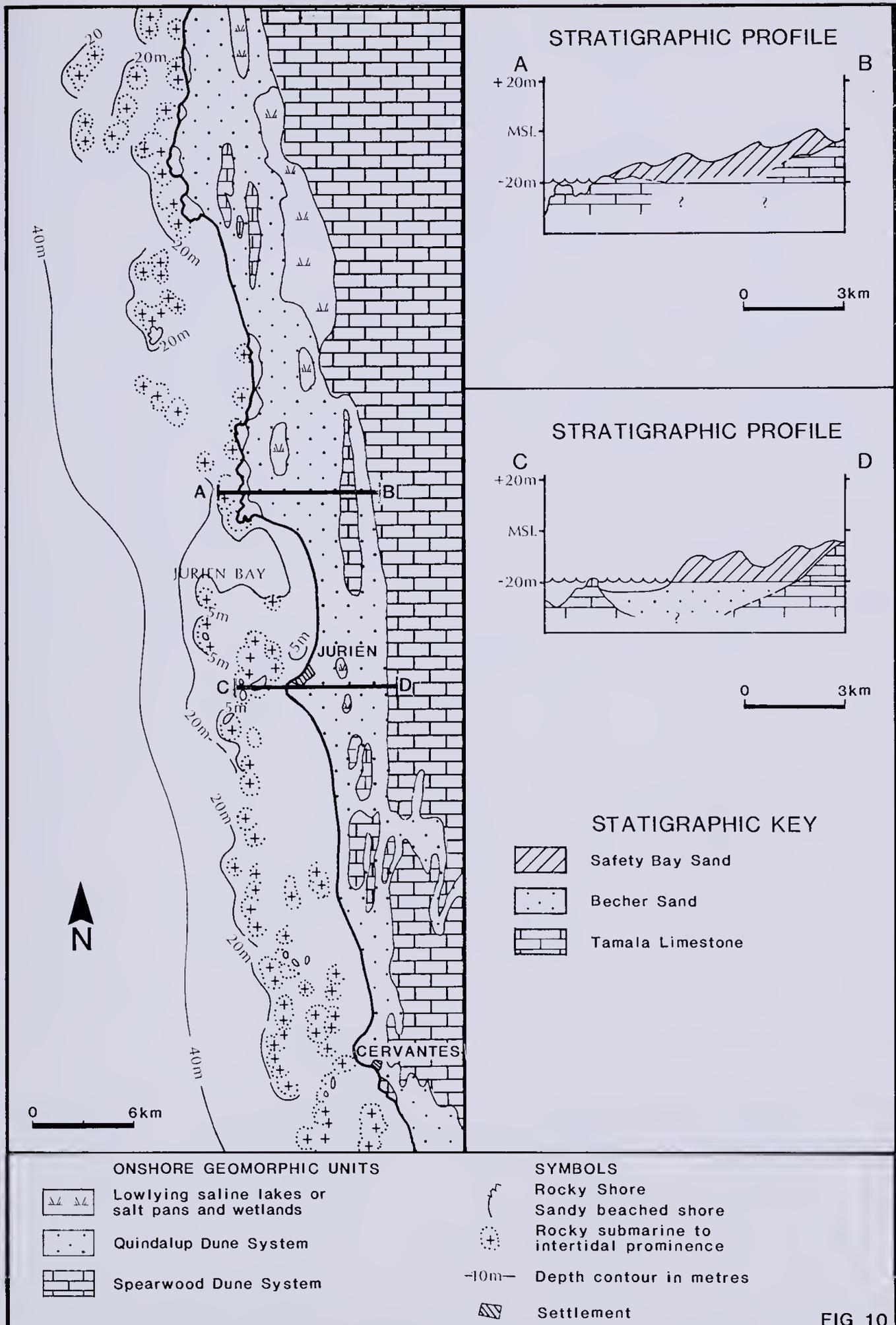


Figure 10.—Portion of coast of Wedge Island-Dongara Sector showing: small isolated Holocene accretionary cusps, large-scale erosionally-scalloped coastal form, geomorphic units, complex nearshore bathymetry of ridges and depressions, and selected stratigraphic profiles. Map modified after Lowry (1974), with information supplemented by the authors.

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Dune vegetation of the Swan Coastal Plain, Western Australia

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Abstract

A study of vegetation on the aeolian deposits of the Swan Coastal Plain, using classification techniques, revealed 49 vegetation units. These units were agglomerated into plant communities and complexes, on the basis of floristic composition. A Conspectus to the vegetation classification is provided.

Vegetation in this region is generally considered to be species-rich. Vegetation on the oldest (Bassendean) dune system was most species-rich. The complexity of vegetation pattern (vegetation texture) was greatest on the intermediate aged (Spearwood) dune system. Vegetation on the Quindalup dune system was both species-poor and had the simplest texture relative to the other two dune systems.

It is postulated that species-richness and vegetation texture change dynamically through time, as the dune systems become more stabilised and leached.

A key to the described communities is provided to allow researchers, conservation managers, teachers and other interested persons to allocate vegetation of particular bushland sites to a plant community described in the Conspectus, and thus increase knowledge of the vegetation variation in bushland remnants across this region.

Introduction

Much of the work on vegetation description in Western Australia has used a structural or physiognomic approach, e.g. Diels (1906), Speck (1952), Seddon (1972). Recent work (e.g. Heddle (1979), Heddle *et al.* (1980)) utilised floristic attributes, within a structural framework, based on the work of Havel (1968) who invoked the concept of site-vegetation types using a quantitative ordination-type approach to the analysis of floristically based data.

Heddle (1979) emphasised what she saw as a confusion of vegetation pattern, caused by the apparently continuous nature of vegetation change. She states:

"For the vast majority of the area investigated in the Perth Region the pattern of vegetation has been detected on the localized scale but not over larger areas. Possibly one of the reasons was the difficulty encountered by earlier workers in classifying large areas of vegetation. This was due to the fact that the vegetation is a complex, predominantly continuous population pattern, with both individual species and groups of species having dissimilar distribution patterns, vegetation in the field being consequently mixtures in varying proportions of continuity and discontinuity. This multi-dimensional nature of the vegetation is by no means a feature unique to Western Australia."

We believe that vegetation of the Swan Coastal Plain (Fig. 1) is amenable to treatment by classificatory techniques; the sharply changing nature of the soil systems and a highly seasonal climate are environmental controls which favour sharp, rather than diffuse, boundaries in vegetation.

The very high species richness of the Coastal Plain vegetation can, however, obscure these boundaries and produce an illusion of vegetation complexity. A great many species occur spasmodically in space and time, reacting to seasonal perturbations and irregular environmental features such as fire. Other reasons for high species-richness are advanced by Lamont *et al.* (1984). Previous work by Bridgewater (1982) showed that a classification strategy could be used

successfully in this vegetation, and the late Prof R. Tüxen (*pers. com.*) remarked, on seeing some of the raw data from this study, that this must surely be one of the best areas in the world to apply classification techniques!

Methods and results

(a) Data collection and analysis

In the present study, over 400 separate samples of vegetation were collected from about 100 sites on the aeolian derived dune systems of the Swan Coastal Plain (Fig. 1). Each sample was a quadrat of 10 m², from which all vascular plant species were listed. Each species was allocated a value on the Braun-Blanquet (1964) cover/abundance scale.

