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The first section of this volume contains papers from the symposium 'Living in a Fire Prone Environment' which was organised by the Linnean Society of NSW and ANZAAS (NSW), with financial assistance from the NSW National Parks and Wildlife Service. The symposium was held in March 1995 at the University of New South wales. Papers in this section were sub-edited by Helene Martin.

The second section of this volume contains research reports submitted for publication in accordance with the publication procedures of the society, which can be obtained from the secretary.

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VOLUME 116

Introduction to the Symposium: Living in a Fire Prone Environment

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In early January 1994 Sydney was ringed by raging bushfires. Simultaneously other extensive fires were burning on the central and north coasts of NSW. The bushfires became the focus of national and international media. In the immediate aftermath of the fires considerable discussion ensued, with claim and counterclaim about the need for more frequent and extensive hazard reduction burning, the desirability of adopting burning regimes similar to those practised prior to European settlement and the need to change building controls and planning practices so as to reduce the loss of life and property in future fires.

Since European settlement our history has been punctuated by notable bushfires (for example Black Friday (January 13 1939), Hobart 1967, Ash Wednesday 1983, and now January 1994). In the folk memory these events are more deeply etched than most of national and international political history. While there is a deeply engrained fear of fire we also, perversely, take a curious pride in bushfires. They are one of the features of Australian life which distinguishes us from other countries (and most particularly Britain). While there are many other fire prone landscapes in the world (including California, the Mediterranean basin, South Africa) it is Australian fires which get the greater global media coverage.

In recent decades major fires have given rise to inquiries, reports and renewed bursts of research activity. These proceedings themselves form part of the response to the 1994 fires. Unfortunately, the urgency of addressing questions raised by each fire diminishes with the passing of time, until the next fires ignite a flurry of renewed activity. These episodic periods of concern about fire have a ratchet effect; incrementally public awareness about fire increases and the knowledge base on which to base management decisions is improved. Nevertheless a more consistent sustained attempt to understand the implications of living in a fire prone environment would be desirable.

The symposium 'Living in a Fire Prone Environment' was organised by the Linnean Society of NSW, ANZAAS (NSW) and the School of Biological Science, University of New South Wales, with financial assistance from the NSW National Parks and Wildlife Service. The aim was to take a very broad perspective of fire and fire management, spanning a range of disciplines from geology to psychiatry. The symposium showed that fire was a natural part of the environment long before humans evolved. However, the role of fire in the evolution of Australia's biota is still to be resolved. The Aborigines successfully used fire as a tool, and in so doing, undoubtedly altered the distribution and composition, at least locally, of vegetation. The importance of weather patterns and their influence on bushfires was discussed, importantly emphasising that January 1994 was not exceptional in terms of weather immediately before and during the bushfire emergency. The human emotional response to bushfires and the management of post traumatic distress are topics rarely considered by ecologists or fire managers. The discussion of these issues in this symposium gives us plenty to think about as we prepare for future fires. While in times past we may have been exhorted 'to keep the home fires burning', clearly we wish to avoid homes being destroyed by fire, with suggestions for improving design and construction to minimise risk of damage.

The task of managing for bushfire has become increasingly complex. The objectives of management have gone beyond consideration of protection of life and property (vitally important as these remain). Today's managers must be aware of the environmental impact of fire management and of the necessity for fire management strategies to meet additional conservation objectives. Ecological research clearly shows that a fire regime favourable to one particular group of species may be disadvantageous to others. Not only must we be aware of the response of species to particular fire regimes we must set very explicit goals for management for particular areas. This will require greater dialogue between researchers and managers, and greater involvement of the public, both in setting broad goals for management and in understanding the social and behavioural constraints which may be imposed by adoption of particular bush fire strategies.

The symposium attracted an extremely diverse audience and thus contributed to fostering exchange between different interest groups. These proceedings provide a permanent record of the symposium and an opportunity for extending the debate into the broader community.

Wildfires in Past Ages

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Wildfires are a natural part of most ecosystems throughout the world today. Evidence from fossilised charcoal shows that wildfires have occurred in past ages ever since the Devonian. Lightning has been the major source of ignition for wildfires before humans appeared on the planet and it is still responsible for most outbreaks today.

Australian Tertiary examples where the palaeobotanical record indicates a modification of the vegetation associated with fossil charcoal layers is presented here. Even when there was high humidity throughout the year, there would have been dry periods and perhaps droughts when the rainforest dried out sufficiently to burnt, but they were rare. Peat swamps were burnt periodically, but the drier parts burnt more often. After the demise of rainforest in the mid–late Miocene, when *Eucalyptus* became common, burning on a frequent basis became an integral part of the environment. These examples show a close association of vegetation, climate and fire history in a manner compatible with what is seen today.

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KEYWORDS: Tertiary, Fire history, Vegetation history, Fusain, Charcoal, palynology, palaeobotany.

INTRODUCTION

Fire is a natural part of most ecosystems in the world today. Under climates with a well marked dry season, wildfires are regular events and the frequency of firing may be every 3–5 years in the most fire-prone vegetation. In wet climates where the vegetation is too wet to burn, e.g. tropical rainforests, droughts may allow sufficient drying for occasional wildfires. For examples, in mid 1982, an unprecedented drought struck East Java, Sarawak, Sulawesi, Sabah and Kalimantan. A major fire in east Kalimantan burnt between 35,000 and 37,000 square kilometres of tropical rainforest, including the peat-forming areas, where the peat was burnt to a depth of 1–2 m. In these peat swamps, 98–100% of the trees were killed. Records show a drought of almost similar proportions occurred about 90 years earlier (Johnson 1984). Even the tundra may burn. Summer lightning strikes may set fire to the peats which may smoulder, and at times flare up, for months (Komarek 1964). With wildfires a possibility almost everywhere in the world today, were wildfires a part of the ecosystems of past ages?

Microscopic charcoal fragments have long been recognised amongst pollen recovered from swamp sediments. The preserved charcoal has been shown to reasonably reflect fire history constructed from other sources and has led to valuable insights in the dynamics of the vegetation and of human interaction with the environment, where the sediments are only thousands of years old (Singh et al. 1981, Clark 1982, Kershaw 1985, 1986, Patterson et al. 1986).

Macroscopic charcoal is known as fusain of fusinite and may be abundant in lignites and coals, but is also found in other sediments. Although it is generally accepted that fusain is fossilized charcoal, this has not always been the case

The origin of fusain

As early as 1844, it was proposed that lightning fires were the cause of the formation of fusain (Komarek 1972). Physical and chemical evidence gathered from the charcoal burning industry supported this view (Francis 1961). Early in the 1900's, these views were challenged, even though satisfactory alternative hypotheses about the formation of fusain were not proposed. At this time, when the science of forestry was beginning to make a real impact, fire ecology was not understood and the philosophy of the time was that all fires were man-made. As a consequence, all forest fires were regarded as destructive and there were total fire exclusion policies. Komarek (1972) considers it curious, if coincidental, that Germany was the cradle of forestry and the home of some of the world's foremost coal petrologists as well.

In the last decade and a half, there have been a number of studies using modern methods such as scanning electron microscopy and electron spin resonance, to compare fusain, charcoal from forest fires, experimentally burnt and artificially charred plant material. The main results of these studies comparing fusain and charcoal are summarised below.

Physical properties.

Fusain has good three-dimensional structure and fractures along planes into rectangular blocks. It is brittle and is easily pulverised with light pressure. It is fibrous (if the plant material was originally wood), has a low density (unless impregnated with mineral matter), a silky lustre and high reflectance (Jones et al. 1991). These properties are very similar to those of charcoal and fusain has the general appearance of charcoal (Harris 1958, Francis 1961, Cope and Chaloner 1980, Scott 1989).

Chemical properties.

Analysis of fusain shows 77–94% carbon and 2–3% hydrogen, an analysis also typical of charcoal (Francis 1961, Scott 1989). Both fusain and charcoal are inert and resistant to maceration (Harris 1958, Sander and Gee 1990). Fusain has low flammability and does not catch alight, it merely glows, as does charcoal. Fusain is unaffected by pyrolysis and electron spin resonance studies suggest that the origin of fusain involve exposure of wood to temperatures of 400–600°C (Austen et al. 1966, Teichmüller 1982). These temperatures are commonly encountered in wildfire (see Scott 1989). In natural fires, temperatures vary enormously (Whittaker 1961, Kenworthy 1963), producing anything from partially charred plant material which remains biodegradable to completely charred material, and if temperatures are extreme, complete combustion may reduce it to ash (Harris 1981, Scott 1989).

Being mainly inert carbon, charcoal is not biodegradable, hence preservation is usually excellent. It has long been known that the charring of wood aids in its preservation. The early pioneers of the U.S.A. superficially charred the fence posts before placing them in the ground (Komarek 1972).

Microscopic examination

Both fusain and charcoal may show excellent cell detail and even delicate structures such as pits are well preserved. The cells retain their three dimensional character and are not deformed, but they may be crushed, whereas cellular tissue preserved by other means (e.g., in swamps and bogs) shows characteristic deformations with pressure. The cell wall has been homogenised and no structures are visible, whereas cells preserved by other methods may show the middle lamella (McGinnes et al. 1974, Cope and Chaloner 1980, Prior and Alvin 1983, Scott 1989, Sander and Gee, 1990). Experiments show that the microfibrillar structure of wood subjected to temperatures up to 240°C is not visibly altered (Beck et al. 1982) but charring in a commercial charcoal kiln where maximum temperatures reached are 280–400°C, the original fibrillar arrangement of the wall is replaced with an amorphous-appearing wall structure (McGinnes et al. 1971).

Most fusain originates from wood, but leaves and flowers showing excellent cell detail have been found also (Alvin 1974, Friis et al., 1982, Scott 1989). Experiments (Harris 1981) in which dry *Pteridium* fronds were set alight, produced burnt fragments retaining their delicate cell structure, and these fragments are similar to carbonized fossil leaves of ferns showing cell detail of the palisade and spongy mesophyll. Even stomates and the hairs on the surface of the leaf may be found in burnt litter after a wildfire Other dry leaves may be more delicate and burn completely to ash in experiments, but they may retain their cell structure if on the forest floor, where temperatures are lower during a forest fire (Harris 1958, 1981). Delicate leafy liverworts have been observed to be carbonized and preserved in brown coals (Blackburn and Sluiter 1994). Charring by a peat fire, some 50 cm below the surface, produced excellent preservation of roots (Teichmüller 1989).

Modification of the vegetation

Changes in the vegetation following modern fires are well known, and modifications in the spore–pollen composition associated with layers of fusain in Tertiary peat environments have been reported. Grebe (1953) examined the pollen floras associated with layers of fusain in some German brown coals. In one layer, the fusain had been transported in by water. In another layer, where the habitat was quite damp, it was only lightly burnt and the forest was not changed by the fire. The interpretation of yet another layer is that the peat had burnt and afterwards, the pollen of a number of ferns and insect pollinated plants, usually rare in these coals, had become common. The fire and the changes in the coal vegetation are comparable to those seen on moors today (Grebe 1953). Such changes have been observed following wildfires in the Okefenokee swamp of the eastern coastal plain of the U.S.A., after a severe drought. When the peat burns, it destroys the root systems of the trees and lakes or 'prairies' are formed. The peat fires are localized and spotty. Eventually, the swamp forest returns (Cypert 1972).

Alternative hypotheses

The evidence for wildfires being the origin of fusain would seem convincing, but there are alternative hypotheses still accepted by some. Aerobic bacterial attack or oxidation of plant material at the surface of a swamp may be proffered, but the high content of volatile matter in material subjected to these processes distinguishes it from fusain. Moreover, bacterial attack would degrade the fine cellular structure and could not produce the excellent preservation of fusain. Wood suffering attack by dry rot fungi shrinks and cracks like charcoal, but the cell walls are grossly degraded, unlike those of fusain (Harris 1952). There are other hypotheses (see Scott 1989), but they seem to result from a disbelief that there could have been wildfires in the past. For example, 'The charcoal theory of origin of fusain is principally objectionable because it is commonly taken to be an indication of periodic drought and a susceptibility of vegetation to conflagration for which all other evidence is lacking … For some and probably the majority of the occurrences of fusain, the forest fire seems ruled out. It is unfortunate that I am not able to suggest any generally applicable alternative hypotheses' (Schopf 1975, p 45). There may be so much fusain that if produced by wildfire, the past would have been a 'fiery nightmare'. Over-representation, when unburnt material has decayed (Harris 1952), or the peat has burnt (Scott 1989), leaving only the fusain, may account for these quantities. For a detailed review of this old controversy, see Scott (1989).

The principal objectors to the theory that fusain is fossilised charcoal come thus from those who are unfamiliar with the behaviour of forest fires and who cannot believe that wildfires may burn out swamps or forests in very wet climates, and that periodic droughts occur, even in the wettest of climates. There is, however, ample evidence to show that this disbelief is mistaken. During an extreme drought in 1954 and 1955, fires swept over the Okefenokee Swamp, burning out approximately 128,700 hectares of swamp and 56,660 hectares of upland (Cypert 1972). Many such swamps are known as fire environments (Komarek 1972) and 'most Holocene peats are subject to destruction by erosion, fire and …' (Cameron et al. 1989, p 105). The fauna of marshes and swamps may rely on regular burning to keep the habitat open and maintain their food supplies. Some of these environments in the eastern coastal plain of the U.S.A. are managed with planned burning, for they are important feeding grounds for migrating birds (Komarek 1974).

Studies of surface sediments and cores from the Florida Everglades traced the development of peat from plant material in an attempt to explain the origin of the coal fractions (Cohen and Spackman 1977). In these studies, the highest content of fusain is found in the driest of the swamp environment. 'No evidence is found to support the hypothesis that fusinite in coal can be derived from any process other than fire' (Cohen and Spackman 1977, p.72). In these environments, fires spread through the vegetation above water and the stems below water remain unburnt (Teichmüller 1982). There is no evidence to support alternative hypotheses of the formation of fusain

Charcoal in the geological record

Charcoalified plant material may be locally abundant in many post-Devonian sediments (Cope and Chaloner 1980). It is not restricted to coal, but may be abundant in silts and clays. Charcoal, being light, would be easily transported by water or air currents, particularly at the time of the fire. The evidence from fusain in Lower Carboniferous rocks of Ireland indicates a 'catastrophic palaeowildfire' (Nichols and Jones 1992, p 487). The volume of fusain is compared with the charcoal production from modern fires and it has been calculated that around 95,000 square kilometres were burnt. This fire resulted in increased runoff and increased sediment deposition in the tidal environment, probably an estuary (Nichols and Jones 1992). Scott (1989, p 445) concludes 'that wildfires have been a feature of terrestrial ecosystems from at least the Late Devonian'. Jones and Chaloner (1991) review wildfires through geological time and conclude that spontaneous wildfires are, perhaps, an essential element in the evolution of the ecosystem.

The source of ignition

The main source of ignition for these wildfires would have been lightning strikes (Scott 1989). Even today, up to 80% of fires in western Queensland are started by lightning and 'lightning causes more fires in Australia than is generally realised' (Luke and McArthur 1978, p.61). In North America, frontal weather systems in summer sweep down the eastern side of the Rockies at about 7–14 day intervals, bringing with them thunderstorms and lightning and setting fires as they travel southeastwards (Komarek 1972). Lightning is of such frequency and magnitude that most ecosystems are subjected to recurring lightning fires. For a fascination account of 'The Natural History of Lightning', see Komarek (1964).

Under certain circumstances, lightning striking an exposed sandy surface may fuse the grains into glassy, dendritic shapes called fulgurites. There may be woody fragments in a central hollow tube, suggesting that the lightning travelled down a stem or root. Fulgurites are common in Quaternary sands near Perth (Kemp 1981), but they may be of any age. Harland and Hacker (1966) report fulgurites from the Palaeozoic. Komarek (1964) records a lightning fire in a Florida forest, but the ranger was unable to find the struck tree. About a week later, a wilting cabbage palm tree (*Sabal palmetto*) was noted. When cut down it was found that the lightning had apparently gone down the inside of the tree, then through the sandy soil a metre or so, apparently igniting a clump of palmetto bushes which contained much flammable material. Where the discharge had gone through the sand, it had fused some of the grains into fulgurites (Komarek 1964).

Where coal seams outcrop, they may ignite spontaneously, thus being a source of ignition for wildfires (Kemp 1981). In New South Wales, a burning coal seam at Wingen has been known from earliest European settlement (Rattigan 1967) and the same seam is still burning at Burning Mountain. Intense localised heat from coal seam fires may fuse the sedimentary rock, and such evidence has been found in the Bowen Basin of Queensland, Leigh Creek of South Australia and other locations in the Sydney Basin, as well as Wingen. For a full review of geological evidence of fire, see Kemp (1981).

In the thick brown coals of the Latrobe Valley, Victoria, there are a number of fire holes. These depressions in the coal have carbonised coal, similar to charcoal at the base and are filled with clay. In some holes, the clay has been baked into a brick-like material due to the fire continuing to burn after the deposition of the clays (Gloe 1960).

Glowing ash and lava fragments from volcanic activity are another potential source of ignition. Volcanoes were active in the southeastern highlands during the Tertiary and more recently in the southwest of Victoria and southeast of South Australia. There is a report of carbonized tree trunks in the Triassic Brisbane Tuffs (Kemp 1981).

The impact of meteorites may be another source of ignition, although rare. Studies of the Cretaceous–Tertiary boundary clays in Europe and New Zealand (Wolbach et al. 1988) show an enrichment in elemental carbon, mainly soot. (Soot forms in the higher temperatures found in flames whereas charcoal is formed by charring at lower temperatures). This enrichment of carbon is associated with the iridium layer (Wolbach et al. 1988), which is thought to be of extraterrestrial origin (Alvarez et al. 1988). The soot is isotopically uniform, suggesting that it comes from a single global fire. Most likely, major wildfires were triggered when trees were killed and dried by the impact, both by the prompt heating of the atmosphere and by strong winds capable of flattening forests out to a distance of 500–1,000 km, and subsequent heating by the ejecta plume and hot fallout (similar to volcanic ash). The soot from these fires settled together with the iridium (Wolbach et al. 1988).

CHANGES IN THE VEGETATION ASSOCIATED WITH CHARCOAL LAYERS

Australian examples of changes in the Tertiary vegetation associated with charcoal layers are discussed here

The Latrobe Valley Brown Coals

The Latrobe Valley Depression, in the western part of the onshore Gippsland Basin (Fig. 1), contains some of the thickest and most continuous deposits of brown coal in the world (Gloe 1960). The extensive coal swamps were vegetated raised bogs (Blackburn 1981) with lakes around much of their margins, thus isolating them from sediment input (Holdgate 1985). The swamps were essentially rain-fed and would have been poor in nutrients, most of the nutrients coming from recycling. The deposits are mid Eocene to mid Miocene in age.

Because of their economic importance, there have been numerous studies of the geology, assessment of the coal and the palaeobotany, both macro- and microfossils (see the review by Blackburn and Sluiter 1994). This paper concentrates on the palaeobotanical studies which show changes in the vegetation associated with charcoal layers.

Earlier workers on the Latrobe Valley brown coals (e.g. Edwards 1953, Baragwanath 1962) rejected the notion that fusain originated from fire, in keeping with the general opinion of the time. Recent workers, however, accept that the fusain is indeed fossil charcoal (Teichmüller 1982, Blackburn 1981)

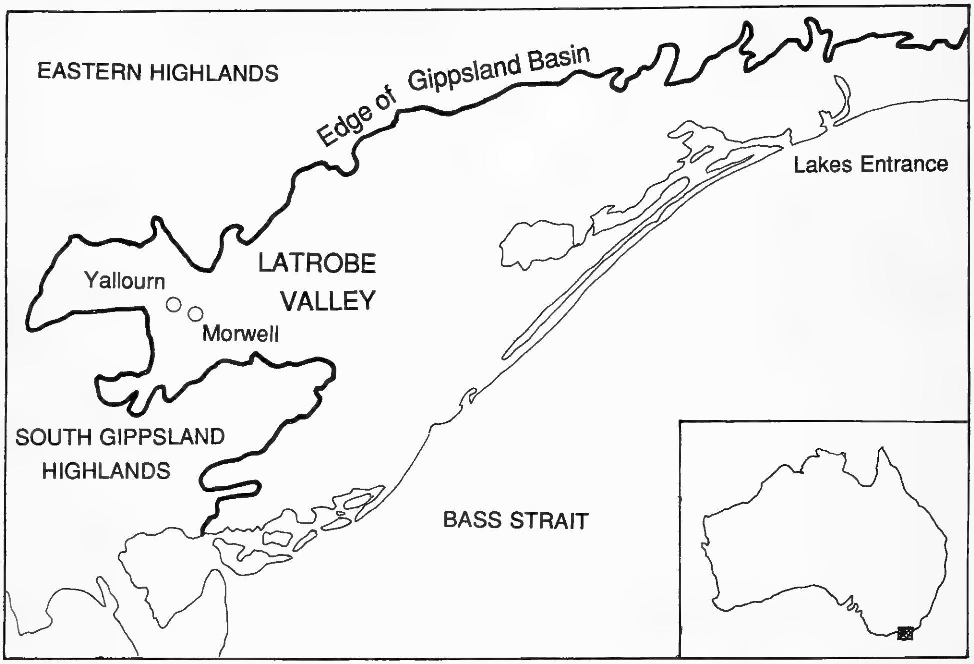

Fig. 1. Locality map of the Latrobe Valley brown coals.

The brown coal resembles peat and macroscopic remains of plants are clearly visible (Teichmüller 1989). The coal varies in colour from light or pale to very dark and a number of lithotypes have been defined using colour. Very dark, dark, medium dark and medium light lithotypes were formed from swamp forests, with the peat surface being generally (dark) or seasonally (medium light) emergent. The very dark coals have a high charcoal content and are indicative of the driest environments. The light to pale lithotypes were probably formed under inundated conditions (Blackburn and Sluiter 1994). The coal usually shows light and dark banding (Blackburn 1981).

The Yallourn seam coals are latest early Miocene to mid Miocene. The basal coals have a high fusain content (35–60%). The vegetation had abundant monocotyledons (Typhaceae, Sparganiaceae, Restionaceae) and Proteaceae (*Banksia, Xylomelum* and others). The Myrtaceae in these coals are those of modern swamp heaths (*Baeckea, Leptospermum, Melaleuca*). Carbonised leafy liverworts are common. Gleicheniaceae is also common in coals with a high fusain content. These reedy swamps with ferns and sclerophyllous shrubs dried out seasonally and the community was largely controlled by fire (Blackburn and Sluiter 1994).

The medium dark to light coals are dominated by Podocarpaceae (*Dacrydium* and *Dacrycarpus*, with *Phyllocladus* locally common), Araucariaceae *(Agathis* and locally *Araucaria)* and Oleaceae. Myrtaceae are also widely distributed and may be assigned to *Syzygium, Tristania* and *Acmena* (Blackburn and Sluiter 1994). The relationships between the vegetation with water levels and the influence of fire is illustrated in Fig. 2.

An erosional layer 5 cm thick, containing abundant charcoal, identifiable over an area of approximately 8 square km, is found in the Morwell Coal Seam. This layer is late Oligocene in age. A section 1.3 m in thickness was sampled at 5 cm intervals across this layer, approximately 60 cm below and 70 cm above it. The darkest coal colour occurs at the

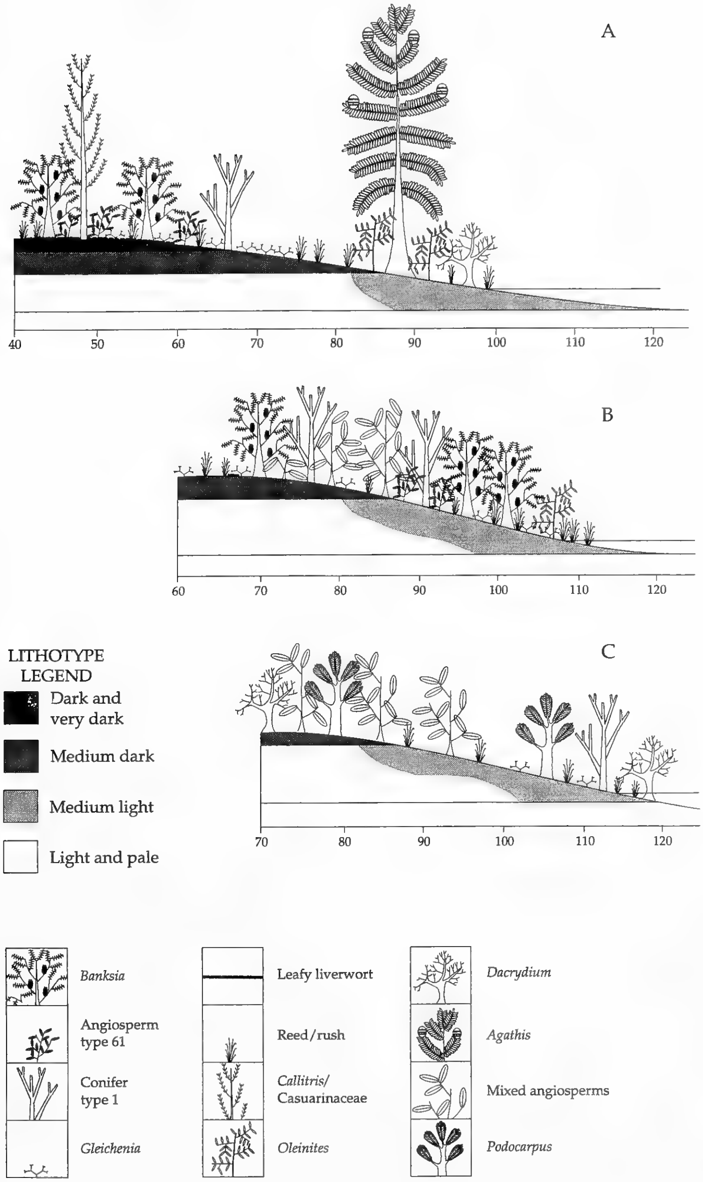

Fig. 2. Hydroseral and pyric succession for three intervals from Yallourn open cut. A to C are arranged in order of decreasing fire influence. Water levels indicate probable permanent inundation. A. Succession under the influence of frequent fires. The margins of open water are essentially a *Dacrydium–Oleinites–Agathis*-reed/rush swamp. On drier areas above this is a reed/rush–*Gleichenia* moor. This grades into a *Banksia–Gleichenia*-conifer type 1-reed/rush scrub. Rare *Callitris* and Casuarinaceae occur on the driest parts with leafy liverworts. B. Succession under the influence of infrequent fires. The margins of open water are occupied by an *Oleinites–Gleichenia*-reed/rush swamp. On drier areas above this is a *Banksia–Gleichenia*–angiosperm type 61-conifer type 1 scrub. Above this again is a region having a mixed angiosperm scrub. On the driest parts *Banksia–Gleichenia*-reed/rush scrub dominates. C. Succession under the influence of very infrequent fires. The margins of the open water are colonised by *Dacrydium–Gleichenia*–conifer type 1-reed/rush swamp. On the drier areas there is a mixed angiosperm–*Podocarpus–Dacrydium* scrub. Reprinted from Blackburn and Sluiter (1994), with permission of Cambridge University Press.

base of the charcoal layer and the colour becomes progressively lighter above it, terminating in light colour at the top. The macrofossils present would have been growing close to the site of deposition, but the microfossils (spores and pollen) could have come from afar.

Major changes in the contributions of the dominant macro- and microfossil plant groups are observed, particularly in the vicinity of the charcoal layer. Some taxa tend to be most abundant below the layer whereas others are more common above it. There is a group which does not change much, above and below the layer. (Blackburn and Sluiter 1994). These major changes are summarized in Table 1.

TABLE 1

Summary of the major changes in dominants from before to after a 'big burn' in the Morwell Coal Seam, age late Oligocene. From Blackburn and Sluiter (1994).

REGIONAL VEGETATION	
Dominant — *Nothofagus* — not growing in swamp (pollen blown in on the wind)	
Swamp Vegetation	
Dominant Taxa	
1. After the fire	
Casuarinaceae	*Allocasuarina*
	Gymnostoma
Cunoniaceae	'*Phyllites*' and others
Myrtaceae	*Tristania* (most)
	Acmena
	Baeckia/Leptospernum
	Syzygium, Austromyrtus
Gleicheniaceae	*Gleichenia*
Typhaceae / Sparganiaceae	
Erosional Layer 'Big Burn' with Charcoal	
2. Before the fire	
Proteaceae	*Banksia*
	Xylomelum and other taxa
Podocarpaceae	*Dacrydium*
	Dacrycarpus
Araucariaceae	*Araucaria/Agathis*
Cunoniaceae	*Ceratopetalum*
Saxifragaceae	*Quintinia*
Liliaceae/Restionaceae	

Murray Basin

The Murray Basin (Fig. 3) was a giant flood plains complex, fed by the major rivers draining the Eastern Highlands. From time to time, the rivers would change course, dumping the sediment load elsewhere and former swamps would develop soil horizons. There was thus a shifting pattern of swamps and dry land. The pollen bearing deposits are late Eocene to mid Miocene in age. Unfortunately, the top 50–100 m of sediment rarely contain pollen (Martin 1984a, 1984b, Brown 1989, Macphail and Truswell 1989). The pollen from about 100 bores in the Basin have been studied (Martin 1993).

From late Eocene to mid Miocene, the vegetation was predominantly rainforest and *Nothofagus* spp. were common. *Podocarpus* was usually the most common gymnosperm, with *Dacrydium* and *Dacrycarpus* usually present. *Lagarostrobos* and Araucariaceae were

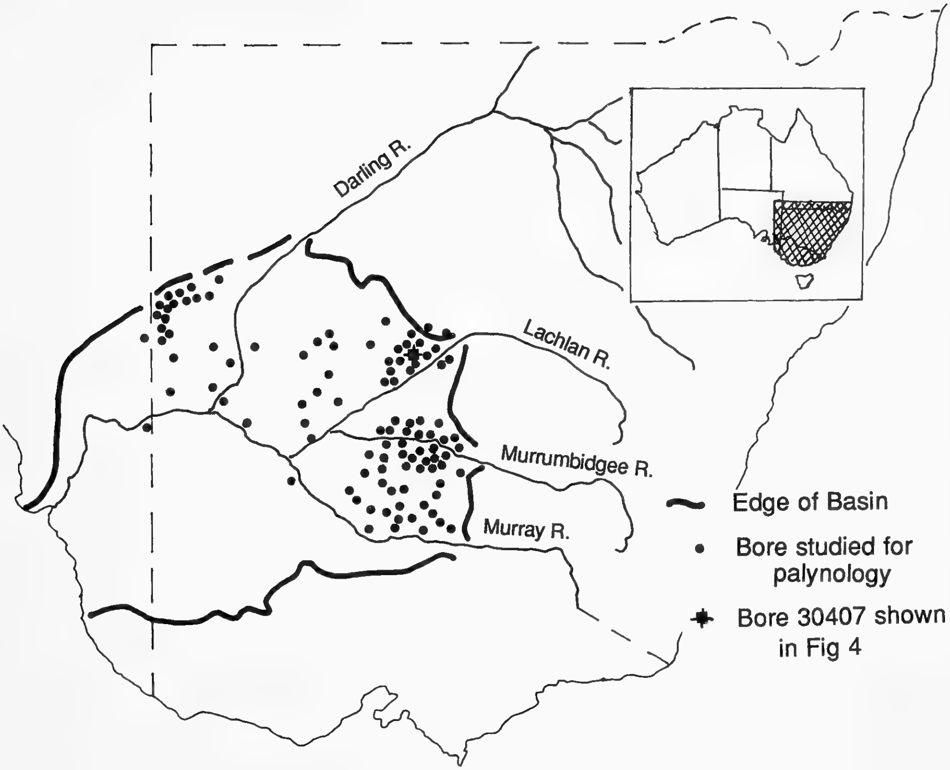

Fig. 3. Locality map of the Murray Basin.

sometimes abundant. Myrtaceae (mostly pollen of rainforest taxa with few of eucalypts) were usually present and Casuarinaceae, generally in low frequencies, was sometimes abundant. Herbaceous or low growing taxa, e.g. Restionaceae, Cyperaceae, Sparganiaceae and rarely Poaceae and Asteraceae were present in low frequencies. There was a wealth of other angiosperm taxa which, being under represented in the pollen fall-out, were only recorded in low frequencies (see Martin 1993).

The climate was very wet and the precipitation would have been above 1500 mm, with relatively high humidities throughout the year (Martin 1987). Such a climate would not be conducive to wildfires.

There is a low frequency of small carbonised particles in most of the sediments (discussed further, below). Charcoal is relatively inert, and may be reworked, with larger pieces being broken into smaller pieces, thus maintaining a low background count. Higher counts are extremely rare in the Murray Basin. In one bore, however, (Fig. 4) one sample shows unusually high Casuarinaceae and exceptionally low *Nothofagus* counts. The counts for fern spores and herbs are high also. This anomalous sample has an unusually high content of carbonized particles. The samples above and below it, both with abundant *Nothofagus*, are more or less average for this time. The *Nothofagus* rainforest had been replaced by more open forest with Casuarinaceae dominant after a fire, which after time, reverted to the usual *Nothofagus* forests (Fig. 4). Even though the climate was very wet, there would have been dry spells and droughts when the vegetation may have dried out sufficiently to burn, but such events were extremely rare (Martin 1993).

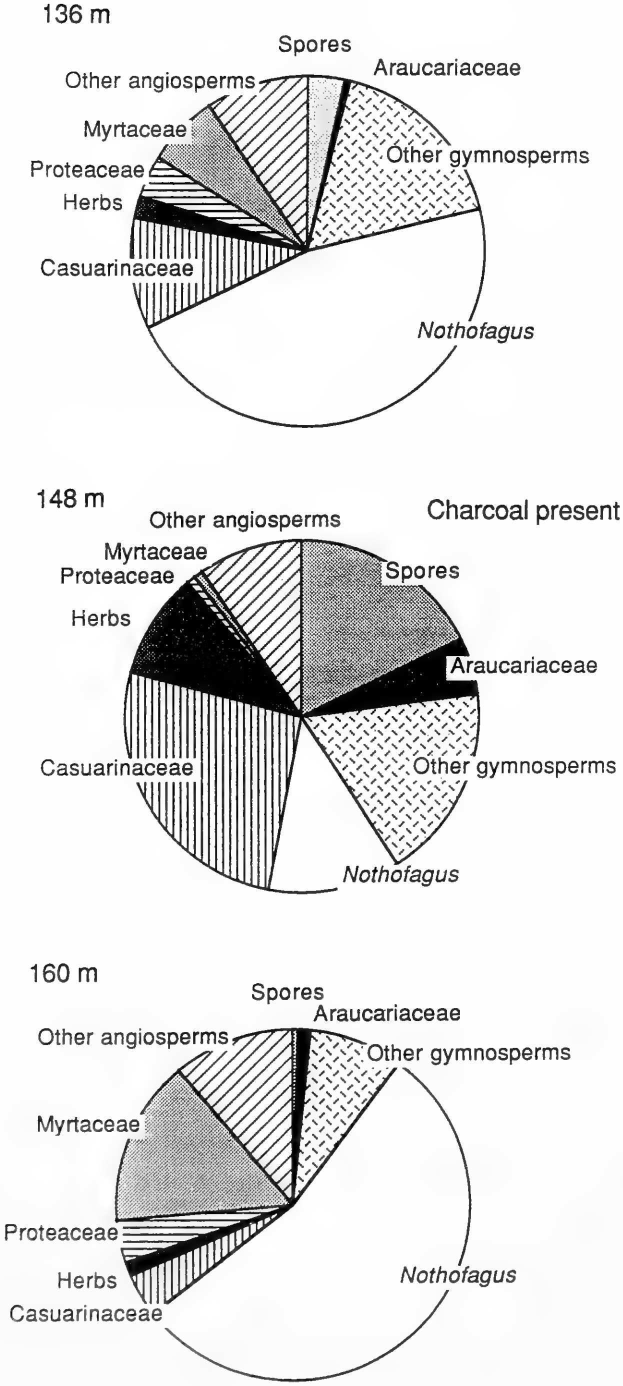

Fig. 4. A sequence of three consecutive samples from bore 30407 (see Fig. 3 for locality). The spectra from 136 m and 160 m are more or less 'average' and that from 148 m is most likely a modification after burning, from Martin (1993).

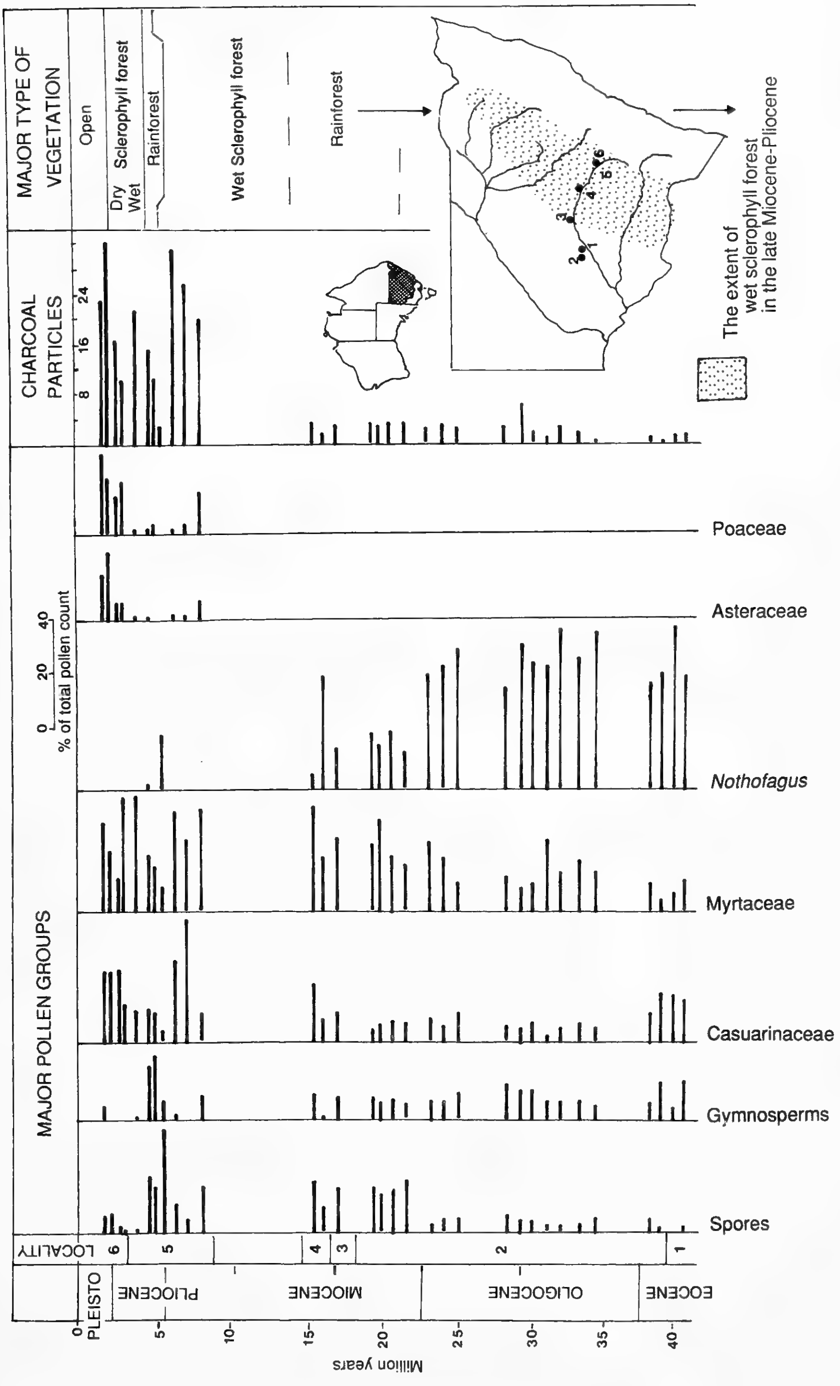

Fig. 5. The major pollen groups, carbonised particle counts (expressed as the ratio carbonised particles/total spores and pollen) and type of vegetation of the Lachlan River Valley. The sequence is a composite of bores, with the locations shown on the inset map (Martin 1978). For further explanation, see text..

The Lachlan River Valley

A series of bores along the Lachlan River presents an almost continuous record from the late Eocene to late Pliocene–Pleistocene. Fig. 5 shows counts of the major pollen groups, and carbonized particles together with interpretations of the palaeovegetation.

From late Eocene to mid Miocene, the major type of vegetation was rainforest. *Nothofagus* was usually common and the Myrtaceae group included mainly rainforest taxa. The pollen assemblages for this time period shown here in Fig. 5 are very similar to the upper and lower levels of the bore represented in Fig. 4, but this latter bore has not been used in this section along the Lachlan River Valley. The charcoal or carbonized particle count is the low background count throughout.

In the mid–late Miocene, there was a drastic change. *Nothofagus* and many other rainforest taxa disappear or are drastically reduced. Myrtaceae has become the dominant group and although much of the Myrtaceae pollen is difficult to identify, the eucalypt type is fairly common. This change is accompanied by a dramatic increase in charcoal particles, suggesting that fire had become an integral part of the environment, and that eucalypts were common in the vegetation (Martin 1987).

TABLE 2

Rainforest taxa in the late Miocene–Pliocene of the Lachlan River Valley, from Martin (1978).

Family	Taxon
Gymnosperms	
Araucariaceae	Araucariaceae
Cupressaceae	Cupressaceae
Podocarpaceae	*Podocarpus*
	Dacrydium
	Dacrycarpus
	Phyllocladus
Angiosperms	
Aquifoliaceae	*Ilex* (rare)
Elaeocarpaceae	Elaeocarpaceae
Euphorbiaceae	*Coelybogyne*
	Macaranga–Mallotus
Proteaceae	*Helicia–Orites*
Rubiaceae	*Gardenia*
Sapindaceae	Cupaneae
Saxifragaceae	*Quintinia*
Symplocaceae	*Symplocos*
Winteraceae	*Tasmannia*

The late Miocene–Pliocene palaeovegetation with abundant Myrtaceae (mostly eucalypts), with some rainforest taxa (see Table 2) and in which burning would have occurred on a regular basis, best fits wet sclerophyll forest which has a tall open canopy of *Eucalyptus*, rainforest taxa in the understorey or as a small tree layer and in which 'fire is an integral part of the environment' (Ashton and Atiwill 1994). Tree ferns (*Cyathea*) may be abundant in wet sclerophyll forest, and spores of *Cyathea* are common amongst the pollen counts. This palaeovegetation is unlikely to have been rainforest, for rainforest rarely burns (Webb 1970, Luke and McArther 1978). If wet sclerophyll forest remains unburnt, it will revert to rainforest, but if the climate has a marked dry season conducive to wildfires on a regular basis, then this reversion is unlikely.

There is one level in the early Pliocene (see Fig. 5) where *Nothofagus* and some other rainforest taxa make a brief comeback. At this level, the carbonized particle count is much reduced and is similar to that of the older part of the sequence when rainforest flourished (Martin 1987). This level marks a short-lived increase in rainfall which would have reduced the fire frequency and allowed rainforest to increase.

The Lachlan River Valley has the best sequence and is shown in Fig. 5, but the other major river valleys down the Western Slopes have very similar sequences (Martin 1991). The likely extent of wet sclerophyll forest in the late Miocene–Pliocene is shown on Fig. 5 also.

DISCUSSION

In view of the experimentation and the number of studies comparing fusain to charcoal, there seems little doubt that fusain is fossilised charcoal and it may be recovered from sediments in considerable quantity. Wildfires may burn in practically every kind of vegetation today, even that growing in very wet climates during times of drought, hence it is not unreasonable to expect wildfires in past ages. The prerequisites for wildfires are: 1, fuel, the vegetation: 2, the fuel must dry out sufficiently to burn, i.e., a climatic prerequisite and 3, there must be a source of ignition, usually lightning before the arrival of man. It is not difficult to realise these three conditions.

Modifications of vegetation following fire are well known today, and the palaeobotany indicates modifications in the vegetation associated with fossil charcoal layers. There are several Australian examples of such modifications of mid–late Tertiary age, when the climate was wetter than that of today.

Examples from the Latrobe Valley and Murray Basin are late Oligocene–mid Miocene in age, and the dominant type of vegetation was rainforest with common *Nothofagus.* The example from the Murray Basin records modifications in the vegetation associated with a charcoal layer. The *Nothofagus* rainforest was replaced by a more open forest with Casuarinaceae dominant, which in turn reverted to *Nothofagus* rainforest. The coal swamp vegetation in the Latrobe Valley did not contain *Nothofagus* which, however was present in the surrounding regional vegetation. Sclerophyllous taxa, e.g., *Banksia* and other Proteaceae were common and sometimes abundant in these swamps, not because of xeric conditions but because of the low nutrient status (Blackburn and Sluiter 1994). Changes in the composition of the vegetation associated with charcoal are complex, but they usually include increased Casuarinaceae. It is interesting to note that although *Eucalyptus* had evolved by this time (Martin 1994), it was not common and not involved with fire ecology in these examples from the Tertiary rainforests. *Eucalyptus* of the late Oligocene–mid Miocene thus responded in a very different manner to that of today when it replaces rainforest after burning.

The mid–late Miocene of the Lachlan River Valley registers the demise of rainforest as the major type of vegetation and the establishment of burning as an integral part of the environment. The charcoal particle frequencies are closely correlated with the spore–pollen frequencies. *Eucalyptus* and Casuarinaceae were dominant in the vegetation. No doubt, these levels of *Eucalyptus* were maintained by burning which was part of the late Miocene and Pliocene environment. There is a minor resurgence of rainforest in the early Pliocene and the charcoal particle frequency drops to the level of that associated with the Oligocene–mid Miocene rainforest.

CONCLUSIONS

Numerous studies on apparent fossilized charcoal show that it has all the properties of charcoal and it has been formed from burning of plant material.

Fossilized charcoal, may be found in sediments of post-Devonian age and is evidence that wildfires were part of the environment of past ages.

Increased concentrations of charcoal may be accompanied with modifications in the vegetation compatible with what is seen today.

In the Oligo–Miocene *Nothofagus* rainforests, wildfires were extremely rare. One instance of an increase in charcoal concentration was accompanied with a change to Casuarinaceae dominated, more open vegetation, which, after a time, reverted to *Nothofagus* forests.

In Oligo–Miocene nutrient-poor sclerophyllous swamp vegetation, an increase in charcoal concentration is also accompanied by a change to more Casuarinaceae in the vegetation.

In the late Miocene–Pliocene, when widespread rainforest had been mostly replaces by *Eucalyptus* forests, there is a consistently higher level of charcoal particles when compared with the former rainforests.

These associations of fire history and modifications in the vegetation, when considered together with the climate of the time, are entirely compatible with what is observed today.

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REFERENCES

Alvarez, L.W. Alvarez. W., Asaro, F. and Michel, H.V. (1980). Extraterrestrial cause for the Cretaceous Tertiary extinction. *Science* **208,** 1095–1108.

Alvin, K.L. (1974). Leaf anatomy of *Weichselia* based on fusainized material. *Palaeontology* **17,** 587–598.

Ashton, D.H. and Atiwill, M.P. (1994). Tall open-forests. In 'Australian Vegetation' Second Edition (Ed. R.H.Groves) pp 121–151. (Cambridge University Press, Cambridge).

Austen, D.E.G., Ingram, D.J.B., Given, P.H., Binder, C.R. and Hill, L.W., (1966). Electron spin resonance study of pure macerals. In: R.F. Gould (Editor), Coal Science. *American. Chemical Society, Advances in Chemistry Series* **55,** 344–362.

Baragwanath, G.E. (1962). Some aspects of the formation and nature of brown coal, and the behaviour of brown coal ash in water tube boilers with special reference to Victorian deposits. *Proceedings, Australian Institute of Mining and Mineralogy* **202,** 131–249.

Beck, C.B., Coy, K. and Schmid, R., (1982). Observations on the fine structure of *Callixylon* wood. *American Journal of Botany* **69,** 54–76.

Blackburn, D.T., 1981. Plant fossils of the Latrobe Valley. International Botanical.Congress Field Trip 37. (Unpubl.) 13 pp.

Blackburn, D.T. and Sluiter, I.R. 1(994). The Oligo–Miocene coal floras of southeastern Australia. In . ''History of the Australian vegetation: Cretaceous to Recent' (Ed. R.S. Hill) pp. 328–367. (Cambridge University Press, Cambridge).

Brown, C.M. (1989). Structural and stratigraphic framework of groundwater occurrence and surface discharge in the Murray Basin, southeastern Australia. *B.M.R. Journal of Australian Geology and Geophysics* **11,** 127–146.

Cameron, C.C., Esterle, J.S. and Palmer, C.A. (1989). The geology, botany, and chemistry of selected peat-forming environments from temperate and tropical latitudes. In 'Peat and Coal: Origin, Facies, and Depositional Models'. (Eds P.C. Lyons and B. Alpern). *International Journal of Coal. Geology* **12,** 105–156

Clark, R.J. (1982). Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et Spores* **24,** 523–535.

Cope, M.J. and Chaloner, W.G. (1980). Fossil charcoal as evidence of past atmospheric composition. *Nature (London)* **283,** 647–649.

Cohen, A.D. and Spackman, W. (1977). Phytogenic organic sediments and sedimentary environments in the Everglades–mangrove complex. *Palaeontographica Abt. B* **162,** 1–144.

Cypert, E. (1972). Plant succession on burned areas in Okefenokee swamp following the fires of 1954 and 1955. *Proceedings of the Tall Timbers Fire Ecology Conference* **12,** 199–217.

Edwards, A.B. 1953 Fusain in some Victorian brown coals. *Proceedings of the Australasian Institute of Mining Metallurgy* **170,** 47–66.

Francis, W. (1961). 'Coal' Second Edition. (Edward Arnold, London)

Friis, E.M. and Skarby, A. (1981). Structurally preserved angiosperm flowers from the Upper Cretaceous of southern Sweden. *Nature (London)* **291,** 485–486.

Gloe, C.S. (1960). The geology of the Latrobe coalfield. *Proceedings of the Australasian Institute of Mining Metallurgy* **194,** 57–125.

Grebe, H. (1953). Beziehungen zwischen Fusitlagen und Pollenführung in der Rheinischen Braunkohle. *Palaeontology* **27,** 12–15.

Harris, T.M. (1958). Forest fire in the Mesozoic. *Journal of Ecology* **46,** 447–453.

Harris, T.M. (1981). Burnt ferns from the English Wealden. *Proceedings of the Geologists Association, London* **92,** 47–58.

Harland, W.B. and Hacker, J.L. (1966). 'Fossil' lightning strikes 250 million years ago. *Advances in Science* **22,** 663–671.

Holdgate, G.R. (1985). Latrobe Valley brown coals, their geometry and facies equivalents as a guide to depositional environment. *Australian Coal Geology* **5,** 53–68.

Johnson, B., 1984. The Great Fire of Borneo. (World Wild Life Fund, Godalming, Surrey, U.K.) 24 pp.

Jones, T.P. and Chaloner, W.G. (1991). Les Feux du passé. *La Recherche* **22,** 1148–1156.

Jones, T.P., Scott, A.C. and Cope, M. (1991). Reflectance measurements and the temperature of formation of modern charcoals and implications for studies of fusain. *Bulletin de la Société géologique France* **162,** 193–200.

Kemp, E.M. (1981). Pre-Quaternary fire in Australia. In 'Fire and the Australian biota' (Eds A.M. Gill, R.A. Groves and I.R. Noble) pp 3–21. (Australian Academy of Science: Canberra)

Kenworthy, J.B. (1963). Temperatures in heather burning. *Nature (London)* **200,** 1226.

Kershaw, A.P. (1985). An extended late Quaternary vegetation record from north-eastern Queensland and its implications for the seasonal tropics of Australia. *Proceedings of the Ecological Society of Australia* **13,** 179–189.

Kershaw, A.P. (1986). Climatic changes and aboriginal burning in north-east Australia during the last two glacial/interglacial cycles. *Nature* **322,** 47–48.

Komarek, E.V., Sr. (1964). The natural history of lightning. *Proceedings of the Tall Timbers Fire Ecology Conference* **3,** 139–183.

Komarek, E.V., Sr. (1972). Ancient fires. *Proceedings of the Tall Timbers Fire Ecology Conference* **12,** 219–240.

Komarek, E.V., Sr. (1974). The effects of fire on temperate forests and related ecosystems, southeastern United States. In 'Fire and Ecosystems' (Eds T.T. Kozlowski. and C.E. Ahlgren) pp 251–277. (Academic press, New York)

Luke R.H., and McArthur, A.G. (1978). 'Bushfires in Australia'. (Australian Government Publishing Service: Canberra) 359 pp.

Macphail, M.K. and Truswell, E.M. (1989). Palynostratigraphy of the central west Murray Basin. *BMR Journal of Australian Geology and Geophysics* **11,**301–331

Martin, H.A (1984a). The stratigraphic palynology of the Murray Basin in New South Wales. II. The Murrumbidgee area. *Journal and Proceedings of the Royal Society of New South Wales* **117,** 35–44.

Martin, H.A (1984b). Stratigraphic palynology of the Murray Basin in New South Wales III. The Lachlan area. *Journal and Proceedings of the Royal Society of New South Wales* **117,** 45–51.

Martin, H.A. 1(987). The Cainozoic history of the vegetation and climate of the Lachlan River Region, New South Wales. *Proceedings of the Linnean Society of New South Wales* **109,** 214–257.

Martin, H.A (1991). Tertiary stratigraphic palynology and palaeoclimate of the inland river systems in New South Wales. In 'The Cainozoic of Australia: a re-appraisal of the evidence' (Eds M.A.J. Williams, P. De Dekker and A.P. Kershaw) *Special Publication of the Geological Society of Australia* **18,** 181–194

Martin, H.A. (1993). The palaeovegetation of the Murray Basin, late Eocene to mid Miocene *Australian Systematic Botany* **6,** 491–531.

Martin, H.A. (1994). Australian Tertiary phytogeography: evidence from palynology. In 'History of the Australian vegetation, Cretaceous to Recent' (Ed. R.S. Hill) pp. 104–142. (Cambridge University Press: Cambridge)

McGinnes, R.A., Kandeel, S.A. and Szopa, P.S.(1971). Some structural changes observed in the transformation of wood into charcoal. *Wood and Fibre* **3,** 77–83.

McGinnes, R.A., Szopa, P.S. and Phelps, J.E. (1974). Use of Scanning Electron Microscopy in studies of wood charcoal formation. In 'Scanning Electron Microscopy 1974 Part II' pp 469–476. (ITT Research Institute, Chicago, IL)

Nichols, G. and Jones, T. (1992). Fusain in Carboniferous shallow marine sediments, Donegal, Ireland: the sedimentological effects of wildfire. *Sedimentology* **39** 487–502.

Patterson, W.A., Edwards, K.J. and Macguire, D.J. (1987). Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews* **6,** 3–23

Prior, J. and Alvin, K.L. (1983). Structural changes on charring woods of *Dichrostachys* and *Salix* from Southern Africa. *IAWA Bulletin New Series* **4,** 197–206.

Rattigan, J.H. (1967). Phenomena about Burning Mountain, Wingen, New South Wales. *Australian Journal of Science* **30,** 183–84.

Sander, P.M. and Gee, C.T. 1(990). Fossil charcoal: techniques and applications. *Review of Palaeobotany and Palynology* **63,** 269–279.

Schopf, J. (1975). Modes of fossil preservation. *Review of Palaeobotany and Palynology* 20, 27–53.

Scott, A.C. (1989). Observations on the nature of fusain. *International Journal of Coal Geology* **12,** 443–475.

Singh, G., Kershaw, A.P. and Clark, R. (1981). Quaternary vegetation and fire history in Australia. In 'Fire and the Australian Biota' (Eds A.M. Gill, R.A. Groves and I.R. Noble) pp 23–54. (Australian Academy of Science: Canberra).

Teichmüller, M. (1982). Origin of petrographic constituents of coal. In 'Stach's Textbook of Coal Petrology' (Eds E. Stach, et al.) 3rd ed, English translation pp 219–294. (Gebrüder Borntraeger: Berlin).

Teichmüller, M. (1989). The genesis of coal from the viewpoint of coal petrology. *International Journal of Coal Geology* **12,** 1–87.

Webb, L.J. (1970). Eastern Australian environments in relation to fire. In 'Environments in order?' pp 5–8. Proceedings of a symposium, Australian Museum, 8th Aug. 1970 (unpubl.)

Whittaker, E. (1961). Temperatures in heath fires. *Journal of Ecology* **49,** 709–715.

Wolbach, W.S., Lewis, R.S., and Anders, E. (1985). Cretaceous extinctions: Evidence for wildfires and search for meteoritic material. *Science* **230,** 167–170.

Aboriginal Use of Fire in Southeastern Australia

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When European settlement began in southeastern Australia, Aboriginal people were observed using fire as a land management tool. Fire was used to clear the underbrush and make travel easier, to hunt large and small game, and to increase the abundance of certain types of plant foods. As a consequence of regular and systematic burning, vegetation mosaics were created which maximised and maintained species diversity. Many of the vegetation associations observed by Europeans in 1788 were artefacts of human intervention. When traditional burning stopped, those areas which had been created by Aboriginal firing changed in species composition. A lower frequency fire regime resulted in more woody understorey plants dominating. A consequence was that when a fire did occur, the fuel load was greater and the fire more intense. The suggestion that Aboriginal fire regimes should be re-introduced to minimise the impact of bushfires ignores the spatial variability inherent in traditional Aboriginal burning regimes, and also ignores the fact that the aims and consequences of hazard reduction burning are very different from the aims and consequences of Aboriginal burning practices.

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INTRODUCTION

In January 1994, following the devastating bushfires which swept through southeastern Australia, an article was published in one of the Sydney newspapers under the heading ‘Libs to seek aid of tribal elders in fire policy’. The article went on to explain that ‘Land management techniques used by Aborigines for thousands of years including regular burning may be incorporated to the policy in an effort to prevent a repeat of the disaster’ (Crouch 1994).

In other parts of Australia, Aboriginal knowledge is being put to good use in the co-operative management of National Parks (Birckhead et al. 1993), so at first glance there may also appear to be some merit in this approach for the more populated parts of Australia. However, a more detailed investigation would strongly suggest that seeking the advice of ‘tribal elders’ or indeed other Aboriginal people on fire policy in southeastern Australia in the 1990s is at best not relevant, and probably totally inappropriate.

Aboriginal people in various parts of Australia have used, and in some cases still do use, fire as a land management tool. However, the relationship between traditional Aboriginal burning and current attempts to maintain biodiversity and reduce property loss due to wild fire in the 1990s is tenuous. While many Aboriginal people have a detailed understanding of the characteristics and control of fire, the motivation for using fire and indeed the consequences of its use are determined by an Aboriginal cultural perspective.

USES OF FIRE BY ABORIGINAL PEOPLE

When Europeans first arrived in Australia, there were between one and two million Aboriginal people speaking over 600 distinct languages and utilising every single ecological zone right across the continent (Butlin 1983; 1993). They had developed technologies and social systems which allowed them to exist and indeed flourish in arid areas where Europeans have found it difficult to survive, even with the advantages of modern technology. Aboriginal people adapted to the environment in which they found themselves, and over time they changed their technology and land management practices in response to changes in the environment. They used the land effectively and efficiently, maximising the productivity in a sustainable way.

Archaeological evidence suggests that Aboriginal people arrived on the Australian continent at least 40,000 years ago, probably 50,000 years ago, and possibly 60,000 years ago (Roberts et al. 1991). When they came, they brought with them knowledge of fire. Just how important fire was to them during the early period of occupation of Australia is largely a matter of conjecture. Certainly, the presence of humans using fire to cook and keep warm would lead to a higher frequency of bush fires, but there is no direct evidence to suggest that fire was used extensively as a land management tool at that early period. From an evolutionary perspective, fire was an important component of the Australian environment long before Aboriginal people arrived. Because fire has been a component of the Australian biota for a considerable period of time, much of the Australian vegetation is therefore fire-adapted, or at least fire-resistant. Many Australian animals have also been shown to be adapted to regular fires (Catling 1991).

One claim for early and systematic Aboriginal use of fire is that of Gurdip Singh, from the Australian National University in Canberra (Singh et al. 1981). Singh studied pollen and charcoal in sediments from Lake George, a large freshwater lake just north of Canberra, and he found significant changes in the vegetation pattern and charcoal content of his cores at around 120,000 years ago. The fire-resistant species, like the eucalypts, began to dominate at this time. Singh suggested that these changes were the result of Aboriginal people first arriving in Australia and bringing with them techniques of firing the landscape (Singh and Geissler 1985).

Although there has been no direct confirmation of Singh's work, similar patterns of vegetation change have been detected in deep sea cores from off the Queensland coast at broadly the same time (Kershaw et al. 1993), and at a later date, around 38,000 years ago, in pollen cores from the Atherton Tablelands in north Queensland (Kershaw 1986, 1993). Here we have the first suggestions that Aboriginal people may have had an active role in creating and changing the environment in which they lived by their use of fire.

However, the period around 120,000 years ago was relatively warm, just the kind of environmental conditions which might be expected to support forests including fire-resistant vegetation such as eucalypts. Since there is no archaeological data to support such an early human occupation of Australia, it seems likely that climate change was responsible for the vegetation changes.

During the periods of extreme low sea level around 18,000 years ago, the average temperature fell by somewhere between 4 and 7 degrees Celsius, while the rainfall may have decreased by as much as 50% (Dodson 1991). The implications of such changes are clear. The lush forests were reduced, and many areas in the south of the continent became grasslands and open woodlands. Such large scale changes in vegetation were primarily responses to climatic change, and cannot be attributed to Aboriginal burning.

During the coldest periods, parts of Tasmania became glaciated. The Tasmanian data presents us with an interesting set of problems. Some Aboriginal burning seems to have occurred in the southwest during the terminal Pleistocene, perhaps between 18,000 and 12,000 years ago. With the greater rainfall of the Holocene, rainforests developed, probably because the wetter conditions. Fire was acting in opposition to the direction of climatic change — burning favours sclerophyll vegetation, while the moister climate favoured rainforest plants (Pyne 1991). Climate won. The same may be said of Lynch's Crater in North Queensland, where rainforests returned within the last five to six thousand years (Kershaw 1986). Perhaps what we are observing in the last few thousand years is the struggle between anthropogenic fires and climate, with climate seeming to come out in front in most situations.

So did Aboriginal people have any significant impact on the Australian environment? Did they effect the distribution of plants and animals across the landscape, particularly though their use of fire? David Horton (1982: 237) has argued that: 'Aboriginal use of fire had little impact on the environment and ... the patterns of distribution of plants and animals which obtained 200 years ago would have been essentially the same whether or not Aborigines had previously been living here'.

Horton takes the extreme position — little or no human impact. He believes that it was climatic change which was the driving force behind the development of contemporary Australian vegetation patterns. Consequently, since the Holocene period has been relatively stable, he must also argue that these changes were virtually completed by 10,000 years ago. Yet there is evidence for some important changes in some vegetation associations during the Holocene.

At the other end of the spectrum, Singh and Kershaw have both argued that fire-induced changes in the Australian vegetation began around 120,000 years ago with the arrival of the Aborigines. Horton argues that fire has always been a component of Australian ecosystems and Aborigines had no impact — Singh and Kershaw argue that fire only became important with the advent of the Aborigines. The truth probably lies somewhere between these two extreme views.

Fire as a land management tool

Before we can adopt traditional Aboriginal burning as a land management tool, there are a number of important questions which need to be answered about Aboriginal burning practices. How long have Aborigines been burning intensively, and what does this burning do to the vegetation, and as a consequence, to the fauna? Many of these basic questions have yet to be satisfactorily answered.

Robyn Clark (1983) believes that on the basis of the palynological evidence: 'Aborigines neither created nor maintained vast areas of grassland, although their burning may have been responsible for the continuation of patches of grassland or woodland within larger forested regions. Climate has been and is far more important than fire in determining the distribution of Australian vegetation, but Aboriginal burning might have effected the rate of vegetation change'.

One complicating factor is that Aboriginal burning methods may not have always been the same. The use of the ethnographic analogy — making the assumption that what we see in the ethnographic present is the same as what existed in the prehistoric past — is fraught with danger. The same cautious approach which is used by prehistorians in assessing artifact functions or cultural practices must be used when investigating Aboriginal burning practices.

On balance, the archaeological, palynological and geomorphological evidence suggests that regular intensive Aboriginal burning is a relatively recent event. Beaton (1982) has studied the Aboriginal use of cycads, a group of plants which contain highly toxic compounds. He documents increases in the number of edible cones after firing, and suggests that one of the uses of fire was to increase the yield of these plants. On the basis of his archaeological studies, he also believes that they were first exploited around 4,000 years ago when the technological processing to remove the poisonous components became known to Aboriginal people. This period of around 4,000 years ago is a time when major technological changes are evident in the archaeological record throughout southeastern Australia. The term 'Intensification' is used to describe the range of changes in site usage, settlement pattern and social interaction which characterised Aboriginal culture in the late Holocene (see Lourandos and Ross 1994). This may well be when intensive use of fire to increase the availability of specific resources was initiated.

There are other forms of evidence which support the view that intensive Aboriginal burning is a relatively late phenomenon in terms of human occupation of Australia. Hughes (1981) and Hughes and Sullivan (1981) have argued that the increase in valley fills in eastern Australia during the last 3,000 years was caused by increased Aboriginal burning. Fires removed the ground cover and understorey, and allowed the sandstone slopes to erode more rapidly, filling up the valley floors with deposit. Hickin and Page (1971) reported that valley fills from the Wollombi valley had been dated to the last 4,000 years. Clearly these recent dates for valley fills in the Sydney region indicate some kind of geomorphic process initiated by something other than climate. Hughes and Sullivan point the finger at Aboriginal burning, and it is difficult to find any other satisfactory explanation. So while regular low-intensity burning as practiced by Aboriginal people in some areas may indeed reduce the severity of wildfires, it may also increase the rates of soil erosion, at least on sensitive geological substrates like Hawkesbury Sandstone.

Spatial and temporal variability in Aboriginal burning patterns

In any understanding of traditional Aboriginal burning practices, it is necessary to look at both the spatial and temporal variability — which parts of the landscape were burned, and when were they burned. Gamble (1986) concludes that much of Arnhem Land is an ‘artificial wilderness’. Gould (1971) demonstrated that fire was an important aspect of traditional culture in the Western Desert. Clark and McLoughlin (1986) believe that sandstone and shale substrates were burned at different frequencies in the Sydney region. Head (1989) points out that in recent times, contemporary Aboriginal groups have been maintaining both fire-dependent and fire-resistant communities. Indeed, what Aboriginal people were trying to achieve was a balance between the need to burn some areas to promote certain resources, and the need to protect other areas from fire where particular plant foods grew, particularly rainforests and wet sclerophyll forests. Aboriginal burning often produced a mosaic of vegetation associations, maximising the diversity and therefore the productivity of an area (Kohen and Downing 1992). Rather than suggesting that Aborigines burned the landscape, perhaps it is better to say that they managed the landscape, and that fire was one of the tools which they used. Indeed, some burning was clearly used to prevent wild fires destroying some fire-sensitive areas.

Rhys Jones was the one of the first to suggest that this burning was controlled or directed (Jones 1969). He saw fire as an important tool in increasing the productivity of the land, by replacing mature forests with open woodlands and grasslands. It seems likely that Aborigines contributed little to this process until the late Holocene, when their increased population and more intensive use of fire promoted certain species to the disadvantage of others, but generally on a local scale. Before this time, the direction and extent of vegetation change was largely directed by climate.

The increase in Aboriginal burning was probably a consequence of the introduction or invention of new technologies which allowed Aboriginal people to focus on those large resources which were previously so difficult to capture — kangaroos, large wallabies and emus. The advent of spearthrowers and multi-barbed spears probably facilitated greater exploitation of these resources. Fire was initially used to promote and retain the environments which were most suitable for these large animals, and fire was subsequently used for maximising the productivity of these areas after the Aboriginal population increase which occurred largely because of the greater access to these abundant resources (Kohen 1995).

Vegetation associations generated or maintained by Aboriginal burning

In the ethnographic present Aboriginal people use fire as a multipurpose tool. It is used to open up the vegetation to make travel easier (in their words to ‘clean up the country'); it is used to hunt large game like kangaroos directly; it is used to hunt possums in hollow trees; it is used to promote the growth grass to attract large herbivores; and it is used to promote some types of plants, particularly cycads and tuber-bearing orchids and lilies which grow in open woodlands. One of the consequences of regular burning is that it may increase nesting sites for arboreal animals by increasing the numbers of hollows in trees. Certainly fire is used to drive snakes away from the camp sites, and to maintain contact between groups.

In order to understand what traditional burning patterns may have been like in southeastern Australia, it is useful to see how and why contemporary Aboriginal communities burn in other parts of the continent. While the marked seasonality of the tropical north strongly influences the way in which Aboriginal people use fire, their reasons for burning and the mechanisms for controlling fire are similar to those documented ethnographically for the southeast. Stephen Pyne (1991: 122) recorded the burning patterns of the Gunei tribe in Arnhem Land, and presents a picture of highly controlled burning patterns, tied to the season. He suggests that: 'Burning actually starts at special sites while the rainy season is still in progress. It escalates as drying spreads, … and it culminates at the end of the Dry with a conflagration of those places destined for burning but not yet fired'.

However, not all of the area was burned with the same frequency: 'The fires were sequential, and burning a composite of practices in a mosaic of environments that extended over nine to ten months. Most of the grasslands and savannas burned; portions of the floodplains burned twice; the woodlands and the forests on the order of a fourth to a half their area (ibid: 123).

Local environmental variables are clearly taken into account, with different environments being burned at different frequencies. Some areas were not burned at all.

The other factor which is fundamentally important is the familiarity with the landscape and the knowledge of how to control fires on a local level. Again, Pyne suggests: 'They exercise control by timing the fires with diurnal wind shifts, by relying on the evening humidity, and by exploiting topographic features like cliffs and streams and old burns' (ibid).

So the burning practices in Arnhem Land are based on an intimate knowledge of local conditions. Such a burning regime is only possible when the people lighting and controlling the fires are familiar with the local topography and the means of controlling the intensity, direction and duration of the fire, that is, when they are burning their own land and for their own purposes.

Historical records of burning in southeastern Australia

If we use the Sydney region as an example of southeastern Australia, there are many ethnographic descriptions of Aboriginal land use and settlement pattern detailed in the early historical records. Aborigines were concentrated on the coast in the summer at relatively large and semi-permanent camps. Both Cook and Phillip reported seeing coastal 'villages' of up to a dozen huts housing 50–60 people. This number of people corresponds to a clan (the land owning group) or a band (the land using group), the social entities referred to as 'tribes' by the early settlers. Yet we know that in the Sydney area many of these 'tribes' did not come to the coast at all. The people who lived west of Parramatta were referred to as the woods tribes, and they even spoke a different dialect of the local Darug language (Kohen 1988). It is clear that large numbers of people, at least several thousand, could be supported at a high population density in the Sydney region.

One important aspect of Aboriginal economy was the practice of regularly burning the underbrush. Aborigines were still burning large tracts of land at Castlereagh as late as the 1820s (Kohen 1986). Phillip (1791) observed 'the natives so frequently setting fire to the country, which they do to catch the opossum, flying squirrel, and other animals …'.

When expeditions began exploring the countryside around Sydney, they encountered a range of vegetation associations, some of which were very different to those which we see in the National Parks around Sydney today. On soils derived from Hawkesbury sandstone, Wianamatta shale, Tertiary alluvial deposits, and igneous intrusions, they found environments which reminded them of the manicured parks of England, with trees well spaced and a grassy understorey. Peter Cunningham (1827) described the country west of Parramatta and Liverpool as: ‘A fine timbered country, perfectly clear of bush, through which you might, generally speaking, drive a gig in all directions, without any impediment in the shape of rocks, scrubs, or close forest’.

This confirmed earlier accounts by Governor Phillip (1791), who suggested that the trees were ‘growing at a distance of some twenty to forty feet from each other, and in general entirely free from brushwood ...’.

It is clear that it was primarily Aboriginal burning practices which maintained an open environment dominated by well spaced trees and a grassy understorey. However, not all areas were burned. There are descriptions of rainforest pockets and wet-sclerophyll associations which were not burned. The margins of the creeks and rivers were mostly left intact, as evidenced by the descriptions of Watkin Tench when his party first travelled along the banks of the Nepean and Hawkesbury Rivers (Tench 1791).

The fact that many of the yam beds along the Hawkesbury provided a regular food resource suggests that some care may have been taken to ensure that the resource was renewable. Fire-breaks may have been created so that these areas did not burn. As Hallam suggests, ‘Gathering yams (Dioscorea) was anything but a random process ... it was certainly not a matter of digging out a root here and there, but of returning regularly to extensively used tracts’ (Hallam 1979: 12).

While Aboriginal people used fire as a tool for increasing the productivity of their environment, Europeans saw fire as a threat. Without regular low intensity burning, leaf litter accumulates, and crown fires can result, destroying everything in their path. European settlers feared fire, for it could destroy their houses, their crops, and it could destroy them. Yet the physical environment which was so attractive to them as farmers and graziers was created by fire. Indeed, it has been suggested that the European settlement of Tasmania followed almost exactly those areas which the Tasmanian Aborigines had regularly burned (Pyne 1991).

Consequences of the cessation of Aboriginal burning

As European settlement spread out from Sydney, traditional Aboriginal burning practices ceased. Once this happened, vegetation associations changed, animals which were once common rapidly declined, and in some cases disappeared altogether. Once the Aborigines stopped burning, the underbrush returned where none had previously existed. Benson and Howell (1990) suggest that the growth of *Bursaria spinosa* in the Sydney area in the 1820s was probably related to a changed fire regime with the cessation of Aboriginal burning.

Europeans land use practices were destructive, and totally different from Aboriginal methods. The first white settlers dug up the ground along the banks of the Hawkesbury River to plant their crops, and in the process destroyed the yam beds which the Darug people depended on (the word Darug means yam). Over 40,000 years of practicing a balanced control over the environment was destroyed in the short space of a few years.

In the more remote areas, this process took longer. In western New South Wales it happened in the 1840s and 1850s. In parts of Central Australia, the extinctions and declines still continue, although other factors are now involved. However, it can be argued that many of these changes are the result of changed fire regimes. Certainly some of the extinctions of the smaller terrestrial mammals in arid Australia occurred long before the introduction of competitors such as the rabbit and predators like the fox and cat.

SHOULD TRADITIONAL ABORIGINAL BURNING REGIMES BE RE-INTRODUCED IN SOUTHEASTERN AUSTRALIA?

Should traditional burning regimes be re-introduced into southeastern Australia? Should Aboriginal people be asked to contribute their knowledge to current land management practices? The answer must clearly be no. Aboriginal burning was used when Aboriginal people were managing the land in a particular way. It was used to maximise the productivity of the landscape. Some areas were not burnt at all, while others were burnt at frequencies varying between twice a year and once every five to ten years. Such fires would have varying degrees of impact. Certainly, those regularly burnt areas would be more open — more grass and well-spaced trees, but not all areas would look like that. Some parts of southeastern Australia were rarely if ever burned. The rugged southwest of Tasmania is unlikely to burn, because of its high rainfall. Parts of the Blue Mountains were probably not burned because of the low value in burning those areas which have steep slopes and rough topography — the very inaccessible areas which may require hazard reduction burning if conservation or prevention of property loss are of prime concern. Relatively flat areas like the Cumberland Plain and the valley floors are much more likely to have been burnt regularly, and these are areas which are unlikely to require hazard-reduction burning.

The consequences of the re-introduction of a traditional Aboriginal burning regime, even if it could be determined what that regime actually was, would not produce the same results now as it did two hundred years ago. European activities such as farming, logging, and the introduction of feral animals have all contributed to dramatic declines and extinctions of many mammal species. Many of the species which appear to be fire specialists, such as the bettongs, have become extinct over most of their previous range (Christensen 1980; Taylor 1993). Indeed an increase in fire frequency may adversely impact on some threatened species because of the increased risk of predation by foxes and feral cats.

For most of southeastern Australia, the re-introduction of traditional Aboriginal burning is not a satisfactory alternative to sound management policies based on systematic scientific study. However, with the potential of the Native Title legislation for Aboriginal people regain control of some of their land in southeastern Australia, it may well be that regular burning is entirely appropriate as a land management tool within their own land and for their own culturally-based reasons.

REFERENCES

Beaton, J. (1982). Fire and water: aspects of Australian Aboriginal management of cycads. *Archaeology in Oceania* **17**: 51–8.

Benson, D. and Howell, J. (1990). 'Taken for granted. The bushland of Sydney and its suburbs'. (Kangaroo Press in association with the Royal Botanic Gardens: Sydney).

Birckhead, J., De Lacy,, T. and Smith, L. (eds). (1993). 'Aboriginal involvement in parks and protected areas'. (Australian Institute of Aboriginal and Torres Strait Islander Studies Report Series, Aboriginal Studies Press: Canberra).

Butlin, N. (1983). 'Our Original Aggression'. (George Allen and Unwin: Sydney).

Butlin, N. (1993). 'Economics and the dreamtime. A hypothetical history'. (Cambridge University Press: Cambridge).

Catling, P.C. (1991). Ecological effects of prescribed burning practices on the mammals of southeastern Australia. In 'Conservation of Australia's forest fauna' (Ed. D. Lunney) pp. 354–363. (Royal Zoological Society of NSW: Mosman).

Christensen, P.E.S. 1980. The biology of *Bettongia penicillata* Gray 1837 *and Macropus eugenii* Desmarest 1804 in relation to fire. *Forest Department of Western Australia Bulletin* **91**.

Clark, R.L. (1983). Pollen and charcoal evidence for the effects of Aboriginal burning on the vegetation of Australia. *Archaeology in Oceania* **18**: 32–7.

Clark, S.S. and McLoughlin, L. (1986). Historical and biological evidence for fire regimes in the Sydney region prior to the arrival of Europeans. *Australian Geographer* **16**: 101–112.

Crouch, B. (1994). *Sunday Telegraph*, January 16 1994, p 9.

Cunningham, P. (1827). 'Two years in New South Wales'. (reprinted 1966, Angus and Robertson: Sydney).

Dodson, J. (ed). (1991). 'The Naive Lands. Prehistory and environmental change in Australia and the Southwest Pacific'. (Longman Cheshire: Melbourne).

Gamble, C. (1986). The artificial wilderness. *New Scientist*, **10/4/1986**, pp 50–54.

Gould, R.A. (1971). Uses and effects of fire among the western desert Aborigines of Australia. *Mankind* **8**, 14–24.

Hallam, S.J. (1975). 'Fire and Hearth. A study of Aboriginal usage and European usurpation in South-western Australia'. (Australian Institute of Aboriginal Studies: Canberra).

Head, L. (1986). Palaeoecological contributions to Australian prehistory. *Archaeology in Oceania* 21(2): 121–9.

Head, L. (1989). Prehistoric Aboriginal impacts on Australian vegetation: an assessment of the evidence. *Australian Geographer* **20**, 37–46.

Hickin, E.J. and Page, K.J. (1971). The age of valley fills in the Sydney Basin. *Search* **2**, 383–4.

Horton, D.R. (1982). The burning question: Aborigines, Fire and Australian ecosystems. *Mankind* **13**, 237–251.

Hughes, P.J. (1981). The impact of bushfires on soils and soil erosion. In 'Bushfires. Their effect on Australian Life and Landscape' (Ed. P. Stanbury). (The Macleay Museum: Sydney).

Hughes, P.J. and Sullivan, M.E. (1981). Aboriginal burning and late Holocene geomorphic events in eastern NSW. *Search* **12**, 277–8.

Jones, R. (1969). Firestick farming. *Australian Natural History* **16**, 224–8.

Kershaw, A.P. (1986). Climatic change and Aboriginal burning in north-east Australia during the last two glacial/ interglacial cycles. *Nature* **322**, 47–9.

Kershaw, P. (1993). Palynology, biostratigraphy and human impact. *The Artefact* **16**, 12–18.

Kershaw, A.P., McKenzie, G.M. and McMinn, A. (1993). A quaternary history of northeastern Queensland from pollen analysis of ODP site 820. *Proceedings of the Ocean Drilling Program, Scientific Results* **133**, 107–114.

Kohen, J.L. (1986). Prehistoric settlement in the western Cumberland Plain: resources, environment and technology. PhD thesis, Macquarie University.

Kohen, J.L. (1988). The Dharug of the western Cumberland Plain: ethnography and demography. In 'Archaeology with ethnography: an Australian perspective' (Eds. B. Meehan and R. Jones). (Department of Prehistory, Research School of Pacific Studies, Australian National University: Canberra).

Kohen J.L. (1995). 'Aboriginal Environmental Impacts'. (University of New South Wales Press: Kensington).

Kohen, J.L. and Downing, A.J. (1992). Aboriginal use of plants on the western Cumberland Plain. *Sydney Basin Naturalist* **1**, 1–8.

Lourandos, H. and Ross, A. (1994). The great 'Intensification Debate': its history and place in Australian Archaeology. *Australian Archaeology* **39**, 54–63.

Phillip, A. 1791 (1963). 'Extracts of letters from Arthur Phillip Esq. Governor of New South Wales to Lord Sydney'. (Public Library of South Australia: Adelaide).

Pyne, S.J. (1991). 'Burning Bush. A Fire History of Australia'. (Henry Holt and Co.: New York).

Roberts, R.G., Jones, R. and Smith, M.A. (1990). Themoluminescence dating of a 50,000-year-old human occupation site in northern Australia. *Nature* **345**, 153–6.

Singh, G., Kershaw, A.P. and Clark, R. (1981). Quaternary vegetation and fire history in Australia. In 'Fire and the Australian Biota' (Eds. A.M. Gill, R.H. Groves and I.R. Noble). (Australian Academy of Science: Canberra).

Singh, G. and Geissler, E.A. (1985). Late Cainozoic history of vegetation, fire, lake levels and climate, at Lake George, New South Wales, Australia. *Philosophical Transactions of the Royal Society London*, **311**, 379–447.

Taylor, R.J. (1993). Habitat requirements of the Tasmanian Bettong (*Bettongia gaimardi*), a mycophagus marsupial. *Wildlife Research* **20**, 711–23.

Tench, W. (1791). 'Sydney's first four years'. (reprinted 1979, Library of Australian History in association with the Royal Australian Historical Society: Sydney).

Regional and Historical Fire Weather Patterns Pertinent to the January 1994 Sydney Bushfires

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The bushfires in Sydney during January 1994 drew an unprecedented response from the public, the media and fire-fighters across the nation. While ignition sources, fuels, terrain and suppression forces affected the number, severity, spread and impact of the fires, weather also had a major effect. We examined the historical weather record maintained by the Bureau of Meteorology for 7 weather stations in the region of Sydney (Wollongong, Sydney, Liverpool, Parramatta, Bankstown, Richmond and Katoomba). Weather data were considered in the form of the McArthur forest fire danger index (FFDI). The FFDI has a maximum of 100 and registers 'extreme' if over 50. During the 1994 fire period, the maximum 3 pm value among all stations was 93 at Richmond. Record January values of FFDI were noted for 5 of the 7 stations (the exceptions being Katoomba and Wollongong). Data for January 1994 from Richmond and Bankstown stood out in that: one 3pm FFDI value at Bankstown was a record for any month while one for Richmond was an equal record; both stations had unprecedented numbers of 'extreme' days (Richmond had 5 in 6 days while Bankstown had 4).

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KEYWORDS: Bushfire, Sydney, weather, Blue Mountains, Wollongong

INTRODUCTION

The fires in the Sydney region in January 1994 resulted in loss of about 230 houses or similar major buildings (C. Ramsay, personal communication) and human life. Most of the damage was around a relatively small fire (Como–Jannali). Fires included those burning in and around Royal National Park, Ku-Ring-Gai National Park, Lane Cove National Park, The Glen Reserve (Como–Jannali) and the Blue Mountains. Fire fighters came from all over Australia to assist. On January 8, approximately 10,000 fire fighters with around 1,000 fire-fighting 'units' were engaged in the greater Sydney Region (including the Blue Mountains — Department of Bush Fire Services 1994). The fires elicited a Coronial Enquiry, a NSW Cabinet Enquiry and a NSW Legislative Assembly Select Committee of Enquiry. The main fire period in the greater Sydney area was between January 3 and January 9, 1994.

For major building damage to result from bushfires it is necessary to have ignitions, fuels, buildings in close vicinity to the bush, and inadequate suppression. The last of these is exacerbated by high fire intensities, strong winds, spot-fire generation, steep inaccessible topography, multiple fire events and, controversially, removal of able-bodied residents from their houses.

Inevitably, the question of the possibility of a recurrence of the January 1994 fires arises. Leaving aside social and fuel aspects of the problem, attention focuses on the weather. Was the weather unprecedented? Can the same conditions recur? The latter question could be answered after consideration of the first. Thus, we examined the fire weather of January 1994 in relation to the history of fire weather in the greater Sydney area.

METHODS

We chose 7 meteorological stations in a transect from Wollongong on the coast to Katoomba in the Mountains (Table 1). Fire weather for all stations was examined using the McArthur forest fire danger index (FFDI). This index was developed by McArthur (1967) to provide the basis for the prediction of the rates of spread of fires burning with the wind in eucalypt litter fuels, as well as to indicate fire danger. In this paper FFDI is used only as an index of the severity of fire weather. FFDI was calculated using the equations of Noble et al. (1980). The FFDI has a maximum value of 100 and registers 'extreme' if over 50, 'very high' if between 24 and 49. If calculated values exceeded 100, they were set at 100. (This happened on only two occasions: once for Wollongong and once for Liverpool, neither in 1994). All weather data were purchased from the Bureau of Meteorology.

TABLE 1

Selected weather data for the meteorological stations used in the study together with some geographical data (from Bureau of Meteorology 1988 and maps).