As an anonymous reviewer indicated, choice of any technique is largely a matter of convenience and purpose, a point with which we concur. In the present study we have opted for a classification technique, with the aim of identifying and clarifying the main vegetation variation, despite the apparent confusion caused by high levels of species richness.

Initially vegetation samples were allocated to groups using the cluster analysis technique of Carlson (1972). These were then further refined using computer program VEGCLASS (Bridgewater and Morales, 1982). VEGCLASS is a computer-aided system of tabular synthesis, which simplifies analysis of large data sets. These analyses revealed 49 vegetation units, which were arranged in a hierarchical classification based on floristic relationships, following the *schema* used by Pen (1983). Details of these vegetation units appear in the following conspectus, and full floristic tables are included in Cresswell (1982). Vegetation from Rottnest Island, and other offshore islands, has some special features which are not treated in this paper.

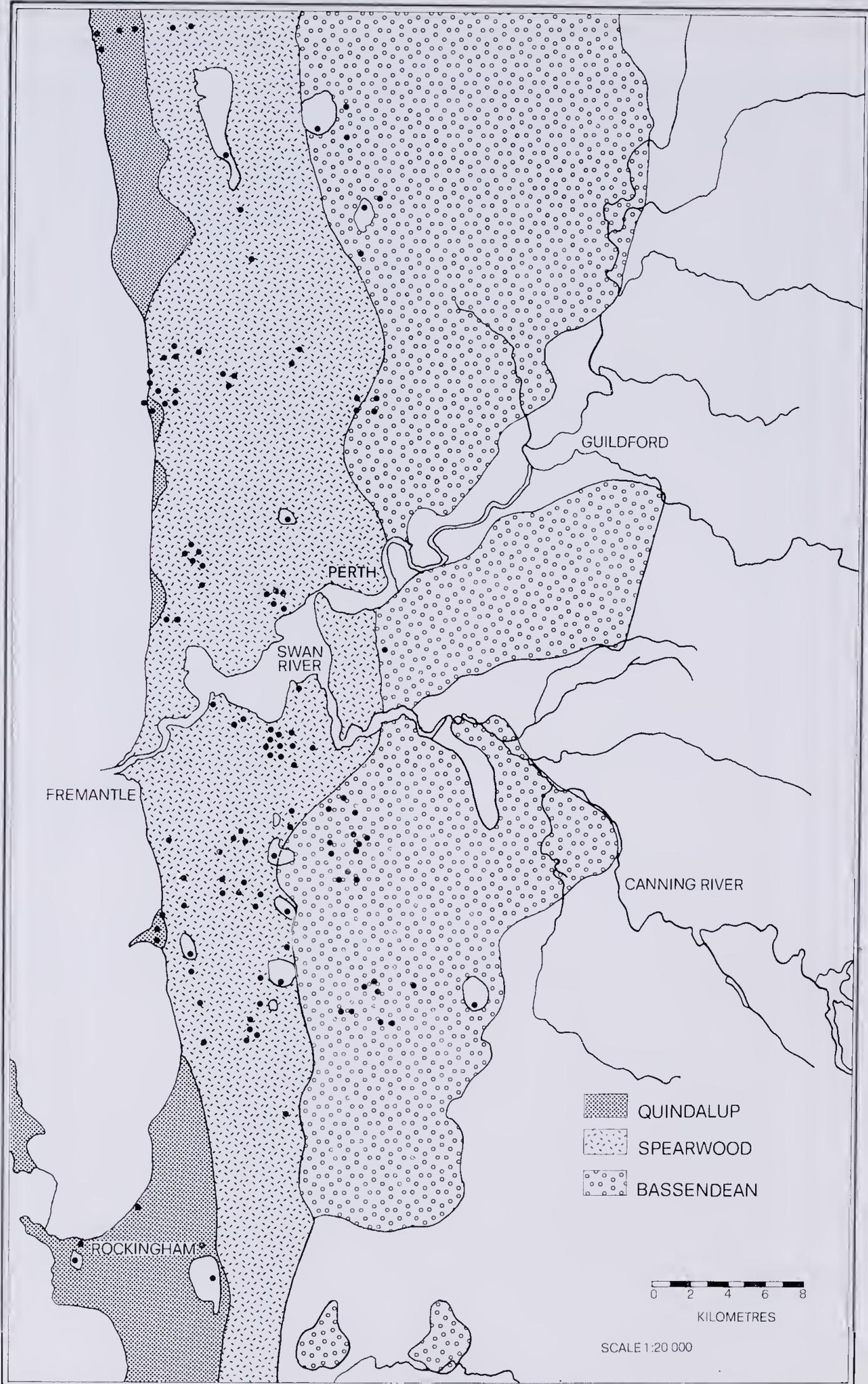


Figure 1.—Map of the Swan Coastal Plain, showing sample sites (•), and the boundaries of aeolian deposits.

(b) *Conspectus of vegetation units*

Vegetation units identified in the study are described in this section, from floristic and structural viewpoints. A key to the vegetation units is included as an appendix. This key should enable workers in the field to identify particular vegetation sites within the region described.

The base unit in the hierarchy is the community, analagous to the association of the Zürich-Montpellier System (Bridgewater 1981). Communities are divided into sub-communities and variants, and aggregated to form complexes. In most cases sub-communities are named after a distinguishing species. Where a sub-community has the same species complement as that for the community the epithet "typical" is used. Use of the community-complex nomenclature follows that of Pen (1983) and should not be confused with the use of complex by Heddlé *et al.* (1980).

For the lowest level of hierarchical division some distributional and ecological notes are included. Distribution of the vegetation units across the Swan Coastal Plain is shown in Figure 2. Species nomenclature is that of Marchant (in prep.). Specimens of most species named are lodged with the Western Australian Herbarium. Terminology of the geomorphic units used in the text follow Bettenay *et al.* (1960).

Tables 1-3 are summaries of species occurrences in the vegetation units. Identifying species for each unit are those with presences of 4 or 5 in each table. Tables 4 and 5 summarise the congruence between these vegetation units and the structural formations of Specht *et al.* (1974).

A. *Stirlingia latifolia*—*Oxylobium capitatum* complex

A.1. *Dasyogon bromeliifolius*—*Lyginia barbata* community

A.1.a. *Scaevola paludosa* sub-community

A.1.a.i. *Monotaxis grandiflora* variant

Usually restricted to the tops of dune ridges in the Karrakatta soil association. Occasionally *Xylomelum occidentale* occurs as extensive patches, more or less replacing *Banksia* species as dominants.

A.1.a.ii. *Acacia willdenowiana* variant

Localised on dune slopes at the junction between Karrakatta and Bassendean soil associations.

A.1.b. *Hardenbergia comptoniana* sub-community

A.1.b.i. *Leucopogon propinquus* variant

Localised on the upper slopes of dune ridges in the eastern sector of the Karrakatta soil association.