Station	Ave. 3pm screen temperature for January (°C)	Ave. 3pm screen relative humidity for January (%)	Mean annual rainfall (mm)	Mean annual raindays (number)	Elevation of station (m)	Distance from the ocean (km)
Wollongong	23.6	67	1420	132	19	1.5
Sydney	24.5	61	1212	139	42	7
Liverpool	26.5	53	851	104	21	32
Bankstown	26.6	52	905	112	9	26
Parramatta	26.2	56	935	112	60	26
Richmond	27.9	47	805	109	19	51
Katoomba	21.2	58	1412	126	1030	92

To calculate FFDI, data on drought status (*via* a 'drought index' and a 'drought factor'), recent precipitation, time since rain, ambient humidity and temperature, and wind speed in the open at a height of 10 meters are needed. Relatively few stations have all these data. 'Sydney' (Observatory Hill) has the data at 3-hr intervals, at least, while some other stations have the data available at only 9am and 3pm. Few stations have all the data needed for routine calculation of FFDI. Data at 3pm were examined for Wollongong University ('Wollongong'), Sydney Regional Office ('Sydney'), Liverpool Council ('Liverpool'), Bankstown Airport ('Bankstown'), Parramatta North ('Parramatta'), Richmond Airport ('Richmond') and Katoomba Composite ('Katoomba'). The 3-hr data from Sydney have been outlined elsewhere (Gill and Moore 1994).

The drought factor was calculated as the deficit of water in the soil for a hypothetical soil profile holding 200 mm of water. We used the 'soil dryness index' of Mount (1972) for this calculation. In the calculations of evaporation — needed for the daily estimation of water loss from the hypothetical soil profile — equations relating maximum daily temperature to evaporation for both Sydney and Canberra were used — rather than Tables of Mount (1972). The Canberra equations were used for Katoomba because the climate there is closer to that of Canberra rather than that of Sydney. Drought index was initialized by assuming a starting point of 200 mm (i.e. completely dry) and running the calculations until the hypothetical profile was near filled to capacity (within a few mm).

Because daily values of drought index were essential to the calculations of FFDI, missing data disrupt the record. Most of the stations examined had missing data to the extent that initializing the drought index was necessary not just at the beginning of the record but also where a new record began following a break (Table 2). Sydney data for windspeed and direction was also composite (Table 3). The few impossible values in the data were screened out and replaced by values averaged from surrounding data.

TABLE 2

Time periods over which Forest Fire Danger Index (FFDI) calculations were made for each meteorological station (SDI-initializing periods excluded). The numbers of 'extreme' FFDI days for the whole length of record are shown also.

Station	Periods used for FFDI calculations (dates)	Length of record (years)	Ave. 'Extreme' days per annum (number)	'Extreme' days in Jan. 1994 (number)	Ave. 'very high' days per annum (number)
Wollongong	1.1.71–30.6.75				
	1.2.76–31.3.76				
	1.8.76–31.1.94	22	13/22 = 0.6	0	3.7
Sydney	1.3.55–28.2.94	39	25/39 = 0.6	1	4.6
Liverpool	1.1.63–31.12.67				
	1.2.70–31. 1.94	29	17/29 = 0.6	2	6.1
Bankstown	1.3.69–31.12.78				
	1.4.88–31. 1.94	16	24/16 = 1.5	4	7.3
Parramatta	1.9.67–28.2.91				
	1.7.91–31.1.94	26	16/26 = 0.6	2	4.7
Richmond	1.7.64–30.4.69				
	1.2.80–31.1.94	19	40/19 = 2.1	5	16.5
Katoomba	1.3.57–31.12.66				
	3.7.74–31. 1.94	30	6/30 = 0.2	1	4.3

TABLE 3

Locations of anemometers for 'Sydney' data during the FFDI-calculation period.

Dates	Anemometer location
1.3.55–30.4.92	Observatory Hill
1.5.92–28.2.94	Sydney Airport (Kingsford Smith)

Wind data were received in the unit of 'knots' but converted by us to km hr^{-1}. Although noted in 'knots', the original data for Liverpool, Parramatta and Katoomba were taken as Beaufait readings, *i.e.* an ordered multiscale, and expressed as 'knots' on the computer file.

Daily 3pm values of FFDI for each station were averaged for each month of the year, i.e. all January values, all February values etc. Maximum values for each month of each year (e.g. maximum for January 1980, January 1981, January 1982 etc.) were also averaged. These results were plotted together with record maxima for each month.

'Extreme' values of FFDI were identified for each station. Then the relative contributions of wind and dryness to these extreme values were charted (using components of the FFDI equation from Noble et al. 1980). The wind factor was the value 0.0234∗V, an exponent in the FFDI equation. V is the windspeed in the open at 10m height above datum in km hr^{-1}. The 'dryness factor' was [$\log_e$ (non-wind portion of FFDI + 1)]. Part of the 'dryness factor' defined here is the 'drought factor' , a variable that has positive values up to 10 (McArthur 1967). For all 'extreme' values for all stations the 'drought factor' was greater than 9.

Wind 'roses' showing frequencies of occurrence of wind directions on the days of 'extreme' FFDI were graphed.

Wind speeds at 3pm for all stations between 1.12.91 and 22.1.94 were compared by regression without transformation of the data. Visual inspection suggested that variance was independent of the mean. Similarly, FFDI values were compared.

Data for '3pm' were 'normally' those for 3pm clock time rather than 3pm Eastern Standard Time during periods of 'Daylight Saving' (Bureau of Meteorology 1988).

RESULTS

During the 1994 fire period, the maximum 3 pm value of FFDI for the region was 93 at Richmond. Record January values of FFDI were recorded at 5 of the 7 stations (the exceptions being Katoomba and Wollongong). FFDI at Bankstown in 1994 was the highest on record for that station. Peak 3pm FFDI for Richmond in January 1994 was equal highest on record. Bankstown had the shortest duration weather data (16 years) and Richmond the next shortest (19 years). For all stations other than Bankstown and Richmond January 1994 values were lower than the highest ever recorded.

Monthly variations in FFDI are shown in Fig. 1. Graphs of Parramatta data have been omitted because of similarities with Bankstown. Sydney data (Fig. 1b) have been presented previously by Gill and Moore (1994). Average FFDI values (lowermost graph in each chart) showed little variation throughout the year for all stations. Higher values were apparent for Richmond. Average maxima (middle graph in each chart) showed marked seasonality. At Wollongong on the coast, peak values occurred in September and December. Data for Bankstown and Liverpool (middle charts) showed a seasonal peak in December. The relatively high values for Richmond showed a broad 'peak' from October to January. Katoomba, at higher elevation and further inland than all other stations, showed a relatively sharp December–January peak. Record values for each month (uppermost graph in each chart) showed peaks between October and March.

Because of the fragmented nature of the data (Table 2), FFDI values were not available for all stations at equivalent times. Twenty two time periods were necessary to enable comparisons of FFDI to be made across stations at any common time. The only year in which all available stations (where two or more stations had data) recorded 'extreme' FFDI's was 1971. Of particular significance was the the first of October 1971 when all stations with available data showed 'extreme' FFDI values. Stations with no data at this time were Katoomba and Richmond. The only station without an 'extreme' value in January 1994 was Wollongong.

'Extreme' FFDI values were scattered in time and space but also often clustered in time at any one station. Thus two or more 'extremes' were often clustered to the extent that they occurred in the same month or week or on successive days. Bankstown had 4 successive days with FFDI in the 'extreme' range in January 1994 while Richmond had 5 'extremes' in 6 days in the same month. In November 1982, Richmond had 4 days — 2 consecutive — where 'extreme' FFDI values occurred. Bankstown had 3 consecutive 'extremes' in December 1972. Richmond and Bankstown had the highest average number of 'extreme' FFDI values per year despite having the shortest periods of data availability (Table 2). These results did not seem to be affected by the actual periods for which data were available.

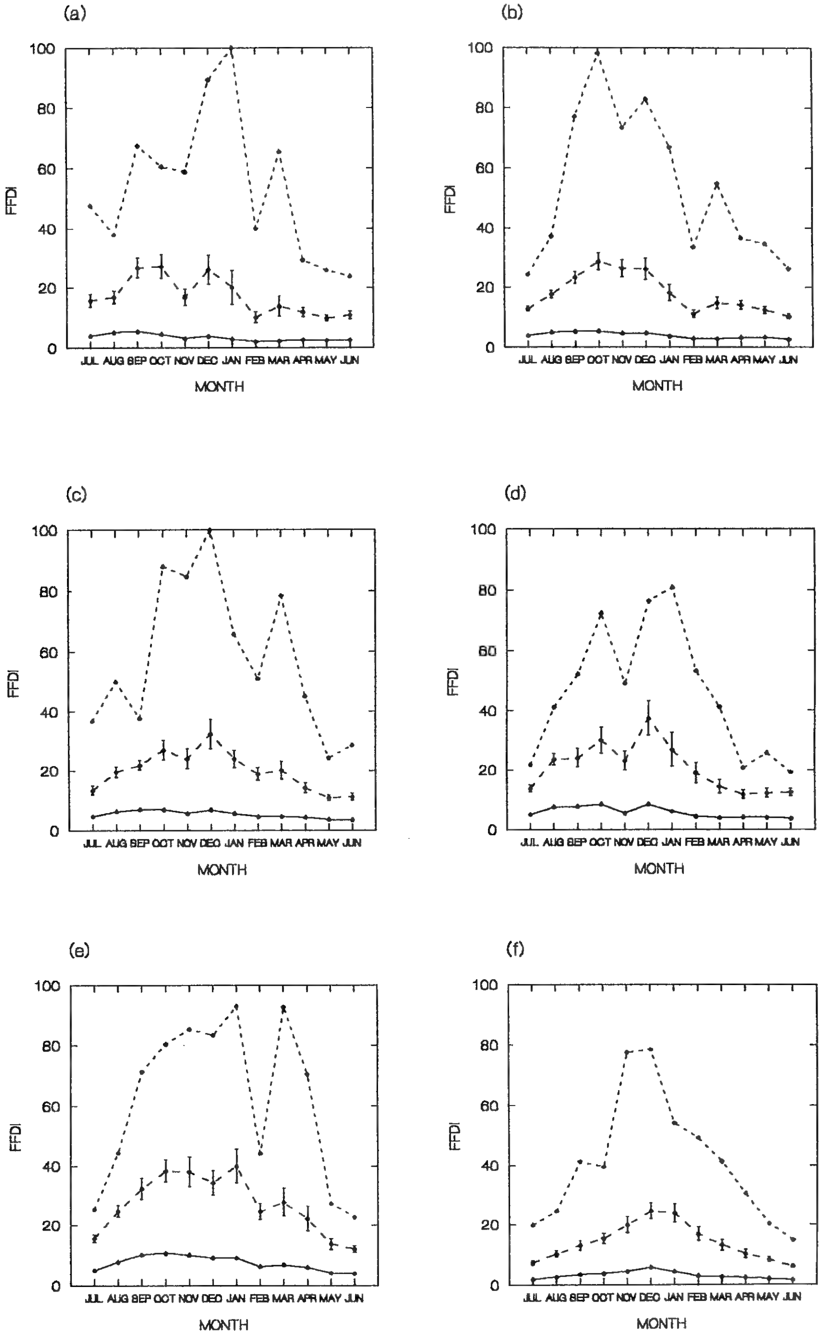

Fig. 1. Seasonal variations in Forest Fire Danger Index (FFDI). The lowermost line in each chart is the average daily 3pm FFDI. The middle line is the average maximum value of FFDI per month. The uppermost line is the highest value recorded for each month over the period of data availability. (a) Wollongong; (b) Sydney; (c) Liverpool; (d) Bankstown; (e) Richmond; (f) Katoomba.

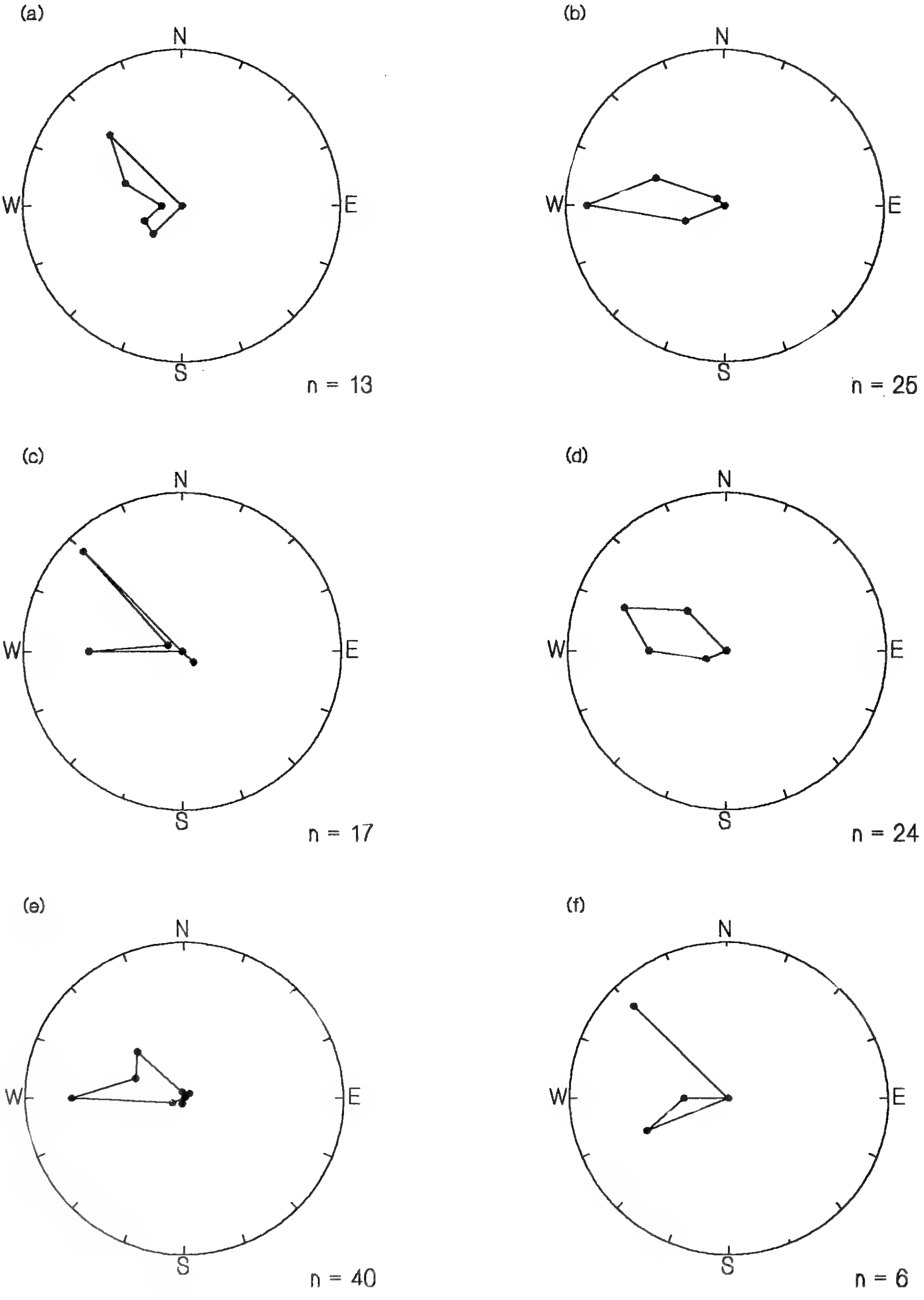

Fig. 2. Frequencies of wind directions when values of the Forest Fire Danger Index (FFDI) are 'extreme'.(a) Wollongong; (b) Sydney; (c) Liverpool; (d) Bankstown; (e) Richmond; (f) Katoomba.

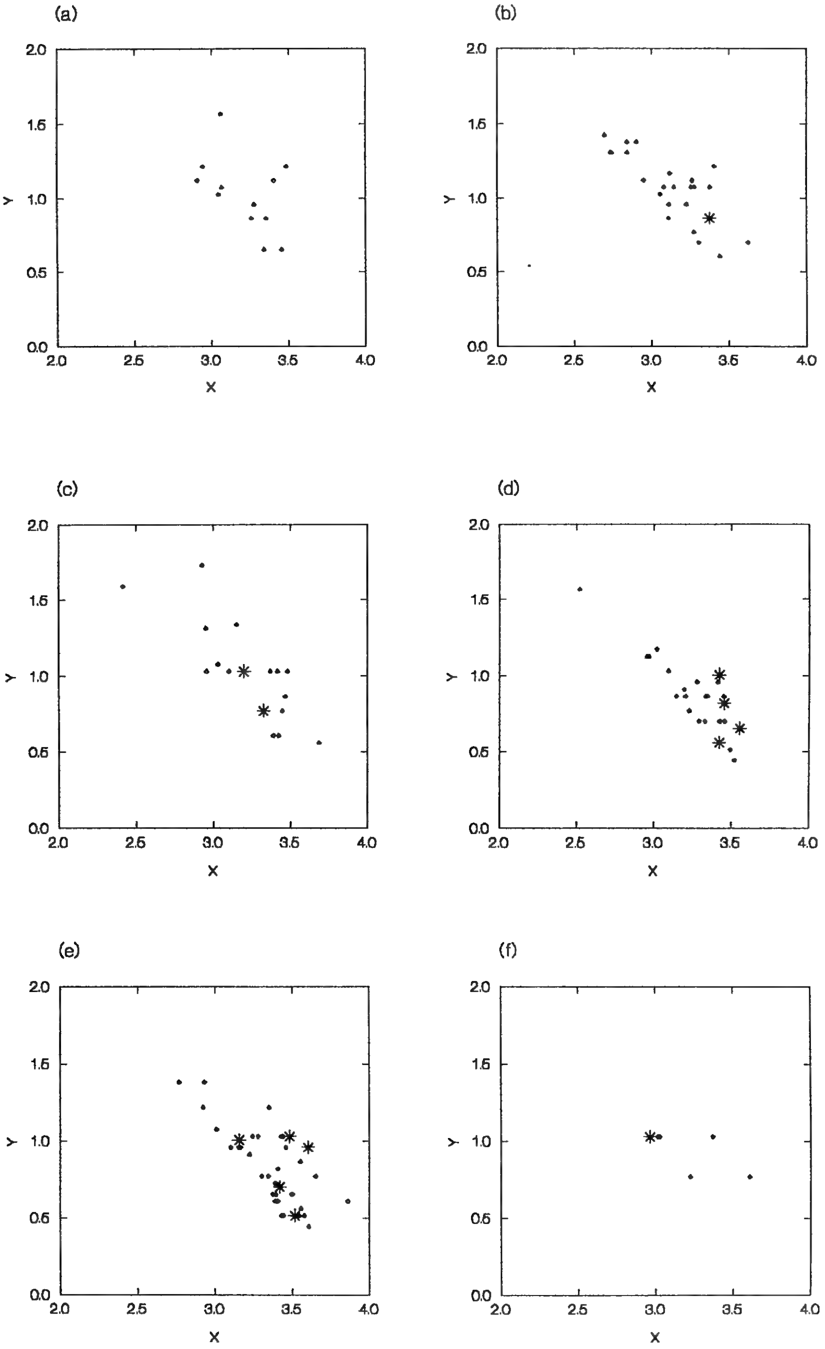

Fig. 3. 'Extreme' days plotted to reveal the contributions of wind (y-axis) or dryness (x-axis) to the value of Forest Fire Danger Index (FFDI). The further to the right the value is, the greater the dryness. The higher on the graph the value is the windier the condition. (a) Wollongong; (b) Sydney; (c) Liverpool; (d) Bankstown; (e) Richmond; (f) Katoomba. The asterisks refer to January 1994 data.

On 'extreme' days at 3pm, winds were predominantly from the westerly sector, especially the west and northwest (Fig.2). Separation of the wind and dryness contributions to FFDI (Fig.3) did not reveal any general trend in the January data to indicate unprecedented windiness or dryness in January 1994. However, the January 1994 'extreme' for Sydney was toward the dry end of the range (Fig.3b, also depicted in Gill and Moore 1994) while that for Katoomba was at the windy end (Fig. 3f).

For the 784 days between 1.12.91 and 22.1.94, wind speeds were all very highly correlated but the extent of variance explained was always less than 45% suggesting that accurate prediction of windspeed from one station to another is tenuous at best. Even the variance explained by regression of the windspeed at Sydney airport with that at Fort Denison (the new Sydney standard) was low. Correlation co-efficients between FFDI values at different stations were all statistically significant with up to 70% of the variance being explained.

DISCUSSION

Wind data are critical to fire-weather determination. The data may be misinterpreted or misleading if they are unrepresentative. They may be unrepresentative if they are inaccurate (more likely with Beaufait-scale determinations as at Katoomba, Liverpool and Parramatta) or the weather station is inappropriately located. The Bureau of Meteorology (personal communication) advised us of locational features of the pertinent meteorological stations. At Observatory Hill in Sydney itself, the anemometer was located on a 10m mast located on top of a three-storey building at a height of 22m above ground; now (1995) it is located at Fort Denison (on an island in Sydney Harbour) on a flagstaff yardarm. At Parramatta and Liverpool trees and buildings were observed to be close to meteorological screens in 1995 (A.M.Gill personal observations). Wollongong meteorological station was 'not located in accordance with Bureau standards'. Richmond and Bankstown weather stations, at local airports, appear to have been well placed, at least in recent years.

To ascertain the wind condition at a fire from a weather station, extrapolation or interpolation must take place. However, because of the difficulties in obtaining accurate and representative wind data from some of the weather stations used in our analyses, it is difficult to say what the wind conditions were at the various fire areas during January 1994 even if the ground there was flat. Given that the land in the fire areas often had a steep topography, local terrain effects on windspeed and direction seem likely. One wonders whether or not models 'anchored' to regional stations — selected by a process of systematic testing and cross regression against many sites — would allow more confident interpolations to be made in the future. Our correlation analyses showed non-predictive, but statistically significant relationships between windpeeds at various stations for a portion of the dataset.

FFDI was poorly predicted between stations but more variance was explained than that with wind. Record values at 3pm were recorded for a number of stations in January 1994 but these were not always the highest ever recorded when all months were considered. The most significant statistic for January 1994 may be the unprecedented (in time or at any station examined) 4 consecutive days with extreme FFDI values at Bankstown and the 5 days out of 6 with extreme FFDI values at Richmond. The length of the data set is relatively short for these stations but they are the stations with most 'very high' days as well as 'extremes' (Table 2).

Most of the data available was for 3pm, a time when FFDI may be expected to be at its highest for the day. This proposition has been tested with 3-hr data from Sydney by Gill and Moore (1994) and found to be reasonable — being much better than the use of either 6pm or 12 noon data.

Housing and other losses do not occur only at 3pm when FFDI reaches 'extreme' values. However, the maximum 3pm value for the day often provides a useful indicator for high values at other times of day. FFDI may have very low values in the mornings of days that reach 'extreme' values (e.g. Gill and Moore 1994 for Sydney).

Most fire–weather literature in the Sydney Region seems to be associated with the Blue Mountains. Colquhoun (1981) examined the synoptic situation and fire–weather indexes for Katoomba and Richmond for December 1977. The 16th December 1977 was one of the few 'extreme' days for Katoomba in our data set. Fifty houses were lost in the Blue Mountains on that day (Cunningham 1984). Other 'extreme' days in our Katoomba data set fall within, and only within, the 'bushfire seasons' determined by Cunningham (1984) from newspapers and travellers narratives, viz. 1977–78, 1979–80 and 1982–83. The 1994 events obviously occurred after Cunningham's study. Most losses of houses in the Blue Mountains have occurred in the November–December period (Cunningham 1984) when unprecedented values of 3pm FFDI have occurred (Fig. 1f). Fires that cause housing losses travelled mainly from the west and northwest, but also from the southwest (Cunningham 1984); these are the same directions from which the wind blows on 'extreme' days in the wider Sydney region (Fig.2).

Whether or not a series of fires similar to those of January 1994 can occur in the Sydney region again depends on the likelihood of a similar conjunction of weather conditions, fuels, ignition sources, locations of ignitions and suppression capabilities. As far as the weather is concerned, some aspects of the weather of January 1994 were unprecedented but, given the short period for which data were available (16 to 39 years), it seems likely that similar weather conditions will recur.

CONCLUSION

The January 1994 bushfires in Sydney were a major event. At a number of the regional weather stations, record 3pm fire–weather peaks were recorded for **January** of the weather data at hand. However, at some stations, peak values had been previously recorded at other times in other months. One Bankstown 3pm FFDI for January 1994 was an all-time record for 3pm but weather data were only available for a 16-year period. Successive days with 'extreme' FFDI values were an unprecedented feature of the data. The meteorological stations supplying data for these analyses were not necessarily well located to provide weather data pertinent to the fires.

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REFERENCES

Bureau of Meteorology. (1988). 'Climatic Averages Australia'. (Australian Government Publishing Service: Canberra).

Colquhoun, J.R. (1981). Meteorological aspects of the December 1977 Blue Mountains Bushfires. *Bureau of Meteorology, Meteorological Note* **116**, 17p.

Cunningham, C.J. (1984). Recurring natural fire hazards: a case study of the Blue Mountains, New South Wales, Australia. *Applied Geography* **4**, 5–27.

Department of Bush Fire Services. (1994). Service information. *Bush Fire Bulletin, January Bush Fires Special Issue*, pp. 45, 47, 50 and 53.

Gill, A.M. and Moore, P.H.R. (1994). Some ecological research perspectives on the disastrous Sydney fires of January 1994. *Proceedings of the 2nd International Forest Fire Research Conference, Coimbra, Portugal*. Pp. 63–72.

McArthur, A.G. (1967). Fire behaviour in eucalypt forest. *Commonwealth of Australia Forestry & Timber Bureau Leaflet* **107**, 25p.

Mount, A.B. (1972). The derivation and testing of a soil dryness index using run-off data. *Tasmanian Forestry Commission Bulletin* **4**, 31p.

Noble, I.R., Bary, G.A.V. and Gill, A.M. (1980). McArthur's fire danger meters expressed as equations. *Australian Journal of Ecology* **5**, 201–3.

Fire-Driven Extinction of Plant Populations: a Synthesis of Theory and Review of Evidence from Australian Vegetation

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Much of Australia's native vegetation is prone to recurring fires. Any desire to conserve the diversity of Australia's fire-prone plant communities must be backed by an understanding of how various regimes of fire affect processes that drive population and community change. Only with such understanding is it possible to predict which fire regimes are associated with high probabilities of population declines and extinctions so that these may be avoided in management. Several ecological concepts contribute to our ability to predict these outcomes. These include: description of temporal and spatial patterns of fires in terms of their frequency, intensity, season (fire regimes); characterisation and analysis of vegetation change in terms of population processes; and the definition of life-cycle attributes that allow species with similar responses to fire regimes to be classified into functional groups.

Using a demographic approach, I identified a number of fire-driven mechanisms of plant extinction. These include seven mechanisms related to death of standing plants and seeds, four mechanisms relating to failure of seed release and/or germination; four mechanisms relating to failure of seedling establishment; two mechanisms relating to the interruption of maturation or developmental growth; and three mechanisms relating to the failure of seed production. These processes may interact with each other, with co-occurring organisms, and with stochasticity in the physical environment. Such interactions may result in accelerated rates of population decline. Fire regimes associated with multiple mechanisms of plant population decline and extinction include high frequency fires, low frequency fires and repeated fires that result in little vertical penetration of heat and possibly smoke derivatives.

Many deficiencies remain in knowledge of the effects of fire on plant species and communities. Despite these deficiencies, mechanisms of plant extinction and the fire regimes with which they are associated are sufficiently well understood that they, along with existing theories of diversity and practical management tools, provide a strong scientific basis for the management of fire for conservation of plant populations and communities.

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INTRODUCTION

The influence of fire extends through virtually all terrestrial habitats in Australia, as it does in many other tropical and temperate parts of the world. In these areas fire may be viewed as an ecological process that mediates between maintenance and loss of biological diversity (Gill and Bradstock 1995). It is one of the few such processes that may be manipulated so readily (though not always successfully) by humans (Shea et al. 1981, van Wilgen et al. 1994, Bradstock et al. 1995), as indeed it has been over millennia to meet a wide variety of ends (Kohen, this volume). In Australia, conservation of biological diversity has become an explicit goal of contemporary fire management in many natural areas under public ownership (Shea et al. 1981, Conroy, this volume, Moore and Shields, this volume) and some areas under private ownership. The fulfilment of this goal, and its integration with other fire management goals, is contingent upon the use of knowledge on how fires affect ecological processes. With this knowledge, circumstances where fires cause loss of biological diversity can be *predicted*, so that they may be avoided or minimised in management practice (Bradstock et al. 1995). In this paper I review concepts that underpin predictive knowledge of the effects of fire, identify fire-driven mechanisms that cause plant populations to decline to extinction and examine some recent approaches to fire management directed at conservation. The emphasis here will be on plants (nomenclature of which follows Harden, 1990–1993) , while the effects of fire on animals is reviewed by Whelan et al. (this volume).

Concepts in fire ecology

1). Fire regimes

Gill (1975) introduced the concept of fire regimes, whereby sequences of recurring fires are characterised in terms of their frequency, intensity, season and fuel type. Fire regimes may thus be used to describe temporal patterns in the occurrence of fires over varying spatial scales across a landscape (e.g. Hobbs and Atkins 1988b, Gill and Bradstock 1995). Although some earlier workers had already begun to examine the ecological effects of fire explicitly in terms of the components of fire regimes (e.g. Gilbert 1959, Jackson 1968), many studies have taken a descriptive approach to fire ecology in which fires are viewed as single events followed by a process of recovery or succession (e.g. Jarret and Petrie 1929, Russell and Parsons 1978, Bell and Koch 1980). While the ‘single fire’ approach has yielded knowledge on ecological changes that occur during an interval between successive fires, it has contributed little to understanding changes that occur over a period interspersed by multiple fires (Morrison et al. 1995), which are the primary concern for conservation. The study of species responses in relation to fire regimes, rather than fire *per se*, is thus an essential basis for predictive knowledge on fire effects (Gill 1975, Noble and Slatyer 1981, Gill and Bradstock 1995).

2). The demographic processes underpinning ecosystem dynamics

Changes in the structure and composition of ecosystems are fundamentally driven by processes that operate within and between populations of organisms (Harper 1977). With an understanding of these fine-scale mechanisms, it should therefore be possible to predict outcomes in terms of composition, diversity and structure at higher levels of scale. Thus in this review I have taken a population approach (cf. Attiwill 1994), emphasising the effects of fire on survival, growth and reproduction within each stage of the plant life cycle (Fig. 1). A population may decline if fire causes the pool of individuals in each life stage to be reduced or interrupts the transfer of individuals between these stages. Extinction results when all pools decline to zero. In such an approach, the mechanisms and causes of population decline and extinction may be identified directly and consequent changes in community structure, composition and diversity may be logically predicted. It should be emphasised that interactions between species (e.g. competition, predation) and with the physical environment (e.g. through environmental stochasticity) are an essential component of a population approach (Fig. 1), as these factors may profoundly influence processes within populations (Harper 1977).

Studies of plant community structure, species composition and richness have a role in testing predicted outcomes of plant population processes (e.g. Morrison et al. 1995) but, on their own, are of limited value in generating predictive knowledge of fire-driven vegetation dynamics. Generalisations about dynamics that are derived from community patterns without reference to population processes as underlying mechanisms (e.g. Attiwill 1994) may sometimes lead to misinterpretations. The frequently cited observation of declining plant species richness with time since fire provides a cogent example. Decline in standing plant richness (e.g. Specht et al. 1958, Bell and Koch 1980) may reflect little or no loss of species from the community, depending on the richness of

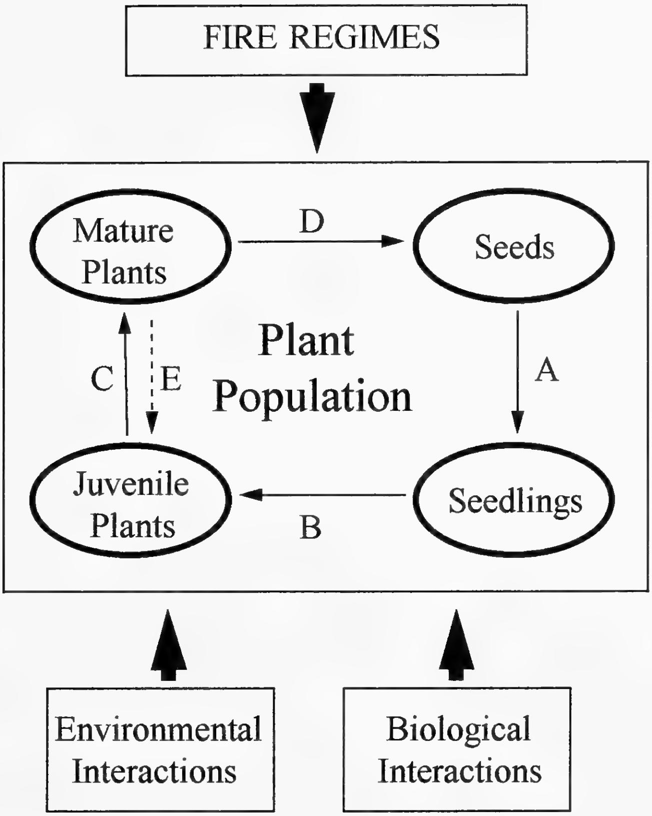

Fig 1. Diagrammatic representation of the processes involved in plant population dynamics of a flowering plant species (analogous schemes can be developed for non-flowering plants). Ellipses represent pools of individuals within each of four life stages. Arrows represent the flux of individuals between life stages: A — germination and emergence; B — seedling establishment; C — maturation and vegetative development; D — flowering, seed production and dispersal; E — establishment of vegetative propagules. Interactions with fire regimes, other organisms and the physical environment that influence rates of flux between life stages and rates of mortality within life stages are shown as arrows from external boxes. Interactions among these exogenous factors have been omitted for simplicity. Mechanisms of population decline and extinction are related to mortality in all life-stages (Mechanisms 1a–1g) and life-cycle fluxes as follows: A (Mechanisms 2a–2d); B and E (Mechanisms 3a–d); C (Mechanisms 4a–4b); and D (Mechanisms 5a–5c).

species represented in soil seed banks which may be substantial. The flux of individuals between these life stages (a population process) is often neglected, but is critical to the dynamics of vegetation after the next fire. It is also true that compositional studies may fail to detect effects of fire that may otherwise be evident from population studies (Lonsdale and Braithwaite 1991 *cf.* Bowman et al. 1988).

3). Life-history attributes

Life-history characteristics of plants vary greatly among species (e.g. Raunkaier 1934). The relevance of plant life history to fire response was discussed by Gill (1975, 1981), who identified traits such as the capacity to resprout after fire, fire stimulated release and germination of seed and post-fire flowering. Possession of particular life-history traits will determine the kinds of fire regimes likely to cause population decline by influencing the responses of particular life stages and rates of transfer between them

(Fig. 1). These traits will also determine which life stages or processes have a critical influence on the population response to particular fire regimes. Plant species that lack a capacity to resprout, for example, may be susceptible to decline under frequent fire regimes depending on the length of time required for maturation (see below).

Life-history attributes may be used to group species that have functionally similar fire responses and hence similar mechanisms of decline and extinction (Gill 1975, Noble and Slatyer 1980, Moore and Noble 1990, Keith 1991, Gill and Bradstock 1992, Keith and Bradstock 1994). Functional classifications of species offer a powerful means of ordering knowledge into generalisations (Verner 1984), as well as a guide for determining research priorities and applying fire management to species for which data are scarce. The latter is an important consideration, particularly in diverse ecosystems where species-by-species acquisition of knowledge may be desirable but is precluded by constraints on available research time and resources.

FIRE-DRIVEN MECHANISMS OF DECLINE/EXTINCTION IN PLANT POPULATIONS

Through each life stage represented in Fig. 1, there is a flux of individuals over time that may be broken down into several components (Harper 1977). Within a given time step, individuals in each life stage may have one of three fates: death; persistence within their present life stage; or passage into the next life stage. Individuals entering a given life stage from within the population must develop from the preceding stage. For mobile life stages (seeds and vegetative propagules), there may be additional fluxes of individuals to and from other populations. The relative magnitude of these fluxes determine whether a population will increase, decline or remain stable through time (Harper 1977).

The role of fire in the life cycles of plants is through its effect on survival of individuals in all life stages and its function as a cue for transfers between life stages. The cues provided by fire are critical for many plant species in which life-stage transfers (e.g. seed production, seed release, germination) do not operate continuously. Thus, a plant population may decline possibly to extinction whenever fire regimes interrupt the transfers between its life stages or deplete the pools of individuals within these life stages by mortality without commensurate replacement over an appropriate time scale (Fig. 1). The mechanisms through which these declines take place may be considered under five headings, depending on the life stages and processes that are affected (Fig. 1): death of standing plants and seeds; failure of seed release or germination; failure of seedling establishment; interruption of maturation and developmental growth; and failure of seed production. Below I examine how these mechanisms operate directly on individuals within plant populations and indirectly through interactions with the physical environment or populations of other organisms (Fig. 1) and identify a wide range of fire regimes implicated in decline and extinction of plant populations (Table 1). It should be noted that the processes discussed below do not act independently of one another. Rather, they interact within the context of whole populations, their habitat and associated species. I discuss the implications of these interactions in the next section (Vegetation Dynamics at Higher Levels of Organisation).

Death of Standing Plants and Seeds

There are at least seven mechanisms of plant population decline and extinction related to the death of standing plants and/or seeds caused by certain fire regimes (Table 1). Some of these mechanisms relate to fire regimes associated with the exposure of vital plant tissues to lethal temperatures (Mechanisms 1a, 1b and 1c, Table 1) or more gradual depletion of reserves essential for survival (Mechanism 1d). These regimes involve high intensity fires, fires causing penetration of high temperatures into the soil profile (i.e. due to consumption of extreme ground fuel loads and very long fire residence times), peat fires and high frequency fires. Other mechanisms relate to fire regimes involving long fire intervals that allow death through senescence or competitive elimination without commensurate replacement (Mechanisms 1e and 1f, Table 1).

Population declines and extinctions caused by fire-related mortality, where neither standing plants nor seeds survive in significant numbers are best known, both from direct observation and inference from historical evidence, in habitats that rarely experience fire. These include rainforests (e.g. Webb 1968, Ashton and Frankenberg 1976, Hill and Read 1984, Podger et al. 1988, Melick and Ashton 1991, Russell-Smith 1985, Russell-Smith and Bowman 1992) and alpine vegetation (e.g. Kirkpatrick 1983, Kirkpatrick and Dickinson 1984). However, high levels of fire-related mortality have been demonstrated in both standing plants (e.g. Noble 1989) and seed banks (e.g. Bradstock et al. 1994) of plant species typical of more fire-prone environments. Below I discuss evidence for each of these mechanisms and identify the environments and life-history types in which they are most likely to operate.

Survival under high fire temperatures depends on life-history characteristics. In some species fire may cause mortality of all standing plants in a population, given complete leaf scorch, so that population persistence is entirely dependent on seed (obligate seeders, Gill 1975). In other species a wide range of vegetative structures may confer the capacity for some or all standing plants to survive the passage of a fire by (i) protecting vital tissues from lethal temperatures; and (ii) harbouring buds that are the basis for vegetative recovery (resprouters, Gill 1975). The recovery buds in resprouters may be dormant (e.g. in mallee *Eucalyptus*) or actively growing (e.g. *Xanthorrhoea*) at the time of fire. Dormant seeds may similarly survive the passage of fire within storages known as seed banks.

In species that have neither a persistent seed bank nor vegetative structures allowing post-fire survival of standing plants, a single fire may cause catastrophic mortality. Some of the best known examples of these are alpine gymnosperms, particularly *Athrotaxis, Diselma, Microcachrys, Microstrobos* and *Podocarpus*, and the deciduous beech, *Nothofagus gunnii* (Kirkpatrick and Dickinson 1984). Other species lacking fire recovery traits are found in rainforests (e.g. Webb 1968, Melick and Ashton 1991), although a few examples (e.g. mistletoes) are known from more fire-prone environments (Gill 1981). Re-occupation of burnt sites by such species is dependent upon dispersal of propagules from unaffected populations (see below).

Mechanism 1a

Some woody shrubs and trees have recovery buds located above the ground. These include species with dormant epicormic buds protected by thick bark (e.g. most arborescent *Eucalyptus* species) and species with actively growing buds protected by crowded leaf bases (e.g. arborescent members of Arecaceae, Pandanaceae, Xanthorrhoeaceae and Kingiaceae). Seeds may also be stored above ground within woody fruits that are retained in the plant canopy for one or more years (see text on serotinous seed banks below). Temperatures to which aerial buds and seeds are exposed depend on fire intensity, the thickness of protective tissue and its thermal diffusivity (Gill and Ashton 1968, Vines 1968, McArthur 1968). Thus fires of high intensity will cause higher levels of mortality than those of low intensity (Mechanism 1a, Table 1), particularly among stems of trees or shrubs with thin or combustible bark (Penfold and Willis 1961, Cremer 1962, Gill 1981, Williams 1995) and among seeds within relatively thin-walled or unclustered fruits (Ashton 1986, Judd and Ashton 1991, Bradstock et al. 1994). The insulating properties of woody fruits may vary with age. Three year-old capsules of *Leptospermum continentale* (formerly included within *L. juniperinum*) subject to experimental heating reached lower internal maximum temperatures than one year-old fruits because their fruit walls were thicker and had greater moisture content, while *E. obliqua* showed the reverse response (Ashton 1986).

TABLE 1

Fire-driven mechanisms of plant population decline and extinction.