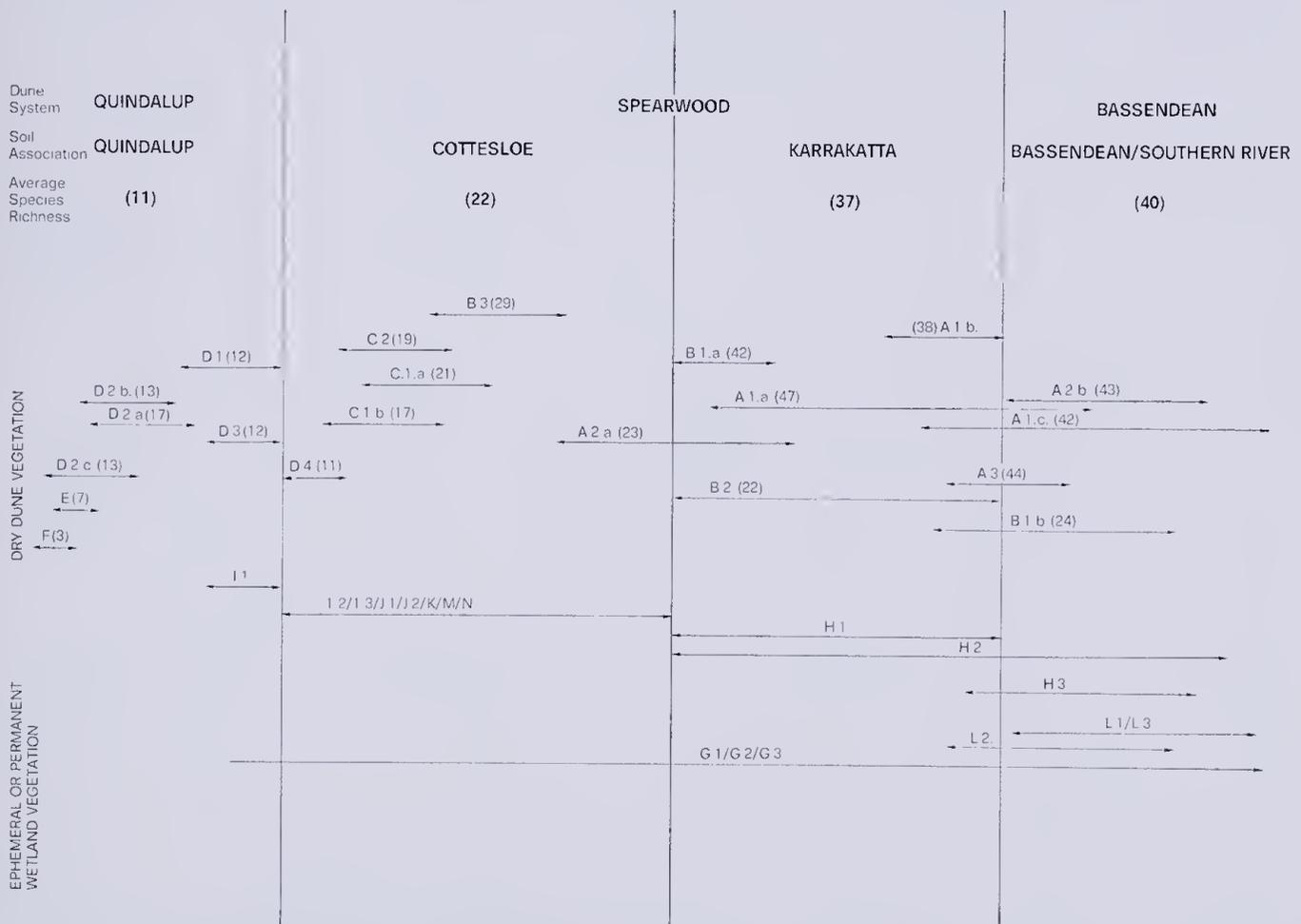


Figure 2.—Distributions of plant communities across the Swan Coastal Plain. The length and position of the lines is an indication of the breadth of the community distribution across the soil associations. Numbers in parentheses are the average species richness for vegetation samples which make up the communities.

A.1.b.ii. *Allocasuarina fraseriana* variant
Common on dune slopes of the Karrakatta soil association.

A.1.c. *Patersonia occidentalis* community

Restricted to swales and lower dune slope in the Bassendean, Southern River and eastern Karrakatta soil associations. Excessive disturbance to this community by mechanical activity can cause a shrub community dominated by *Adenanthos cygnorum* to develop. Many road cuttings and housing developments in the eastern Bassendean system clearly show this.

A.2. *Allocasuarina humilis*—*Synaphea spinulosa* community

A.2.a. *Acacia pulchella*—*Conostephium pendulum* sub-community

Localised on dune slopes of the Cottesloe and Karrakatta soil associations.

A.2.b. *Scholtzia involucrata*—*Banksia ilicifolia* sub-community

Lower dune slopes throughout the Bassendean soil associations, primarily found on slopes verging on ephemeral wetlands.

A.3. *Jacksonia sternbergiana*—*Pimelea rosea* community

Common on dune slopes of the eastern Karrakatta and western Bassendean soil association. Where this community abuts wetlands a transitional vegetation frequently occurs, with *Eucalyptus rudis* as the tree layer, and *Jacksonia furcellata*, *Lechenaultia biloba* and, at Thompsons Lake, *Dodonaea hackettiana* common in the shrub layer. The width of this transitional band depends on the slope of the dune—being most extensive where gently sloping dunes grade into wetland.

B. *Xanthorrhoea preissii*—*Mesomelaena stygia* complex

B.1. *Allocasuarina fraseriana*—*Hardenbergia comptoniana* community

B.1.a. *Leucopogon propinquus* sub-community

Common on upper slopes in the western Karrakatta soil association. This sub-community includes *Eucalyptus gomphiocephala* open-forest, and is frequently degraded, with many exotic species present. Degraded stands of this sub-community often key out as B.2. *Banksia grandis* is an occasional component of the tree layer in this and the next sub-community.

B.1.b. *Alexgeorgea arenicola* sub-community

Localised on the lower slopes of the eastern Karrakatta soil association, and western Bassendean soil association.

B.2. *Dianella revoluta*—*Mesomelaena stygia* community

Found throughout the Karrakatta soil association. Typically species poor, possibly due to extensive physical and environmental disturbance. The number of exotic species is greater in this sub-community than in any other vegetation unit. As such, it forms a synthetic plant community (Backshall & Bridgewater (1981)) which may be transitional in nature, or represent new metastable vegetation.

B.3. *Dryandra nivea*—*Lechenaultia linarioides* community

Occurs on ridge tops in the Cottesloe soil association, with limestone cap rock slightly exposed, or near to the surface. In some localities *Agonis flexuosa* occurs in the tree layer.

C. *Dryandra sessilis*—*Calothamnus quadrifidus* complex

C.1. *Dryandra nivea*—*Phyllanthus calycinus* community

C.1.a. *Hakea prostrata* sub-community

Confined to the western parts of Cottesloe soil association, on shallow soils with large proportion of limestone rock outcrop. This community is synonymous with the Dryandro-*Calothamnium haketosum* (Bridgewater and Zammit (1979)). Exposed outcrops frequently have *Acacia cochlearis*, *A. lasiocarpa* and *Melaleuca luegelii* as the dominant species.

C.1.b. *Templetonia retusa* sub-community

Found in area frequently subject to seaspray on shallow soils of the Cottesloe soil association; typically limestone outcrops present. This sub-community is synonymous with the Dryandro-*Calothamnium templetonietosum* (Bridgewater and Zammit (1979)).

C.2. *Olearia axillaris*—*Rhagodia baccata* community

Summit of dune ridges, typically with exposed limestone cap-rock, in the extreme west of the Cottesloe soil association.

D. *Olearia axillaris*—*Rhagodia baccata* complex

D.1. *Callitris preissii* community

Confined to the Quindalup soil association. This community was formerly common along the coast, but is now depleted in area and in floristic quality, due both to urban development and greater fire frequency.

D.2. *Lepidosperma gladiatum* community

D.2.a. *Acacia xanthina* sub-community

Common on dune ridges and upper slopes of the Quindalup soil association, occurring occasionally in deep gullies with a scattered overstorey of *Eucalyptus gomphiocephala*, and shrubby *Agonis flexuosa* (e.g. at City Beach). Localised on the edges of limestone cliffs in the Cottesloe soil association.

D.2.b. *Acacia cyclops* sub-community

Occurs on the eastern slopes of fore-dunes formed by the Quindalup soil association (referred to as the "youngest" phase by Bettenay *et al.* (1960)). As with the previous sub-community, *Agonis flexuosa* may be a component of mature stands of the sub-community.

D.2.c. *Acacia rostellifera* community

Best developed on low ridges of the more exposed areas of the Quindalup soil association.

D.3. *Eucalyptus gomphiocephala* community

Confined to sheltered depressions of the Quindalup soil association, becoming more frequent south of Rockingham. This unit is floristically unrelated to

the *Eucalyptus gomphocephala* alliance (Specht *et al.* (1974)) of the Cottesloe soil association, which is included under B.1.a.

D.4. *Threlkeldia diffusa*—*Frankenia pauciflora* community

Confined to exposed limestone cliffs of the Cottesloe soil association, and subject to seaspray. In the north of the region *Nitraria billardieri* and *Melaleuca cardiophylla* occur as components of the community.

E. *Tetragonia implexicoma* complex

E.1. *Tetragonia implexicoma* community

Confined to upper slopes and ridges of the Quindalup fore-dunes.

F. *Cakile maritima* complex

F.1. *Cakile maritima* community

The most seaward of dune vegetation, occupying the strandline of the Quindalup dune system. This community is remarkable because two of its three identifying species are regarded as introductions to Australia (*C. maritima* and *Arctotheca populifolia*). It must also be regarded as a synthetic community, with European man both enabling species vagility, and creating appropriate environmental conditions.

The remaining vegetation units are all from wetland vegetation. Riverine vegetation, associated with the Swan and Canning rivers, is not covered in this account, as Pen (1983) has a detailed review of such vegetation. Where vegetation units described below also occur in riverine systems, they are cross-referenced to Pen (op. cit.). Occasionally units defined by Pen as "complexes" have been reduced to community status, by the inclusion of material from this wider study. Communities restricted to tidal marshes along river margins are not included in this present account, and the reader is referred to Pen (op. cit.) for details.

G. *Typha-Baumea* complex.

G.1. *Typha orientalis* community

Identified by the dominance of *T. orientalis* and presence of few other species. Widespread throughout lentic wetlands and in riverine situations, but absent from the most saline sites.

G.2. *Typha orientalis*—*Baumea articulata* community

Identified by the co-dominance of the two naming species, and presence of few other species. Possibly a short-lived dynamic phase transitional from the *Baumea articulata* community to the *Typha orientalis* community.

G.3. *Baumea articulata* community

Identified by the dominance of *B. articulata*, and presence of few other species, this community is found only in freshwater sites. In the majority of the areas where it occurs there is evidence of invasion by *Typha orientalis*. Disturbance, eutrophication and changes to wetland water levels (both raising and lowering) all appear to facilitate this invasion.

H. *Melaleuca rhapsiophylla* complex

H.1. *Schoenoplectus validus* community

Identified by the dominance of *S. validus* with *Polygonum salicifolium* as a prominent understory species. Typically occurs as fringing vegetation of lakes in the Karrakatta soil association. Severely degraded or exposed sites may be species poor, with *S. validus* being dominant, *M. rhapsiophylla* infrequent and few other species present. *Phyla nodiflora* is abundant in such sites, as a ground cover.

H.1.a. typical sub-community

This sub-community occurs in swamps, often with a permanent water table above soil level, and in thin zones along the upper reaches of the major rivers, where it is expressed as monospecific stands of *Schoenoplectus* (Pen 1983).

H.1.b. *Carex fascicularis* sub-community

Identified by an abundance of *C. fascicularis* in the lower sedge stratum. Localised as vegetation fringing lakes, particularly abundant in the northern sector of the study area.

H.2. *Melaleuca rhapsiophylla*—*Eucalyptus rudis* community

Widely distributed throughout the Karrakatta and Bassendean soil associations. The three sub-communities represent a transition from semi-open water (H.2.a.) to dry soil surface (H.2.c.) Pen (1983) defines a *Eucalyptus*—*Melaleuca* Complex, which would form part of this community, defined in the broader terms of the whole coastal plain.

H.2.a. *Polygonum salicifolium* sub-community

P. salicifolium is present as the dominant understory species, typically submerged or floating in open water at the edge of lakes and swamps.

H.2.b. *Centella asiatica* sub-community

C. asiatica is present as the major understory species. The sites occupied by this sub-community are ephemeral winter swamps.

H.2.c. typical sub-community

This sub-community is found on the driest sites around lakes.

H.3. *Melaleuca rhapsiophylla* community

Identified by the dominance of *M. rhapsiophylla* with few other species present. Structurally this community is a tree overstorey on open water. In some sites *Lemna* spp. occur as floating aquatics on the water surface.

I. *Juncus kraussii* complex

I.1. *Centella asiatica* community

Identified by the dominance of *Baumea juncea*, with *C. asiatica* the major understory species. This is a very restricted community, apparently confined to wetlands in the Quindalup soil association.

I.2. *Juncus kraussii* community

Restricted to wetlands whose waters have relatively high conductivities. This community appears as a brackish water vicariant to the *Baumea articulata*

community. Also frequent along the rivers upstream from the Narrows—termed *Melaleuca-Juncus* Complex by Pen (1983).

I.2.a. *typical* sub-community

I.2.b. *Melaleuca raphiophylla* sub-community

In some localities *Melaleuca raphiophylla* is present as an overstorey species, and such vegetation has been called the *Melaleuca raphiophylla* sub-community. The typical sub-community lacks the overstorey. This is a particular example of vegetation nomenclature where importance is placed on the lower stratum being of greater environmental indicator value than the upper stratum.

I.3. *Melaleuca raphiophylla*—*Baumea juncea* community

I.3.a. *Juncus kraussii* sub-community

J. kraussii and *B. juncea* are co-dominant in the understorey, with few other species present. This sub-community is closest to the waterline.

I.3.b. *Aster subulatus* sub-community

A. subulatus and *Cotula coronopifolia* are constantly present in the understorey, typically with a number of other ephemeral species. This sub-community occurs landward of I.3.a.

I.3.c. *Melaleuca teretifolia* sub-community

M. teretifolia is present as co-dominant with *M. raphiophylla*, with *Ruppia polycarpa* and *Chara* spp. (Charophyta: Algae) occurring as submerged macrophytes in open water amongst the *B. juncea* layer. Occurs only south of the Swan River.

I.3.d. *typical* sub-community

This species-poor sub-community occurs occasionally within the study area.

J. *Sarcocornia quinqueflora* complex

J.1. *Sarcocornia quinqueflora* community

Identified by the dominance of *S. quinqueflora* and the occasional presence of *Suaeda australis* and/or *Samolus* spp. Restricted to the most westerly wetlands, this community is typically associated with estuarine salt marshes, and occurs extensively along the fringes of the Swan and Canning Rivers, as well as in lentic wetlands. Equivalent to the *Sarcocornia* Community (Pen 1983).