Life-cycle Process	Fire Regime Characteristics	Mechanism of Decline/Extinction	Life-history Types Affected
1. Death of standing plants & seeds	a) High intensity fires	Depletion of standing plants and seed banks through heat death of vital tissues above ground	Epicormic resprouters, passive fire tolerators and species with serotinous seed banks
	b) Fires consuming extreme quantities of ground fuel and with long residence times, especially when soil moisture is low	Depletion of standing plants and seed banks through heat death of vital tissues below ground	Resprouters, passive fire tolerators and species with soil seed banks. Especially when vital tissues are buried at shallow depths
	c) Peat fires	As for 1b.	As for 1b. Especially when peat is deep
	d) High frequency fires	Depletion of standing plants through depletion of bud banks, starch reserves or structural weakening	Resprouters and passive fire tolerators
	e) Low frequency fires	Depletion of standing plants and seed banks through senescence	Species with standing plants & seed banks that are short-lived relative to fire intervals
	f) Low frequency fires	Depletion of standing plants through competition with community dominants	Competitively subordinate species with short-lived seed banks
	g) High frequency fires	Depletion of standing plants through competition with opportunistic exotics	Species with slow-growing seedlings and resprouts in modified habitats
2. Failure of seed release and/or germination	a) Low frequency fires	Low rate of recruitment (relative to mortality) due to infrequent germination events	Species with limited seed release or germination in the absence of fire
	b) Low intensity fires	Low rate of recruitment (relative to mortality) due to release of few seeds	Species, especially trees, with serotinous seed banks and heat-dependent seed release
	c) Fires consuming small quantities of ground fuel and with short residence times, especially when soil moisture is high	Low rate of recruitment (relative to mortality) due to germination of few seeds caused by poor soil heating	Species with soil seed banks and heat-dependent dormancy
	d) Fires resulting in poor penetration of smoke derivatives into the soil profile	Low rate of recruitment (relative to mortality) due to germination of few seeds	Species with soil seed banks and smoke-dependent dormancy
3. Failure of seedling establishment	a) Low frequency fires	High mortality of seedlings emerging in the absence of fire due to resource deprivation, competition, predation and disease	Species whose seedlings are intolerant of conditions in 'mature' plant communities

	b) Fires preceding dry conditions (e.g. fires preceding summer, fires preceding drought)	High post-fire seedling mortality due to desiccation	Obligate seeders affected more rapidly than facultative seeders and vegetative increasers
	c) Extreme intensity fires, high frequency fires and peat fires with or without subsequent soil erosion	Physical change to habitat rendering it less amenable to seedling survival	Species occurring on organic or highly erodable substrates and in habitats rarely prone to fire
	d) Small or patchy fires and low intensity fires	High post-fire seedling mortality due to predation	Species with palatable seedlings. Obligate seeders affected more rapidly than facultative seeders and vegetative increasers
4. Interruption of maturation and developmental growth	a) High frequency fires	Fire-induced death of pre-reproductive juvenile plants	Obligate seeders affected more rapidly than resprouters
	b) High frequency fires	Fire-induced death of pre-resistant juvenile plants	Resprouters and passive fire tolerators
5. Failure of seed production	a) Low frequency fires	Low rate of recruitment due to infrequent flowering cues and seed production	Species whose flowering is stimulated only by the passage of fire
	b) Autumn/winter fires	Low rate of seed production (hence low recruitment rate) due to 'suboptimal' flowering cues	Species whose flowering is stimulated only by the passage of spring and summer fires
	c) Low frequency fires, small or patchy fires and low intensity fires	Low seed availability caused by high rates of predation (failure of predator satiation)	Species with fire-stimulated, flowering seed release or germination

Contrasting with species that survive fire actively by resprouting from dormant aerial buds protected from lethal temperatures are some arborescent obligate seeders whose actively growing shoots may avoid lethal temperatures (passive fire tolerators, Morrison 1995). Examples include *Leptospermum laevigatum* (Burrell 1981), species of *Callitris* (Bradstock 1989), *Allocasuarina littoralis, Acacia binervia* and *A. parramattensis* (Morrison 1995). These species may survive the passage of some fires if their actively growing canopy is held above scorch height and their bark is sufficiently thick within the scorch zone to protect vascular tissues from lethal temperatures. Operation of Mechanism 1a (Table 1) therefore depends on the developmental stage of the tree and flame height, which is related to fire intensity (Cheney 1981). Older trees with a high canopy, thick bark and discontinuous vertical fuel structure are more likely to survive than young trees (Morrison 1995).

Some plant species appear to influence community structure in a way that reduces the likelihood of lethal temperatures above ground during fires (Mechanism 1a, Table 1). In dense stands of some passive fire tolerators, such as *Allocasuarina littoralis* and *Callitris verrucosa*, heavy fall and compaction of litter and exclusion of understorey species may result in a ground fuel structure that reduces the chance of lethal canopy fires with post-fire age (Withers and Ashton 1977, Bradstock 1989). An analogous relationship may exist in alpine bolster heaths whose compact habit provides a fuel structure unfavourable to propagation of fire, allowing high rates of survival even when the margins of plants are scorched by ignition of adjacent fuels (Kirkpatrick 1983, Kirkpatrick and Dickinson 1984). Conversely, frequent firing may increase the ability of ground fuels to carry fire by stimulating vegetative recruitment in herbaceous resprouters, thereby increasing their density and possibly biomass. Tolhurst and Oswin (1992) demonstrated such a response in *Pteridium esculentum* when burnt by successive spring fires three years apart. Leigh and Noble (1981) also suggest a relationship between ground fuel structure and frequent fire in subalpine woodland, where high densities of leguminous shrubs may replace a less flammable groundcover of snow grass in response to frequent fire.

Mechanism 1b

In many resprouters the recovery organs, such as lignotubers (e.g. mallee *Eucalyptus*), bulbs, tubers, corms (e.g. various members of the Liliales) and rhizomes (e.g. various members of the Cyperaceae and Restionceae) are located underground. A large proportion of plant species (resprouters and obligate seeders) also have seed banks located underground (Auld 1994). Here, buds and seeds may be protected from lethal temperatures (Mechanism 1b, Table 1), not only by the insulating properties of the soil, but by the behaviour of fire which ensures that only about 5% of the heat that is generated travels in a downward direction (Packham 1970). The temperatures to which buried structures are elevated during the passage of fire are not directly related to fire intensity. Rather, these temperatures are related positively to the amount of ground fuel consumption and residence time of fire, and inversely to depth of burial and moisture content of soil at the time of fire (Beadle 1940, Bradstock et al. 1992, Valette et al. 1994, Bradstock and Auld 1995). These factors have, in turn, been related to levels of mortality among lignotubers of *Eucalyptus* (Noble 1984), *Banksia* (Bradstock and Myerscough 1988) and *Angophora* (Auld 1990), among rhizomes of several restionaceous sedges (Pate et al. 1991) and among soil-stored seed of native legumes (Auld 1987a, Auld and O'Connell 1991). Thus Mechanism 1b (Table 1) may be expected to operate on buried seeds and vegetative organs when depth of burial is shallow, ground fuel consumption is high, fire residence time is long and/or when soil moisture content is low.

Mechanism 1c

Where the soil itself is fuel, as is the case in peat fires, soil temperatures may reach 200 to 600°C and be sustained in that range for hours or days (Wein 1981, Frandsen 1991). Exposure to these levels and durations of heating causes high levels of mortality among standing plants (Mechanism 1c, Table 1) (Cremer 1962, Wein 1981, Hill 1982, Hill and Read 1984, Kirkpatrick and Dickinson 1984). Levels of mortality in soil seed banks are also likely to be high during peat fires (Wein 1981). The consequences of seed bank losses after peat fires have been examined in the northern hemisphere (e.g. Flinn and Wein 1977, Moore and Wein 1977), but few data exist for Australian plant communities (e.g. Cunningham and Cremer 1965). Hill and Read (1984), for example, inferred that seedlings of *Coprosma quadrifa* and *Pimelea drupacea* were confined to sites where peat remained unburnt because seeds stored in the soil were killed where the peat burned. The likelihood of peat combustion depends on its depth and moisture content (Wein 1981, Hill 1982).

A mechanism of fire evasion apparently operates in some species of trees subject to peat fires. Hill (1982) reported that tree mortality occurred where peat had combusted at their base, presumably killing their cambium (Cremer 1962), while trees generally survived where peat burnt incompletely around their base. Certain trees may evade death by: (i) having large irregularly shaped butts, increasing the chances of strips of cambium being sheltered from fire; or (ii) occurring preferentially in sites where peat depth is insufficient for combustion. Hill and Read (1984) suggested that these mechanisms, respectively, were responsible for rates of survival in *Eucalyptus nitida* and *Leptospermum scoparium* that were markedly higher than those of co-occurring rainforest tree species after a peat fire at Savage River, Tasmania. In a different fire, mortality among large trees of *Nothofagus cunninghamii* and *Eucryphia lucida* was higher than in smaller trees of the same species and *Atherosperma moschatum* and *Anodopetalum biglandulosum.* Hill (1982) suggested that these latter trees were more likely to evade lethal fires because of the shallower and less combustible accumulation of peat around their bases compared to large individuals of *N. cunninghamii* and *E. lucida.*

Mechanism 1d

Post-fire survival of standing plants may also depend on the distribution of recovery buds and/or the level of stored starch reserves (Pate et al. 1990, 1991). Resprouters may be killed if pools of dormant buds or stored starch reserves are exhausted by repeated fires or by fires at certain times of the annual growth cycle (Mechanism 1d, Table 1). Stands of mallee eucalypts, *E. incrassata*, a species that is well known for its resistance to fire, suffered extreme mortality when experimentally subjected to high-frequency fire (Noble 1989). The level of mortality increased with increasing fire frequency and reached a maximum of 95% after 4 successive fires one year apart (Noble 1989). *Stirlingia latifolia*, a resprouting heath shrub, is apparently more resilient to frequent fire regimes. Starch reserves held in its lignotuber were depleted by 50–75% in the period 2–5 months after a single fire, but were fully replenished by 1.5–2 years after fire (Bowen and Pate 1993). Starch reserves were exhausted, resulting in death, only after 10–12 monthly defoliation treatments. In *Banksia oblongifolia*, Zammit (1988) inferred that 70 % of dormant lignotuber buds were exhausted after a single clipping treatment and completely exhausted after four successive treatments, suggesting an intermediate level of resilience between *E. incrassata* and *S. latifolia*. However, pools of dormant buds were apparently restored after six months' growth. The ability to replenish dormant buds or starch reserves may diminish with age so that large old plants may suffer greater mortality in response to fire than younger, presumably more vigorous plants as observed, for example, in *Banksia grandis* (Burrows 1985). It has also been suggested that frequent fires cause tree death through structural weakening and eventual collapse (Benson 1985a) or by exposure of sensitive tissues to subsequent fires (Ashton and Frankenberg 1976, Russell-Smith and Dunlop 1987).

Noble's (1989) experiments also demonstrate the effect of fire season on mortality of standing plants. Repeated fires in spring resulted in lower mortality after 4 fires than repeated fires in autumn, presumably because spring fires preceded the annual growth season (summer–early autumn), whereas autumn fires coincided with a time when starch reserves had been depleted by recent growth (Noble 1989). Tolhurst and Oswin (1992) suggested that depletion of starch reserves may have been responsible for an observed reduction in density of *Poa sieberiana* after successive spring fires 3 years apart, relative to a single spring fire over the same period which resulted in increased density. A similar response to fire season may be expected in geophytic species, but I know of no available data on this topic.

Mechanism 1e

Fire may influence the number of individuals in various life stages of a plant population indirectly, through its absence, where transfers between these stages are dependent on fire (Fig. 1). If both standing plants and seeds are short-lived, and germination, seedling establishment or fruit production are constrained to the occurrence of fire (see below), then regimes of infrequent fire may cause decline and elimination of the population at a rate determined by senescence of standing plants and stored seeds (Mechanism 1e, Table 1). Many species with short-lived populations of standing plants apparently have persistent soil seed banks (e.g. Auld 1987a, though see Witkowski et al. 1991 for an exception, *Banksia coccinea*). Thus many reports that show a decrease in species richness of plant communities with time since fire (e.g. Specht et al. 1958, Russell and Parsons 1978, Bell and Koch 1980, Fox 1988) may be more likely to reflect a shift in the population structure of some species (i.e. from standing plants to buried seed), rather than a real loss of species from the community.

Survivorship or longevity data for standing plant populations in the absence of fire are available for a range of species (e.g. Ashton 1976, Lamont and Downes 1979, Wellington and Noble 1985a, Auld 1987a, Williams and Ashton 1988, Bradstock and

O'Connell 1988, Witkowski et al. 1991). The longevity of individual plants varies from less than a year in ephemeral herbs (e.g. Pate et al. 1985) to hundreds of years in woody perennials (e.g. Wellington et al. 1979, Lamont and Downes 1979, Head and Lacey 1988).

There are few data on the longevity of seed banks. Serotinous seed banks may persist for many years, but are unlikely to remain viable for long after senescence of parent plants (Gill and McMahon 1986, Witkowski et al. 1991, Lamont et al. 1991). Transient soil seed banks are even shorter-lived and have a discontinuous existence of a few months after flowering events (e.g. Gill and Ingwerson 1976, Auld 1987b, Auld 1990, Bradstock 1995). Experimental burial of seeds of forbs in the Asteraceae and Liliales that are typical of fire prone temperate grasslands yielded seed bank half-lives of two months to one year (Lunt 1995). Persistent soil seed banks may provide a basis for regeneration long after senescence of standing plant populations (e.g. Ewart 1908, Gilbert 1959). Auld (1994) summarised available data from burial experiments to estimate the longevity of persistent soil seed banks in fire-prone heath and woodland in the Sydney region. The results indicated a group of species with seed bank half-lives of 1–3 years duration (e.g. *Darwinia biflora, Zieria involucrata, Anisopogon avenaceus*), a group of species with seed bank half-lives in the order of a decade (e.g. *Acacia suaveolens, Grevillea linearifolia, Kunzea ambigua*) and a group of species with seed bank half-lives possibly in the order of several decades (e.g. *Gahnia sieberiana, Velleia perfoliata, Stackhousia viminea*). Inference from non-overlapping patterns of fruit production and seedling emergence at sites where dispersal from fruiting populations was unlikely also suggests that substantial quantities of buried seed of some herbaceous species may remain viable for well in excess of 10 years (e.g. Pate et al. 1985, Keith 1991, Lamont and Runciman 1993).

Mechanism 1f

Another mechanism of decline and extinction involves density-dependent interactions that lead to dominance of some species and competitive elimination of others as a consequence of resource deprivation (Keddy 1989). Competitive elimination (Mechanism 1f, Table 1) may be interrupted by disturbances, such as fire, if they allow recovery of suppressed individuals and recruitment of seedlings. Competitive effects may accelerate population declines that occur as a consequence of senescence, since both mechanisms operate during long fire intervals (1e and 1f, Table 1). However, these competitive interactions only affect the standing plant life stages of populations. Thus dormant propagules, depending on their longevity, may continue to persist in a community long after standing plants have been eliminated, perhaps to re-emerge as standing plants when fire reduces the biomass of the dominant species (Keith and Bradstock 1994).

Few Australian studies have examined the role of competition in terrestrial vegetation directly by experimental manipulation (e.g. Aarson and Epp 1990). Nonetheless, given sufficiently long fire-free intervals, there is evidence for decline and eventual competitive elimination of subdominant species in forests (e.g. Gilbert 1959, Ashton 1981), heathlands and woodlands (Withers 1979, Specht and Morgan 1981, Burrell 1981, Molnar et al. 1989, Keith and Bradstock 1994) and grasslands (Lunt 1991, Tremont and McIntyre 1994, Morgan 1994, in press). Species most prone to competitive elimination are subordinate in stature relative to community dominants and intolerant to conditions associated with the 'mature' community such as shade and leaf litter. Examples include interstitial herbs of grassland (Tremont and McIntyre 1994) and slow-growing sub-shrubs of heathlands (Keith and Bradstock 1994). Competitive elimination is also mediated by the structure of the community itself, particularly the density and spatial pattern of the dominant species which may be dependent on fire regimes and their spatial pattern, as well as seed dispersal mechanisms (Molnar et al. 1989, Lamont et al. 1993, Keith and Bradstock 1994, Morgan 1994).

Mechanism 1g

Where fires enhance invasion of herbaceous weeds they may cause decline and extinction of indigenous species through competition (Mechanism 1g, Table 1). By exploiting gaps and growing rapidly after fire, opportunistic weed species are able to exclude their slower growing neighbours from the community (McIntyre and Lavorel 1994). This mechanism of decline and extinction operates most rapidly under frequent fire regimes (Table 1), since these provide more gaps for the opportunists to exploit over a given time. Milberg and Lamont (1995), for example, showed experimentally how the abundance of exotic weeds increased at the expense of indigenous plant species after a single fire and that these changes persisted for at least 7 years. They suggested that increasing the frequency of fire would excerbate the transformation from native to exotic vegetation. Similar conclusions were reached by Hobbs and Atkins (1990). Some plant communities are apparently less susceptible to weed invasion after fire than others, since dispersal of weed propagules into burnt areas is not always followed by establishment (Hobbs and Atkins 1988a, Hester and Hobbs 1992). The reasons for these differences apparently involve other sources of disturbance that cause habitat modification as commonly occurs in agricultural and urban landscapes. These include water and nutrient enrichment, increased herbivory and physical disturbance to vegetation (Tremont and McIntyre 1994, McIntyre and Lavorel 1994).

Failure of Seed Release and/or Germination

These mechanisms of decline and extinction relate to the part of the plant life cycle where individuals are transferred from stored seeds to seedlings (Fig. 1). Certain kinds of fires provide cues to release seeds from serotinous seed banks and to break dormancy of seeds in soil seed banks, resulting in mass germination events (Gill 1981). Fire regimes that fail to provide cues that stimulate the release and germination of seeds at a rate sufficient to replace deaths of standing plants will cause a plant population to decline, possibly to extinction. This may occur if fire regimes stimulate germination infrequently or if they result in germination events that involve relatively few seeds. In the first instance declines and extinctions may be associated with infrequent fire regimes (Mechanism 2a, Table 1). In the second instance declines and extinctions may be associated with aspects of fire behaviour that influence the generation of heat and the dispersal of smoke and ash (Mechanisms 2b–d, Table 1), since these in turn influence the size and timing of germination events (Auld and O'Connell 1991, Dixon et al. 1995). The critical aspects of fire behaviour depend on whether seed storage is in the plant canopy or in the soil and on the nature of seed dormancy.

Mechanism 2a

When fires occur infrequently, there will be few opportunities for seed release or germination, thereby limiting seedling recruitment, so that a population may decline at a rate determined by the rate of death in each life stage (Mechanism 2a, Table 1). Where death rates among standing plants and seeds are high (i.e. where all life-stages are short-lived), frequent germination events that involve large numbers of seeds are required if population decline is to be avoided, unless deaths are offset by immigration. Conversely, where death rates are low, infrequent germination events or those that involve small numbers of seeds may be sufficient to maintain population stability.

Operation of Mechanism 2a (and Mechanisms 2b–d) may be offset if the rate of spontaneous seed release and germination (i.e. the extent to which seeds germinate independently of fires) is substantial and results in seedling recruitment. The extent to which the availability of seeds for germination is constrained by the occurrence of fire varies among both serotinous species and those with soil seed banks. Seeds may be released and germinate independently of fire either through spontaneous release of seeds from woody fruits (Ashton 1979, Abbott 1985, Cowling and Lamont 1985a, Wellington and Noble 1985a, Bradstock and O'Connell 1988, Lamont and van Leeuwin 1988, Zammit and Westoby 1988, Enright and Lamont 1989b, Bradstock 1990, Davies and Myerscough 1991, Pannell 1995), by continued production of a fraction of non-dormant seeds (Auld and O'Connell 1991, Morrison et al. 1992) or by spontaneous release from dormancy

(Baskin and Baskin 1989, Morrison et al. 1992, Auld et al. 1993). An obvious corollary of spontaneous germination is depletion of regeneration capacity after the next fire, particularly if germinated seeds fail to grow into established plants, because these seeds are lost from storage and will not contribute to any subsequent post-fire germination event.

The extent to which seeds are retained in serotinous fruits until fire or released spontaneously through time varies between and within species. Spontaneous release of seed from serotinous seed banks may occur when fruits are desiccated during branch senescence or in response to wet–dry cycles. Davies and Myerscough (1991), for example, estimated that serotinous seed in *Eucalyptus luehmanniana* had a turnover time of 1–2 years. Wet–dry cycles were apparently responsible for spontaneous release of 90% of seeds independently of fire in the first year after fruit maturation in *Banksia grandis* (Abbott 1985). Cowling and Lamont (1985a) demonstrated that levels of serotiny varied within *Banksia* species in relation to moisture status of the habitat, xeric habitats supporting populations with more serotinous seed banks.

Levels of dormancy in soil seed banks vary between populations and with seed age (Bradstock 1989 *cf.* Bogusiak et al. 1990, Auld and O'Connell 1991, Morrison et al. 1992, Auld et al. 1993, Bell et al. 1993, Dixon et al. 1995). This variation is attributable to several different mechanisms and may contribute to a substantial capacity for germination independent of fire. Auld and O'Connell (1991) reported that the non-dormant fraction of annual seed lots varied between zero and 59% among 35 native legume species. In some species the non-dormant fraction of seeds is small at the time of release but increases with seed age, a process that has been attributed to mechanical abrasion, action of digestive juices, microbial or fungal attack, high or fluctuating ambient temperatures and high relative humidity (e.g. Mott 1972, Cavanagh 1987). Morrison et al. (1992) found that seed dormancy may also decrease in dry storage, a process known as after-ripening. They detected after-ripening over three years in several species of legumes in the tribes Bossiaeeae and Phaseoleae, but not in numerous species from other tribes of the family. Finally, there is a possibility that seed dormancy may vary in a reversible manner. Auld et al. (1993) found that dormancy of experimentally buried seeds of *Darwinia* and *Grevillea* was reduced over summer, but restored in the following winter.

Mechanism 2b

Species of Proteaceae (*Banksia, Dryandra, Hakea, Petrophile, Isopogon, Strangea, Xylomelum*), Myrtaceae (*Eucalyptus, Leptospermum, Melaleuca, Callistemon, Kunzea, Agonis, Astartea, Calothamnus, Beaufortia, Eremea, Regelia, Phymatocarpus, Pericalymma*), Casuarinaceae (*Casuarina, Allocasuarina*) and Cupressaceae (*Callitris, Actinostrobos*) have serotinous seed banks. In many of these taxa, seed release occurs whenever the fruit is desiccated, as is the case when their branches are scorched by fire. Thus, low intensity fires may result in only partial seed release if scorching does not reach the height of some or all fruit-bearing branches, unless the entire plant is killed by basal scorching. The outcome may be limited seedling recruitment and population decline (Mechanism 2b, Table 1).

In many *Banksia* species, release of seeds requires exposure to temperatures well above ambient levels to rupture an abscission zone of cells in the fruit (Gill 1976). The temperature to which *Banksia* fruits are exposed affects not only the ultimate proportion of seeds released, but also their rate of release over the first post-fire year (Bradstock and Bedward 1992), a factor that may have implications for seedling survival (see next section). Enright and Lamont (1989a) have shown that threshold temperatures required for 90% seed release varied from 175 to 500°C among 10 *Banksia* species. Temperature-dependent seed release was also shown by Zammit and Westoby (1987a). Low intensity fires are less likely to produce temperatures required for seed release than high intensity fires, particularly where serotinous fruits are held high above the ground. Mechanism 2b (Table 1) is therefore likely to be associated with more rapid population declines in serotinous species with arborescent growth forms than in those with non-arborescent growth forms.

Mechanism 2c

The widely observed phenomenon of pulsed post-fire seedling recruitment (Specht et al. 1958, Purdie 1977b, Hobbs and Atkins 1990, Clark 1988, Tolhurst and Oswin 1992, Auld and Tozer 1995) suggests that large numbers of species in fire-prone environments have soil seed banks whose dormancy is broken by fire-related cues. Seed dormancy mechanisms are well known in leguminous species: seeds have hard impermeable seed coats which may be ruptured by heat or physical damage, allowing them to imbibe and germinate (Baskin and Baskin 1989). A germination response to heat has been demonstrated in a wide range of Australian legumes and other taxa (Table 2). Auld and O'Connell (1991) have shown that threshold temperatures for germination varied from 40 to 80°C among 34 legume species, while germination response was relatively insensitive to duration of exposure to these temperatures. Fires consuming 0.6 to 2.0 kg.m^{-2} of fine ground fuel are required to generate these temperatures to depths of 1–3 cm below ground surface (Bradstock et al. 1992, Bradstock and Auld 1995), where most soil seed capable of emergence is located (Auld 1986a, unpubl. data). Fires that fail to meet these conditions may be associated with low levels of germination from soil seed banks and hence population declines (Mechanism 2c,Table 1).

TABLE 2

Genera with persistent soil seed banks for which an enhanced germination response to heat (H) or smoke (S) have been demonstrated experimentally and genera in which such responses have been tested but not found (h and s, respectively). Results should be treated with some caution because experimental methods vary between authors and responses are likely to vary within genera, species and populations.

Genus	Family	Response	Source
Acacia	Fabaceae	H	Beadle 1940, Floyd 1966, 1976, Shea et al. 1979, Warcup 1980, Vlahos and Bell 1986, Auld 1987a, Hodgkinson and Oxley 1990, Auld and O'Connell 1991, Bell et al. 1993
Actinodium	Myrtaceae	s	Dixon et al. 1995
Actinostrobos	Cupressaceae	S	Dixon et al. 1995
Actinotus	Apiaceae	H	Auld, Bradstock and Keith, unpubl.
Adriana	Euphorbiaceae	s	Dixon et al. 1995
Agrostocrinum	Anthericaceae	s	Dixon et al. 1995
Alogyne	Malvaceae	s	Dixon et al. 1995
Amphipogon	Poaceae	s	Dixon et al. 1995
Andersonia	Epacridaceae	S	Dixon et al. 1995
Anigozanthos	Haemodoraceae	S	Dixon et al. 1995
Anisopogon	Poaceae	h	Auld, Bradstock and Keith, unpubl.
Anthibolus	Santalaceae	s	Dixon et al. 1995
Aotus	Fabaceae	H	Auld and O'Connell 1991
Asterolasia	Rutaceae	H	Auld, unpubl.
Astroloma	Epacridaceae	s	Dixon et al. 1995
Billardiera	Pittosporaceae	S	Dixon et al. 1995
Blandfordia		h	Auld, Bradstock and Keith, unpubl.
Boronia	Rutaceae	s	Dixon et al. 1995
		H	Auld, Bradstock and Keith, unpubl.
Bossiaea	Fabaceae	H	Warcup 1980, Auld and O'Connell 1991, Bell et al. 1993
Brachyloma	Epacridaceae	s	Dixon et al. 1995
Burchardia	Colchicaceae	S	Dixon et al. 1995
		h	Auld, Bradstock and Keith, unpubl.
Chamaescilla	Anthericaceae	S	Dixon et al. 1995
Choretrum	Santalaceae	s	Dixon et al. 1995

Chorizema	Fabaceae	H	Bell et al. 1993
Codonocarpus	Gyrostemonaceae	S	Dixon et al. 1995
Comesperma	Polygalaceae	H	Auld, Bradstock and Keith, unpubl.
Commersonia	Sterculiaceae	H	Floyd 1976
Conospermum	Proteaceae	S	Dixon et al. 1995
		H	Auld, Bradstock and Keith, unpubl.
Conostephium	Epacridaceae	s	Dixon et al. 1995
Conostylis	Haemodoraceae	H	Bell et al. 1987, Bell et al. 1993,
		S	Dixon et al. 1995
Convolvulus	Convolvulaceae	H	Warcup 1980
Croninia	Epacridaceae	s	Dixon et al. 1995
Darwinia	Myrtaceae	H,h	Auld et al. 1991, 1993
Daviesia	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Deyeuxia	Poaceae	H	Warcup 1980
Dichondra	Convolvulaceae	H	Warcup 1980
Dillwynia	Fabaceae	H	Auld and O'Connell 1991
Dodonaea	Sapindaceae	H	Floyd 1966, 1976, Warcup 1980, Hodgkinson and Oxley 1990, Auld, Bradstock and Keith, unpubl.
Drosera	Droseraceae	s	Dixon et al. 1995
Epacris	Epacridaceae	H	Warcup 1980, Auld, Bradstock and Keith unpubl.
Eriostemon	Rutaceae	S	Dixon et al. 1995
Exocarpos	Santalaceae	s	Dixon et al. 1995
Gahnia	Cyperceae	h	Auld, Bradstock and Keith unpubl.
		s	Dixon et al. 1995
Gastrolobium	Fabaceae	H	Bell et al. 1993
Geleznowia	Rutaceae	S	Dixon et al. 1995
Geranium	Geraniaceae	H	Warcup 1980
Glycine	Fabaceae	H	Auld and O'Connell 1991
Gompholobium	Fabaceae	H	Vlahos and Bell 1986, Auld and O'Connell 1991, Bell et al. 1993
Goodenia	Goodeniaceae	s	Dixon et al. 1995
Grevillea	Proteaeceae	S	Dixon et al. 1995
		h	Auld and Tozer 1995
Gyrostemon	Gyrostemonaceae	S	Dixon et al. 1995
Hardenbergia	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Hemiandra	Lamiaceae	s	Dixon et al. 1995
Hibbertia	Dilleniaceae	S	Dixon et al. 1995
		h	Auld, Bradstock and Keith, unpubl.
Hovea	Fabaceae	H	Vlahos and Bell 1986, Bell et al. 1993
Hybanthus	Violaceae	S	Dixon et al. 1995
Hypocalyma	Myrtaceae	S	Dixon et al. 1995
Isolepis	Cyperaceae	H	Warcup 1980
Jacksonia	Fabaceae	H	Bell et al. 1993
Johnsonia	Anthericaceae	s	Dixon et al. 1995
Juncus	Juncaceae	H	Warcup 1980
Kennedia	Fabaceae	H	Floyd 1966, 1976, Vlahos and Bell 1986, Auld and O'Connell 1991, Bell et al. 1993
Kunzea	Myrtaceae	H	Auld, Bradstock and Keith unpubl.
Lachnostachys	Chloanthaceae	s	Dixon et al. 1995
Lepidosperma	Cyperaceae	s	Dixon et al. 1995
Leschnaultia	Goodeniacaeae	S	Dixon et al. 1995
Leucopogon	Epacridaceae	s	Dixon et al. 1995
Lomandra	Lomandraceae	s	Dixon et al. 1995
Lysinema	Epacridaceae	S	Dixon et al. 1995
Macropidia	Haemodoraceae	s	Dixon et al. 1995

Mirbelia	Fabaceae	H	Shea et al. 1979, Auld and O'Connell 1991, Bell et al. 1993
Neurachne	Poaceae	S	Dixon et al. 1995
Olearia	Asteraceae	h	Auld, unpubl.
Opercularia	Rubiaceae	H	Warcup 1980
Oxylobium	Fabaceae	H	Bell et al. 1993
Ozothamnus	Asteraceae	H	Floyd 1976
Paraserianthes	Fabaceae	H	Bell et al. 1993
Patersonia	Iridaceae	S	Dixon et al. 1995
Pelargonium	Geraniaceae	H	Warcup 1980
Persoonia	Proteaeceae	s	Dixon et al. 1995
		h	Auld, Bradstock and Keith, unpubl.
Petrophile	Proteaceae	S	Dixon et al. 1995
Phebalium	Rutaceae	s	Dixon et al. 1995
Phyllota	Fabaceae	H	Auld and O'Connell 1991
Pimelea	Thymelaeaceae	H	Auld, Bradstock and Keith unpubl.
		S	Dixon et al. 1995
Platylobium	Fabaceae	H	Auld and O'Connell 1991
Platysace	Apiaceae	H	Warcup 1980
Pomaderris	Rhamnaceae	H	Warcup 1980, Coates 1991, Auld, Bradstock and Keith, unpubl.
Poranthera	Euphorbiacae	H	Warcup 1980
Pultenaea	Fabaceae	H	Warcup 1980, Auld and O'Connell 1991
Ricinocarpos	Euphorbiaceae	h	Auld, Bradstock and Keith, unpubl.
Rulingia	Sterculiaceae	S	Dixon et al. 1995
Scaevola	Goodeniaceae	S	Dixon et al. 1995
Scholtzia	Myrtaceae	s	Dixon et al. 1995
Senna	Fabaceae	H	Hodgkinson and Oxley 1990
Seringia	Sterculiaceae	H	Floyd 1976
Siegfriedia	Rhamnaceae	S	Dixon et al. 1995
Sorghum	Poaceae	H	Andrew and Mott 1983
Sowerbaea	Anthericaceae	s	Dixon et al. 1995
Sphaerolobium	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Sphenotoma	Epacridaceae	S	Dixon et al. 1995
Sprengelia	Epacridaceae	H	Warcup 1980, Auld, Bradstock and Keith unpubl.
Spyridium	Rhamnaceae	H	Warcup 1980
		S	Dixon et al. 1995
Stackhousia	Stackhousiaceae	S	Dixon et al. 1995
		H	Auld, Bradstock and Keith, unpubl.
Stirlingia	Proteaeceae	S	Dixon et al. 1995
Stylidium	Stylidiaceae	H	Tozer, unpubl.
Styphelia	Epacridaceae	s	Dixon et al. 1995
Synaphea	Proteaceae	s	Dixon et al. 1995
Tetratheca	Tremandraceae	S	Dixon et al. 1995
Thomasia	Sterculiaceae	s	Dixon et al. 1995
Thysanotus	Anthericaceae	S	Dixon et al. 1995
Triptercoccus	Stackhousiaceae	s	Dixon et al. 1995
Trymalium	Rhamnaceae	H	Bell et al. 1987
Velleia	Goodeniaceae	H	Auld unpubl.
		s	Dixon et al. 1995
Verticordia	Myrtaceae	S	Dixon et al. 1995
Viminaria	Fabaceae	H	Auld and O'Connell 1991, Bell et al. 1993
Xanthorrhoea	Xanthorrhoeaceae	h	Auld, Bradstock and Keith, unpubl.
Xanthosia	Apiaceae	s	Dixon et al. 1995
Zieria	Rutaceae	H	Floyd 1976, Auld unpubl.

Mechanism 2d

Fire-related germination cues other than heat include chemical responses from smoke (van der Venter and Esterhuizen 1988, de Lange and Boucher 1990, Brown 1993, Dixon et al. 1995) and charred wood (Keeley et al. 1985, Keeley and Pizzorno 1986). The active chemical agents within smoke are not known, but are apparently widespread in occurrence and act relatively indiscriminately on germination across a wide range of taxa (Dixon et al. 1995). Dixon et al. (1995) found positive germination responses to smoke in 45 of 94 south-western Australian plant taxa, some of which also responded positively to heat (Table 2). They suggested that seed banks of certain species may require exposure sequentially or possibly additively to a number of stimuli before dormancy is broken. However, approximately half of the taxa exhibiting a positive germination response to smoke were not germinable by other means and several others showed greater germinability after smoke treatment than after heat treatment (Dixon et al. 1995). Further, Dixon et al. (1995) were able to stimulate additional seedling emergence from residual seed banks in recently burnt areas by applying smoke experimentally to the soil *in situ* using fumigation apparatus. The experimental site had been previously burnt by a low intensity fire which presumably resulted in little penetration of heat or smoke derivatives into the soil profile.

The factors affecting generation of smoke derivatives and their penetration into the soil profile are currently unknown, but are likely to be critical in the determining the magnitude of germination responses and hence the likelihood of population declines (Mechanism 2d, Table 1). Given that heat and smoke derivatives may penetrate the soil profile in different ways, smoke derivatives may be important in breaking dormancy of seeds buried at depths beyond those subject to elevated temperatures during fire (e.g. Bradstock and Auld 1995).

Failure of Seedling Establishment

Seedling establishment refers to the transfer of individuals from the seedling stage to the juvenile stage (Fig. 1). If seedling establishment fails to replace deaths among standing plants over time, a population will decline, possibly to extinction. There are at least four mechanisms by which fire regimes may cause population declines and extinctions by limiting seedling establishment (Fig. 1, Table 1). Infrequent fire regimes may limit seedling recruitment by limiting the number of opportunities for establishment, assuming the timing of seedling establishment is constrained to the immediate post-fire period (Mechanism 3a, Table 1). In many species seedling establishment is at least partly constrained to the immediate post-fire period by mechanisms of seed release and dormancy (see preceding section). Below I examine processes affecting seedling survival that act to further constrain seedling survival to the post-fire period. Other mechanisms of population decline and extinction involve limitations on seedling survival in the post-fire environment imposed by limited moisture supply (Mechanism 3b, Table 1), physical changes to the habitat wrought by extreme fire events (Mechanism 3c, Table 1) and predators (Mechanism 3d, Table 1).

Mechanism 3a

Evidence that seedling establishment is greater immediately after fire than in an established (unburnt) community has been documented in Australian forests (Beadle 1940, Christensen and Kimber 1975, Ashton 1976, Hill and Read 1984, Tolhurst and Oswin 1992), woodlands (Purdie 1977b, Withers 1978, 1979, Clark 1988, Hobbs and Atkins 1990, Auld and Tozer 1995), heathlands (Beadle 1940, Specht et al. 1958, Zammit and Westoby 1987a, Cowling and Lamont 1987, Meney et al. 1994), swamps (Keith 1991), grasslands (Westoby et al. 1988, Gilfedder and Kirkpatrick 1993, Tremont and McIntyre 1994, Morgan in press) and arid and semi-arid shrublands (Griffin and Friedel 1984, Wellington and Noble 1985a, Hodgkinson 1991). In combination, intolerance to shade and increased susceptibility to fungal pathogens, desiccation and predators may severely limit seedling establishment of many species in a wide range of habitats, except when the passage of a fire liberates resources (particularly light, water and nutrients), reduces competition and facilitates predator satiation. Where fires occur rarely, as in low frequency fire regimes, population declines may occur at a rate determined by the mortality of standing plants (Mechanism 3a, Table 1).

Prolonged exposure to shade and consequent fungal disease have been implicated as major factors responsible for high seedling mortality in the absence of fire in wet forest eucalypts (Gilbert 1959, Ashton and MacCauley 1972), in a range of understorey species and eucalypts of dry grassy woodlands (Purdie 1977b, Withers 1978, 1979) and in fire-prone swamp vegetation (Keith 1991). In the latter community high seedling mortality is correlated with a dense canopy of resprouting graminoids and ferns that reduces light intensity at the soil surface by two orders of magnitude (Keith 1991). Desiccation is a second cause of high mortality of seedlings in unburnt vegetation. Studies of heathlands on both sides of the continent showed mortality of newly emerged *Banksia* seedlings was significantly higher in vegetation unburnt for at least 3 years compared with vegetation burnt immediately prior to sowing and this difference was ascribed to desiccation (Cowling and Lamont 1987, Zammit and Westoby 1988). Similar differences in seedling mortality have also been ascribed to desiccation in a diverse range of species and habitats: epacridaceous shrubs and restionaceous sedges in heathland (Meney et al. 1994); numerous eucalypt and understorey species in temperate woodlands (Purdie 1977b, Withers 1978, Auld 1987a, Davies and Myerscough 1991, Tozer unpubl.); and mallee eucalypts and shrubs in semi-arid shrublands (Wellington and Noble 1985a,b, Bradstock 1989). In all cases few or none of the seedlings in unburnt vegetation survived the first summer after emergence, while a larger but variable fraction survived to become established in recently burnt vegetation. Predation is another cause of seedling mortality that appears to have a greater impact in unburnt conditions than after a recent fire (Purdie 1977b, Wellington and Noble 1985a,b, Bradstock 1989). Similar fire-mediated predator satiation may operate on newly emerged seedlings to that described below for post-dispersal seeds (see text on Mechanism 5c).

Some species are apparently capable of spontaneous seedling establishment in ‘mature’ unburnt communities at rates that may be sufficient to prevent population declines through Mechanism 3a (Table 1). Ashton (1976) recorded substantial recruitment of woody understorey species, notably *Coprosma quadrifida* and *Cyathea australis*, between 28 and 48 years post-fire in a regenerating south-eastern Australian forest. This appears to be a common phenomenon among rainforest elements in the understoreys of wet eucalypt forests (Webb 1968, Ashton 1976, Ashton and Frankenberg 1976, Read and Hill 1988). Similarly, Abbott (1985) observed continuous recruitment of seedlings of *Banksia grandis* in wet eucalypt forests of south-western Australia, apparently at a rate sufficient for populations to persist in the absence of fire. Species of *Allocasuarina* and *Acacia* are apparently capable of persistence by continual recruitment in the absence of fire, even though growth rates are 1.5 to 5 times slower than in burnt sites (Withers and Ashton 1977, Withers 1978). In tropical savanna woodlands seedling recruitment occurs seasonally and independent of fire in annual grasses (e.g. Andrew and Mott 1983, Mott and Andrew 1985) and some trees and shrubs (Price and Bowman 1994). Spontaneous recruitment appears to be very uncommon in heathlands. *Leptospermum laevigatum* is able to recruit seedlings and invade heathland in the absence of fire, however, its establishment may be aided by other forms of disturbance such as grazing and past clearing activities (Burrell 1981, Bennett 1994). Indeed, Australian heathlands, appear to be unique among temperate heathlands globally, in having very few woody species able to recruit seedlings in the absence of fire (Keeley 1995).

The senescence of dominant plants in a community may create conditions suitable for seedling establishment where this is otherwise limited in ‘mature communities’ by scarcity of light and space. Data on the dynamics of long unburnt plant populations in Australian fire-prone habitats are scarce but there is evidence for seedling recruitment into small gaps caused by senescence in rainforests (Webb 1968), eucalypt forests (Abbott 1985) and woodlands (Withers 1978, 1979), lowland heaths (Witkowski et al. 1991), subalpine heaths (Williams and Ashton 1988) and grasslands (Tremont and McIntyre 1994, Morgan in press). Nonetheless, for the majority of species in these habitats except rainforests, recruitment that may occur in long unburnt stands is unlikely to be sufficient to replace spontaneous deaths of standing plants (e.g. Withers 1978,1989, Ashton 1981, Gill and McMahon 1986, Bradstock and O'Connell 1988, Williams and Ashton 1988, Bradstock 1990, Witkowski et al. 1991, Burgman and Lamont 1992).

The relationship between the occurrence of fire and vegetative recruitment in clonal species (Fig. 1) may be analogous to that between fire and seedling recruitment. Few data exist on this topic, but there is evidence of increased vegetative recruitment after fire in *Pteridium esculentum* (Tolhurst and Oswin 1992, Tolhurst and Burgman 1994) and members of the Haemodoraceae (Lamont and Runciman 1993). In *P. esculentum*, vegetative recruitment appears to increase with fire frequency, since the annual rate of recruitment decreases with time since fire. Vegetative recruitment is influenced by fire season, increases in recruitment being greater and sustained for longer after spring fires than after autumn fires (Tolhurst and Oswin 1992). However, it is not known whether exclusion of fire over a long period results in continued decline in density and eventual elimination of any species dependent on vegetative recruitment. Thus, further research is necessary to determine the applicability of Mechanism 3a (Table 1) to clonal species.

Mechanism 3b

The role of soil moisture in seedling mortality (e.g. Wellington and Noble 1985a, Cowling and Lamont 1987, Bradstock and O'Connell 1988), suggests that opportunities for seedling recruitment may be constrained not only by the occurrence of fire, but the weather conditions that follow it. Population declines and extinctions are likely where fires are followed by dry conditions in the first year, curtailing the rate of recruitment (Mechanism 3b, Table 1). The likelihood of conditions unfavourable to seedling establishment is influenced by season of fire (on average, declines are more likely in response to winter and spring fires than fires in other seasons), as well as year to year variations in weather and fine-scale spatial variability in availability of moisture and nutrients.

Several authors have emphasised the stochastic nature of the relationship between the occurrence of fire, post-fire rainfall and seedling recruitment (Bradstock and Bedward 1992, Burgman and Lamont 1992). The coincidence of events when a fire is followed by a sequence of seasons suitable for germination and seedling establishment is likely to be rare in some habitats. Wellington and Noble (1985a), for example, estimated that recruitment of *Eucalyptus incrassata* occurred after only about 10% of fires. In south-western Australia where there is a predictable mean winter maximum rainfall, seedling recruitment varies substantially in response to fire season. Seedlings emerging after fires in spring are exposed to hot dry conditions at a younger age than those emerging after fires in summer or autumn and consequently suffer greater rates of mortality (Cowling and Lamont 1987, Cowling et al. 1990, Hobbs and Atkins 1990, Lamont et al. 1991). A similar trend has been demonstrated in South Africa (Bond et al. 1984). However in eastern Australia, where rainfall is less predictably seasonal and has a mean summer maximum, the response of recruitment to fire season, although still evident, is weaker (Clark 1988, Hodgkinson 1991, Tolhurst and Oswin 1992, Bradstock and Bedward 1992, Whelan and Tait 1995). As a consequence, fires in summer and autumn may sometimes be less favourable to seedling recruitment than fires in winter and spring (e.g. Noble 1989, Whelan and Tait 1995), even though the reverse is more usually true. Factors that influence the timing of seed release and germination may also offset seasonal effects on desiccation of seedlings. Cowling and Lamont (1985b) suggested that wet–dry cycles had a role in regulating the season of seed release after fire. Wet–dry cycles resulted in greater seed release under cool ambient temperatures (15–20°C) than warm temperatures (c. 20°C), so that more rapid seed release would be expected in autumn than in spring or summer (Cowling and Lamont 1985b, Enright and Lamont 1989a). Secondary dormancy mechanisms related to ambient temperature may have a similar role (e.g. Andrew and Mott 1983, Mott and Andrew 1985, Bradstock and Bedward 1992).

An analogous relationship may exist between spatial variability in resource supply and the establishment and maturation of seedlings. Sites with locally abundant supplies of moisture or nutrients may favour higher rates of seedling establishment (Tongway et al. 1989, Tongway and Ludwig 1990) and maturation (Keith unpubl. data) and thus act as important refuges or core habitat for plant populations under adverse fire regimes. In some cases, however, the advantages to growth and maturation in resource-rich patches may be offset by other interactions such as competition (Morris and Myerscough 1988, Lamont et al. 1993).

Mechanism 3c

Certain fire regimes or even single fire events may modify some landscapes in a way that makes them no longer suitable for habitation by certain plant species, particularly through the prevention of seedling establishment (Mechanism 3c, Table 1). Fires associated with habitat change may also cause extreme mortality in all life stages of the population (Mechanism 1a, Table 1), resulting in sudden and long-lasting local extinctions. The fire regime itself may change physical characteristics of the habitat either directly, or in concert with other events such as erosive rainfall (Table 1). The best examples of this mechanism of extinction come from habitats where fire may be a rare phenomenon such as peatlands, alpine vegetation, rainforests and, to a lesser extent deserts.

Peat fires may expose coarse gravel or rocky substrates largely unsuitable for seedling establishment (Wein 1981), at least in certain species. Removal of peat also holds consequences for the nutrient status and water retention capacity of remaining soil, which may affect seedling establishment. These habitat changes may be compounded by further soil losses from the erosive effects of subsequent rainfall and frost heave (Wein 1981). Landscapes subjected to such fires may thus remain uninhabitable to certain plants over long time scales. The consequences of habitat change by peat fires has received some attention in the northern hemisphere (e.g. Tallis 1987, Maltby et al. 1990), however, data for Australian peat landscapes are scarce (Wein 1981).

Several coniferous species and *Nothofagus gunnii* have been eliminated from Tasmanian alpine vegetation by catastrophic fires within the last 40 years (Kirkpatrick and Dickinson 1984). These species generally failed to re-establish at the burnt sites, despite availability of seed in adjacent unburnt stands. Similarly, Podger et al. (1988) described the elimination of Tasmanian rainforest dominated by *Phyllocladus aspleniifolius* and *Agastachys odorata* by a single fire in 1881 and its subsequent replacement by sedgeland. Palynological evidence suggests there may be many instances where catastrophic elimination of alpine conifers, *N. gunnii* and species of cool temperate rainforest is not followed by re-establishment, despite fire-free periods of decades or centuries (e.g McPhail 1979, 1981). Failure of these species to re-establish has been attributed partly to soil degradation through erosion and loss of peat and nutrients, partly to poor dispersal of seeds and partly to competitive exclusion by shorter-lived shrub species (Kirkpatrick and Dickinson 1984). However, the relative roles of these factors are not known and require experimental investigation.

There is circumstantial evidence that fires may also mediate extinctions through habitat change (Mechanism 3c, Table 1) in tropical and arid environments. In arid rangelands, mulga (*Acacia aneura*) occupies groves where soils are deeper and more fertile than those occupied by hummock grasses (*Triodia* spp.) (Tongway and Ludwig 1990, Bowman et al. 1995). Bowman et al. (1995) suggested that soil erosion resulting from severe fire followed by intense rain may convert stands of mulga to grassland by creating unsuitable soil conditions for establishment of the former. Stands of tropical monsoon forest have apparently been eliminated by fire regimes involving frequent and/or intense fires (Russell-Smith 1985). Repeated fires cause weakening and eventual death of the dominant tree, *Allosyncarpia ternata*, and its replacement by more flammable grasses and shrubs (Russell-Smith and Dunlop 1987). Conversely, expansion of *A. ternata* into surrounding savanna is thought to be very slow due to intolerance of its seedlings to exposed microclimates and fire (Russell-Smith and Dunlop 1987).

Mechanism 3d

Fire regimes may influence decline of plant populations through high seedling mortality caused by post-fire predation (Mechanism 3d, Table 1). By triggering a transition to seedlings, fires transform the structure of plant populations into a state that is predisposed to much higher levels of mortality than they would otherwise experience because seedlings and vegetative recruits are generally more palatable and more accessible to predators and have less capacity for recovery from herbivory than foliage of established plants (Cremer 1969, Purdie 1977b, Leigh and Holgate 1979, Dickinson and Kirkpatrick 1986, Leigh et al, 1987, Wimbush and Forrester 1988). The extent to which these effects may be offset by predator satiation and post-fire reduction of predator populations is apparently influenced by characteristics of fire behaviour (see text on Mechanism 5c).

Greater losses to predation may be expected after fires, such as those with low scorch heights and little soil heating, that result in relatively low levels of seed release or seedling emergence, since predator populations are less likely to be satiated. The size and patchiness of the burnt area also appears to be an important factor influencing the impact of predation. Predators are more likely to congregate in high densities and may forage more exhaustively within post-fire vegetation when the area burnt is small and/or patchy than when the area burnt is large and/or less patchy. Small, patchy, low intensity fires have been shown to cause greater mortality of seeds (Mechanism 2d, Table 1), seedlings and vegetative regrowth (Mechanism 3d, Table 1) than after larger, less patchy, high intensity fires as a consequence of both invertebrate (Whelan and Main 1979) and vertebrate (Dickinson and Kirkpatrick 1986, Whelan 1986) predators in forests, woodlands and heathlands. However, it is important to emphasise the highly variable nature of predation (Lowman 1985) which limits the portability of research findings between species, sites and different times (Williams et al. 1994, Whelan et al. this volume). Factors that influence variability in predation are inadequately investigated and include palatability and quantity of food availability, the timing and spatial pattern of food availability, the availability and palatability of alternative food sources, weather and social behaviour of the predators (e.g. Ashton 1979, Andersen and Ashton 1985, Lowman 1985, Lowman and Heatwole 1987, Landsberg 1988, Andersen 1989).

Interruption of Maturation and Developmental Growth

There are two mechanisms of population decline and extinction whereby fire regimes interrupt the transfer of individuals from the juvenile life stage to the mature stage (Fig. 1). They involve the effect of frequent fire, respectively, on obligate seeders (Mechanism 4a, Table 1) and resprouters (Mechanism 4b, Table 1).

Mechanism 4a

The rate at which seed banks are replenished after fire depends on the time required for seed production to commence and the subsequent rate of seed production. Gill (1975) distinguished the time required for post-fire seedlings to mature and produce their first flowers, the 'primary juvenile period', from the time required for pre-fire plants that survive complete leaf scorch to recommence flowering, the 'secondary juvenile period'. Both primary and secondary juvenile periods vary between and within species. In resprouters, the primary juvenile period is generally longer than the secondary juvenile period (Bradstock and Myerscough 1988, Keith 1991). In general, primary juvenile periods are longer for woody species than herbaceous species (Benson 1985b, Keith 1991) and longer for woody resprouters than woody obligate seeders (Bradstock 1990, Keith 1991, Auld unpubl. data). Primary juvenile periods of obligate seeders range from less than six months for herbs such as *Gonocarpus micranthus* (Keith 1991) up to twenty years for trees such as *Eucalyptus regnans* (Ashton 1976), while secondary juvenile periods are less variable (Table 3).

TABLE 3

Primary (1) and secondary (2) juvenile periods for selected plant species. (Acacia species in mallee examined by Bradstock (1989) include A. rigens, A. wilhelmiana, A. brachybotrya and A. havilandii).*

Species	Habit	Juvenile Period (yrs)	Source
Obligate Seeders			
Acacia spp. (mallee)*	shrub	2–4 (1)	Bradstock 1989
Acacia myrtifolia	shrub	3 (1)	Keith 1991
Acacia suaveolens	shrub	1 (1)	Auld and Myerscough 1986
Cryptandra ericoides	shrub	3 (1)	Benson 1985b, Keith 1991
Eucalyptus regnans	tree	15–20 (1)	Ashton 1976
Banksia ericifolia	shrub	5 (1)	Bradstock and O'Connell 1988
		7–8 (1)	Benson 1985b
Callitris verrucosa	tree	11–13 (1)	Bradstock 1989
Dillwynia floribunda	shrub	3 (1)	Keith 1991
Dillwynia retorta	shrub	5 (1)	Benson 1985b
Epacris microphylla	shrub	5 (1)	Keith 1991
Epacris obtusifolia	shrub	3 (1)	Keith 1991
Epacris pulchella	shrub	6 (1)	Benson 1985b
Eriostemon buxifolius	shrub	5 (1)	Benson 1985b
Gonocarpus micranthus	herb	0.5 (1)	Keith 1991
Gonocarpus teucrioides	shrub	2–4 (1)	Benson 1985b
Grevillea buxifolia	shrub	8 (1)	Benson 1985b
Hemigenia purpurea	shrub	2 (1)	Benson 1985b
Leptospermum laevigatum	shrub	5 (1)	Burrell 1981
Mitrasacme polymorpha	shrub	2–3 (1)	Benson 1985b
Opercularia varia	herb	2 (1)	Keith 1991
Petrophile pulchella	shrub	4 (1)	Bradstock and O'Connell 1988
		6–9 (1)	Benson 1985b
Poranthera ericifolia	herb	1 (1)	Benson 1985b
Triodia irritans	grass	3–5 (1)	Bradstock 1989
Woollsia pungens	shrub	3 (1)	Benson 1985b
Resprouters			
Aotus ericoides	shrub	>5 (1), 3 (2)	Keith 1991
Banksia oblongifolia	shrub	>17 (1), 2 (2)	Keith 1991
		>23 (1), 1–2 (2)	Zammit and Westoby 1987b
Boronia parviflora	shrub	>5 (1), 1 (2)	Keith 1991
Epacris paludosa	shrub	5 (1), 1 (2)	Keith 1991
Eucalyptus obstans	shrub	>15, 4 (2)	Keith (unpubl.)
Goodenia dimorpha	herb	>6 (1), 1 (2)	Keith 1991
Isopogon anemonifolius	shrub	>7 (2), 2 (2)	Keith 1991
Melaleuca uncinata	shrub	15–20 (1), 5–7 (2)	Bradstock 1989
Mitrasacme polymorpha	herb	5 (1), 1 (2)	Keith 1991
Xanthorrhoea resinifera	shrub	>21 (1), 1 (2)	Keith (unpubl.)

Seed production may reach a peak rapidly after maturation and then decline, or build gradually from low levels to a maximum over several seasons. Contrasting examples include: *Acacia suaveolens*, in which seed production reaches a maximum of 10–21 fruits per plant per year at age 2–3 years and declines asymptotically to less than 4 fruits per plant in 14–16 year-old plants (Auld and Myerscough 1986); and *Banksia cuneata* which reaches maturity at five years of age, establishes a modest seed bank (average of 18 seeds per plant) between ages five and 12 and builds a superabundant seed bank (over 17 000 seeds per plant) by age 25 (Lamont et al. 1991).

Primary juvenile periods and rates of seed production vary between populations within species according to environmental conditions, particularly habitat productivity and post-fire rainfall. In general, longer juvenile periods and slower rates of subsequent fruit production are associated with less productive habitats and low levels of post-fire rainfall than the reverse conditions (Bradstock and O'Connell 1988, Cowling et al. 1990, Keith unpubl. data).

Decline and elimination of plant populations whose fruit production is interrupted by frequent fires (Mechanism 4a, Table 1) has been documented in a wide range of fire-prone habitats (Gilbert 1959, Jackson 1968, Ashton 1976, Siddiqi et al. 1976, Gill 1981, Benson 1985b, Fox and Fox 1986, Nieuwenhuis 1987, Bradstock and O'Connell 1988, Lamont and Barker 1988, Burgman and Lamont 1992, Morrison et al. 1995, Gill and Bradstock 1995, Cary and Morrison 1995). The rate of decline will be most rapid, possibly resulting in local extinction after a single short fire interval, in populations in which all standing plants are killed when scorched and in which the seed bank is completely exhausted by a single fire. The best-known examples of this response are obligate seeders with serotinous seed banks such as *Eucalyptus regnans, Hakea teretifolia, Banksia ericifolia, B. prionotes, B. leptophylla, B. cuneata, Allocasuarina distyla* and *Leptospermum laevigatum* (Ashton 1976, Siddiqi et al. 1976, Burrell 1981, Niewenhuis 1987, Bradstock and O'Connell 1988, Lamont et al. 1991, Pannell and Myerscough 1993, Morrison et al. 1995, Cary and Morrison 1995).

If some proportion of the pre-fire standing plant population survives fire (as in resprouters) or if some proportion of the seed bank remains dormant after fire, then decline that results from interruption of seed production by frequent fire (Mechanism 4a, Table 1) is likely to be less rapid than in populations without these characteristics. Populations of resprouters are rarely eliminated by a single short fire interval, but may decline at a slower rate if deaths of established plants are not replaced by new recruits (Fig. 1, see below). The retention of residual post-fire seed banks may be another buffer against short-term elimination by fires that occur frequently enough to preclude or limit seed production (Noble and Slatyer 1980). In general, serotinous seed banks are completely exhausted by a single fire (e.g. Gill and McMahon 1976, Bradstock and Myerscough 1981, O'Dowd and Gill 1984). In contrast, a residual proportion of soil seed banks may be retained in a dormant state, depending on penetration of heat and smoke derivatives during and after fire, thus providing a capacity for seedling recruitment after a subsequent fire even if no new seeds are produced (Auld 1987a, Auld and O'Connell 1991, Dixon et al. 1995). However, some species with soil seed banks apparently retain few viable seeds after fire (Meney et al. 1994) or at certain times of their annual cycle (Morgan 1995a) and may therefore have limited potential for recovery even if a single short fire interval is followed by longer intervals.

Mechanism 4b

In resprouters and fire tolerators, the time it takes for seedlings to develop fire resistant structures (lignotubers, thick bark, rhizomes, protective leaf bases, corms, buried buds, etc.) is demographically analogous to the primary juvenile period in obligate seeders. If successive fires occur at intervals of less than this duration, then new recruits to the population will be killed without contributing to future generations. Thus population size will decline if recruitment is insufficient to replace deaths of established plants (Mechanism 4b, Table 1).

Vegetative structures that enable resprouting and fire tolerant plants to survive the passage of a fire may remain undeveloped for several years during the juvenile stage of the life cycle, leaving the plants vulnerable to fire during this period (Fig. 1). A positive relationship between post-fire survival and lignotuber size has been demonstrated in species of *Eucalyptus, Banksia, Isopogon, Angophora* and *Telopea* (Noble 1984, Bradstock and Myerscough 1988, Auld 1990, Bradstock 1995). Bradstock and Myerscough (1988) found that juveniles of *B. serrata* and *I. anemonifolius* failed to survive fire if their lignotubers were less than 4 cm and 2 cm diameter, respectively. The fastest growing lignotubers of *B. serrata* reached this critical size at age 5–7 years and a large proportion were predicted to reach it by age 10 years (Table 4, Bradstock and Myerscough 1988). However, in *I. anemonifolius* no 5 year-old juveniles survived fire and only a small proportion of lignotubers were predicted to reach their critical size for survival by age 15 years (Table 4, Bradstock and Myerscough 1988). Observations on other species fall within this range (Table 4), suggesting that the development of fire-resistant lignotubers in a significant proportion of a seedling cohort takes between 6 and 15 years. Observations and inferences of some authors (e.g. Henry and Florence 1966, Zammit and Westoby 1987b) suggest more rapid lignotuber development in some species, however their data do not allow direct comparison with values in Table 4.

TABLE 4

Post-fire survival in juvenile and adult plants of woody species. Age is in years and corresponds to time since previous fire except in T. speciosissima *where 1-and 6-year old cohorts emerged 3 years after previous fire. The age of juveniles of* E. dalrympleana, E. dives *and* E. pauciflora *is not known, but the previous fire was >45 years before the experimental burn. Size is diameter of lignotuber (cm) for all species except* X. resinifera, *number of leaves. Fire severity: low — scorch and partial consumption of ground fuel and shrub foliage; high — complete consumption of ground fuel and shrub foliage. Response based on observed samples except * predicted from size of smallest survivor and mean growth rate (see Bradstock and Myerscough (1988) for method). Sources: Noble (1984) for* E. dalrympleana, E. dives *and* E. pauciflora*; Bradstock and Myerscough (1988) for* B. serrata *and* I. anemonifolius*; Auld (1990) for* A. hispida*; Bradstock (1995) for* T. speciosissima*; and Keith (unpubl. data) for* B. oblongifolia, E. obstans *and* X. resinifera.

Species	Age	Size	Fire severity	Response
Angophora hispida	9	1–3	low	37% survived (n = 27)
Banksia oblongifolia	5	1–3	high	12% survived (n = 188)
Banksia serrata	5–7	<4	low–high	nil survived (n = 13)
	5–7	4–5	low	100% survived (n = 3)
	10	>5	low–high	most survived*
Eucalyptus dalrympleana	?	?	high	63% survived (n = 35)
Eucalyptus dives	?	?	high	59% survived (n = 59)
Eucalyptus obstans	5	0.5–1	high	<1% survived (n = 126)
Eucalyptus pauciflora	?	?	high	59% survived (n = 49)
Isopogon anemonifolius	5–7	<0.5	low–high	nil survived
	10	c. 1	low	nil survived*
	15	c. 2	low	small proportion survived*
Telopea speciosissima	1		high	nil survived (n = 93)
	6		high	22% survived (n = 50)
Xanthorrhoea resinifera	5	1–4	high	38% survived (n = 141)

Few data are available for species with other kinds of recovery organs. In *Xanthorrhoea*, recovery is by continued growth of an apical shoot that is insulated from heat by crowded leaf bases and, in subterranean species, soil. After germination the apical shoot is drawn below the soil surface by contractile roots. Gill (1981) estimated the rate of downward movement to be up to 1 cm per month in cultivated seedlings of *X. australis*. The rate at which apical buds of juvenile plants are drawn down in the field is likely to be slower. However, this mode of recovery may be attained more quickly than development of lignotubers in woody dicotyledonous species. Survival in five year-old cohorts of *X. resinifera* plants was 38% after a fire that consumed all ground fuel and shrub foliage (Table 4). As discussed earlier, some arborescent obligate seeders may survive fires passively by avoiding exposure of tissues to lethal temperatures through development of thick bark and an arborescent habit (see text on Death of Standing Plants and Seeds). The rate at which juveniles develop sufficient bark thickness and canopy height to tolerate fires of various scorch heights is not known, but likely to be more than a decade.

The response of resprouters to frequent fire regimes (Mechanism 4b, Table 1) is analogous to decline of populations of obligate seeders under frequent fire (Mechanism 4a, Table 1), but differs in two important aspects. First, comparison of values in Tables 3 and 4 indicate that seedlings of obligate seeders become reproductive earlier than seedlings of resprouters develop fire-resistant structures. Thus, fire regimes that involve fire intervals long enough to maintain stable populations of most obligate seeders may still cause declines in populations of resprouters, at least woody species. For example, under recurring fire intervals of 10–12 years populations of *Isopogon anemonifolius*, a resprouter, are predicted to decline (Bradstock 1990), while populations of *Petrophile pulchella*, a co-occurring obligate seeder, are likely to remain stable or increase (Bradstock and O'Connell 1988). Second, rates of decline are likely to be slower in resprouters than obligate seeders and are more likely to be reversed by a single long fire interval that provides a window of opportunity for recruitment (Bradstock 1990). This is because the pool of established plants that survive fires in resprouters provide a capacity for population recovery that is not present in obligate seeders, even though this pool may diminish rapidly when high fire frequency is sustained (see text on Death of Standing Plants and Seeds). The nature of these differences between the responses of resprouters and obligate seeders to frequent fire regimes has lead to the perception that resprouters are generally more resilient to frequent fire than obligate seeders (e.g. Zammit and Westoby 1987b, Fox and Fox 1986). Indeed, most of the fire-driven extinctions reported in the literature involve elimination of obligate seeders by frequent fire regimes (Gill and Bradstock 1995). However, this may in part reflect an observational bias, since elimination of obligate seeders involves a mechanism often causing abrupt decline, whereas declines of resprouters are likely to involve time scales beyond the scope of many ecological studies.

Failure of Seed Bank Accumulation

Seed bank accumulation involves the transfer of individuals from the mature stage to the seed stage (Fig. 1). When a seed bank fails to accumulate, seedling recruitment may be limited and a plant population may decline at a rate determined by the death rate among standing plants. Fire regimes may influence such declines directly through the role of fire as a cue for seed production, or indirectly through an interaction with predation during and after production and release of seeds. In the first instance seed production may be limited by infrequent fire regimes (Mechanism 5a, Table 1) or by fires that occur consistently in seasons that do not provide the appropriate cue to stimulate mass flowering (Mechanism 5b, Table 1). In the second instance, a high proportion of seeds produced may be consumed by predators after fires of low intensity, high patchiness or limited spatial extent (Mechanism 5c, Table 1).

Mechanism 5a

The passage of a fire stimulates flowering and subsequent seed production (Fig. 1) in a range of plant species that also have transient seed banks, whereby seeds either germinate soon after their release or lose viability in a short time (Gill 1981, Auld 1994). In some of these species flowering is extremely restricted in the absence of fire so that opportunities for seedling recruitment are essentially constrained to a short period after post-fire seed release (Gill and Ingwerson 1976, Lamont and Downes 1979, Auld 1987b, Lamont and Runciman 1993, Johnson et al. 1994, Lunt 1994, Bradstock 1995). When fires occur infrequently, there will be few opportunities for flowering and seedling recruitment so that populations will decline at a rate determined by mortality among standing plants (Mechanism 5a, Table 1). This type of decline is analogous to that which occurs in response to low frequency fire regimes in species whose seed release or germination is cued to fire (Mechanism 2a).

Many of the Australian species that may be affected by such declines are from monocotyledonous families, although a few dicotyledonous taxa also have essentially obligate pyrogenic flowering (Table 5, Gill 1981). On other continents, pyrogenic flowering is well represented among geophytic members of the Amaryllidaceae, Iridaceae, Liliaceae (*sensu lato*) and Orchidaceae (Kruger 1977) in South Africa and in the Poaceae of North America (e.g. Daubenmire 1968) and New Zealand (e.g. Rowley 1970).

TABLE 5

Resprouting plant species in the Sydney region that flower abundantly only after fire. See Gill (1981) for further examples.

Species	Family	Source
Angophora hispida	Myrtaceae	Auld 1987b
Baumea teretifolia	Cyperaceae	Keith 1991
Baumea rubiginosa	Cyperaceae	Keith 1991
Blandfordia nobilis	Phormiaceae	Keith 1991, Johnson et al. 1994
Chorizandra cymbaria	Cyperaceae	Keith 1991
Chorizandra sphaerocarpa	Cyperaceae	Keith 1991
Cyathochaeta diandra	Cyperaceae	Keith 1991
Deyeuxia decipiens	Poaceae	Keith 1991
Drosera binata	Droseraceae	Keith 1991
Genoplesium filiforme	Orchidaceae	Keith, unpubl. obs.
Haemodorum corymbosum	Haemadoraceae	Keith 1991, unpubl. data
Lepidosperma neesii	Cyperaceae	Keith, unpubl. data
Lomatia silaifolia	Proteaeae	Keith 1991
Prasophyllum australe	Orchidaceae	Keith 1991
Prasophyllum brevilabre	Orchidaceae	Keith 1991
Prasophyllum elatum	Orchidaceae	Keith, unpubl. obs.
Ptilothrix deusta	Cyperaceae	Keith 1991, unpubl. data
Telopea speciosissima	Proteaceae	Pyke 1983, Bradstock 1991
Villarsia exaltata	Menyanthaceae	Keith 1991
Xanthorrhoea media	Xanthorrhoeaceae	Keith, unpubl. data
Xanthorrhoea resinifera	Xanthorrhoeaceae	Keith 1991, unpubl. data

The fire-related cues that stimulate flowering may vary among species, and apparently include ash bed effects, hormonal responses brought on by leaf removal or ethylene, and release from the effects of neighbouring plants and litter. In *Xanthorrhoea australis* 67–87% plants were stimulated to produce inflorescences when subject to burning, leaf clipping or exposure to ethylene (a constituent of smoke and product of injured tissues) relative to 37% in untreated plants (Gill and Ingwerson 1976). In some other *Xanthorrhoea* species fruit production is close to zero at post-fire periods of greater than

2 years (Keith unpubl. data). In *Blandfordia nobilis* post-fire inflorescence production was greatest in the first post-fire year (50–68% plants flowering) and diminished over 3–4 years and correlated with changes in soil chemistry (Johnson et al. 1994). In *Anigozanthos pulcherrimus* and *Macropidia fuliginosa* flowering was enhanced experimentally in the field by burning or by fertiliser application, and to a lesser extent by leaf clipping and clearing of adjacent litter and plant material, relative to untreated controls, but flowering was not enhanced by application of ash or heat (Lamont and Runciman 1993). Inflorescence production was greatest in the first year after fire (10–70% culms flowering) and declined sharply to negligible levels after five years (Lamont and Runciman 1993). Daubenmire (1968) and Rowley (1970) ascribed increased flowering after fire in North American prairie grasses and New Zealand snow grass, respectively, to elevated ambient temperature experienced by stem apices during the summer floral inductive period, decreased shading and increased tillering.

Mechanism 5b

Fire regimes that involve a succession of cool-season fires may fail to stimulate prolific flowering in some species, or at least delay flowering and seed release until the second post-fire year. If these 'sub-optimal' flowering events result in seedling recruitment at insufficient levels to replace losses of established plants, then a population will decline (Mechanism 5b). This mechanism of decline and extinction remains largely uninvestigated, particularly in geophytic species that remain as dormant subterranean vegetative propagules unless stimulated to emerge and flower by the passage of a fire (e.g. Jones 1988). For these species, further research is needed to test expected declines, which may be slow and cryptic.

Gill (1981) reported an experiment on *X. australis* showing that inflorescence production in the first post-fire year was greater in response to fires in November and February than in response to fires in May and August. However, many more plants in the latter treatments flowered in their second post-fire year. Thus, the principal difference between treatments was that flowering in most plants was delayed by one year after a cool-season fire compared with a warm-season fire. The delay in seed availability may have implications for seedling establishment (see text on Failure of Seedling Establishment). Experimental observations on *X. media* show that more plants were stimulated to flower in the first two years after a fire in January than in the first two years after a fire in October (Keith, unpubl. data). A prolific flowering response in the South African iris, *Watsonia pyramidata* (>50% ramets flowering), occurred in response to autumn and possibly late summer fires, but not in response to spring fires (Kruger 1977). After spring fires, flowering remained at levels typical of unburnt vegetation (c. 5% of ramets flowering) or less.

Mechanism 5c

Predation may limit the number of viable seeds in the seed bank even in cases where the production of large quantities of seed may have been initiated. When predation consistently limits the availability of seed for germination and recruitment, a population may decline at a rate determined by the death rate of standing plants (Fig. 1). Fire regimes may affect the impact of predation on seed availability by influencing the relative abundance of predators and their food source (Mechanism 5c, Table 1).

The passage of certain fires that maximise the quantity of seed released relative to predator abundance may be critical in the avoidance of this mechanism of decline in many plant species whose spontaneous rate of production or release of seeds is small compared with the maximum post-fire rate or where the post-fire rate of seed production and release varies depending on aspects of fire behaviour. Species potentially affected have palatable seeds and include those with serotinous seed banks, those with a pyrogenic flowering response and some short-lived obligate seeders whose germination and emergence is constrained by the timing of fire (e.g. Pate et al. 1985). In such cases predator populations may be satiated by a superabundance of seeds caused by massive post-fire seed release, allowing greater numbers to escape predation and germinate than in unburnt conditions (Ashton 1979, O'Dowd and Gill 1984, Auld and Myerscough 1986, Andersen 1988). A similar outcome (i.e. temporary increase in edible seeds per predator) may be achieved if fire reduces the density of predator populations. This appears to be the case in species of Lepidoptera (Friend 1995), some of which, in their larval stage, are pre-dispersal predators of developing seeds and fruits (Gill 1981 and unpubl., Zammit and Hood 1986, Lamont and van Leeuwin 1988, Wallace and O'Dowd 1989).

When seeds are released spontaneously, the availability of seeds more closely matches the ability of predators to consume them because seed release occurs at a slower rate than immediately after the passage of a fire (O'Dowd and Gill 1984, Auld 1987b, Bradstock and O'Connell 1988, Bradstock 1990, Witkowski et al. 1991, Lamont et al. 1991). Rates of seed removal by predatory animals in unburnt vegetation vary up to 100% within a few days of experimental placement and have been shown in a variety of species and habitats to be significantly greater than rates of removal immediately after certain fires (Ashton 1979, O'Dowd and Gill 1984, Abbott and van Heurck 1985, Andersen and Ashton 1985, Wellington and Noble 1985b, Andersen 1988, Auld 1995a, Pannell 1995). The effect of predation is thus to strengthen the dependence of recruitment on fire-related cues for flowering (Mechanism 5a and 5b, Table 1), as well as seed release and germination (Mechanisms 2a–2d, Table 1).

Fires may vary in the extent to which predator satiation is effected, depending on fire characteristics. Greater losses to predation may be expected after fires with low flame heights, little soil heating and patchy spatial pattern because such fires result in relatively low levels of seed release and germination so that predator populations are less likely to be satiated. While empirical evidence for this effect refers primarily to seedlings and vegetative recruits (Whelan and Main 1979, Whelan 1986, Dickinson and Kirkpatrick 1986), analogous effects involving seeds have been inferred (Gill 1981, Bradstock and Bedward 1992, Auld et al. 1993) and warrant further investigation.

Other Mechanisms of Decline and Extinction

There may be other mechanisms of plant population decline and extinction related to fire regimes that are, at present, poorly known. Some of these may involve complex biological interactions between plants, other organisms and fire, such as mutualistic relationships (e.g. Lamont 1995) and pathogenic relationships (e.g. Shea 1979, Keith 1995a).

Lamont (1995) described mutualistic relationships in eucalypt forests between fungi, terrestrial marsupials and woody understorey plants that were mediated by fire. Seedling growth of various shrub species is curtailed in the absence of the fungi which form mycorrhizae enhancing uptake of nutrients. Dense groves of these shrubs provide essential shelter for marsupials, which also depend on the sporocarps of the fungi for a food source, particularly after fire. The fungi, whose sporocarps are subterranean, depend on the marsupials for spore dispersal and possibly for digestive pretreatment for spore germination. The fungi also depend on their plant hosts for organic nutrition. Fires interact with all components of this partnership: the canopies of shrubs are consumed; fungal mycelia in the litter layer are consumed; soil seeds are stimulated to germinate and fungi may be stimulated to sporulate; a proportion of the marsupial population may be killed; but their enhanced foraging activity in the days after fire disperses fungal spores and enhances inoculation of post-fire seedlings which grow rapidly to restore shrub cover (Lamont 1995). Clearly, fire regimes that cause declines in any one component of the partnership (e.g. through poor germination of soil seed, high levels of marsupial mortality, etc.) may also cause declines in populations of the other organisms.

Pathogenic interactions are another mechanism of decline or extinction of plant populations that is potentially influenced by fire. The introduced pathogenic root-rot fungus, *Phytophthora cinnamomi*, causes high levels of mortality among some tree and shrub species in temperate Australia (Weste and Marks 1987). It has been suggested that the impact of the pathogen may be controlled by reducing the abundance of its major hosts (Shea 1979). Abbott (1985) and Burrows (1985) have explored how populations of one such host, *Banksia grandis*, may be reduced through management of fire regimes. Conversely, Burdon (1991) argued that there is little possibility of any susceptible plant species escaping disease through low density because of the pathogen's extreme aggressiveness, wide host range and persistence in the soil after invasion. It has also been suggested that the timing of fire after invasion is critical to the recovery of species with soil seed banks (Keith 1995a). Soil seed banks may provide a 'refuge' in which some individuals of a population evade death during the initial phase of the disease epidemic. With time after invasion, the abundance of the pathogen and hence its effects on standing plants apparently decline (Weste and Ashton 1994). The passage of a fire after decline of the pathogen population, but before soil seed is lost through senescence, may allow replenishment of the standing plant population by stimulating germination from the soil seed bank (Keith 1995a). The interactions between fire regimes, plant populations and their fungal pathogens clearly warrant more research.

VEGETATION DYNAMICS AT HIGHER LEVELS OF ORGANISATION

Whole Plant Populations, their Habitats and Associated Species

Much of the preceding discussion has focussed on processes that operate within various parts of the plant life cycle (Fig. 1, Table 1). These processes do not act independently of one another and, at higher levels of organisation, this has consequences in physical and biotic environments that are heterogeneous in space and time. Explicit mathematical models and computer simulations (see below) are powerful tools for predicting the outcomes of these interactions which may be compensatory, favouring population stability, or complementary, favouring accelerated rates of increase or decline. High intensity fires in mature wet temperate eucalypt forests provide one example where opposing effects may produce a neutral outcome in terms of population persistence and community composition (Ashton 1981). On one hand these fires cause high levels of mortality among standing plants, and on the other hand, they stimulate high levels of seedling establishment through mass seed release, predator satiation, and diminished effects of resource limitation, competitors and pathogens. Indeed without such fires populations of these eucalypts may eventually decline to extinction through senescence (Gilbert 1959, Ashton 1981).

When life-cycle processes interact in a complementary manner, the risk of extinction may be amplified. Consider, for example, populations of woody plants subject to a fire regime comprising frequent, low intensity, patchy fires which occur invariably just before a dry season. Multiple mechanisms of decline and extinction may operate under such a regime. Depending on the life-history characteristics of the species these may include: decline of standing plant numbers through depletion of stored buds and starch or structural weakening (Mechanism 1d) or through weed competition (Mechanism 1g); low rates of germination and seedling emergence due to slow rates or low levels of seed release (Mechanism 2b) or to low rates of release from dormancy (Mechanisms 2c and 2d); low rates of seedling survival due to desiccation (Mechanism 3b) or predation (Mechanism 3d); interruption of maturation (Mechanism 4a) or the development of fire resistant structures (Mechanism 4b) in juvenile plants; and depletion of the potential seed bank by predation (Mechanism 5c). Decline and extinction may be expected to eventuate more rapidly when these mechanisms are considered as operating concurrently on different parts of the plant life cycle (Fig. 1) than if they are considered to operate in isolation.

Many of the examples of plant extinctions cited by Gill and Bradstock (1995) were related to variations of the above scenario. Indeed, fire regimes that involve frequent fire, fires resulting in little vertical penetration of heat (and possibly smoke derivatives) and fire exclusion are associated with multiple mechanisms of decline and extinction (Table 1) and therefore must be the foci of fire management for conservation. At higher levels of organisation, these types of fire regimes have been widely implicated in the simplification of vegetation structure and the loss of ecosystem diversity, particularly through local extinctions of woody plants (e.g. Gilbert 1959, Siddiqi et al. 1976, Fox and Fox 1986, Clark 1988, Morrison et al. 1995, Clark and Morrison 1995) and their dependent biota (e.g. Rowley and Brooker 1987, Lindenmayer et al. 1990, Catling 1991, York 1993).

Metapopulation dynamics: environmental correlations and dispersal among populations

The significance of any given extinction must be measured in terms of its spatial and genetic scales. Local extinctions may be of little consequence to conservation of metapopulations and species if they result in no net loss of genetic diversity and are balanced over some relevant time scale by establishment of new populations. Dynamics of this type may be expected in organisms with a panmictic metapopulation structure and widely dispersed propagules. Possible examples are mistletoes and short-lived wind-dispersed Asteraceous species known as fire weeds. Conversely, local extinctions may be of great significance in species with poor dispersal capability or with a high proportion of genetic diversity apportioned between, relative to within, their populations.

The spatial arrangement of populations in a landscape will influence whether different populations share similar fire regimes. Populations in close geographic proximity and aligned to common fire pathways are more likely to share a common fire regime than if they are separated by large distances or by significant barriers to fire spread (e.g. expanses of water or developed areas). Populations in close proximity are also more likely to share similar post-fire environmental conditions and similar predator pressures that may influence the likelihood of their decline and extinction (Mechanisms 3b, 3d and 5c) than populations separated by larger distances. When different populations are likely to experience the same fire events, droughts, predator fluxes, etc., their probabilities of extinction will be correlated, resulting in a higher probability of extinction for the entire metapopulation than if all populations had independent probability of extinction (Burgman et al. 1993).

The importance of dispersal in the persistence of metapopulations cannot be overemphasised (Burgman et al. 1993), yet data on dispersal of plants are conspicuously scarce in the literature. For species in which all effective seed dispersal occurs immediately after fire, Bradstock et al. (in press) have shown that the spatial extent of fire mediates the persistence of populations within landscapes by influencing the amount of seed released and the extent of habitat available for establishment. The probability of seed dispersal to neighbouring patches in their model was critical to population persistence.

Average dispersal distances may be limited to a few metres or tens of metres in a large majority of species in the Australian fire-prone flora, particularly species that have heavy winged propagules or smaller propagules without wings or hairs (e.g. Lamont 1985, Wellington and Noble 1985b, Auld 1986, 1987b, Morgan 1995b, Keith, unpubl. data). Experimental studies on perennial herbs in North America suggest similarly short dispersal distances (e.g. Primack and Miao 1992, Weiblen and Thomson 1995). Longer dispersal distances are possible in species whose propagules are dispersed by wide-ranging vertebrates. Fleshy-fruited species are known to be consumed by frugivorous birds and bats and may be deposited kilometres from their origin after digestion (Date et al. 1991, Eby 1991, Overton 1994). However, fleshy-fruited species are relatively uncommon in the Australian fire-prone flora (French 1991).

Although most studies point to the limited dispersal capability of the fire-prone Australian flora, dispersal of plant propagules over long distances remains conjectural.

Very infrequent long-distance dispersal events are by and large intractable topics for research and may therefore have escaped detection (Levin 1981). Whelan (1986) suggested that the convection column of a fire could promote long-distance dispersal of wind-dispersed seeds, provided propagules were drawn into the updraught without heat damage. Although there appear to be no reports of such occurrences, there are some anecdotal reports of charred and uncharred leaves falling to ground many kilometres from large fires (Whelan 1986, pers. obs.). These events are potentially most important in metapopulation dynamics and gene flow (Portnoy and Willson 1993), but the likelihood that they will lead to establishment of new populations will be further limited by the chance of dispersal to suitable habitats, as well as the factors that limit germination and establishment (see text on Failure of Seed Release and/or Germination and Failure of Seedling Establishment).

FIRE MANAGEMENT FOR CONSERVATION

The wide range of fire regimes associated with mechanisms of decline and extinction (Table 1) pose a quandary for fire managers who may be looking for simple prescriptions to meet conservation objectives. There are many apparent contradictions in the requirements of fire frequency, intensity and season for survival of species coexisting within one community. If, for example, frequent fires may cause declines in some species through interruption of life-cycle processes, while infrequent fires may cause declines in others through senescence or competitive elimination (Table 1), how can extinctions be avoided? Similarly, the season in which fire stimulates greatest vegetative recruitment and flowering and results in least mortality in resprouters (i.e. spring) is apparently the same season in which fire exposes subsequently emerged seedlings to greatest risks of mortality from desiccation (Table 1). A means of addressing such conflicts in fire management is offered firstly by reference to theories of species coexistence and diversity for the development of management principles, and secondly by a wide range of practical tools for experimental management.

Theories of coexistence and diversity

The intermediate disturbance hypothesis states that maximum diversity will be maintained when disturbances of intermediate intensity and size occur at intermediate frequencies (Connell 1978). Many of the fire regimes associated with population decline and extinction reviewed here are indeed associated with extremes in fire frequency, intensity and size (Table 1). It follows that avoidance of these extremes in fire management should minimise the chance of extinctions and favour maintenance of diversity (Hobbs and Huenneke 1992). Floristic diversity may be maintained by promoting fire intervals that are intermediate between the time of maturation and the time of senescence (Hobbs and Huenneke 1992). However, the fire requirements of some co-existing species may not overlap when defined in this manner (e.g. Keith and Bradstock 1994, Keith 1995b), so that sustained, invariant intermediate regimes of fire, in themselves, may be insufficient to maintain full diversity (van Wilgen et al. 1994).

In the mosaic paradigm the focus of fire management is maintenance of diversity within heterogeneous landscapes. In other words, the goal of conservation is maintenance of species somewhere within a landscape, but not necessarily at all inhabitable sites or at any one site continuously. Thus different fire regimes may be prescribed for different parts of the landscape to ensure conservation of different components of the biota. Species may either persist within a subset of patches or persist in some dynamic equilibrium by migrating from patch to patch as the suitability for habitation of patches changes through time.

Maintenance of fire mosaics, in particular those involving patches of different post-fire ages, has been widely advocated and applied in Australia, particularly for fauna conservation (e.g. Saxon 1975, Christensen and Kimber 1975, Bradstock et al. 1995). However, implementation of fire mosaics in management has largely been governed by logistical considerations and demands of management goals other than conservation, such as protection of property and timber production (Williams et al. 1994, Bradstock et al. 1995). Consequently, some aspects of deterministically managed fire mosaics such as the size and spatial pattern of patches may not be sufficient to avoid extinctions. As discussed previously, fire patch size may mediate persistence of some plant populations through the outcomes of predation (Whelan and Main 1979) and dispersal (Bradstock et al. in press). Hence, some deterministically managed mosaics may involve patches that are too small to maintain populations of some species (McCarthy and Burgman 1995). Williams et al. (1994) and McCarthy and Burgman (1995) point out other features of highly deterministic mosaics as maintained, for example, in production forests that may make them unsuitable for conservation of some species. Further, the assumption that mosaics of patches of different post-fire age help to maintain populations of animal species through dynamic equilibria has been called into question by recent empirical studies (e.g. Short and Turner 1994). Another potential limitation to some systems of mosaic management concerns the role of unplanned fires (Williams et al. 1994, Bradstock et al. 1995). Deterministic mosaic management systems that aim to maintain rigid patch boundaries or fine-scale patterns of fire history are unlikely to be viable in the face of unplanned ignitions and weather conditions of high fire danger (Bradstock and Scott 1995).