J.2. *Juncus kraussii*—*Sarcocornia quinqueflora* community

Confined to the western-most lakes, presumably influenced by sea spray drift, as well as high levels of solutes from surface limestone rock. Also in saltmarshes along the lower reaches of the rivers. Equivalent to the *Juncus* typical Community (Pen, 1983).

J.2.a. *Suaeda australis*—*Samolus* spp. sub-community

Suaeda australis, *Samolus repens* and *Samolus junceus* are present as co-dominants in the understorey. Usually found in standing water at lake edges.

J.2.b. *Melaleuca raphiophylla* sub-community

M. raphiophylla is present as an overstorey, with *J. kraussii* and *Gahnia trifida* present as co-dominants in the understorey. This sub-community is found in ephemeral swamps, and up-shore of H.2.a. in lakes.

K. *Melaleuca cuticularis* complex

Identified by the dominance of *M. cuticularis* with the presence of few other species. This community is confined to wetlands where waters have very high conductivities (>25 mho/cm in winter). Also represented in small relict patches along the shore of Melville Water, as the *Juncus-Melaleuca* Community of Pen (1983).

L. *Lepidosperma longitudinale* complex

L.1. *Melaleuca teretifolia*—*Lepidosperma longitudinale* community

This is one of three communities which are of importance in separating the wetlands in the south of the study area from those of the north, being abundant in ephemeral wetlands in the Bassendean soil association.

L.2. *Viminaria juncea* community

This community forms dense thickets at the extreme littoral fringe of fresh water lakes and swamps.

L.3. *Astartea fascicularis*—*Schoenus subfascicularis* community

Restricted to ephemeral wetlands recharged during winter from ground water flows and surface water seepage in the Bassendean soil association.

L.3.a. *Banksia littoralis*—*Melaleuca preissiana* sub-community

B. littoralis and *M. preissiana* are present as co-dominant tree species over a species-rich understorey. There are a number of variants of this sub-community, which require further study before their status can be established.

L.3.b. *Eutaxia virgata* sub-community

E. virgata is present in a species-poor shrubland, with no trees present.

M. *Bulboschoenus caldwellii* complex

M.1. *Bulboschoenus caldwellii* community

Confined to areas of standing water in the western-most brackish swamps. Two *Chara* species and *Ruppia polycarpa* are present as submerged macrophytes in this community, which is the only community of the complex. Clearly related to the *Bulboschoenus* Community of Pen (1983), which lacks submerged macrophytes, perhaps because of more rapid water movement.

N. *Melaleuca teretifolia* complex

N.1. *Melaleuca teretifolia* community

Identified by the dominance of *M. teretifolia* with the presence of few other species. Like the *M. teretifolia*—*Lepidosperma longitudinale* complex, this is confined to the southern sector of the study area, and has only one component community.

O. *Polypogon monspeliensis* complex

The identifying species is an exotic grass, which underlies the major feature of all quadrats allocated to this complex—they all suffer from gross physical disturbance, and are best regarded as degraded variants of some of the previously described communities.

Table 1

Summary table of the major species composition of vegetation units from the *Stirlingia latifolia*—*Oxylobium capitatum* complex (A), and the *Xanthorrhoea preissii*—*Mesomelaena stygia* complex (B). Numerical values in the table indicate the percentage occurrence of the species in the quadrats sampled for the respective vegetative unit, as follows:

1. species present in 1-9% of the samples
2. species present in 20-39% of the samples
3. species present in 40-59% of the samples
4. species present in 60-79% of the samples
5. species present in 80-100% of the samples

Complex code:	A	A	A	A	A	A	A	A	B	B	B	B
Association code:	1	1	1	1	1	2	2	3	1	1	2	3
Sub-Association code:	a	a	b	b	c	a	b		a	b		
Variant code:	i	ii	i	ii								
Number of samples:	5	3	12	8	30	5	6	3	13	6	8	4
Species												
<i>Banksia attenuata</i>	3	5	4	5	5	5	5	4	5	5	3	2
<i>Hibbertia hypericoides</i>	5	5	5	5	4	5	5	5	5	4	3	4
<i>Gompholobium tomentosum</i>	4	5	3	3	4	5	5	4	4	4	3	3
<i>Banksia menziesii</i>		5	3	3	5	5	5	5	4	4	2	
<i>Xanthorrhoea preissii</i>	4	5	5	4	2	3	2	4	4	5	2	5
<i>Macrozamia riedlei</i>	3	2	5	4	2	3	2	5	5	5	2	3
<i>Burchardia umbellata</i>	5	5	5	4	5	2	5	5	5	2	4	2
<i>Mesomelaena stygia</i>	5	5	3	2	2	5	4	4	4		4	5
<i>Stirlingia latifolia</i>	4	4	2	4	4	3	4	5	1		1	
<i>Petrophile linearis</i>	5	2	4	4	5	3	5	4	4	2	1	
<i>Diplopogon setaceus</i>	5	2	1	2	4	4	4	5	1		1	2
<i>Hypocalymma robustum</i>	5	5	4	4	3	2	4	5	4		1	
<i>Oxylobium capitatum</i>	4	5	3	3	2	2	5	5	3			
<i>Daviesia triflora</i> (M. Crisp inedit)	5	5	3	4	4	4	1		3	1	2	
<i>Conostephium pendulum</i>	3	5	3	2	4	5	2		1		1	
<i>Lyginia barbata</i>	3	5	3	2	4		5		2			
<i>Dasyopogon bromeliifolius</i>	5	5	2	3	4		2	5	2			
<i>Drosera macrantha</i>	5	5	5	4	3						2	
<i>Lepidosperma angustatum</i>	5	2	4	4	3						2	
<i>Tetraria octandra</i>	3	4	5	4		2		2	3		2	
<i>Isotropis cuneifolia</i>	3	4	4	2					1		1	
<i>Scaevola pabudosa</i>	5	4	1	1	1		4		2	1	2	
<i>Hypolaena exsulca</i>	4	4	1	1	2		2					
<i>Macarthuria australis</i>	4			1	1		3	2			1	
<i>Monotaxis grandiflora</i>	4			2	1	2	2		1			
<i>Haemodorum spicatum</i>	5		1	1	1		1		1	1	1	
<i>Calectasia cyanea</i>	4		1		2		2		1	1		
<i>Anigozanthos humilis</i>	5		1	1	1	2	1	2			1	2
<i>A. manglesii</i>	4		2	1	2		1		2		1	
<i>Acacia stenoptera</i>	4		2	2	1			2	2		2	
<i>Eriostemon spicatus</i>	4	2	1	2	2			2			1	
<i>Astroloma pallidum</i>	4		1		1		5	3	2		2	2
<i>Allocasuarina fraseriana</i>	5		1	4	2	3	2	2	4	5		
<i>Eucalyptus marginata</i>		5	5	4	1	3			5	5	1	
<i>Hibbertia huegelii</i>	2	5	1	2	2	2	1					
<i>Phlebocarya ciliata</i>		4	1		2							
<i>Pimelea sulphurea</i>	2	5		1	2	5			1			
<i>Opercularia vaginata</i>	2	5	2	2	1	4	1		1		2	
<i>Acacia willdenowiana</i>		5	2	1			1					
<i>Alexgeorgea arenicola</i>	3	5		2	1	5	2		2	4	2	
<i>Allocasuarina humilis</i>	2	4			3	5	4		1			2
<i>Lagenifera huegelii</i>			4	2	1							
<i>Kennedia prostrata</i>	2		4	1	1				2	1	1	
<i>Leucopogon propinquus</i>	2		4	2	1	2	4	2	5		1	
<i>Eryngium rostratum</i>			3	2	1			4	5		2	
<i>Dianella revoluta</i>	4		3	2	1			5	4	3	4	
<i>Xanthosia huegelii</i>		2	3	2	2		1	4	1	1		
<i>Hardenbergia comptoniana</i>	3		4	4	1	2			5	4	1	2
<i>Patersonia occidentalis</i>	2	5		2	5		5		2			
<i>Leucopogon conostephioides</i>				1	3	4	3					
<i>Eremaea pauciflora</i>	2	2			3	2	4					
<i>Synaphaea spinulosa</i>	2		1	2	1	5	5		1	3	1	
<i>Acacia pulchella</i>			2	1	3	5		2	1		2	
<i>Waitzia suaveolens</i>					1	4	2					4
<i>Hakea lissocarpha</i>						4				3	1	4
<i>Calothamnus quadrifidus</i>						4	1					3
<i>Dryandra nivea</i>	3		1	1	1	4		4	2		2	5
<i>Banksia ilicifolia</i>		3			1	1		5	2	1		
<i>Scholtzia involucrata</i>					3			5				
<i>Drosera microphylla</i>								5				
<i>Calytri fraseri</i>					1			4				
<i>Jacksonia sternbergiana</i>	2		1	2	1		1	5	2	3	3	2
<i>Hakea prostrata</i>					1	3		5	1	2		3
<i>Acacia saligna</i>	2		1	1		2	1	5	1	1		2
<i>Hybanthus calycinus</i>	3		1	1			2	4	2			2
<i>Eucalyptus calophylla</i>			2					5	2			
<i>Pimelea rosea</i>			1	1	1	1	1	5	1			
<i>Acacia huegelii</i>	2	2	1	2	2		1	4	2			
<i>Hibbertia racemosa</i>			2	3	3		1		4		1	
<i>Haemodorum laxum</i>							2		1	4		3
<i>Phyllanthus calycinus</i>			1	2	1				1			4
<i>Stipa elegantissima</i>	2		2	1	1	3	1		2		2	4
<i>Lechenaultia linarioides</i>											1	4