Where mosaics concern variability of fire regimes in space, lottery models concern the variability of fire regimes in time. The relevance of lottery theory to fire-prone vegetation has recently been demonstrated by Laurie and Cowling (1995) and Lamont and Witkowski (1995). Its relevance to conservation is predicated upon: differing requirements for survival and establishment among species; and rates of population decline and elimination that are slow relative to the recurrence of recruitment events (Chesson and Warner 1981). Thus a sequence of different recruitment and mortality events that alternately favour establishment in populations of different species may be sufficient to maintain full species diversity (Cowling et al. 1990, Keith 1995b). In practical terms this means that a site must experience fires of varying intensity, season, size and at varying intervals if its full complement of species is to be maintained. Van Wilgen et al. (1994), Bradstock and Scott (1995), Keith (1995) and Bradstock et al. (1995), for example, have stressed the importance of variability in the length of fire intervals, within certain thresholds, for the maintenance of full diversity. Species that decline under say frequent fires could coexist with species that decline under infrequent fires, so long as a favourable fire interval occurred often enough to reverse any trends of population decline before extinction took place. Rates of decline are therefore crucial. A lottery approach to fire management is unlikely to be successful where single fires may cause sudden elimination (e.g. Mechanism 3c, Kirkpatrick and Dickinson 1984). Further, it should be recognised that some of the environmental viability required for lottery coexistence, such as landscape pattern, post-fire weather conditions and aspects of fire behaviour under certain conditions, may be influenced only partly through management.

Practical Tools for Decision Support in Experimental Fire Management

While each of the three theories has limitations, together they provide some principles for the management of fire for conservation. There are also a number of practical tools that assist in the planning and implementation of fire management in specific areas. General principles could be translated into specific guidelines through the use of thresholds in fire regimes as suggested by Bradstock et al. (1995). Fire regimes likely to cause catastrophic, widespread and long-lasting declines or elimination could be identified in such thresholds which are expressed in terms of the components of the fire regime (i.e. upper and/or lower limits to frequency, intensity, season, type) and its and spatial pattern. Avoidance of fire regimes beyond the thresholds is in accordance with the intermediate disturbance hypothesis. The risk of more subtle declines and extinctions would be reduced by promoting variability in fire regimes within the thresholds. Variability should be on both spatial and temporal scales in accordance with the mosaic paradigm and lottery theory, respectively. Bradstock et al. (1995) give an example of a set of fire regime thresholds for management of a coastal heathland, though these do not address the spatial component of fires.

The extremely high species richness of some fire-prone plant communities may pose a problem for the development of management thresholds (e.g. George et al. 1979, Keith and Sanders 1990, Keith and Myerscough 1993). In such cases data may be available for only a fraction of the species that need to be considered. Functional classifications of species provide one means for effective use of this limited information (Verner 1984). As discussed earlier, such classifications could be constructed using life-history attributes to group species with similar mechanisms of decline and extinction. Examples of the application of such classifications to fire-driven vegetation dynamics are both practical (e.g. Purdie 1977a,b, Keith and Bradstock 1994) and theoretical (Noble and Slatyer 1980, Moore and Noble 1990). Information on life-history attributes, such as ability to resprout and type of seed bank, is available for a wide range of species (Gill and Bradstock 1992) and is easy to obtain in the field (e.g. Keith 1991). Within functional groups, the species most susceptible to decline under particular fire regimes would be the focus for defining thresholds. For example, within a group of serotinous obligate seeders, the primary juvenile period of the slowest maturing species should be considered when defining the upper threshold for fire frequency (Bradstock and Auld 1988, Bradstock and O'Connell 1988).

Predictive models of the dynamics of plant populations and communities are another set of practical tools available to fire managers for the translation of principles into strategies and prescriptions. Models provide powerful tools for understanding the outcomes of complex interactions between life-cycle processes (e.g. Auld 1987a, Bradstock and O'Connell 1988), between species (e.g. Noble and Slatyer 1980, Moore and Noble 1990), in temporally heterogeneous environments (e.g Burgman and Lamont 1992) and in spatially heterogeneous landscapes (e.g. Green 1989, Bradstock et al. in press). Models allow their users to explore the consequences of alternative actions before they are implemented. Through sensitivity analyses, they also allow salient factors for research and management to be singled out from a morass of potentially important variables (Burgman et al. 1993). Models that incorporate stochastic variability in environmental conditions and disturbance regimes are potentially the most useful for decision support in management. These allow risks of extinction associated alternative management options to be assessed explicitly in the face of uncertainty (Burgman et al. 1993, McCarthy and Burgman 1995). Management options may be ranked accordingly. However, predictive ecological models in general are yet to realise their potential in practical fire management, partly because of limited data on life-cycle processes and partly because researchers have had limited success in fostering their wide use among managers.

Knowledge of the local landscape, its biota and its fire history is one of the most important requisites for fire management. Systems of experimental management and monitoring, as proposed for example by Gill and Nicholls (1989), offer a sound framework for the acquisition of such knowledge, as well as a means for ongoing assessment of both fire regimes and biotic responses in relation to the goals of fire management (Bradstock et al. 1995). Hypothesis testing of this kind is an essential but often neglected aspect of natural area management (Murphy 1991). Ongoing assessment and judicious acquisition of knowledge is essential if management is to be flexible and responsive to changes in biota and fire regimes over dynamic landscapes (Bradstock et al. 1995, Keith 1995).

Geographic information systems provide powerful tools for organising this information into a wide range of forms for display, analysis and interpretation (van Wilgen et al. 1994, Garvey this volume). This technology has to a large degree outstripped the availability of spatial information on fire history and vegetation which, in most areas, is unavailable at resolutions and accuracies required for sound ecological decisions in fire management.

CONCLUSION

Many potential mechanisms of plant extinction and the fire regimes with which they are associated have been identified (Table 1). Fire regimes associated with multiple mechanisms of decline and extinction, particularly of woody species (obligate seeders and resprouters), include high fire frequency, low fire frequency and repeated fires that result poor vertical penetration of heat. However, many other, possibly overlapping, fire regimes may be associated with high risks of extinctions within any given area. Minimisation of these risks by avoiding detrimental fire regimes may therefore be prove to be a complex management task.

Our knowledge of the plant ecology of fire is still deficient on some important aspects. However, existing knowledge on mechanisms of decline and extinction, combined with ecological theories and practical management tools, is enough to predict how some populations and communities of plants may respond in landscapes subject to a wide range of fire regimes. Ongoing acquisition and evaluation of predictive knowledge of this kind are essential for a strong scientific basis for the management of fire for conservation.

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REFERENCES

Aarson, L.W., and Epp, G.A. (1990). Neighbour manipulation in natural vegetation: a review. *Journal of Vegetation Science* **1**, 13–30.

Abbott, I. (1985). Recruitment and mortality in populations of *Banksia grandis* Willd. in Western Australian forests. *Australian Journal of Botany* **33**, 261–270.

Abbott, I., and van Heurk, P. (1985). Comparison of insects and vertebrates as removers of seed and fruit in a Western Australian forest. *Australian Journal of Ecology* **10**, 165–168.

Andersen, A.N. (1988). Immediate and longer-term effects of fire on seed predation by ants in sclerophyllous vegetation in south-eastern Australia. *Australian Journal of Ecology* **13**, 285–293.

Andersen, A.N. (1989). Pre-dispersal seed losses to insects in species of *Leptospermum* (Myrtaceae). *Australian Journal of Ecology* **14**, 13–18.

Andersen, A.N., and Ashton, D.H. (1985). Rates of seed removal by ants at heath and woodland sites in south-eastern Australia. *Australian Journal of Ecology* **10**, 381–390.

Andrew, M.H., and Mott, J.J. (1983). Annuals with transient seed banks: the population biology of indigenous *Sorghum* species of tropical north-west Australia. *Australian Journal of Ecology* **8**, 265–276.

Ashton, D.H. (1976). The development of even-aged stands of *Eucalyptus regnans* F. Muell. in Central Victoria. *Australian Journal of Botany* **24**, 397–414.

Ashton, D.H. (1979). Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Ecology* **4**, 265–277.

Ashton, D.H. (1981). Fire in tall open forests (wet sclerophyll forests). In 'Fire and the Australian Biota'. (Eds Gill, A.M., Groves, R.H., and Noble, I.R.) pp. 339–366. (Australian Academy of Science: Canberra.)

Ashton, D.H. (1986). Viability of seeds of *Eucalyptus obliqua* and *Leptospermum juniperinum* from capsules subjected to a crown fire. *Australian Forestry* **49**, 28–35.

Ashton, D.H., and Frankenberg, J. (1976). Ecological studies of *Acmena smithii* (Poir.) Merrill and Perry with special reference to Wilson's Promontory. *Australian Journal of Botany* **24**, 453–487.

Ashton, D.H., and MacCauley, B.J. (1972). Winter leaf spot disease of seedlings of Eucalyptus regnans and its relation to forest litter. *Transactions of the British Mycological Society* **581**, 377–386.

Attiwill, P.M. (1994). Ecological disturbance and the conservative management of eucalypt forests in Australia. *Forest Ecology and Management* **63**, 301–346.

Auld, T.D. (1986). Population dynamics of the shrub *Acacia suaveolens* (Sm.)Willd.: dispersal and dynamics of the soil seed bank. *Australian Journal of Ecology* **11**, 235–254.

Auld, T.D. (1987a). Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd: survivorship throughout the life cycle, a synthesis. *Australian Journal of Ecology* **12**, 139–151.

Auld, T.D. (1987b). Post-fire demography in the resprouting shrub *Angophora hispida* (Sm.) Blaxell: flowering, seed production, dispersal, seedling establishment and survival. *Proceedings of the Linnean Society of New South Wales* **109**, 259–269.

Auld, T.D. (1990). The survival of juvenile plants of the resprouting shrub *Angophora hispida* (Myrtaceae) after a simulated low-intensity fire. *Australian Journal of Botany* **38**, 255–260.

Auld, T.D. (1994). The role of soil seedbanks in maintaining plant communities in fire-prone habitats. In 'Proceedings of the Second International Conference on Forest Fire Research'. pp. 1069–1078. (Coimbra.)

Auld, T.D. (1995). Burning grevilleas, ants, rats and wallabies. *CALMScience Supplement* **4**, 159–164.

Auld, T.D., Bradstock, R.A., and Keith, D.A. (1991). 'Germination of rare plants in relation to fire.' (World Wide Fund for Nature: Sydney).

Auld, T.D., Bradstock, R.A., and Keith, D.A. (1993). 'Fires as a threat to populations of rare plants.' (Australian National Parks and Wildlife Service: Canberra)

Auld, T.D., and Myerscough, P.J. (1986). Population dynamics of the shrub *Acacia suaveolens* (Sm.)Willd.: Seed production and pre-dispersal seed predation. *Australian Journal of Ecology* **11**, 219–234.

Auld, T.D., and O'Connell, M.A. (1991). Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* **16**, 53–70.

Auld, T.D., and Tozer, M. (1995). Patterns in emergence of *Acacia* and *Grevillea* seedlings after fire. *Proceedings of the Linnean Society of New South Wales* **115**, 5–16.

Baskin, J.M., and Baskin, C.C. (1989). Physiology of dormancy and germination in relation to seed bank ecology. In 'Ecology of soil seed banks'. (Eds Leck, M.A., Parker, V.T., and Simpson, R.L.) (Academic Press: San Diego.)

Beadle, N.C.W. (1940). Soil temperatures during forest fires and their effect on the survival of vegetation. *Journal of Ecology* **28**, 180–192.

Bell, D.T., and Koch, J.M. (1980). Post-fire succession in the northern jarrah forest of Western Australia. *Australian Journal of Ecology* **5**, 9–14.

Bell, D.T., Plummer, J.A., and Taylor, S. K. (1993). Seed germination ecology in southwestern Western Australia. *The Botanical Review* **59**, 24–73.

Bell, D.T., Vlahos, S., and Watson, L.E. (1987). Stimulation of seed germination of understorey species of the northern jarrah forest of Western Australia. *Australian Journal of Botany* **35**, 593–599

Bennett, L.T. (1994). The expansion of *Leptospermum laevigatum* on the Yankie Isthmus, Wilsons Promontory, under changes in the burning and grazing regimes. *Australian Journal of Botany* **42**, 555–564.

Benson, D.H. (1985a). Aspects of the ecology of a rare tree species, *Eucalyptus benthamii*, at Bents Basin, Wallacia. *Cunninghamia* **1**, 317–338.

Benson, D.H. (1985b). Maturation periods for fire sensitive shrub species in Hawkesbury sandstone vegetation. *Cunninghamia* **1**, 339–349.

Bogusiak, A., Rice, B., and Westoby, M. (1990). Seedling emergence of hummock grasses in relation to the effects of fire. *Australian Rangelands Journal* **12**, 25–28.

Bond, W.J., Vlok, J., and Viviers, M. (1984). Variation in seedling recruitment of Cape Proteaceae after fire. *Journal of Ecology* **72**, 209–221.

Bowen, B.J., and Pate, J.S. (1993). The significance of root starch in post-fire shoot recovery of the resprouter Stirlingia latifolia R.Br. (Proteaceae). *Annals of Botany* 72, 7–16.

Bowman, D.M.J.S., Latz, P.K., and Panton, W. J. (1995). Pattern and change in an *Acacia aneura* shrubland and *Triodia* hummock grassland mosaic on rolling hills in central Australia. *Australian Journal of Botany* **43**, 25–37.

Bowman, D.M.J.S., Wilson, B.A., and Hooper, R.J. (1988). Response of *Eucalyptus* forest and woodland to four fire regimes at Munmarlary, Northern Territory, Australia. *Journal of Ecology* **76**, 215–232.

Bradstock, R.A. (1989). Dynamics of a perennial understorey. In 'Mediterranean landscapes in Australia: Mallee ecosystems and their management'. (Eds Noble, J.C., and Bradstock, R.A.) pp. 141–154. (CSIRO: Melbourne.)

Bradstock, R.A. (1990). Demography of woody plants in relation to fire: *Banksia serrata* L.f. and *Isopogon anemonifolius* (Salisb.) Knight. *Australian Journal of Ecology* **15**, 117–132.

Bradstock, R.A. (1995). Demography of woody plants in relation to fire: *Telopea speciosissima. Proceedings of the Linnean Society of New South Wales* **115**, 25–33.

Bradstock, R.A., and Auld, T.D. (1988). Effects of fire on plants: case studies in the Proteaceae and Fabaceae in the Sydney region and the implications for fire management in conservation reserves. In 'Bushfire management in natural areas'. (Ed Conroy, R.) pp. 91–119. (NSW National Parks and Wildlife Service: Sydney.)

Bradstock, R.A., and Auld, T.D. (1995). Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* **32**, 76–84.

Bradstock, R.A., Auld, T.D., Ellis, M.E., and Cohn, J.S. (1992). Soil temperatures during bushfires in semi-arid mallee shrublands. *Australian Journal of Ecology* **17**, 433–440.

Bradstock, R. A., and Bedward, M. (1992). Simulation of the effect of season of fire on post-fire seedling emergence of two *Banksia* species based on long-term rainfall records. *Australian Journal of Botany* **40**, 75–88.

Bradstock, R.A., Bedward, M., Scott, J., and Keith, D.A. (in press). Cellular analysis of fire and extinction. *Conservation Biology*.

Bradstock, R.A., Gill, A.M., Hastings, S.M., and Moore, P.H.R. (1994). Survival of serotinous seed banks during bushfires: Comparative studies of *Hakea* species from southeastern Australia. *Australian Journal of Ecology* **19**, 276–282.

Bradstock, R.A., Keith, D.A., and Auld, T.D. (1995). Managing fire for conservation: imperatives and constraints. In 'Conserving biodiversity: threats and solutions'. (Eds Bradstock, R.A., Auld, T.D., Keith, D.A., Kingsford, R.T., Lunney, D., and Sivertsen, D.) pp 323–333. (Surrey Beatty and Sons Pty. Ltd.: Chipping Norton.)

Bradstock, R.A., and Myerscough, P.J. (1981). Fire effects on seed release and the emergence and establishment of seedlings in *Banksia ericifolia* L.f. *Australian Journal of Botany* **29**, 521–531.

Bradstock, R.A., and Myerscough, P.J. (1988). The survival and population response to frequent fires of two woody resprouters *Banksia serrata* and *Isopogon anemonifolius*. *Australian Journal of Botany* **36**, 415–431.

Bradstock, R.A., and O'Connell, M.A. (1988). Demography of woody plants in relation to fire: Banksia ericifolia L.f. and Petrophile pulchella (Schrad) R.Br. *Australian Journal of Ecology* **13**, 505–518.

Bradstock, R.A., and Scott, J. (1995). A basis for planning fire to achieve conservation and protection objectives adjacent to the urban interface. *CALMScience Supplement* **4**, 109–116.

Brown, N.A.C. (1993). Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytologist* **122**, 1–9.

Burdon, J.J. (1991). Fungal pathogens as selective forces in plant populations and communities. *Australian Journal of Ecology* **16**, 423–432.

Burgman, M.A., Ferson, S., and Akcakaya (1993). 'Risk assessment in conservation biology.' (Chapman and Hall: London)

Burgman, M.A., and Lamont, B.B. (1992). A stochastic model for the viability of *Banksia cuneata* populations: environmental demographic and genetic effects. *Journal of Applied Ecology* **29**, 719–727.

Burrell, J.P. (1981). Invasion of coastal heaths of Victoria by *Leptospermum laevigatum* (J.Gaertn.) F. Muell. *Australian Journal of Botany* **29**, 747–764.

Burrows, N.D. (1985). Reducing the abundance of *Banksia grandis* in the jarrah forest by the use of controlled fire. *Australian Forestry* **48**, 63–70.

Cary, G.J., and Morrison, D.A. (1995). Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: combinations of inter-fire intervals. *Australian Journal of Ecology* **20**, 418–426.

Cavanagh, A K. (1987). Germination of hard-seeded species (Order Fabales). In 'Germination of Australian native plant seed'. (Ed P. Langkamp) pp58–70. (Inkata Press: Melbourne.)

Catling, P. (1991). Ecological effects of prescribed burning practices on the mammals of south-eastern Australia. In 'Conservation of Australia's forest fauna'. (Ed Lunney, D.) pp. 353–363. (Surrey Beatty and Sons: Sydney.)

Cheney, N.P. (1981). Fire behaviour. In 'Fire and the Australian Biota'. (Eds Gill, A.M., Groves, R.H., and Noble, I.R.) pp. 151–175. (Australian Academy of Science: Canberra.)

Chesson, P.L., and Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**, 923–943.

Christensen, P.E., and Kimber, P. C. (1975). Effects of prescribed burning on the flora and fauna of southwest Australian forests. *Proceedings of the Ecological Society of Australia* **9**, 85–106.

Clark, S.S. (1988). Effects of hazard-reduction burning on populations of understorey plant species on Hawkesbury sandstone. *Australian Journal of Ecology* **13**, 473–484.

Coates, F. (1991). The conservation ecology and management of five rare species in the Rhamnaceae family. 91/3. Department of Parks, Wildlife and Heritage, Hobart

Connell, J.H. (1978). Diversity in tropical rainforests and coral reefs. *Science* **199**, 1302–1210.

Cowling, R.M., and Lamont, B.B, (1985a). Variation in serotiny of three *Banksia* species along a climatic gradient. *Australian Journal of Ecology* **10**, 345–350.

Cowling, R.M., and Lamont, B.B. (1985b). Seed release in *Banksia*: The role of wet–dry cycles. *Australian Journal of Ecology* **10**, 169–171.

Cowling, R.M., and Lamont, B.B. (1987). Post fire recruitment of four co-occurring Banksia species. *Journal* *of Applied Ecology* **24**, 645–658.

Cowling, R.M., Lamont, B.B., and Enright, N.J. (1990). Fire and management of south-western Australian banksias. *Proceedings of the Ecological Society of Australia* **16**, 177–183.

Cremer, K.W. (1962). The effect of fire on eucalypts reserved for seeding. *Australian Forestry* **26**, 129–154.

Cremer, K.W. (1969). Browsing of mountain ash regeneration by wallabies and possums in Tasmania. *Australian Forestry* **33**, 201–210.

Cunningham, T.M., and Cremer, K.W. (1965). Control of the understorey in wet eucalypt forest. *Australian Forestry* **29**, 4–14.

Date, E.M., Ford, H.A., and Recher, H.F. (1991). Frugivorous pigeons, stepping stones and weeds in northern New South Wales. In 'Nature Conservation 2: the role of corridors' (Eds D.A. Saunders, and R.J. Hobbs), pp241–245. (Surrey Beatty and Sons: Sydney.)

Daubenmire, R. (1968). Ecology of fire in grasslands. *Advances in Ecological Research* **5**, 209–266.

Davies, S.J., and Myerscough. P.J. (1991). Post-fire demography of the wet mallee *Eucalyptus luehmanniana* F. Muell. (Myrtaceae). *Australian Journal of Botany* **39**, 459–466.

de Lange, J.H., and Boucher, C. (1990). Autecological studies on *Audouinia capitata* (Bruniaceae). I. Plant-derived smoke as a seed germination cue. *South African Journal of Botany* **56**, 700–703.

Dickinson, K.J.M., and Kirkpatrick, J.B. (1986). The impact of grazing pressure in clearfelled, burned and undisturbed eucalypt forest. *Vegetatio* **66**, 133–136.

Dixon, K.W., Roche, S., and Pate, J.S. (1995). The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* **101**, 185–192.

Eby, P. (1991). 'Finger-winged night workers', managing forests to conserve the role of Grey-headed Flying Foxes as pollinators and seed dispersers. In *Conservation of Australia's forest fauna* (Ed D. Lunney), pp91–100. (Surrey Beatty and Sons: Sydney.)

Enright, N.J., and Lamont, B.B. (1989a). Fire temperatures and follicle-opening requirements in 10 Banksia species. *Australian Journal of Ecology* **14**, 107–113.

Enright, N.J., and Lamont, B.B. (1989b). Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *Journal of Ecology* **77**, 1111–2222.

Ewart, A.J. (1908). On the longevity of seeds. *Proceedings of the Royal Society of Victoria* **21**, 1–210.

Flinn, M.A., and Wein, R.W. (1977). Depth of underground plant organs and theoretical survival during fire. *Canadian Journal of Botany* **55**, 2550–2554.

Floyd, A.G. (1966). Effect of fire on weed seeds in wet sclerophyll forests of northern New South Wales. *Australian Journal of Botany* **14**, 243–256.

Floyd, A.G. (1976). Effect of burning on regeneration from seeds in wet sclerophyll forest. *Australian Forestry* **39**, 210–220.

Fox, M.D. (1988). Understorey changes following fire at Myall Lakes, New South Wales. *Cunninghamia* **2**, 85–95.

Fox, M.D., and Fox, B.J. (1986). The effect of fire frequency on the structure and floristic composition of a woodland understorey. *Australian Journal of Ecology* **11**, 77–85.

Frandsen, W.H. (1991). Heat evolved from smouldering peat. *International Journal of Wildland Fire* **1**, 197–204.

French, K. (1991). Characteristics and abundance of vertebrate-dispersed fruits in temperate wet sclerophyll forest in southeastern Australia. *Australian Journal of Ecology* **16**, 1–14.

Friend, G. (1995). Fire and invertebrates — a review of research methodology and the predictability of post-fire response patterns. *CALMScience Supplement* **4**, 165–174.

George, A.S., Hopkins, A.J.M., and Marchant, N.G. (1979). The heathlands of Western Australia. In 'Ecosystems of the World 9A. Heathlands and related shrublands'. (Ed Specht, R.L.) pp. 211–230. (Elsevier: Amsterdam.)

Gilbert, J.M. (1959). Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **93**, 129–151.

Gilfedder, L., and Kirkpatrick, J.B. (1993). Germinable soil seed and competitive relationships between a rare native species and exotics in a semi-natural pasture in the Midlands, Tasmania. *Biological Conservation* **64**, 113–119.

Gill, A.M. (1975). Fire and the Australian flora: a review. *Australian Forestry* **38**, 4–25.

Gill, A.M. (1976). Fire and the opening of *Banksia ornata* F. Muell. follicles. *Australian Journal of Botany* **24**, 329–335.

Gill, A.M. (1981). Adaptive responses of Australian vascular plant species to fire. In 'Fire and the Australian Biota'. (Eds Gill, A.M., Groves, R.H., and Noble, I.R.) pp. 243–272. (Australian Academy of Science: Canberra.)

Gill, A.M., and Ashton, D.H. (1968). The role of bark type in relative tolerance to fire of three central Victorian eucalypts. *Australian Journal of Botany* **16**, 491–498.

Gill, A.M., and Bradstock, R.A. (1992). A national register for the fire responses of plant species. *Cunninghamia* **2**, 653–660.

Gill, A.M., and Bradstock, R.A. (1995). Extinction of biota by fires. In 'Conserving biodiversity: threats and solutions'. (Eds Bradstock, R. A., Auld, T. D., Keith, D. A., Kingsford, R. T., Lunney, D., and Sivertsen, D. P.) pp. in press. (Surrey Beatty and Sons Pty. Ltd.: Sydney.)

Gill, A.M., and Ingwersen, F. (1976). Growth of *Xanthorrhoea australis* R.Br. in relation to fire. *Journal of*

Applied Ecology **13**, 195–203.

Gill, A.M., and McMahon, A. (1986). A postfire chronosequence of cone, follicle and seed production in Banksia ornata. *Australian Journal of Botany* **34**, 425–433.

Gill, A.M., and Nicholls, A.O. (1989). Monitoring fire-prone flora in reserves for nature conservation. In 'Fire Management on Nature Conservation Lands'. (Eds Burrows, N., McCaw, L., and Friend, G.) pp. 137–151. 1/89. (Western Australian Department of Conservation and Land Management: Perth.)

Green, D.G. (1989). Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. *Vegetatio* **82**, 139–153.

Griffin, G.F., and Friedel, M.H. (1984). Effects of fire on central Australian rangelands. 2. Changes in tree and shrub populations. *Australian Journal of Ecology* **9**, 395–403.

Harden, G. (1990–1993). Flora of New South Wales. Volumes 1–4. (University of New South Wales Press: Kensington

Harper, J.L. (1977). 'Population biology of plants.' (Academic Press: London)

Head, M.J., and Lacey, C.J. (1988). Radiocarbon age determinations from lignotubers. *Australian Journal of Botany* **36**, 93–100.

Henry, N.B., and Florence, R.G. (1966). Establishment and development of regeneration in Spotted Gum–Ironbark forests. *Australian Forestry* **30**, 304–316.

Hester, A.J., and Hobbs, R.J. (1992). Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science* **3**, 101–108.

Hill, R.S. (1982). Rainforest fire in western Tasmania. *Australian Journal of Botany* **30**, 583–589.

Hill, R.S., and Read, J. (1984). Post-fire regeneration of rainforests and mixed forests in Western Tasmania. *Australian Journal of Botany* **32**, 481–493.

Hobbs, R.J., and Atkins, L. (1988a). Effect of disturbance and nutrient addition on native and introduced annuals. *Australian Journal of Ecology* **13**, 171–179.

Hobbs, R.J., and Atkins, L. (1988b). Spatial variability of experimental fires in south-west Western Australia. *Australian Journal of Ecology* **13**, 295–299.

Hobbs, R.J., and Atkins, L. (1990). Fire-related dynamics of a *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* **38**, 97–110.

Hobbs, R.J., and Huenneke, L.F. (1992). Disturbance, diversity and invasion: Implications for conservation. *Conservation Biology* **6**, 324–337.

Hodgkinson, K.C. (1991). Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *Journal of Applied Ecology* **28**, 60–70.

Hodgkinson, K.C., and Oxley, R.E. (1990). Influence of fire and edaphic factors on germination of the arid zone shrubs Acacia aneura, *Cassia nemophila* and *Dodonaea viscosa*. *Australian Journal of Botany* **38**, 269–279.

Jackson, W.D. (1968). Fire, air, water and earth — an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia* **3**, 9–16.

Jarrett, P.H., and Petrie, A.H.K. (1929). The Vegetation of the Black's Spur Region. A Study in the ecology of some Australian mountain Eucalyptus forests. IV. Pyric succession. *Journal of Ecology* **17**, 249–281.

Johnson, K.A., Morrison, D.A., and Goldsack, G. (1994). Post-fire flowering patterns in *Blandfordia nobilis* (Liliaceae). *Australian Journal of Botany* **42**, 49–60.

Jones, D.L. (1988). 'Native orchids of Australia.' (Reed: Sydney.)

Judd, T.S., and Ashton, D.H. (1991). Fruit clustering in the Myrtaceae: seed survival in capsules subjected to experimental heating. *Australian Journal of Botany* **39**, 241–245.

Keddy, P.A. (1989). 'Competition.' (Chapman and Hall: London)

Keeley, J.E. (1995). Seed germination patterns in fireprone mediterranean climate regions. In 'Ecology and biogeography of mediterranean ecosystems in Chile, California and Australia'. (Eds Kalin Arroyo, M. T., Zedler, P. H., and Fox, M. D.) (Sprenger-Verlag: New York.)

Keeley, J.E., Morton, B.A., Pedrosa, A., and Trotter, P. (1985). Role of allelopathy, heat, and charred wood in the germination of chaparral herbs and suffrutescents. *Journal of Ecology* **73**, 445–458.

Keeley, S.C., and Pizzorno, M. (1986). Charred wood stimulated germination in two fire-following herbs of the California chaparral and the role of hemicellulose. *American Journal of Botany* **7**, 1289–1297.

Keith, D.A. (1991). Coexistence and species diversity in upland swamp vegetation: the roles of an environmental gradient and recurring fires. Ph.D. Thesis, University of Sydney.

Keith, D.A. (1995a). Surviving fire and fungal pathogens: are there life-history solutions for threatened Tasmanian *Epacris* species? In 'Bushfire '95: Proceedings of the fifth Australian Bushfire Conference' (Eds. T. Blanks, M. Chladil, R. Chuter and K. Green). (Forestry Tasmania, Parks and Wildlife Service, Tasmania Fire Service: Hobart)

Keith, D.A. (1995b). Mosaics in Sydney heathland vegetation: the roles of fire, competition and soils. *CALMScience Supplement* **4**, 199–206.

Keith, D.A., and Bradstock, R.A. (1994). Fire and competition in Australian heath: a conceptual model and field investigations. *Journal of Vegetation Science* **5**, 347–354.

Keith, D.A., and Myerscough, P.J. (1993). Floristics and soil relations of upland swamp vegetation near Sydney. *Australian Journal of Ecology* **18**, 325–344.

Keith, D.A., and Sanders, J.A. (1990). Vegetation of the Eden region, South-eastern Australia: Species composition, diversity and structure. *Journal of Vegetation Science* **1**, 203–232.

Kirkpatrick, J.B. (1983). Treeless plant communities of the Tasmanian high country. *Proceedings of the Ecological Society of Australia* **12**, 61–77.

Kirkpatrick, J.B., and Dickinson, K.J.M. (1984). The impact of fire on Tasmanian alpine vegetation and soils. *Australian Journal of Botany* **32**, 613–629.

Kruger, F.J. (1977). Ecology of Cape fynbos in relation to fire. In 'Proceedings of a Symposium on Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems'. (Eds Mooney, H.A., and Conrad, C.E.) pp. 230–243. (USDA Forest Service General Technical Report WO-3: Washington D.C.)

Lamont, B.B. (1985). Dispersal of the winged fruits of *Nuytsia floribunda* (Loranthaceae). *Australian Journal of Ecology* **10**, 187–194.

Lamont, B.B. (1995). Interdependence of woody plants, higher fungi and small marsupials in the context of fire. *CALMScience Supplement* **4**, 151–158.

Lamont, B.B., and Barker, M.J. (1988). Seed bank dynamics of a serotinous, fire-sensitive *Banksia* species. *Australian Journal of Botany* **36**, 193–203.

Lamont, B.B., Connell, S.W., and Bergl, S.M. (1991). Seed bank and population dynamics of *Banksia cuneata*: the role of time, fire, and moisture. *Botanical Gazette* **152**, 114–122.

Lamont, B.B., and Downes, S. (1979). The longevity, flowering and fire history of the grasstrees *Xanthorrhoea preissii* and *Kingia australis*. *Journal of Applied Ecology* **16**, 893–899

Lamont, B.B., and Runciman, H.V. (1993). Fire may stimulate flowering, branching, seed production and seedling establishment in two kangaroo paws (Haemodoraceae). *Journal of Applied Ecology* **30**, 256–264.

Lamont, B.B., and van Leeuwin, S.J. (1988). Seed production and mortality in a rare *Banksia*. *Journal of Applied Ecology* **25**, 551–559.

Lamont, B.B., Witkowski, E.T.F., and Enright, N.J. (1993). Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology* **74**, 501–512.

Lamont, B.B., and Witkowski, E.T.F. (1995). A test for lottery recruitment among four *Banksia* species based on their demography and biological attributes. *Oecologia* **101**, 299–308.

Landsberg, J. (1988). Dieback of rural eucalypts: Tree phenology and damage caused by leaf-feeding insects. *Australian Journal of Ecology* **13**, 251–268.

Laurie, H., and Cowling, R.M. (1995). Lottery coexistence models extended to plants with disjoint generations. *Journal of Vegetation Science* **6**, 161–168.

Leigh, J.H., and Holgate, M.D. (1979). The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. *Australian Journal of Ecology* **4**, 25–45.

Leigh, J.H., and Noble, J.C. (1981). The role of fire in the management of rangelands in Australia. In 'Fire and the Australian biota'. (Eds Gill, A.M., Groves, R.H., and Noble, I.R.) pp. 471–495. (Australian Academy of Science: Canberra.)

Leigh, J.H., Wimbush, D.J., Wood, D.H., Holgate, M.D., Slee, A.V., Stanger, M.G., and Forrester, R.I. (1987). Effects of rabbit grazing and fire on a subalpine environment. I. Herbaceous and shrubby vegetation. *Australian Journal of Botany* **35**, 433–464.

Levin, D.A. (1981). Dispersal versus gene flow in plants. *Annals of the Missouri Botanic Gardens* **68**, 233–242.

Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., and Smith, A.P. (1990). The conservation of arboreal marsupials in montane ash forests of the central highlands of Victoria: II. The loss of trees with hollows and its implications for the conservation of Leadbeater's Possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). *Biological Conservation* **54**, 133–145.

Lonsdale, W.M., and Braithwaite, R.W. (1991). Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* **16**, 363–374.

Lowman, M.D. (1985). Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology* **10**, 7–24.

Lowman, M.D., and Heatwole, H. (1987). The impact of defoliating insects on the growth of eucalypt saplings. *Australian Journal of Ecology* **12**, 175–182.

Lunt, I.D. (1991). Management of remnant lowland grasslands and grassy woodlands for nature conservation: a review. *Victorian Naturalist* **108**, 56–66.

Lunt, I.D. (1994). Variation in flower production of nine grassland species with time since fire, and implications for grassland management and restoration. *Pacific Conservation Biology* **1**, 359–366.

Lunt, I.D. (1995). Seed longevity of six native forbs in a closed *Themeda triandra* grassland. *Australian Journal of Botony* **43**, 439–449.

Maltby, E., Legg, C.J., and Proctor, M.C.F. (1990). The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. *Journal of Ecology* **78**, 490–518.

McArthur, A.G. (1968). The fire resistance of eucalypts. *Proceedings of the Ecological Society of Australia* **3**, 83–90.

McCarthy, M.A., and Burgman, M.A. (1995). Coping with uncertainty in forest wildlife planning. *Forest Ecology and Management* **74**, 23–36.

McIntyre, S., and Lavorel, S. (1994). How environmenral and disturbance factors influence species composition in temperature Australian grasslands. *Journal of Vegetation Science* **5**, 373–384.

McPhail, M.K. (1979). Vegetation and climates in southern Tasmania since the last glaciation. *Quarternary Research* **11**, 306–341.

McPhail, M.K. (1981). A history of fire in the forest. In 'Fire and forest management in Tasmania'. (Ed Kirkpatrick, J. B.) (Tasmanian Conservation Trust: Hobart.)

Melick, D.R., and Ashton, D.H. (1991). The effects of natural disturbance on warm temperate rainforests in south-eastern Australia. *Australian Journal of Botany* **39**, 1–30.

Meney, K.A., Neilssen, G.M., and Dixon, K.W. (1994). Seed bank patterns in Restionaceae and Epacridaceae after wildfire in kwongan in southwestern Australia. *Journal of Vegetation Science* **5**, 5–12.

Milberg, P., and Lamont, B.B. (1995). Fire enhances weed invasion or roadside vegetation in southwestern Australia. *Biological Conservation* **73**, 45–49.

Molnar, C.D., Fletcher, D., and Parsons, R.F. (1989). Relationships between heath and *Leptospermum laevigatum* scrub at Sandringham, Victoria. *Proceedings of the Royal Society of Victoria* **101**, 77–88.

Moore, A.D., and Noble, I.R. (1990). An individualistic model of vegetation stand dynamics. *Journal of Environmental Management* **31**, 61–81.

Moore, J.M., and Wein, R.W. (1977). Viable seed populations by soil depth and potential site recolonisation after disturbance. *Canadian Journal of Botany* **55**, 2408–2412.

Morgan, J.W. (1994). The ecology of grasses and grasslands in lowland Victoria. *Victorian Naturalist* **111**, 87–92.

Morgan, J.W. (1995a). Ecological studies of the endangered *Rutidosus leptorhynchoides*. I. Seed production seed bank dynamics, population density and their effects on recruitment. *Australian Journal of Botany* **43**, 1–11.

Morgan, J.W. (1995b). Ecological studies of the endangered *Rutidosus leptorhynchoides*. II. Patterns of seedling emergence and survival in a native grassland. *Australian Journal of Botany* **43**, 12–37.

Morgan, J.W. (in press). The effect of grassland gap size on the establishment, survival and flowering of the endangered *Rutidosis leptorhynchoides* (Asteraceae). *Journal of Applied Ecology.*

Morris, E.C., and Myerscough, P. J. (1988). Survivorship, growth and self-thinning in *Banksia ericifolia. Australian Journal of Ecology* **13**, 181–189.

Morrison, D.A. (1995). Some effects of low-intensity fires of co-occurring small trees in the Sydney region. *Proceedings of the Linnean Society of New South Wales* **115**, 103–109.

Morrison, D.A., Auld, T.D., Rish, S., Porter, C., and McClay, K. (1992). Patterns of testa-imposed seed dormancy in native Australian legumes. *Annals of Botany* **70**, 157–163.

Morrison, D.A., Cary, G.J., Penjelly, S.M., Ross, D.G., Mullins, B.G., Thomas, C.R., and Anderson, T.S. (1995). Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Inter-fire interval and time-since-fire. *Australian Journal of Ecology* **20**, 239–247.

Mott, J.J. (1972). Germination studies on some annual species from an arid region of Western Australia. *Journal of Ecology* **60**, 293–304.

Mott, J.J., and Andrew, M. H. (1985). The effect of fire on the population dynamics of native grasses in tropical savannas of north-west Australia. *Proceedings of the Ecological Society of Australia* **13**, 231–239.

Murphy, D.D. (1991). Conservation biology and scientific method. *Conservation Biology* **4**, 203–204.

Nieuwenhuis, A. (1987). The effects of fire frequency on the sclerophyll vegetation of the West Head Peninsula, New South Wales. *Australian Journal of Ecology* **12**, 373–385.

Noble, I.R. (1984). Mortality of lignotuberous seedlings of *Eucalyptus* species after an intense fire in montane forest. *Australian Journal of Ecology* **9**, 47–50.

Noble, I.R., and Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5–21.

Noble, I.R., and Slatyer, R.O. (1981). Concepts and models of succession in vascular plant communities subject to recurrent fire. In 'Fire and the Australian biota'. (Eds Gill, A. M., Groves, R. H., and Noble, I. R.) pp. 311–335. (Australian Academy of Science: Canberra.)

Noble, J.C. (1989). Fire regimes and their influence on herbage and mallee coppice dynamics. In 'Mediterranean Landscapes in Australia, Mallee Ecosystems and their Management'. (Eds Noble, J. C., and Bradstock, R.A.) pp. 168–180. (CSIRO: Melbourne.)

O'Dowd, D.J., and Gill, A.M. (1984). Predator satiation and site alteration following fire: mass reproduction of alpine ash in south-eastern Australia. *Ecology* **65**, 1052–1066.

Overton, J.M. (1994). Dispersal and infection in mistletoe metapopulations. *Journal of Ecology* **82**, 711–723.

Packham, D.R. (1970). Heat transfer above a small ground fire. *Australian Forest Research* **5**, 19–24.

Pannell, J.R. (1995). Factors affecting seedling recruitment of *Allocasuarina distyla* and *A. nana* at burnt and unburnt sites. *Proceedings of the Linnean Society of New South Wales* **115**, 121–133.

Pannell, J.R., and Myerscough, P. J. (1993). Canopy-stored seed banks of *Allocasuarina distyla* and *A. nana* in relation to time since fire. *Australian Journal of Botany* **41**, 1–9.

Pate, J.S., Casson, N.E., Rullo, J., and Kuo, J. (1985). Biology of the fire ephemerals of the sandplains of the kwongan of south-western Australia. *Australian Journal of Plant Physiology* **12**, 641–655.

Pate, J.S., Froend, R.H., Bowen, B.J., Hansen, A., and Kuo, J. (1990). Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S.W. Australia. *Annals of Botany* **65**, 585–601.

Pate, J.S., Meney, K.A., and Dixon, K.W. (1991). Contrasting growth and morphological characteristics of fire-sensitive (obligate seeder) and fire-resistant (resprouter) species of Restionaceae (S. Hemisphere

Restiads) from south-western Australia. *Australian Journal of Botany* **39**, 505–525.

Penfold, A.R., and Willis, J.L. (1961). 'The eucalypts.' (Leonard Hill: London)

Podger, F.D., Bird, T., and Brown, M.J. (1988). Human activity, fire and change in the forest at Hogsback Plain, southern Tasmania. In 'Australia's Ever Changing Forests'. (Eds Frawley, K. J., and Semple, N.) pp. 119–142. Special Publication No. 1. (Australian National University, Australian Defence Force Academy: Canberra.)

Portnoy, S., and Willson, M.F. (1993). Seed dispersal curves: behaviour of the tail of the distribution. *Evolutionary Ecology* **7**, 25–44.

Price, O., and Bowman, D.M.J.S. (1994). Fire-stick forestry: a matrix model in support of skilful fire management of *Callitris intratropica* R.T. Baker by north Australian aborigines. *Journal of Biogeography* **21**, 573–580.

Primack, R.B., and Miao, S.I. (1992). Dispersal can limit local plant distribution. *Conservation Biology* **6**, 513–519.

Purdie, R.W. (1977a). Early stages of regeneration after burning in dry sclerophyll vegetation. I. Regeneration of the understorey by vegetative means. *Australian Journal of Botany* **25**, 21–34.

Purdie, R.W. (1977b). Early stages of regeneration after burning in dry sclerophyll vegetation. II. Regeneration by seed germination. *Australian Journal of Botany* **25**, 35–46.