Table 2

Summary table of the major species composition of vegetation units from the *Dryandra sessilis*—*Calothamnus quadrifidus* complex (C), the *Olearia axillaris*—*Rhagodia baccata* complex (D), the *Tetragonia implexicoma* complex (E) and the *Cakile maritima* complex (F). Numerical values in the table are as Table 1.

Complex code:	C	C	C	D	D	D	D	D	D	E	F
Association code:	1	1	2	1	2	2	2	3	4		
Sub-association code:	a	b			a	b	c				
Number of samples:	6	4	13	4	8	1	5	5	1	5	5
Species											
<i>Calothamnus quadrifidus</i>	5	4	3	3	2						
<i>Dryandra sessilis</i>	5	4	3					1			
<i>Grevillea thelemantiana</i>	4	5	3								
<i>Lomandra suaveolens</i>	4	5	3								
<i>Melaleuca acerosa</i>	5	5	2	3	4		3	3			
<i>Dryandra nivea</i>	5	5	1								
<i>Phyllanthus calycinus</i>	5	5	1		2				4		
<i>Acacia littorea</i>	4	5	1								
<i>Hibbertia hypericoides</i>	5	3									
<i>Xanthorrhoea preissii</i>	4										
<i>Flakea prostrata</i>	5						1				
<i>Schoenus grandiflorus</i>	4		1		2					3	
<i>Acacia rostellifera</i>	4			2			5		3		
<i>Conostylis candidaus</i>	4	2	1	3	2		2		3		
<i>Stipa elegantissima</i>	3	5	2		4						
<i>Petrophile serruriae</i>	2	5	1				2				
<i>Kenedia coccinea</i>	2	4	1								
<i>Melaleuca huegelii</i>	3	4	2				2				
<i>Templetonia retusa</i>		4	3		4		2				
<i>Olearia axillaris</i>	1	5	5	2	4	5	4	2	5		
<i>Rhagodia baccata</i>		4	5	3	3	5	2	4	5		
<i>Pelargonium capitatum</i>	1	4	4	4	5	5	4	3			
<i>Hardenbergia comptoniana</i>	1	2	4	5	2	5		3			
<i>Callitris preissii</i>				5							
<i>Anthocercis littorea</i>			1	3	1						
<i>Acrotriche cordata</i>				2							
<i>Acanthocarpus preissii</i>		3	3		5	5	4		5		
<i>Lepidosperma gladiatum</i>			1	2	4	5	3				2
<i>Acacia xanthiua</i>		2	1		5		2				
<i>Poa poliflorus</i>			1		3						
<i>Spyridium globulosum</i>			3		3						
<i>Myoporum insulare</i>					2		5	2	3		
<i>Atriplex cinerea</i>							5				
<i>Spinifex longifolius</i>							5				
<i>Acacia cyclops</i>							5				2
<i>Scaevola crassifolia</i>			2		2		5				
<i>Clematis microphylla</i>	1		2		2				5		2
<i>Dianella revoluta</i>	2		1		1		4				
<i>Eucalyptus gonphocephala</i>		2	1		1				4		
<i>Diplolaena dampieri</i>							1		5		
<i>Nitraria billardieri</i>			1						4		
<i>Threlkeldia diffusa</i>			1							5	
<i>Frankenia pauciflora</i>					1					5	
<i>Melaleuca cardiophylla</i>			1							5	
<i>Sporobolus virginicus</i>											2
<i>Tetragonia implexicoma</i>			1		1						4
<i>Isoplepis nodosa</i>											5
<i>Cakile maritima</i>											2
<i>Arctotheca populifolia</i>											5
<i>Spinifex hirsutus</i>											5

Discussion

Havel (1979) noted that two factors appear of major importance in determining the vegetation pattern of the Coastal Plain: soil moisture and level of leaching (especially of soil iron). These factors are undoubtedly important—but seasonality of soil moisture and topographic variation are also important in determining vegetation pattern, e.g. Beard (1984). Havel (1979) also makes the important point that “vegetation is an integral part of the landscape in which it occurs. It is shaped by the landscape, and what vegetation is found at any one locality depends on the climatic, topographic and soil conditions at that locality”.

In the case of the Coastal Plain, historical factors are also important and we propose the following scenario for the development of the present-day flora and vegetation. It is possible to visualise a total dune flora which oscillates through time e.g. species which are now confined to the Quindalup dune system were once common on the Bassendean dune system. As the sands of the Bassendean dunes became leached and Spearwood dunes developed seawards, only species tolerant of nutrient-poor conditions were able to survive. Some species, possibly excluded by competition from species of nutrient-rich habitats, are then able to colonise the newly vacant habitats. Species requiring nutrient-rich conditions, and those tolerant of salt spray and the pioneer dune ecosystem would then colonise the developing Spearwood dune system. This process is now being repeated between the Spearwood and Quindalup dune systems.

Table 3
 Summary table of the major species composition of vegetation units from wetlands. Numerical values in the table are as Table 1. *indicates mixed sward of *Cynodon dactylon* and *Paspalum distichum*.