Pyke, G.H. (1983). Relationships between time since the last fire and flowering in *Telopea speciosissima* R.Br. and Lambertia formosa Sm. *Australian Journal of Botany* **31**, 293–296.

Raunkiaer, C. (1934). 'Life form and terrestrial plant geography.' (Clarendon Press: Oxford)

Read, J., and Hill, R.S. (1988). The dynamics of some rainforest associations in Tasmania. *Journal of Ecology* **76**, 558–584.

Rowley, I., and Brooker, M. (1987). The response of a small insectivorous bird to fire in heathlands. In 'Nature conservation: the role of remnants of native vegetation'. (Eds Saunders, D.A., Arnold, G.A., Burbidge, A.A., and Hopkins, A.J M.) pp. 211–218. (Surrey Beatty and Sons: Sydney.)

Rowley, J. (1970). The effects of burning and clipping on temperature, growth, and flowering of narrow-leaved snow tussock. *New Zealand Journal of Botany* **8**, 264–282.

Russell, R.P., and Parsons, R.F. (1978). Effects of time since fire on heath floristics at Wilson's Promontory, southern Australia. *Australian Journal of Botany* **26**, 53–61.

Russell-Smith, J. (1985). A record of change: studies of Holocene vegetation history in the south Alligator River region, Northern Territory. *Proceedings of the Ecological Society of Australia* **13**, 191–202.

Russell-Smith, J., and Bowman, D.M.J.S. (1992). Conservation of monsoon rainforest isolates in the Northern Territory, Australia. *Biological Conservation* **59**, 51–63.

Russell-Smith, J., and Dunlop, C. (1987). The status of monsoon vine forests in the Northern Territory: A perspective. In 'The Rainforest Legacy'. pp. 277–288. Special Australian Heritage Publication Series. No. 7. (Australian Government Publishing Service: Canberra.)

Saxon, E.C. (1984). 'Anticipating the Inevitable: A Patch-burn Strategy for Fire Management at Uluru (Ayers Rock–Mt Olga) National Park.' (CSIRO: Melbourne)

Shea, S.R. (1979). Forest management and *Phytophthora cinnamomi* in Australia. In 'Phytophthora and forest management in Australia'. (Ed Old, K.M.) pp. 73–100. (CSIRO: Melbourne.)

Shea, S.R., McCormick, J., and Portlock, C.C. (1979). The effect of fires on regeneration of leguminous species in the northern jarrah (*Eucalyptus marginata* Sm.) forest of Western Australia. *Australian Journal of Ecology* **4**, 195–205.

Shea, S.R., Peet, G.B., and Cheney, N.P. (1981). The role of fire in forest management. In 'Fire and the Australian biota'. (Eds Gill, A.M., Groves, R.H., and Noble, I.R.) pp. 443–469. (Australian Academy of Science: Canberra.)

Short, J., and Turner, B. (1994). A test of the vegetation mosaic hypothesis — a hypothesis to explain the extinction of Australian mammal species. *Conservation Biology* **8**, 439–449.

Siddiqi, M.Y., Carolin, R.C., and Myerscough, P. J. (1976). Studies in the ecology of coastal heath in NSW. III. Regrowth of vegetation after fire. *Proceedings of the Linnean Society of New South Wales* **101**, 53–63.

Specht, R.L., and Morgan, D.G. (1981). The balance between the foliage projective covers of overstorey and understorey strata in Australian vegetation. *Australian Journal of Ecology* **6**, 193–202.

Specht, R.L., Rayson, P., and Jackman, M. E. (1958). Dark Island heath (Ninety Mile Plain, South Australia). VI. Pyric succession changes in composition, coverage, dryweight and mineral nutrient status. *Australian Journal of Botany* **6**, 59–88.

Tallis, J.H. (1987). Fire and flood at Holme Moss: erosion processes in an upland blanket mire. *Journal of Ecology* **75**, 1099–1129.

Tolhurst, K.G., and Burgman, M.A. (1994). Simulation of bracken cover in forested areas in Victoria in response to season, overstorey and fire conditions. *Australian Journal of Ecology* **19**, 306–318.

Tolhurst, K.G., and Oswin, D.A. (1992). Effects of spring and autumn low intensity fire on understorey vegetation in open eucalypt forest in west-central Victoria. In 'Ecological impacts of fuel reduction burning in dry sclerophyll forest: first progress report'(Eds Tolhurst, K. G., and Flinn, D.) Research Report No. 349 pp3.1–3.60. (Department of Conservation and Environment: Melbourne.)

Tongway, D.J., Ludwig, J.A., and Whitford, W. G. (1989). Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia. *Australian Journal of Ecology* **14**, 263–268.

Tongway, D.J., and Ludwig, J.A. (1990). Vegetation and soil patterning in semi-arid mulga lands of eastern

Australia. *Australian Journal of Ecology* **15**, 23–34.

Tremont, R.M., and McIntyre, S. (1994). Natural grassy vegetation and native forbs in temperate Australia: structure, dynamics and life histories. *Australian Journal of Botany* **42**, 641–658.

Valette, J., Gomendy, V., Marechal, J., Houssard, C., and Gillon, D. (1994). Heat transfer in the soil during very low-intensity experimental fires: the role of duff and soil moisture content. *International Journal of Wildland Fire* **4**, 225–237.

van der Venter, H.A., and Esterhuizen, A.D. (1988). The effect of factors associated with fire on seed germination of *Erica sessiliflora* and *E. hebecalyx* (Ericaceae). *South African Journal of Botany* **54**, 301–304.

van Wilgen, B.W., Richardson, D.M., and Seydack, A.H.W. (1994). Managing fynbos for biodiversity: constraints and options in a fire-prone environment. *South African Journal of Science* **90**, 322–329.

Verner, J. (1984). The guild concept applied to management of bird populations. *Environmental Management* **8**, 1–14.

Vines, R.G. (1968). Heat transfer through bark and the resistance of trees to fire. *Australian Journal of Botany* **16**, 499–514.

Vlahos, S., and Bell, D.T. (1986). Soil seed-bank components of northern jarrah forest of Western Australia. *Australian Journal of Ecology* **11**, 171–179.

Wallace, D.D., and O'Dowd, D.J. (1989). The effect of nutrients and inflorescence damage by insects on fruit set by *Banksia spinulosa*. *Oecologia* **79**, 482–488.

Warcup, J.H. (1980). Effect of heat treatment of forest soil on germination of buried seed. *Australian Journal of Botany* **28**, 567–571.

Webb, L.J. (1968). Environmental relationships of the structural types of Australian rainforest vegetation. *Ecology* **49**, 296–311.

Weiblen, G.D., and Thomson, J.D. (1995). Seed dispersal in *Erythronium grandiflorum* (Liliaceae). *Oecologia* **102**, 211–219.

Wein, R.W. (1981). Characteristics and suppression of fires in organic terrain in Australia. *Australian Forestry* **44**, 162–169.

Wellington, A.B., and Noble, I.R. (1985a). Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* Labill. in semi-arid, south-eastern Australia. *Journal of Ecology* **73**, 645–656.

Wellington, A.B., and Noble, I.R. (1985b). Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus incrassata* Labill in semi-arid, south-eastern Australia. *Journal of Ecology* **73**, 657–666.

Wellington, A.B., Polach, H.A., and Noble, I.R. (1979). Radiocarbon dating of lignotubers from mallee forms of *Eucalyptus*. *Search* **10**, 282–283.

Weste, G., and Ashton, D.H. (1994). Regeneration and survival of indigenous dry sclerophyll species in the Brisbane Ranges, Victoria, after a *Phytophthora cinnamomi* epidemic. *Australian Journal of Botany* **42**, 239–253.

Weste, G., and Marks, G.C. (1987). The biology of *Phytophthora cinnamomi* in Australasian forests. *Annual Review of Phytopathology* **25**, 207–229.

Westoby, M., Rice, B., Griffin, G., and Friedel, M. (1988). The soil seed bank of *Triodia basedowii* in relation to time since fire. *Australian Journal of Ecology* **13**, 161–169.

Whelan, R.J. (1986). Seed dispersal in relation to fire. In 'Seed dispersal'. (Ed Murray, D. R.) pp 237–271. (Academic Press: Australia.)

Whelan, R.J., and Main, A.R. (1979). Insect grazing and post-fire plant succession in south-west Australian woodland. *Australian Journal of Ecology* **4**, 387–389.

Whelan, R.J., and Tait, I. (1995). Responses of plant populations to fire: fire season as an under-studied element of fire regime. *CALMScience Supplement* **4**, 147–150.

Williams, J.E., Whelan, R.J., and Gill, A.M. (1994). Fire and environmental heterogeneity in southern temperate forest ecosystems: implications for management. *Australian Journal of Botany* **42**, 125–137.

Williams, R.J. (1995). Tree mortality in relation to fire intensity in a tropical savanna of the Kakadu region, Northern Territory, Australia. *CALMScience Supplement* **4**, 77–82.

Williams, R.J., and Ashton, D.H. (1988). Cyclical patterns of regeneration in subalpine heathland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* **36**, 605–619.

Wimbush, D.J., and Forrester, R.I. (1988). Effects of rabbit grazing and fire on a subalpine environment. II. Tree vegetation. *Australian Journal of Botany* **36**, 287–298.

Withers, J. (1978). Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II. The differential seedling establishment of Eucalyptus ovata Labill. and *Casuarina littoralis* Salisb. *Australian Journal of Botany* **26**, 465–483.

Withers, J. (1979). Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. IV. The effect of shading on seedling establishment. *Australian Journal of Botany* **27**, 47–66.

Withers, J., and Ashton, D.H. (1977). Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. I. The structure and regeneration. *Australian Journal of Botany* **25**, 623–637.

Witkowski, E.T.F., Lamont, B.B., and Connell, S. J. (1991). Seed bank dynamics of three co-occurring Banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and interfire establishment. *Australian Journal of Botany* **39**, 385–397.

York, A. (1993). 'Bulls Ground Frequent Burning Study.' (State Forests of New South Wales: Sydney.)

Zammit, C. (1988). Dynamics of resprouting in the lignotuberous shrub *Banksia oblongifolia*. *Australian*

Journal of Ecology **13**, 311–320.

Zammit, C., and Hood, C.W. (1986). Impact of flower and seed predators on seed-set in two *Banksia* shrubs. *Australian Journal of Ecology* **11**, 187–193.

Zammit, C., and Westoby, M. (1987a). Seedling recruitment strategies in obligate-seeding and resprouting *Banksia* shrubs. *Ecology* **68**, 1982–1992.

Zammit, C., and Westoby, M. (1987b). Population structure and reproductive status of two *Banksia* shrubs at various times after fire. *Vegetatio* **70**, 11–20.

Zammit, C., and Westoby, M. (1988). Pre-dispersal seed losses, and the survival of seeds and seedlings of two serotinous *Banksia* shrubs in burnt and unburnt heath. *Journal of Ecology* **76**, 200–214.

To Burn or not to Burn? A Description of the History, Nature and Management of Bushfires within Ku-Ring-Gai Chase National Park

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The January 1994 bushfires in New South Wales has once again brought the issue of bushfire management within natural areas into sharp focus. This paper analyses the bushfire history of Ku-ring-gai Chase National Park (1943–1994) from fire records maintained by the National Parks and Wildlife Service. The patterns of bushfire occurrence for the Park are discussed. The management policies of the National Parks and Wildlife Service for this area are also outlined. The impact of the January 1994 wildfires on the Park is assessed, particularly in relation to the effectiveness of prescribed burning on wildfire control in the Warringah and Pittwater areas. Prescribed burning in the Park was effective in assisting with the containment of the 'Cottage Point' wildfire despite the extreme fire weather conditions experienced. The management policies adopted by the Service were effective in protecting important catchments, important animal species and maintaining refuges from which animals and plants can recolonise burnt patches. The importance of maintaining accurate and relevant fire history records is emphasised.

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KEYWORDS: Ku-ring-gai Chase National Park; bushfire history; January 1994 wildfires.

INTRODUCTION

Gill (1975) describes fire regimes in terms of the combined effects of bushfire frequency, intensity and season of occurrence. Gill and Bradstock (1993) add that the spatial distribution of bushfires, or the 'patchiness' of bushfires, is also an important component of the bushfire regime. Bushfires are an important agent of change in the bushland of south-eastern Australia. The composition and structure of natural plant and animal communities may be altered as a result of imposed changes in the fire regime.

For example Catling (1991) found that the infrequent occurrence of intense wildfires favours the development of a dense understorey which is favoured as habitat by native vertebrate fauna. Catling (1991) also found that frequent, low-intensity burns in autumn will disadvantage native mammal species and advantage many exotic species.

Fox and Fox (1986) report that a shrubby woodland site on the New South Wales mid north coast which had burnt twice within 12 years had significantly more plant species and higher shrub densities than a similar site burnt only once in the same period. Fox (1988) also found differences in plant species richness and diversity and community structure in a mid-north coast open forest at different ages since the last fire. Similarly Morrison et al (1995) found that fire frequency (i.e. time since last fire and inter-fire period) accounted for about 60% of the floristic variation in dry sclerophyll vegetation on the NSW Central Coast. They proposed that variability in the inter-fire period will lead to a greater diversity of plant species within a particular community. Christensen and Kimber (1975) also reported that changes in understorey composition may be brought about by alterations to fire frequency.

Ridley and Garner (1961) report the conversion of large areas of sub-tropical rainforest in Queensland to lantana groves following frequent burning. Rainforest areas are particularly vulnerable to transformation following bushfire and are frequently converted to eucalypt forest after intense bushfires have burnt through them in drought conditions. After long bushfire free intervals (ie > c.150 years) these same areas may convert back to the rainforest that once existed there (Ashton 1981, Hopkins 1981, Smith and Guyer 1983).

The application of different bushfire regimes will also impact on soil fertility and structure. Reduced cover as a result of frequent bushfires or extensive high intensity bushfires will lead to the mobilisation of soil and nutrients and greatly accelerate soil erosion (Lamy and Junor 1965a and 1965b, Harwood and Jackson 1975, Henry 1977, Blong et al. 1982, Adamson et al. 1983, Atkinson 1984). It is reasonable to assume that a close inter-relationship exists between the effects of fire on inducing changes to soil fertility and structure and to subsequent changes in the composition and structure of plant and animal communities. Understanding the spatial and temporal distribution of bushfires and prescribing fire regimes to meet management objectives is therefore a very important task within conservation reserves.

Ku-ring-gai Chase National Park is similar to many other conservation reserves on the fringe of Sydney. The Park is comprised of flammable vegetation types and steep slopes surrounded by urban and rural development. The Park has a history of frequent and extensive wildfires. The Park also contains species which are sensitive to the application of certain bushfire regimes. Management of the Park has to be undertaken in a way which is sensitive to the protection of neighbours and Park visitors but which is also ensures that species and natural communities are conserved.

This paper examines the approach taken by the New South Wales National Parks and Wildlife Service (NPWS) in fire management within the Park. The history and occurrence of bushfires within the Park is analysed and the management response of the NPWS is summarised using specific examples of the approach taken in the management of significant species and landscapes. The success of this approach and the implementation of prescribed burns within the Park over the last five years is assessed in relation to the impact of the January 1994 wildfires.

NSW NATIONAL PARKS AND WILDLIFE SERVICE

The NSW NPWS has statutory responsibility *(inter alia)* for the establishment of national parks and nature reserves; and within parks and reserves for the protection of all plants, animals and landscapes including wilderness areas and the provision of facilities for the use, appreciation and enjoyment of those areas. The Service is also responsible for the protection and care of fauna; the protection of native plants and the care, preservation and the protection of Aboriginal relics and places throughout NSW.

The Service has a statutory responsibility under the Bush Fires Act (1949) for minimising the risk of escape of fires from areas under its care, control and management. The Service co-operates with other fire authorities and land management agencies in bushfire suppression, mitigation and prevention activities within local government areas and as such contributes to the development and implementation of fire operations and fuel management plans under Section 41AB of the Bush Fires Act 1949.

The management of bushfire within national parks and nature reserves is guided by the objectives and strategies identified within plans of management prepared in accordance with Section 72 of the National Parks and Wildlife Act 1974. Section 72 prescribes that for national parks and nature reserves the Service shall have regard (inter alia) to 'the protection … against fire and erosion', 'the protection of special features', 'the preservation … as a catchment area' and 'the conservation of wildfire'.

If no plan of management has been prepared, then bushfire management policies and procedures are specified within non-statutory NPWS bushfire management plans. These same policies and procedures are also negotiated with Bush Fire Management Committees and are adopted for Parks and Reserves within fire operational and fuel management plans prepared under Section 41AB of the Bush Fires Act 1949.

The NPWS must also consider the relevant arrangements made at Commonwealth and State Government level for protecting the environment. These include international treaties, conventions and inter-governmental agreements to which the Commonwealth and NSW State Government are signatories such as the Convention on Biological Diversity and the Inter-Governmental Agreement on the Environment. These conventions and agreements commit the NSW Government to protecting biological diversity, maintaining ecological processes and systems and integrating environmental considerations into all levels of Government decision-making respectively. These conventions and agreements must be taken into account in the planning and implementation of fire management activities.

KU-RING-GAI CHASE NATIONAL PARK

Ku-ring-gai Chase National Park is an area of about 14,700 hectares on the northern outskirts of Sydney. The Park is part of a complex of national parks and nature reserves on the sandstone plateaux surrounding Sydney (eg Blue Mountains National Park, Brisbane Waters National Park, Marramarra National Park, Muogamarra Nature Reserve etc). Responsibility for the management of the Park is vested in the Director-General of the National Parks and Wildlife Service. The objectives of management for the Park are outlined within an adopted plan of management and are consistent with objectives defined in Section 72 of the National Parks and Wildlife Act 1974.

The Park is part of the Hornsby Plateau and is bordered by the drowned river valleys of the Hawkesbury River and the urbanised shale plateaux and ridges of the northern suburbs of Sydney. The topography is characterised by sandstone slopes averaging 10–15° over an elevation range of about 200 metres and plateaux with large outcrops sandstone outcrops covering >50% of the surface area. The sandstone soils of the Park are shallow and infertile, have a low water capacity and are subject to extreme sheet and gully erosion following disturbance (Chapman and Murphy 1989).

The slopes and ridges are covered with a dry sclerophyll vegetation with shrubland, woodland and open forest structural types being the most common. In narrow gullies on Narrabeen Shales and in some of the small volcanic diatremes within the Park, a more mesomorphic vegetation occurs under tall open forest and closed forest structural types. Small areas of sedgeland are found in the hanging swamps of Lambert Peninsula (Thomas and Benson 1985).

Fine fuel types are differentiated mainly on the basis of vegetation structure and density and accumulate quickly in the first 8 years following a fire. From 8 to 15 years, fuels accumulate more slowly and after 20 years, fuel loads appear to stabilise. Maximum fine fuel levels occur in the shrubland fuel type with as much as 35 tonnes/hectare being recorded in 25 year old vegetation (Conroy 1993).

The bushland within and surrounding the Park is one of the most fire prone areas in Australia with very high fine fuel potential, very flammable fuel types, steep slopes, regular occurrence of extreme fire danger weather and large areas of urban-bushland interface. The Park has a total linear boundary of c.116 km. Fifty-six kilometres of this boundary is urban-park interface with c.2000 residential homes being situated on or near the Park boundary.

BUSHFIRE IN THE PARK

Prehistoric Records

Kodela's (1984) study on pollen and charcoal deposits in a 6,000 year old soil profile within a hanging swamp at Salvation Creek on the Lambert Peninsula in Ku-ring-gai Chase NP, revealed widely fluctuating charcoal inputs. Major peaks in charcoal influx, representing high fire activity (either due to high fire frequency and/or high intensity fires) were believed to have occurred around 300, 400, 1300, 1700 and 2300 (main peak) years before present. Low fire activity was recorded approximately 800 and 4200 years before present. Kodela (1984) did not find any evidence of vegetation change with increasing fire frequency.

Martin (1971) recorded pollen of the rainforest genera *Ackama, Nothofagus* and *Rhodomyrtus* in 4,000 year old sediment from the nearby Dee Why Lagoon. These species are fire sensitive and are now not represented in the area. It is possible that fire and/or climatic changes led to these species becoming locally extinct.

Evidence of Aboriginal occupation and burning practices in the area comes from a variety of sources. Hughes and Sullivan (1981) found evidence of increased firing of the landscape over the last c.4000 years in rock shelters in the Mangrove Creek catchment near Sydney, and suggest that this was closely associated with the Aboriginal occupation of the area. They believed that Aboriginal fire regimes lead to episodic and severe erosional and depositional events which greatly exceeded those levels that might be expected under natural firing regimes. Head (1989) however casts some doubt over these conclusions suggesting 'this need not signify anything more than disturbance at the very local scale'.

Historic Records

Clark and McLoughlin (1986) believe that on the basis of available historical and biological evidence from the north shore of Sydney, that Aborigines burnt the bushland frequently. They state that it is likely that burning was more frequent on the shale ridges (c.1–5 year intervals) than on the adjacent sandstone slopes (c.7–15 year intervals). The main evidence to support this notion comes from the accounts of explorers (eg the First Fleeters: Hunter, Phillip and Worgan) of the North Shore of Sydney in the nineteenth century and their descriptions of the nature of the vegetation and of Aboriginal land management practices at the time.

Extreme wildfire events have been recorded in the Sydney Region in 1888, 1928–29, 1936, 1938–39, 1944–45, 1946–47, 1951–52, 1957–58, 1964–65, 1968–69, 1974–75, 1977, 1980–81 and 1983 (Cheney 1979, Cunningham et al. 1994).

Ku-ring-gai Chase Trust records (prior to 1967) and NPWS records (since 1967) reveal extensive wildfire events within the Park during the same time periods, that is 1943, 1946, 1951, 1957/58, 1965, 1967/68, 1977, 1979, 1980, 1983 and 1994. Table 1 shows the location and approximate size of large (ie >500ha) recorded wildfires in the Park over the last 51 years.

Vines (1974) stated that 'severe forest-fire seasons' in southern Australia occurred every 13 years and were associated with regular drought periods. He suggested that for any given region, droughts and possible bushfire seasons are chronologically related to distinctive weather patterns for the area which are quasi-periodic in nature. Most of the major wildfires within the Park (eg Table 1), have coincided with long extended drought periods (ie 1957–58, 1967–68, 1979–83, and 1993–94) and have occurred where fuels had accumulated over large fire prone areas for periods up to and exceeding 10–12 years.

The frequency and extent of wildfires in the Park in the late fifties and sixties was of great concern to the Trustees of the Park and to local fire authorities (Anon 1967). A special study of the impact of these fires was commissioned by the Park Trust (Lamy and Junor 1965). They reported that 'intensely hot fires have repeatedly ravaged this catchment (Porto Bay) and a recent fire caused great damage and destruction of tree cover'. They also stated 'Accelerated erosion has occurred in all catchments of Ku-ring-gai Chase over the past fifty years and, in the main, this can be directly attributed to the damage caused by frequent severe fires'. Similar problems were encountered in nearby areas such as the McDonald River Valley (eg Henry 1977).

TABLE 1

Major wildfires in Ku-ring-gai Chase NP 1943/44–1993/94

00/00/1943	Lambert Peninsula	3,500
28/01/1946	Duckholes/Ingleside	4,000
00/00/1958	Refuge Bay/Lambert Peninsula	4,600
14/11/1965	Refuge Bay/Lambert Peninsula	3,000
27/11/1968	Nth Turramurra/St Ives Chase	850
01/10/1971	Wahroonga/Nth Turramurra	518
16/12/1979	Nth Turramurra/Terrey Hills	5,200
01/11/1980	Shark Rock Ridge/Berowra	1,226
08/01/1983	Govett Ridge/Ten Bob Ridge Cowan	1,400
09/01/1983	Mt Colah	1,320
23/12/1990	Mt Colah/Nth Turramurra	935
07/01/1994	Cottage Point/Lambert Peninsula/Terrey Hills	7,110

From the early 1970's through to the 1980's, reports of an increasing 'shrubbiness' in the nature of the vegetation in the Park was reported. This increased shrubbiness was generally attributed to the reduced frequency of extensive bushfires caused by strategic fuel management programmes and the increased effectiveness of fire suppression and fire prevention programmes. Photographic evidence (ie Park records of oblique 1900–1910 photographs and aerial photographs from 1946–1994) and accounts of bushwalkers and scout leaders who have used the Park over the last 50 years confirm this observation. For example Mr Fred Matthews of Waitara (*pers. comm.*). has used the Park with his scout troop for over 30 years and states that it was possible to walk from one rock outcrop to another within the Park with little difficulty in the 1940's, 50's and 60's. However in the 1980's and 1990's the vegetation has become so dense in some areas that to walk along some of the same plateaux and ridges becomes a real struggle with dense shrubs being encountered all of the way.

This evidence is also consistent with accounts from other areas in the Hawkesbury-Nepean River catchment. Many of the land-owners from the 1940–50's who are still living in the area (eg Woodbury family from Spencer on the Hawkesbury River) report the increased 'shrubbiness' in the bush over the last 50 years and the 'unfortunate' decline in some of the more attractive flowering plant species such as Christmas Bells (*Blandfordia nobilis* Sm.), Flannel Flowers (*Actinotus helianthi* Labill.) and Native Rose (*Boronia serrulata* Sm.) as a result of a decrease in bushfire frequency. Generally a more open understorey and greater ease and comfort of bushwalking is consistently reported by bushwalkers and neighbours who used the Park in the 40's, 50's and 60's (*pers. comms.*).

Experienced volunteer bush fire brigade members from the Coal and Candle VBFB in the Warringah Council area (*pers.comm.*) believe that the installation of authorised fireplaces in the West Head and Duckholes area of the Park in the early to mid-1970's had a very significant impact on reducing the number of wildfires caused by campfires in the Park. Cheney (1979) supports these observations arguing that the fre-

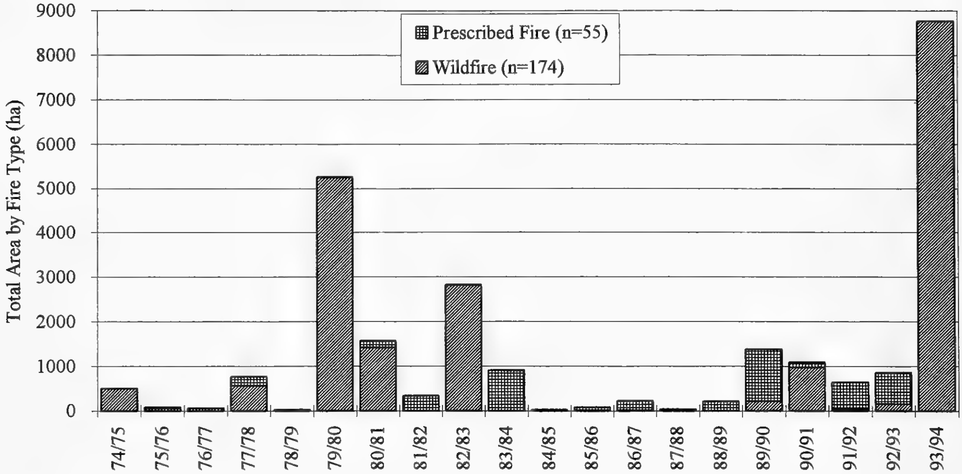

Fig. 1. Total area burnt by bushfire type (n = 229) within Ku-ring-gai Chase NP (1974–94).

quency of large fires in southern Australia has probably decreased recently as a result of greater management and control of bushland, the impact of fire prevention programmes, a decrease in the number of ignition sources, more efficient and effective suppression of fires and increasing fuel management and control by land management authorities. Although conjectural and anecdotal, this information is valuable in understanding the relationship between fire regimes and the landscape and for understanding changes over time in the nature of the vegetation.

Total Area Burnt by Fire

The total area burnt by fire in the Park over the last 20 years is shown in Figure 1 and Figure 2. The total area burnt within the Park over the last 20 years is in excess of 25,000 hectares (ie c. 1,250 $ha.yr^{-1}$) with a large number of fires burning the same area more than once. Unfortunately, reliable fire frequency data for the Park are not yet available to present any analysis of this.

Over the last 20 years, large wildfires (ie >1000 hectares) were recorded in the Park in 1979, 1980, 1983 and 1994. These periods coincide with extended droughts within the Sydney Region. Prescribed burns have not contributed significantly to the total area burnt. At the end of 1993/94, prescribed burning had contributed only 18.25% of the cumulative total area burnt. The average size of recorded wildfires within the Park over the last 20 years (n = 174) is 120.3 ± 782 hectares. In the period before 1974, the average size of recorded wildfires (n = 122) is 103.9 ± 475.6 hectares. The average size of prescribed burns in the last 20 years (n = 55) is 86.1 ± 28.9 hectares. There are no records of the area burnt in prescribed burns prior to 1974.

Cause of Wildfires

Arson is thought to account for 40.8% of the total number of wildfires occurring in Ku-ring-gai Chase NP (Figure 3). If combined with the major proportion of wildfires of 'unknown' cause then an estimate of c.57% of all wildfires can be attributed to arson and related causes.

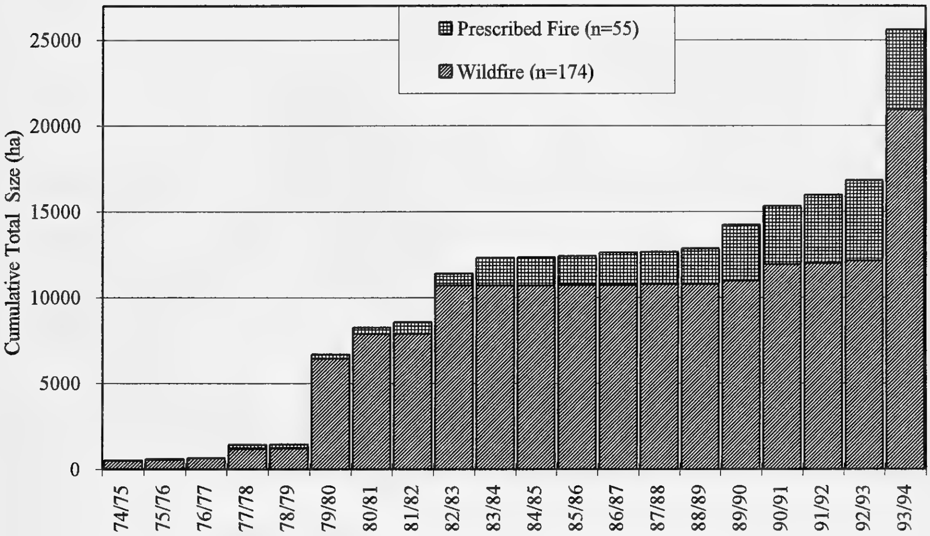

Fig. 2. Cumulative total area burnt by bushfire type (n = 229) within Ku-ring-gai Chase NP (1974–94).

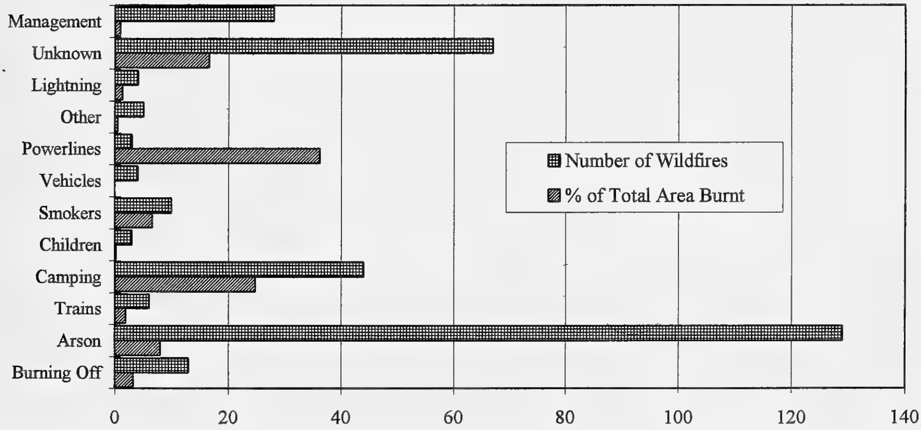

Fig. 3. Total number and % of total area burnt by cause (n = 316) within Ku-ring-gai Chase NP (1943–94).

Natural sources of ignition (ie lightning) account for only 1.3% of all wildfires and 1.3% of the total area burnt by wildfires over the recorded fire history of the Park (ie 51 years) This is because storms of this type, on or near the coast, are usually accompanied by heavy rainfall. This is quite different in the Blue Mountains area (Conroy and Gellie 1987) where lightning may account for up to 28% of wildfire ignitions and where as many as 25 wildfires may be caused by the one thunderstorm event (N. Gellie NPWS *pers comm).*

Although powerlines were not a significant cause of wildfires during the period, comprising only 0.9% of the total number of wildfires, they are significant in terms of the total area burnt, comprising 36.2% of that total. While the average size of an arson fire in the Park is 97.8 hectares, the average size of a powerline fire is 441.2 hectares (Figure 3). Powerline fires are caused by electrical transmission lines striking together in high wind conditions which results in hot metal and insulation material dropping to the ground.

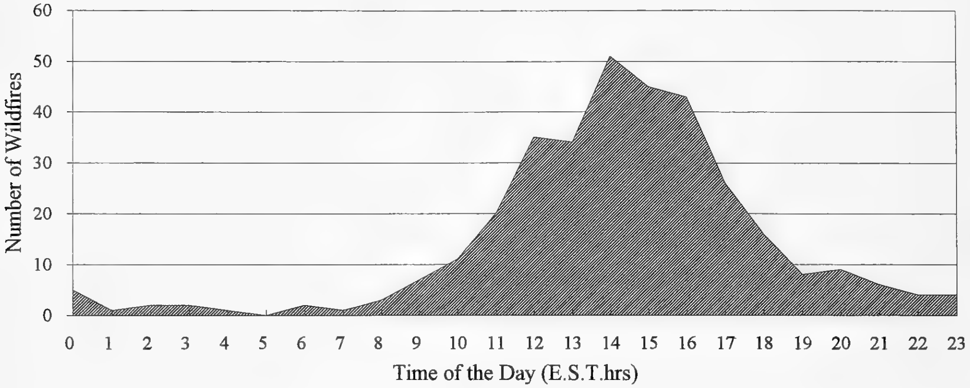

Fig. 4. Number of wildfire ignitions by time (EST) of the day (n = 260) within Ku-ring-gai Chase NP (1943–94).

Time of Ignition of Wildfire

Records of wildfires in the Park (1943–1994) where time of ignition was recorded (n = 260) were analysed. The time of the day when most wildfires are ignited is between 1300hrs and 1600hrs, with 43.8% of all wildfires occurring during this period (Figure 4). The large majority (ie >75%) of wildfires being ignited between 1000–1800hrs. Wildfire ignitions which were recorded between 2300–0100hrs are related to the practice on New Years Eve, of firing boatflares from boats moored in Cowan Waters and Pittwater across the Park on the stroke of midnight. The flares ignite fires in Park areas which are usually difficult to access and at that time of the night, difficult to resource with firefighters.

Time of day and wildfire ignition are likely to be related through a variety of factors including relative humidity and associated fine fuel moisture content. It is very likely that societal routines (eg school times and shift hours) would also influence these figures.

Day of the Week

Wildfire analysis by day of week shows some interesting trends. Most wildfires are ignited on Sundays (22.6%) and Mondays (17.6%) (Figure 5). This trend may be related to the greater number of people using bushland for recreational purposes on weekends and public holidays and to the number of people who leave campfires unattended.

Month of Occurrence

The bush fire danger period in New South Wales is usually 1st October to the 31st March unless modified as a result of local weather conditions. The trends of recorded wildfire occurrence by month within Ku-ring-gai Chase NP are illustrated in Figures 6 and 7. The data show that in terms of area burnt, the most important period is from October to January. There is a large drop in the recorded area burnt by wildfire in February. This may be explained by the slightly wetter conditions which exist in the Sydney Region in February (average wildfire size is 7.6 hectares) and as result of societal factors such as the end of the NSW school Christmas holiday period.

The trend in the number of recorded wildfires by month shows that the six-month period August–January is the most important period for wildfire occurrence with 80% of the total number of recorded wildfires. However the average size of recorded wildfires for August (29.6 ha), September (27.3 ha) and October (27.3 ha) is significantly less than the next period of November (153.2 ha), December (127.9 ha) and January (462.2 ha).

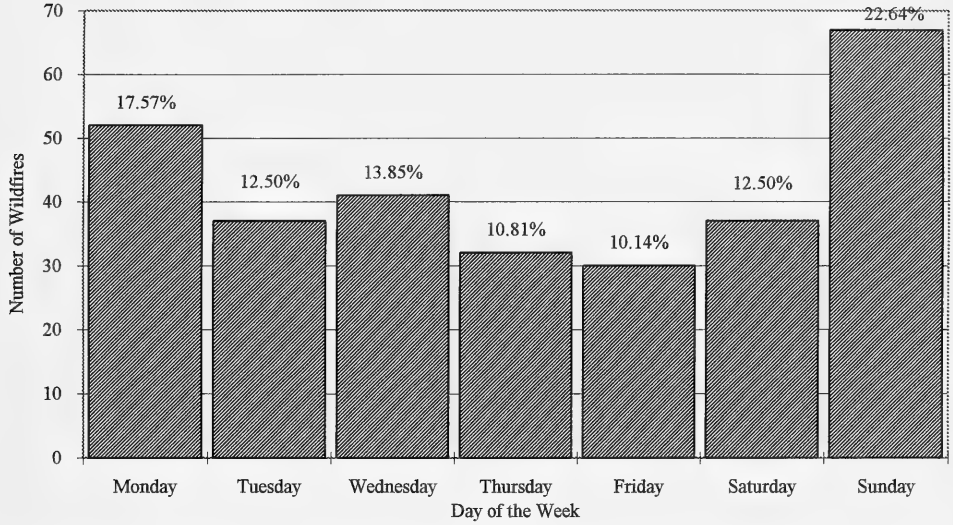

Fig. 5. Number of ignitions by day of the week (n = 296) within Ku-ring-gai Chase NP (1943–94).

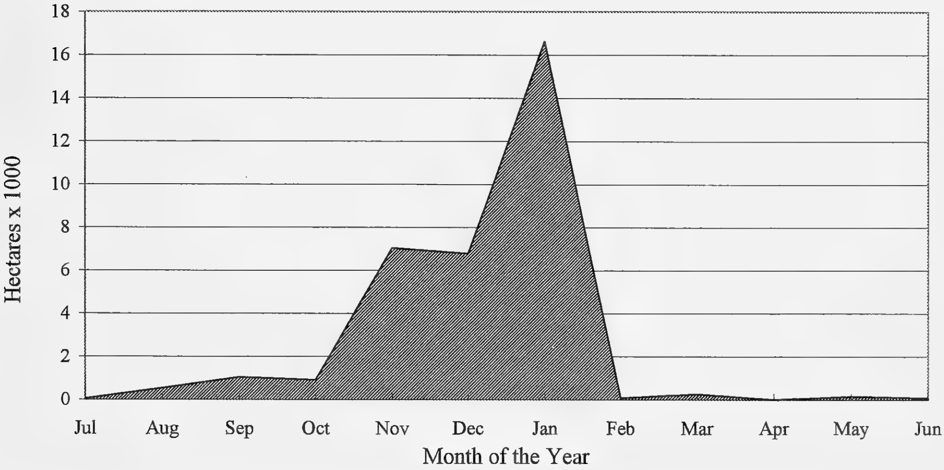

Fig. 6. Total area burnt by month of the year (n = 296) within Ku-ring-gai Chase NP (1943–94).

Number of Wildfires by Size Class

The wildfire data (Figure 8) for Ku-ring-gai Chase NP show that a large proportion of wildfires (69.6%) do not exceed 10 hectares in size, while 86.8% of wildfires do not exceed 100 hectares in size. Trends in the size of wildfires within discrete areas can be used as a very useful performance measure of the effectiveness of strategic fuel management works and the effectiveness of the total wildfire suppression response (ie the detection and suppression of wildfires).

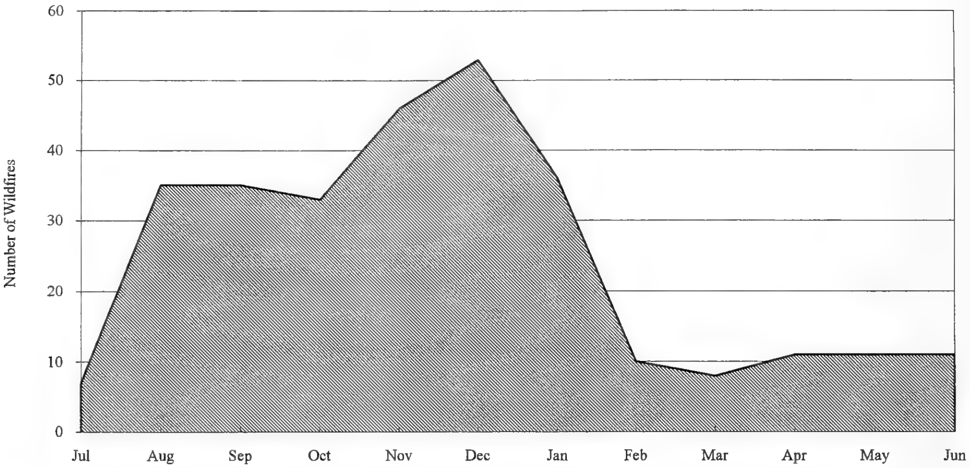

Fig. 7. Number of wildfires by month of the year (n = 296) within Ku-ring-gai Chase NP (1943–94).

Bushfire Management Considerations

The NSW National Parks and Wildlife Service has developed bushfire management policies for Ku-ring-gai Chase National Park (NPWS 1994) which take into account the fire history of the Park as described above and those special features of the Park which may be sensitive to changes in fire regimes. Some of these special features are summarised below.

Grevillea caleyi R.Br.

Grevillea caleyi is an endangered plant (Briggs and Leigh 1988) which is restricted to a 6 x 6 km area centred on the northern Sydney suburb of Terrey Hills (Scott et al. 1995) and which has a some small populations within both Ku-ring-gai Chase and Garigal National Parks. It is a fire sensitive species which relies on germination from a soil seedbank to recover after fire. Senescence is high in populations of *G. caleyi* which are older than about 12 years. Repeated fires at intervals of less than 8 years will cause local extinction of *G. caleyi* (Scott et al. 1995).

Scott et al (1995) also identified the potential negative impacts caused as a result of creating islands of unburnt habitat in areas containing rare or threatened plants, particularly where those species are also obligate seeders. For example seed predators may be drawn to an unburnt site and therefore consume most of the crop of seed produced for that year. *G. caleyi* does not produce a great amount of seed per plant with only 3% of flowers producing viable seed. The seed is relatively long-lived with a half-life of about 7.6 years but 82–92% of the seed is consumed by seed predators. Therefore it is important to minimise the impacts of seed predators on the plant after bushfires.