Complex code:	G	G	H	H	H	H	H	H	H	I	I	I	I	I	I	I	I	J	J	J	J	J	J	K	L	L	L	L	L	M	N						
Association code:	1	2	3	1	1	2	2	2	2	1	2	2	3	3	3	3	3	1	2	2	2	2	2	1	1	2	3	3	3	3							
Sub-association code:			a	b	a	b	c	a	b	a	b	a	b	c	d	a	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a						
Number of samples	8	5	15	5	5	10	8	3	7	7	6	6	4	5	4	5	4	3	3	3	3	3	9	5	3	5	10	6	3	5							
<i>SPECIES</i>																																					
<i>Typha orientalis</i>	5	5					2	2	2	1	1																										
<i>Banmea aritculata</i>	5	5					2	2	2	1	1																										
<i>Polygonum salicifolium</i>	1	1	1	5	4	5																															
<i>Schoenoplectus validus</i>	1	1	1	5	5		1			1																											
* <i>Cynodon/Paspalum</i>																																					
<i>Eucalyptus rudis</i>				2	1	4	4	5	2	2	2																										
<i>Melaleuca raphitophylla</i>	1			2	2	5	4	4	5	5	5																										
<i>Banmea juncea</i>				2	2	5	4	4	5	5	5																										
<i>Cenella asiatica</i>				2	2	5	4	4	5	5	5																										
<i>Juncus kranssi</i>	1									2	5																										
<i>Atriplex hypoleuca</i>																																					
<i>Sarcocornia quinqueflora</i>																																					
<i>Melaleuca cuticularis</i>																																					
<i>M. teretifolia</i>																																					
<i>Deveuxia quadrifida</i>																																					
<i>Lepidosperma longitudinale</i>																																					
<i>Acacia pulchella</i>																																					
<i>Viminaria juncea</i>																																					
<i>Schoenus subfascicularis</i>																																					
<i>Astarea fascicularis</i>																																					
<i>Eutaxia virgata</i>																																					
<i>Gahnia trifida</i>																																					
<i>Chara</i> spp.																																					
<i>Samolus</i> spp.																																					
<i>Ruppia</i> spp.																																					
<i>Bolboschoenus caldwellii</i>																																					
<i>Polygonum monspeliensis</i>																																					
<i>Carex fascicularis</i>																																					
<i>Aster subulatus</i>																																					
<i>Cotula coronopifolia</i>																																					
<i>Suaeda australis</i>																																					
<i>Melaleuca preissiana</i>																																					
<i>Banksia littoralis</i>																																					

Table 4

Congruence between vegetation units of the dryland dune systems and the structural formations, described by Specht *et al.* (1974). A '+' indicates the vegetation unit falls within a particular structural formation.

Floristic Vegetation Unit	A	A	A	A	A	A	A	A	A	A	B	B	B	B	C	C	C	D	D	D	D	D	D	D	E	F
Structural Formation																										
<i>Banksia menziesii</i> — <i>B. attenuata</i> — <i>Casuarina fraseriana</i> — <i>Eucalyptus totitiana</i> Low woodland	+	+																								
<i>Eucalyptus marginata</i> — <i>E. calophylla</i> Woodland																										
<i>B. menziesii</i> Low open-forest																										
<i>B. menziesii</i> Woodland																										
<i>B. menziesii</i> Low woodland																										
<i>E. marginata</i> Low open-forest																										
<i>E. gomphocephala</i> Low open-forest																										
<i>Dryandra</i> spp.— <i>Hakea</i> spp.— <i>Casuarina</i> spp. Open-scrub																										
Proteaceae—Leguminosae—Myrtaceae Open-heath																										
Proteaceae—Leguminosae—Myrtaceae Closed-heath																										
<i>Acacia rostellifera</i> — <i>A. cyclops</i> — <i>A. cochlearis</i> Closed-scrub																										
<i>Melaleuca lacleolata</i> — <i>Callitris preissii</i> Closed-scrub																										
<i>E. gomphocephala</i> Woodland Coastal Complex; Dune vegetation— Southern																										

Table 5

Congruence between vegetation units of the wetland dune system and the structural formations described by Specht *et al.* (1974). A '+' indicates the vegetation unit falls within a particular structural formation.

Floristic Vegetation Unit	G	G	G	H	H	H	H	H	H	H	I	I	I	I	I	I	J	J	J	J	J	J	J	J	K	L	L	L	L	L	M	N		
Structural Formation																																		
Swamp complex																																		
<i>Eucalyptus rudis</i> — <i>Melaleuca</i> spp. Low open-forest																																		
<i>Halophytic complex</i> No described alliance																																		
<i>Astarea fascicularis</i> — <i>Agonis parviceps</i> — <i>Melaleuca preissiana</i> Closed-heath																																		
<i>Viminaria juncea</i> Low open-shrub- land																																		

As Fig. 2 demonstrates, vegetation at the coast, on the most recently formed dunes (Quindalup), is relatively species-poor (average of 11 species per 10 m² quadrat), whereas that of the oldest dunes (Bassendean & Southern River Systems) is species-rich (average of 40 species per 10 m² quadrat). Dry dune vegetation of the Quindalup dune system appears quite distinct from the vegetation of both the Spearwood and Bassendean Systems, which share some species.

Dry dune vegetation on the Bassendean soil association exhibits the greatest species richness for any single soil association, although the vegetation texture (pattern) is greatest in the Karrakatta and Cottesloe soil associations. Again this emphasises the difference between the younger Spearwood dune system and the older Bassendean dune system. The Spearwood dune system has a more diverse landform, containing a greater range of opportunity for vegetation texture to be expressed, compared to the older, less undulating landscape of the Bassendean dune system. Because the Bassendean Landscape is older there are greater opportunities for the factors promoting species richness, noted by Lamont *et al.* (1984), to operate.

Although limestone heath vegetation (basically the *Dryandra-Calothamnus* complex) contains elements of both the *Stirlingia-Oxylobium* complex and the *Olearia-Rhagodia* complex, it also has its own suite of identifying species, showing it clearly as transitional vegetation. Limestone heaths are found on the transition between Quindalup and Cottesloe soil associations, as well as forming the vegetation on limestone cliffs of the Cottesloe soil association.

Vegetation of the coastal plain wetlands also varies from west to east—primarily due to changing conductivity (salinity) of the ground water. This salinity gradient reflects a gradient of species richness. Highly saline wetlands of estuarine origin are species-poor, whilst low saline wetlands of freshwater origin are species-rich by comparison. The wetland communities with greatest species richness occur in the Bassendean dune system.

Wetland vegetation may also be arranged on a gradient of structural change—from sedgeland (swamp complex) to closed-forest (See Table 5). Structural attributes of the wetland communities are environmentally determined, with a variety of structural forms occurring in each soil association. The variation of structural form is strongly linked with the obvious vegetation zonation within wetlands, and has no geographical determination or significance.

Tables 4 and 5 show the relative lack of congruence between floristically based vegetation units, and structurally derived units. Several authors e.g. (Bridgewater (1978), Griffin *et al.* (1983)) have reported this from other vegetation types. This does not mean that either set of units is necessarily "better" than the other. There is evidence that vegetation classifications based on the "dominance type" do not reflect well the nuances of environmental variation (e.g. Griffin *et al.* (1983), Kirkpatrick and Glasby (1981)). For use in areas of great species and vegetation richness, floristically based methods appear the most appropriate to describe the full vegetation variation—an essential prerequisite to the development of adequate conservation plans.

Vegetation of the Swan Coastal Plain, being a mosaic of dryland dune systems, lakes, ephemeral swamps and riverine vegetation represents an

important resource for future generations. It is important that adequate and representative samples of the coastal plain vegetation be conserved, to maintain the maximum representation of plant and animal species in this area. In this regard the difference drawn in this paper between richness of species and richness of vegetation texture is an important consideration in determining the adequacy of conservation measures. The conspectus and key should help to identify vegetation variation and help in the creation of an adequate and satisfactorily managed set of reserves, and provide a useful resource for educators in Biology and Environmental Science.

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Appendix

Key to vegetation units

To use this key it is important to select an area of vegetation approximately 10 metres square, which is not transitional in nature.

Unlike strictly dichotomous keys, there are six main points of entry (I-VI). Each point is defined by well recognised dominant species, or vegetation types. Within each of these six sub-keys are a series of statements. To use the key simply start at the first statement and move through each statement until a positive response is obtained.

Failure to reach an end point may be due to the vegetation selected being transitional in nature, or the vegetation having been particularly disturbed, and subject to invasion by exotic species.

It should, however, be possible to discover which of the six main groups the vegetation is related to, and work through the text description of each vegetation unit included in that group to find the nearest "fit".

As this key represents a new format to aid the recognition of vegetation units, the authors would appreciate comments from users on the degree of difficulty, or ease, in using the key in the field.

I

At least four of the following six species present: *Petrophile linearis*, *Conostephium pendulum*, *Bossiaea eriocarpa*, *Daviesia juncea*, *Hypocalymma robustum*, *Oxylobium capitatum*.

(Not as above—go to II)

**Eucalyptus gomphocephala*, or three of the following species present: *Hakea prostrata*, *Hardenbergia comptoniana*, *Dianella revoluta*, *Leucopogon propinquus*

B.1.

*Three of the following four species present: *Patersonia occidentalis*, *Dasyopogon bromeliifolius*, *Lyginia barbata*, *Tetraria octandra*

A.1.

*three of the following four species present: *Eucalyptus calophylla*, *Eryngium pinnatifidum*, *Dianella revoluta*, *Dasyopogon bromeliifolius*

A.3

**Allocasuarina humilis* and/or *Acacia pulchella* present

A.2

II

Four of the following six species present: *Banksia attenuata*, *Hibbertia hypericoides*, *Mesomelaena stygia*, *Allocasuarina fraseriana*, *Eucalyptus marginata*, *Xanthorrhoea preissii* (not as above, go to III)

*Three of the following five species present: *Phyllanthus calycinus*, *Stipa elegantissima*, *Lectonaultia linarioides*, *Calothamnus quadrifidus*, *Hakea lissocarpha*.

B.3

*Four of the following six species present: *Hardenbergia comptoniana*, *Alexgeorgea arenicola*, *Hibbertia racemosa*, *Leucopogon propinquus*, *Scaevola canescens*, *Acacia pulchella*.

B.1

*None of the above species groups present.

B.2

III

Heath or shrubland with two of the following species present: *Hibbertia hypericoides*, *Melaleuca acerosa*, *Dryandra nivea* OR *Dryandra sessilis* OR at least two of the following species present: *Olearia axillaris*, *Pelargonium capitatum*, *Rhagodia baccata*, *Hardenbergia comptoniana* (If the conditions above do not apply go to (IV))

**Callitris preissii* present

D.1

**Agonis flexuosa*—with *Dryandra sessilis*, *Hardenbergia comptoniana* present

B.3

**Dryandra nivea* and *Melaleuca acerosa* or *Melaleuca luegelii* present with

—*Hakea prostrata*, *Acacia littorea*, *A. cochlearis* or *Templetonia reitusa* present

C.1

—*Acacia xanthina* present

C.2

—neither of those combinations present

C.2

**Acacia rostellifera*;

—with *Eucalyptus gomphocephala* present

D.3

—without *E. gomphocephala*

D.2

**Acacia cyclops* or *A. xanthina* with occasionally

Agonis flexuosa present

D.2

**Threlkeldia diffusa* or *Frankenia pauciflora*

D.4

present

IV

Foredune and Strandline communities (If not as above go to V)

**Cakile maritima* present

F

**Tetragonia implexicoma* present

E

V

Melaleuca raphiophylla present

(If *M. raphiophylla* absent go to VI)

**Baumea juncea* with;

—*Gahnia trifida* and/or *Juncus kraussii* present

I.3.a

—*Cotula coronopifolia* present

I.3.b

—*Rupia polycarpa* present

I.3.c

—none of the above species or combinations present

I.3.d

—*Sarcocornia quinqueflora* present

J.2.b

—*Eucalyptus rudis* present

H.2.b

—*Carex fascicularis* and/or *Polygonum salicifolium* present

H.1.b

**Sarcocornia quinqueflora* present

J.2.b

**Atriplex hypoleuca* present

I.2.b

**Polygonum salicifolium* with;

—*Schoenoplectus validus* present

H.1

—*Eucalyptus rudis* and *Paspalum distichum* or

Cynodon dactylon present

H.2.a

—*Centella asiatica* present

H.2.b

—none of the above species present

H.3

**Schoenoplectus validus* with;

—*Polygonum salicifolium* present

H.1

—*Centella asiatica* present

H.2.b

—*Baumea articulata* present

G.3

VI

Various wetland sites, dominated by sedges or paperbarks

**Juncus kraussii* with;

—*Sarcocornia quinqueflora* present

J.2.a

—*Melaleuca cuticularis* present

K

—*Melaleuca teretifolia* present

L.1

—none of the above species present

L.2.a

**Baumea juncea* with;

—*Aster subulatus* present

I.3.b

—*Centella asiatica* present

I.1

—*Typha orientalis* present

G.1

—none of the above species present

I.3.d

**Sarcocornia quinqueflora* with

—*Melaleuca cuticularis* present

K

—*M. cuticularis* absent

J.1

**Melaleuca cuticularis* present

K

**Melaleuca teretifolia* with;

—*Lepidosperma longitudinale* present

L.1

—*L. longitudinale* absent

N

**Typha orientalis* with;

—*Baumea articulata* present

G.2

—*B. articulata* absent

G.1

**Baumea articulata* present

G.3

**Astartea fascicularis* with;

—*Melaleuca preissiana* and/or *Banksia littoralis*

L.3.a

present

L.3.b

—*Schoenus subfascicularis* present

L.2

—*Viminaria juncea* present

L.2

**Viminaria juncea* present

L.2

*Open water,

Chara spp. present as submerged macrophytes

M

INSTRUCTIONS TO AUTHORS

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PARTS 3 and 4

Contents

	Page
Mangrove environments of Port Darwin, Northern Territory: the physical framework and habitats. By V. Semeniuk	81
The relationship of fire and soil type to floristic patterns within heathland vegetation near Badgingarra, Western Australia. By David T. Bell and William. A. Loneragan	98
The Becher Sand a new stratigraphic unit for the Holocene of the Perth Basin. By V. Semeniuk and D. J. Searle	109
The natural sectors of the inner Rottnest Shelf and coast adjoining the Swan Coastal Plain. By D. J. Searle and V. Semeniuk	116
Dune vegetation of the Swan Coastal Plain Western Australia. By I. D. Cresswell and P. B. Bridgewater	137

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