The NPWS fire management policies prescribe a fire regime for plant communities known to contain *G. caleyi*, which attempts to ensure that fire frequency is variable and where the average fire frequency is less than one fire every 12 years. Populations *of G. caleyi* are also burnt if surrounding areas are burnt and the average fire frequency at the site is >12 years. *G.caleyi* seedlings have been recorded in good numbers in many of the previous known locations which were affected by the January 1994 wildfires.

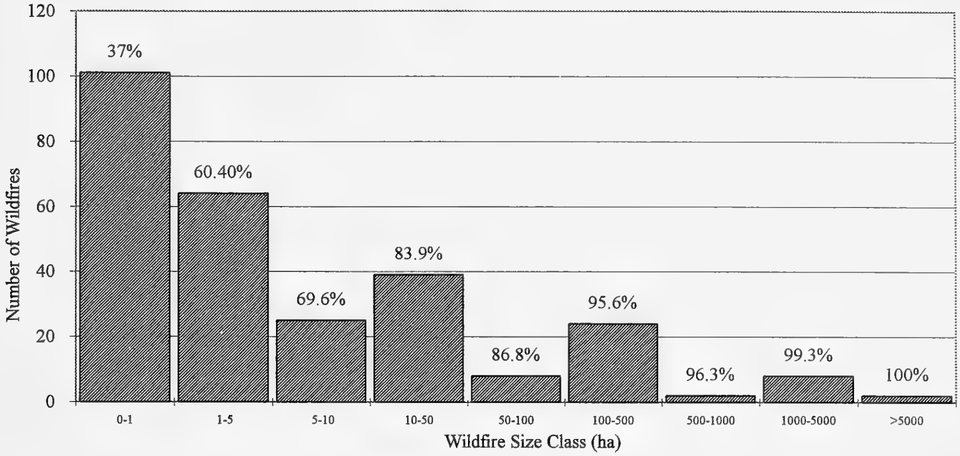

Fig. 8. Number of wildfires by size class (n = 273) showing cumulative total (%) for each size class within Ku-ring-gai Chase NP (1943–94).

Koala Populations

Koalas have been recorded within the Park at various locations (eg West Head, Duckholes, Akuna Bay and Cottage Point). Wildfires have been implicated in the decline of koala populations in New South Wales (Lunney et al. 1988). Tilley and Uebel (1988) describe the effectiveness of the use of selective strategic burning and aerial ignition methods for hazard reduction in assisting to mitigate the effects of wildfires on koala populations in the Upper Nepean catchment area. Koalas appear to be particularly vulnerable to high intensity fires and in the long-term, to the effects of frequent low intensity fires on their habitat as a result of the impacts on soil fertility and food tree species survival.

NPWS Park fire management policies prescribe measures which aim to reduce the risk of high intensity bushfires in areas where koalas have been recorded by strategic fuel reduction burns. This strategy proved to be very effective during the January 1994 wildfires, with known locations of koalas being protected from extreme wildfire behaviour as a result of reduced fuel levels in surrounding areas.

Sensitive Slopes

The major landscape unit of the Park is the Hawkesbury landscape type (after Chapman and Murphy 1989) which consists of shallow discontinuous lithosols or siliceous sands, yellow earths, earthy sands and yellow podzolic soils. This soil type is highly susceptible to concentrated flow erosion and sheet erosion especially when the organic matter is removed by intense bushfires.

Park fire management policies specify that in areas containing a combination of steep slopes and sensitive soils, the application of bushfires should ensure that adequate levels of cover are maintained over slopes to minimise soil erosion within those catchments. For example fuel management burns are staged over several years in fire sensitive catchments to ensure that sufficient vegetation cover is available to reduce the risk of concentrated flow and sheet erosion. The intensity of the burns is also managed to increase the patchiness of vegetation cover in these catchments which further reduces the risk of erosion.

Rainforest

The margins of rainforest with eucalypt forest may be sharp or there may be an ecotone depending on factors which include the time since the last fire and the average fire interval for the area. Rainforest boundaries are often interpreted as advancing at the expense of the eucalypt forest due to an absence of disturbances such as fire (Smith and Guyer 1983). Although rainforest fires have been well documented, rainforests nevertheless provide effective barriers to the progress of wildfires except under the most extreme fire weather conditions.

Rainforest vegetation occupies a very small area (<1%) of the Park (Conroy 1987). It is distributed in very narrow gullies and in volcanic craters (eg Campbells Crater) which are extremely vulnerable to intrusion by wildfire and colonisation by exotic species. Many fire sensitive plant species are only known from these rainforest communities. These species include *Abrophyllum ornans, Cryptocarya spp, Dendrobium striolatum, Polyosma cunninghamii* and *Toona australis*. The NPWS policies are aimed at encouraging the growth of rainforest areas to their maximum available limit within the Park. The NPWS therefore attempts to minimise the impact of bushfires on the ecotonal area of rainforests. For example it is tempting to use rainforest boundaries as natural boundaries for wildfire control and prescribed burns because it is safer and cheaper to do so. The NPWS policies suggest that this is not acceptable and that the extra effort should be taken to avoid impacts on rainforest ecotones.

The policies also state that some areas will be managed to increase opportunities for whole catchments to be kept in an old age class condition (eg Smiths Crater, Campbells Crater and Cicada Glen Creek catchments.)

Old Growth Vegetation

There are very few areas of old growth dry sclerophyll vegetation remaining within the Park or for that matter within the Sydney Region generally. In 1986, only 25% of the area of the Park was older than 21 years (Conroy, 1987). In 1994, following the January fires this figure has declined to about 1% (*pers.obs.*). A similar situation occurs in other conservation areas on Hawkesbury Sandstone soils.

The Park fire management policies state that it is desirable to have at least 50% of the most common plant communities in an old age class condition (ie >20 years in age). This is because of the special needs of some animal species for dense shrub and herb cover (eg lyrebirds, whip birds, pheasant coucals, red-necked pademelons, bandicoots etc), to serve as scientific benchmarks, as a means of implementing the 'precautionary principle' in accordance with Clause 3.5.1 of the Inter-Government Agreement on the Environment and to give managers flexibility in the future management of the Park.

The policies also state that some areas will be managed to increase opportunities for whole catchments to be kept in old age class condition (eg Mt Murray-Anderson, Shark Rock Ridge, Windybanks Ridge). These policies are taken into account when prescribed burns are being planned and during the development of wildfire control strategies.

Special Habitats

There are a few very special sites within the Park that contain vegetation communities which are of conservation and scientific interest. These include sites on volcanic dykes and diatremes (eg West Head Dyke, Campbells Crater and Smiths Crater) and vegetation communities and plant species on sandstone rock outcrops and gnammas (eg *Kunzea rupestris* Blakely and *Micromyrtus blakelyi* J. Green).

These sites are uncommon in Sydney Region and could be irreversibly damaged by the application of the wrong type of fire regime. A conservative approach has been adopted by the Service in managing these plant communities (ie IGAE precautionary principle). Park fire management policies specify that these sites will not be subjected to prescribed burning and that where it is possible and cost-effective to do so, wildfires will be prevented from burning them until the impacts of fire on them are known with some certainty. The nature of wildfires in the Park makes it unnecessary to burn these communities deliberately as that would only reduce future management options.

Prescribed Burning Strategies

Strategies for prescribed burning within the Park have been developed largely from an understanding of wildfires over the last 20–50 years and attempts to minimise unacceptable impacts on species, communities and landscapes from inappropriate fire regimes.

Volunteer bush fire brigades (VBFB's) and the NSW Fire Brigades (NSWFB) concentrate on reducing hazards in close proximity to assets at risk usually on vacant crown lands and private property. Generally NPWS concentrates on Park strategic wildfire control burns; while VBFB's and NSWFB's concentrate on 'off-Park hazard reduction burns'. This arrangement reflects relative funding arrangements, availability of resources of the various organisations and statutory responsibilities. However, there are also many examples where resources and responsibilities are shared to achieve regional fire management objectives and to overcome individual agency funding or resourcing problems.

There had been 30 recorded prescribed burns within the Park in the five years immediately preceding the January 1994 wildfires. Of these 23 (76%) were located on Park boundaries. The total area burnt was 2950 hectares of which 2942 hectares were within the Park. Therefore 19.6% of the total Park area had been treated in prescribed burns in the 5 years prior to the January 1994 wildfires.

A total of 1404ha or 9.4% of the Park had also been affected by wildfires (n = 44) in the previous five years. Therefore 26% of the total area of the Park contained fuel which was less than 5 years old. A large proportion of this area was located on Park boundaries and located in areas affected by the January '94 wildfires.

Many of the prescribed burns over the previous five years had been undertaken to reduce fire threats to neighbouring lands, protect species habitats, protect old growth vegetation and to provide a diversity of age classes in the more common plant communities.

Effect of Prescribed Burning on Containing Wildfires

Buckley (1992) stated that fuel should be reduced across more than 50% of the area of a site to be effective under very high to extreme fire danger conditions. Fuel reduction burning in coastal forests of East Gippsland covering more than 50% of the area of a site provided excellent protection against wildfire spread for at least one-and-half years, but the effectiveness of these burns reduced progressively over a seven year period depending on the fire weather conditions.

The value of prescribed burning in assisting with the containment of wildfires is often questioned and some argue that prescribed burning is of little use in wildfire control. This is not the case (*pers.obs*). There are many examples in the Hornsby and Warringah areas where wildfires have been contained or where the impact of wildfires on assets, species, scenic resources, heritage items and landscapes has been greatly reduced as a result of prescribed burns. Recent examples occurred at Berowra (1985), Cowan (1990), West Head (1994), Belrose (1994), Duffys Forest (1994) and St Ives (1994) where wildfire runs were effectively contained under extreme weather conditions as a result of prescribed burns.

Problems with Implementing Prescribed Burning

Johnson (1984) summarises the many problems involved in implementing prescribed burns. Among these were regulatory constraints (eg clean air legislation), the costs associated with risk of fire escape during high fire danger days (eg in Victoria, December 1994), the costs and risks associated with postponement of prescribed burning programmes due to poor weather conditions, the risks to the safety and welfare of firefighters and controversy over environmental impacts.

Gill et al. (1987) also discuss the difficulties associated with selecting appropriate weather conditions to undertake prescribed burning. They estimated that at fuel weights of 10–40 t/ha^{-1}, optimal weather conditions (ie from Melbourne data) for prescribed burning occurred on only 11.2 days per annum. They state ‘it is probable that several years may pass without there being days optimal to prescribed burning so that fuel weight continues to rise …’. These difficulties are very real to managers and firefighters in the Sydney Region with a large proportion of planned burns being cancelled due to unsuitable weather conditions. Some prescribed burns in the Park (eg 1984 at West Head) and in the nearby Garigal NP (eg April–June 1994 at Middle Harbour Creek) have had to be re-scheduled on four separate occasions over a period of several months as a result of unsuitable weather conditions.

Reliance of land management authorities in the Sydney Region on the support from volunteer bush fire brigades who are mostly available on weekends only, further compounds this problem. It is common for a large number of prescribed burning proposals to be cancelled at short notice due to either lack of available resources, lack of suitable weather conditions or to air pollution problems. For example ‘No-burn notices’ issued under Section 24A of the Clean Air Act (1961) were responsible for cancellation or modification of prescribed burns on 7/05/1992 at Cottage Point in Ku-ring-gai Chase NP; 27/08/1991 at DeBurghs Bridge in Lane Cove NP and more recently on 17/08/1994 at Cattai NP.

Local community groups have also sometimes thrown the prescribed burning programme into disarray. For example at Elvina Bay in 1992 residents were polarised on the issue of whether a burn proposed by NPWS and local VBFB’s should proceed. The residents believed that an alternative method of hazard reduction (manual hazard reduction) should be trialled by them. This was later done and proved very effective in this situation. Community opposition to burning as a means of reducing hazards is a common problem throughout the Sydney Region and needs to be managed more effectively.

One of the problems of fire management in the Park, is that while it is generally not possible to burn an area more frequently than about once every five years during the prescribed burning season (ie March–August), it is possible for a wildfire burning under extreme weather conditions to run through the same area with sufficient intensity to cause property damage. This was seen in a number of localities in the Warringah/Pittwater area during January 1994 (eg Cottage Point, McCarrs Creek and on the Centre Trail in Ku-ring-gai Chase NP) where the Cottage Point fire failed to be contained by prescribed burns implemented between 2 and 5 years ago. However the intensity of the fire was reduced as it burnt through lighter fuel loads. Only those prescribed burns which had been implemented in the last 18 months were effective in containing the Cottage Point wildfire. Similar problems were encountered in other areas during the January’ 94 wildfires (eg at the Howes Valley, Lane Cove and Hornsby fires).

CONCLUSION

To burn or not to burn? The well documented fire history of Ku-ring-gai Chase National Park demonstrates that until the 1970’s, wildfires were more frequent and were widespread throughout the Park. This fire regime resulted in a depleted shrub understorey, the exposure of large amounts of bare soil and subsequent sheet erosion and sedimentation of the waterways. It is likely that this scenario applied to many of the bushland areas around Sydney.

It seems that the implementation of strategic prescribed burns, the better resourcing of volunteer bush fire brigades and NPWS, fire prevention and detection programmes and the installation of authorised fireplaces did much to bring this situation under control.

After 1970, fire suppression became more effective and recreational use of the Park and other fire ignition causes were better managed. Prescribed burns and fire trails were placed in strategic areas which reduced fire spread and wildfires became less frequent but more intense. A fire frequency of 10–15 years for most of the Park particularly the ridges and upper slopes is apparent over the last fifty years. The effect of a reduced fire frequency and the resulting higher fire intensities has extended the age of vegetation in many areas and has thereby increased the 'shrubbiness' of the vegetation.

Regular analysis of fire records provides a good basis for guiding the development of fire management policies and priorities. The analysis of fire cause for example can assist in targeting particular sources of fire (eg firing of boat flares and holiday-makers). The analysis of areas of fire origin will also assist in identifying off-Park sources of fire occurrence. The analysis of average wildfire size will also assist in identifying the success of prescribed burning and detection strategies. Fire frequency data (not analysed here) will also assist Park managers in determining the success of implementing certain fire management policies.

Despite doubts to the contrary by many groups, fuel reduced areas provide a real advantage to the achievement of fire regime prescriptions for natural areas and for locations considered to be significant and sensitive to changes in the fire regime. The implementation of strategic fuel management burns does assist in wildfire control even under extreme fire weather conditions in certain circumstances.

Fire records are an important source of information and the old records maintained by NPWS and Trust staff have proved to be particularly valuable in policy decisions today. This significance is often not recognised by land management agencies. The prescription of bushfires in an area must consider the wildfire history to be relevant and appropriate.

"To burn or not to burn"? — the answer is to burn, but to ensure that it is by prescription in accordance with management objectives and related strategies. Performance in achieving management objectives must be closely monitored and adequate records and maps kept of fire applications and fire effects.

REFERENCES

Anon. (1967). Fires a Problem in Ku-ring-gai Chase. *Bush Fire Bulletin.* **6,** 17–18.

Adamson, D., Selkirk, P.M. and Mitchell, P. (1983). The Role of Fire and Lyre Birds in the Sandstone Landscape of the Sydney Basin. In 'Aspects of Australian Sandstone Landscapes' (Eds. R.W. Young and G.C. Nanson) pp. 81–93. Australian and New Zealand Geomorphology Group Special Publication No. 1. 1983.

Ashton, D.H. (1981). Bushfire in Tall Open Forests (Wet Sclerophyll Forest). In 'Bushfire and the Australian Biota' (Eds. A.M. Gill, R.H. Groves and I.R. Noble). Australian Academy of Science. Canberra.

Atkinson, G. (1984) Erosion Damage Following Bushfires. *Journal of Soil Conservation NSW,* **40**, 4–9.

Auld, T.D., Bradstock, R.A. and Keith, D.A. (1993) Fire as a threat to populations of rare plants. Australian National Parks and Wildlife Service Endangered Species Program ESP No.31. Final Report.

Blong, R.J. Riley, S.J. and Crozier, P.J. (1982) Sediment Yield from Runoff Plots Following Bushfire near Narrabeen Lagoon, NSW. *Search,* **13 (1–2)**, 36–38.

Briggs, J.D. and Leigh, J.H. (1988) 'Rare or Threatened Australian Plants'. Special Publication (14). Australian National Parks and Wildlife Service.

Buckley, A. (1992) Fire Behaviour and fuel reduction burning : Bemm River wildfire, October 1988. *Australian Forestry*, **55**, 135–147.

Catling, P. (1991) Ecological effects of prescribed burning practices on the mammals of southeastern Australia. In 'Conservation of Australia's Forest Fauna'. (Ed. D. Lunney) pp. 353–63. Published by Royal Zoological Society of N.S.W., Mosman.

Chapman, G.A. and Murphy, C.L. (1989) 'Soil Landscapes of the Sydney 1:100,000 sheet'. Soil Conservation Service of N.S.W., Sydney.

Cheney, N.P. (1979) Bushfire Disasters in Australia 1945–75. In 'Natural Hazards in Australia' (Eds. R.L.Heathcote and B.G. Thom) pp. 72–93. Australian Academy of Science. Canberra.

Christensen, P.E. and Kimber, P.C. (1975) Effect of prescribed burning on the flora and fauna of S.W. Australian forests. *Proceedings Ecological Society Australia*, **9**, 85–106.

Clark, S.S. and McLoughlin, L. (1986) Historical and biological evidence for fire regimes in the Sydney Region prior to the arrival of Europeans: Implications for future bushland management. *Australian Geographer*, **17**, 101–111.

Conroy, R.J. and Gellie, N. (1987) Bushfire History Data for Natural Areas. In 'Bushfire Management in Natural Areas' (Ed. R.J. Conroy) pp. 29–42. NSW National Parks and Wildlife Service Unpub.

Conroy, R.J. (1987) Bushfire Management Planning in Natural Areas. In 'Bushfire Management in Natural Areas' (Ed. R.J. Conroy) pp. 1–9. N.S.W. National Parks and Wildlife Service. Unpub.

Conroy, R.J. (1993) Fuel Management Strategies for the Sydney Region. In 'The Burning Question: Fire Management in N.S.W.'. Proceedings of a Conference held at Coffs Harbour, August, 1993 pp. 73–84. N.S.W. Department of Bush Fire Services.

Cunningham, C.J., Hobbs, J.E., Pagram, R., Pisanu, P. and Smith, J.M.B. (1994) 'Management Aspects of the January 1994 Bushfires in New South Wales. A (Draft) report prepared for the Senior Deputy State Coroner'. Department of Geography and Planning and the Centre for Disaster Management. University of New England, Armidale NSW.

DBFS (1990) 'Guide to Preparing Fire Management Plans Under S41A of the Bush Fires Act, 1949'. Co-ordinating Committee of the Bush Fire Council of New South Wales.

DBFS (1991) 'Planning for Bush Fire Protection. A Guide for Land Use Planners, Fire Authorities, Developers and Home Owners'. NSW Department of Bush Fire Services.

Fox, M.D. and Fox, B.J. (1986) The effect of fire frequency on the structure and floristic composition of a woodland understorey. *Australian Journal of Ecology*, **11**, 77–85.

Fox, M.D. (1988) Understorey changes following fire at Myall Lakes, New South Wales. *Cunninghamia,* **2 (1)**, 85–96.

Gill, A.M. (1975) Fire and The Australian Flora: A Review. *Australian Forestry*, **38**, pp. 4–25.

Gill, A.M. and Bradstock, R.A. (1993) Extinction of Biota by Fires. Abstract in 'Conserving Biodiversity: Threats and Solutions' p.24. New South Wales National Parks and Wildlife Service, Sydney.

Gill, A.M., Christian, K.R. and Moore, P.H.R. (1987) Bushfire incidence, fire hazard and fuel reduction. *Australian Journal of Ecology*, **12**, 299–306.

Harwood, C.E. and Jackson,W.D. (1975) Atmospheric Losses of Four Plant Nutrients During a Forest Bushfire. *Australian Forestry,* **38**, 2, 92–99.

Head, L. (1989) Prehistoric Aboriginal Impacts on Australian Vegetation: An Assessment of Evidence. *Australian Geographer*, **20 (1),** 37–46.

Henry, H.M. (1977) Catastrophic Changes in the McDonald Valley, New South Wales, 1949–1955. *Royal Society of New South Wales — Journal and Proceedings,* **110**, 1–16.

Hopkins, A.J.M. and Robinson, C.J. (1981) Fire induced structural change in a Western Australian Woodland. *Australian Journal of Ecology*, **6**, 177–188.

Hopkins, M.S. (1981) Disturbance and change in rainforests and the resulting problems of functional classification. In 'Vegetation Classification in Australia' (Eds. A.N. Gillison and D.J. Anderson) pp. 42–52. Australian National University Press. Canberra.

Hughes, P.J. and Sullivan , M. E. (1981) Aboriginal Burning and Late Holocene Geomorphic Events in Eastern NSW. *Search,* **12**, No. 8, 277–278.

Johnson, Von J. (1984) Prescribed Burning. Requiem or Renaissance. *Journal of Forestry*; **82,** 82–94.

Kodela, P.G. (1984) 'The Vegetation and Fire History of Ku-ring-gai Chase National Park'. Thesis B.App.Sc., School of Geography, University of New South Wales.

Lamy, D.L. and Junor, R.S. (1965a) An Erosion Survey in the Ku-ring-gai Chase and Adjoining Catchments. Part 1. *Extract from the Journal of the Soil Conservation Service of NSW*, **21**, No. 3, 94–174.

Lamy, D.L. and Junor, R.S. (1965b) An Erosion Survey in the Ku-ring-gai Chase and Adjoining Catchments. Part II. *Extract from the Journal Soil Conservation Service of NSW*, **21**, No. 4, 159–174.

Luke, R.H. and McArthur, A.G. (1986) 'Bushfires In Australia'. Australian Government Publishing Service.

Lunney, D., Urquhart, C.A. and Reed, P. (Eds) (1988) 'Koala Summit. Managing Koalas in New South Wales'. NSW National Parks and Wildlife Service.

Martin, A.R.H. (1971) The Depositional Environment of the Organic Deposits on the Foreshore at North Dee Why, New South Wales. *Proceedings of the Linnaean Society of New South Wales,* **96**, Part 4, 278–281.

Morrison, D.A., Cary, G.J., Pengelly, S. G., Ross, D.G., Mullins, B.J., Thomas, C.R. and Anderson, T.S. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Inter-fire interval and time-since-fire. *Australian Journal of Ecology*, **20,** 239–247.

Nieuwenhuis, A. (1987) The effect of fire frequency on the sclerophyll vegetation of the West Head, New South Wales. *Australian Journal of Ecology*, **12**, 373–383.

NPWS (1990) 'Fire Management Manual'. NSW National Parks and Wildlife Service.

NPWS (1993) 'North Metropolitan District Bushfire Management Plan'. NSW National Parks and Wildlife Service.

NPWS (1994) 'Submission to Cabinet Committee: Bush Fire Management and Control'. NSW National Parks and Wildlife Service.

Radtke, K.W-H., Arndt, A.M. and Wakimoto, R.H. (1982) 'Fire History of the Santa Monica Mountains'. Proceedings of the Symposium on Dynamics and Management of Mediterranean Type Ecosystems. General Tech. Report PSW-58. Forest Service. US Dept. of Agriculture.

Ridley, W.F. and Gardner, A. (1961) 'Fires in Rainforest'. *Australian Journal of Science*, **23**, 227–8.

Scott, J., Marshall, A. and Auld, T. (1995) 'Conservation Research Statement and Recovery Plan for *Grevillea caleyi* R.Br'. NSW National Parks and Wildlife Service. Australian Nature Conservation Agency, Endangered Species Program. Endangered Species Project No.456.

Smith, J.M.B. and Guyer, I.J. (1983) 'Rainforest–eucalypt interactions and the relevance of the biological nomad concept.' *Australian Journal of Ecology*, **8**, 55–60.

Standing Committee on Forestry (1987) Australian Bushfire Research. Background Guidelines and Directory. Australian Forestry Council.

Thomas, J. And Benson, D.H. (1985) 'Vegetation Survey of Ku-ring-gai Chase National Park. National Herbarium of New South Wales'. Royal Botanic Gardens, Sydney.

Tilley, D. And Uebel, K. (1988) Observations of koala populations within the Sydney Water Board's Upper Nepean catchment area. In 'Koala Summit Managing Koalas in New South Wales'. (Eds. D. Lunney, C.A. Urquhart and P. Reed) pp. 81–84. NSW National Parks and Wildlife Service, Sydney.

US N.P.S. (1992) 'Yellowstone National Park Wildland Fire Management Plan'. National Parks Service. Department of the Interior. United States of America.

Vines, R.G. (1974) 'Weather Patterns and Bush-Fire Cycles in Southern Australia'. Division of Chemical Technology Paper No. 2. CSIRO.

Responses of Heathland *Antechinus stuartii* to the Royal National Park Wildfire in 1994

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Little is known of the detailed responses of mammal populations to wildfires. Mortality is commonly observed, but trapping studies frequently record that animals have survived the passage of a fire front only to succumb to various causes of mortality thereafter. In particular, previous studies of *Antechinus stuartii* have reported population declines to near zero soon after fire. This study followed an *A. stuartii* population for over a year following the January 1994 wildfire at Royal National Park, between Sydney and Wollongong, New South Wales. The population was sustained through 1994, with many animals recaptured on successive trapping periods. There was successful reproduction in October 1994 to produce a second generation that was sampled in a May 1995 trapping session. We propose that the sustaining of this population, rather than its disappearance (expected based on previous studies), may have been permitted by two factors: (i) the extensive use by these animals of the many rock outcrops in the study area, for foraging, cover and nesting sites (determined by spooling animals), and (ii) the presence of a large energy source in the form of *Xanthorrhoea* nectar throughout the winter of 1994, produced by the fire-stimulated flowering of *X. media*. Pollen from *Xanthorrhoea* was present in the scats of almost all animals sampled and almost all flowering stalks showed evidence of having been climbed by small mammals during the flowering period. The timing of fire determines whether *Xanthorrhoea* will flower in the year immediately following fire or not until the subsequent winter. Thus populations of some small mammals may respond to the timing of fire via the responses of the flora

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INTRODUCTION

Fires are commonly believed to cause the deaths of vertebrate fauna, especially fires of high intensity (Whelan 1995). Observations that lead to this belief include the finding of charred carcasses after fires and failure to find animals in recently burned vegetation. Hemsley (1967), for example, reported that carcasses of 59 bird species were washed up on beaches in Tasmania after a wildfire in *Eucalyptus* forest … an observation supported by observations made after a wildfire at Nadgee Nature Reserve in New South Wales (Recher and Christensen 1981).

In contrast, some studies have reported good survival of fire by vertebrates. For example, Christensen (1980) radio-tracked 19 woylies (*Bettongia penicillata*) during and after high-intensity prescribed fire in south western Australian eucalypt forest. Six of the 19 survived in unburnt patches, nine survived by doubling back through the flames, and four hid in logs. One of the four that sought refuge in logs was killed by suffocation. Many anecdotal observations of animals still alive soon after the passage of a high intensity fire support Christensen's findings (e.g. Newsome et al. 1975, Fox and McKay 1981).

The resolution to this apparent contradiction may be that many animals are able to survive the passage of the fire front, though some succumb, but that the surviving population crashes (or emigrates) soon after the fire (Christensen and Kimber 1975, Newsome et al. 1975, Cheal 1983, Whelan 1995). In particular, Fox (1982) found an absence of *Antechinus stuartii* during the first year after fire in heath at Myall Lakes National Park, north of Newcastle, with the population not increasing until more than two years after the fire. Newsome et al. (1975) found that an *A. stuartii* population in heath at Nadgee Nature Reserve declined to almost zero in heathland during the year after a December wildfire.

The reasons for population decline may include increased predation, shortage of food and changes in vegetation structure (Whelan 1995). It has been further suggested that a succession of small mammal species occurs as the flora recovers and the vegetation structure changes over time (Fox and McKay 1981, Higgs and Fox 1993).

Unburned patches of vegetation and other refuges may provide opportunities for survival of the passage of a fire front, as described above for the woylies studied by Christensen. Newsome et al. (1975), for example, indicated that unburned stream-side vegetation at Nadgee Nature Reserve may have permitted survival of some *Antechinus* individuals and immediate re-establishment of the population after fire in that habitat.

There has been very little detailed study of the importance of unburned patches of vegetation for survival of fires by small mammals, and too little is known of the importance of post-fire habitat in permitting continued occupation of a burned site. The January 1994 wildfire in Royal National Park provided an opportunity to study short- and medium-term survival of *Antechinus stuartii* in a heathland site.

Antechinus stuartii is a widespread small mammal species, occurring in many habitats throughout east, and south east Australia. It is easily trapped and is often common, making it a suitable species for study. It consumes a wide range of both arboreal, and ground-dwelling arthropods, some plant material, nectar, and occasionally vertebrates (Hall 1980, Dickman 1983, Green 1989, Goldingay et al. 1991). Social interaction is common, and communal nests may be found in hollows in trees, rock crevices, and logs (Hyett and Shaw 1980, Cockburn and Lazenby-Cohen 1992).

This study used the opportunity of the high-intensity fire in heathland at Royal National Park to examine the following:

(i) change in *Antechinus stuartii* population after fire;
(ii) potential importance of structural features of the habitat (rock outcrops, unburned patches of vegetation) for *Antechinus stuartii* activity;
(iii) availability and use of some food resources over the winter period.

METHODS

Study area

This study was initiated in the Royal National Park (34°08'S, 151°04'30"E) about a month after the wildfire in January 1994. The fire burned through approximately 95% of the 17,163 ha National Park. The study area was located in open heathland towards the northern end of the Park.

Trapping was also located in a nearby site of similar vegetation that was not burned in the 1994 fires. The Cataract Catchment site (34°16'30"S, 150°53'54"–150°55'E) is 22 km from the Royal National Park site. No appropriate unburnt areas were available in the Royal National Park.

Prior to the 1994 fire in the Royal National Park, the two areas were similar in their fire histories. The Cataract Catchment sites were burnt in a fire in December 1990, and in a hazard reduction burn in 1982 (George Williams, pers. comm.). The Royal National Park sites were last burnt in by a wildfire in the 1987/88 fire season, and before that by a prescribed burn in 1977/78.

The January 1994 fire in Royal National Park occurred during hot, dry, windy weather conditions. These weather conditions, the consumption of all leaf litter by the fire, the presence of white ash on the ground, and the reduction of most plants in the burnt area to charred stems, all suggest that the fire in the heathland was of high intensity.

Small patches of unburned vegetation were scattered throughout the study area (Figure 1). These were extremely variable in both size and shape. They were sometimes associated with sandstone rock outcrops.

Trapping was conducted in four main periods at Royal National Park: (i) March to May 1994 (1185 trap-nights); (ii) June to July 1994 (880 trap nights); (iii) October 1994 (399 trap-nights); and (iv) May 1995 (360 trap-nights). Trapping was conducted in the Cataract Dam catchment only in March–May 1994 (400 trap-nights) and October 1994 (160 trap-nights).

Site Selection

Trapping grids were established in four types of sites:

(i) heathland vegetation that had no rock outcrops and was entirely burned (open-burned: sites 1 & 7);
(ii) no rock outcrops but with a patch of unburned vegetation (open-patch: sites 2 & 5);
(iii) vegetation with rock outcrops but the vegetation was entirely burned (rock-burned: sites 4 & 8);
(iv) rock outcrops and a patch of unburned vegetation (rock-patch: sites 3, 6 & 9).

Sites were chosen so that patches of unburned vegetation within them were roughly comparable in size, to reduce variations in capture rates due to the size of the patch.

Trapping grids were set up at five sites in the Cataract catchment, using locations of similar topography and vegetation to the Royal National Park area pre-fire.

Trapping Methods

A trapping grid was marked in each site. In sites 1–8, grids comprised 5 lines of 8 traps, with traps approx. 10 m apart. Site 9 was the only site that contained a large area of unburned vegetation as well as substantial rock outcrops. This was the site used for the studies of *Antechinus* movements (see below). Trapping here initially comprised 6 rows of 10 traps about 15 m apart, later increased to 80 traps. In June 1994, trapping at site 8 was also increased to 80 traps, by establishing a second grid of 40 traps on the rock outcrop (see'8b' on Figure 1).

Bait used in traps was a mixture of oats, peanut butter, and honey. A mixture of small (22 x 8.5 x 8 cm) and larger (33 x 10 x 9 cm) Elliott traps was used. Traps were always washed after a capture. Traps were set out as close to dusk as was feasible and were checked at dawn or soon after. Animals were tagged by toe-clipping.

Scat Samples

Scats deposited by animals in traps during trapping sessions from May to October 1994 were collected and placed in 70% ethanol for later microscopic examination. Approximately 0.03g (air-dry weight) from each scat was mixed in a droplet of water on a microscope slide. *Banksia* and *Xanthorrhoea* pollen grains were counted in ten scans (400 x magnification) from edge to edge of the cover slip (17.5 mm). Three categories were used for the total pollen grain count for a slide: 0; 1–19; ≥20 pollen grains.

A total of 35 scat samples was collected from The Royal National Park sites: 19 from males and 16 from females: 15 were collected from animals trapped in unburned patches (Sites 2, 3, 5, 6, 9) and 20 from animals trapped in the burned sites. At Cataract Catchment, 7 samples were from males and 7 from females. All these scat samples were scored for *Banksia* pollen. However, some samples were taken before *X. media* had started flowering in Royal National Park, so the only samples scored for *Xanthorrhoea* pollen were those collected during the flowering period: 12 in patches and 10 in burned sites.

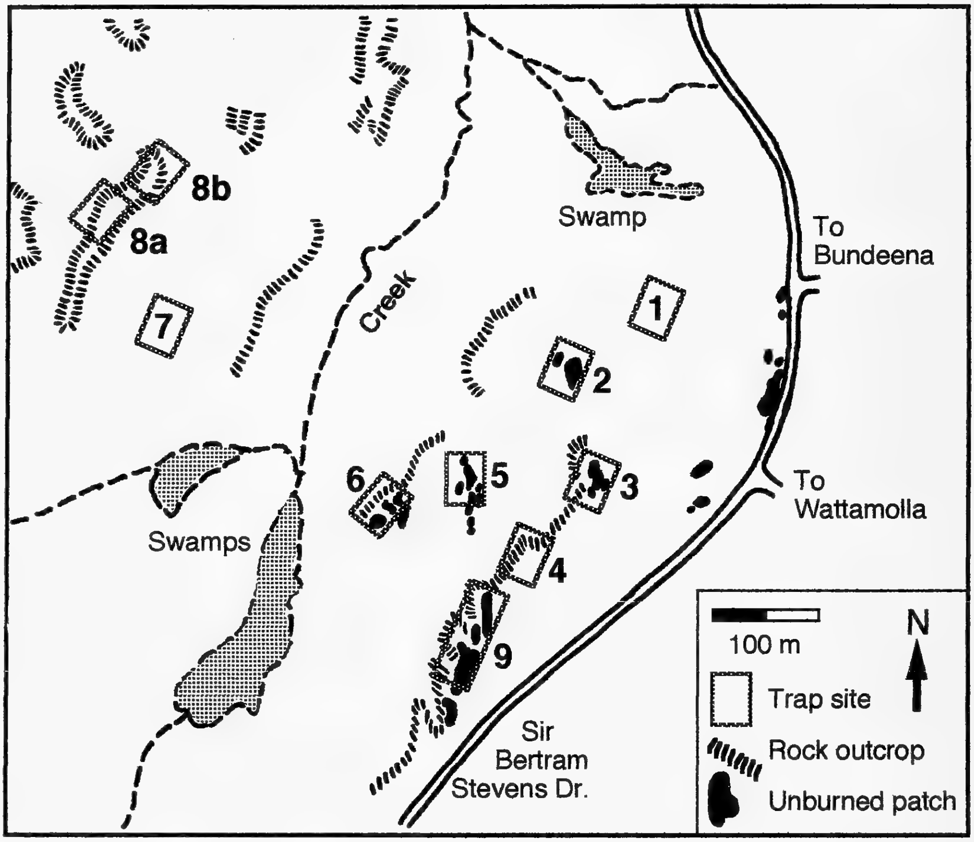


Fig. 1. Map of study sites at Royal National Park, showing locations of trapping grids (numbered 1–9), rock outcrops and unburned patches of heath vegetation.

Antechinus movements

Detailed movements of seven *Antechinus* individuals were recorded in site 9, Royal National Park, between March and May 1994, using the spool-and-line tracking technique (see Carthew 1993). Elliott traps were situated close to flowering *Banksia* plants (*B. ericifolia* and *B. marginata*) and small rock crevices. Traps were set late in the afternoon and checked at dawn. *Antechinus* individuals captured were fitted with a spool of fine thread (nylon quilting thread bobbin 70/2 — Penguin Threads Pty. Ltd., Prahran, Victoria) containing 165 m of thread. The spools, which unravel from the middle, were covered in plastic tape to avoid snagging on vegetation. Spools were stuck to the tips of the fur on the shoulders of the animals with Superglue, and the loose end was secured at the point of release. Threads were followed within 36 hours of release of an animal, and the route was plotted in relation to landmarks within the study site. Only five of the seven spooling attempts were successful.

Antechinus visits to *Xanthorrhoea*

Xanthorrhoea media has a fine white powder on the surface of its flowering stalk. Disturbance of this powder, for example perching by birds or climbing by mammals (even human fingerprints) leaves a long-term record on the stalk. We considered that small mammals, such as *Antechinus stuartii,* may climb flowering stalks to obtain nectar from inflorescences (see Goldingay et al. 1991).

The percentage of flowering stalks used by small mammals was estimated by scoring the percentages of flowering stalks with 'scurry marks' in ten 20 x 20 meter quadrats. This section of field work was conducted on the 11th of September 1994; towards the end of the flowering season for *X. media.*

RESULTS

Species captured

Five species of small-mammals were caught after the fire in the Royal National Park: *A. stuartii, M. musculus* (house mouse), *R. fuscipes* (bush rat), *R. lutreolus* (swamp rat), and *Cercartetus nanus* (Eastern pygmy possum). Only two individuals of *C. nanus* were caught; both in the largest of the patches of unburned vegetation (site 9). Only two species were caught in the Cataract Dam catchment area: *A. stuartii* and *R. lutreolus.*

Capture rates of *A. stuartii*

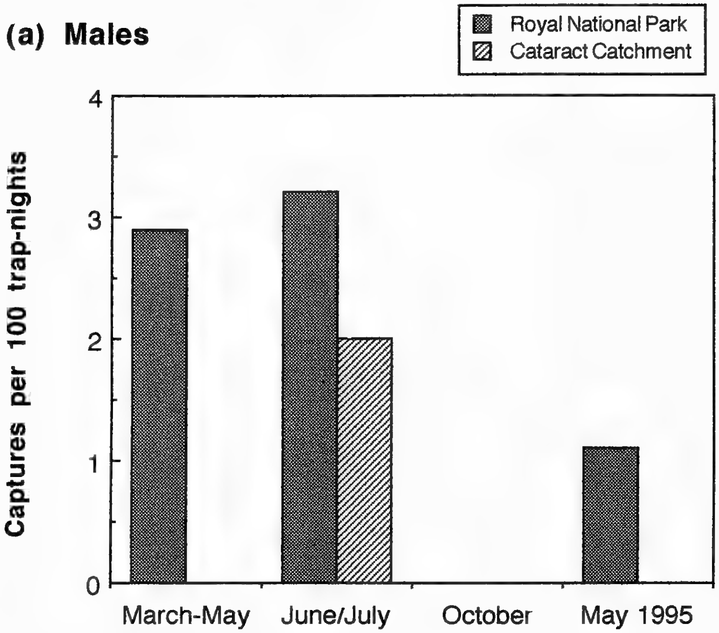
Over all four trapping sessions at Royal National Park, 20 male and 24 female *A. stuartii* were captured. Numbers captured per 100 trap-nights remained quite consistent through the 1994 trapping periods at Royal National Park for both males and females (Figure 2). No males were caught in October 1994 in either study area, because all were dead after the breeding season (Figure 2a). Capture rates of both males and females had declined substantially by the May 1995 trapping period (Figure 2a & b): 38% of March–May 1994 for males and only 14.4% for females. The capture rate per 100 trap nights for males in Royal National Park was about 60% higher than that in the Cataract Dam sites, for the June to July trapping period (Figure 2a). Capture rates for female *A. stuartii* in the Cataract Dam area were higher than that in the Royal National Park, in both the June/July and the October trapping periods.

For both male and female *A. stuartii* in the Royal National Park, at least 60% of captures in the June to July and October 1994 trapping periods were recaptures of individuals initially caught in the March to May trapping period (Figure 3 a & b). No new animals were caught during the October 1994 trapping period, but all captures in May 1995 were new individuals, as would be expected from the 'annual' life history of this species.

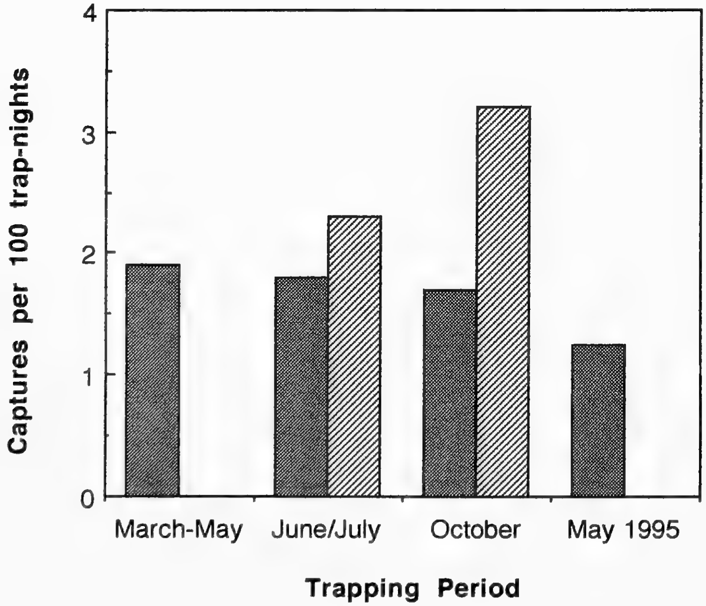
The females with pouch young caught in the October trapping in the Royal National Park and the Cataract Dam were similar in age, with young from both populations being estimated as under 1 week old. A female without young, which appeared to be pregnant, was caught in the Cataract Dam on October 4. The number of young carried by females, excluding the female which appeared to be pregnant, was similar for the Royal National Park and Cataract Dam. In the Royal National Park 7 females had an average (±s.e.) of 7.9 (±0.14) young each, and in the Cataract Dam 4 females had an average of 7.5 (±0.50) young each.

Variation among capture sites at Royal National Park

Male *A. stuartii* showed no consistent difference in capture rates comparing open versus rock outcrop sites, or comparing burnt sites versus those with unburnt patches (Figure 4a). The highest capture rates for female *A. stuartii* were in sites with rock outcrops (Figure 4b) but two sites with both rock outcrops and unburned vegetation (sites 3 and 6) had low capture rates. The highest capture rates for female *A. stuartii* were recorded where the two largest rock outcrop sites were located (sites 8 and 9). Also, site 4, the site with the third highest capture rate of female *A. stuartii* was located close to site 9.



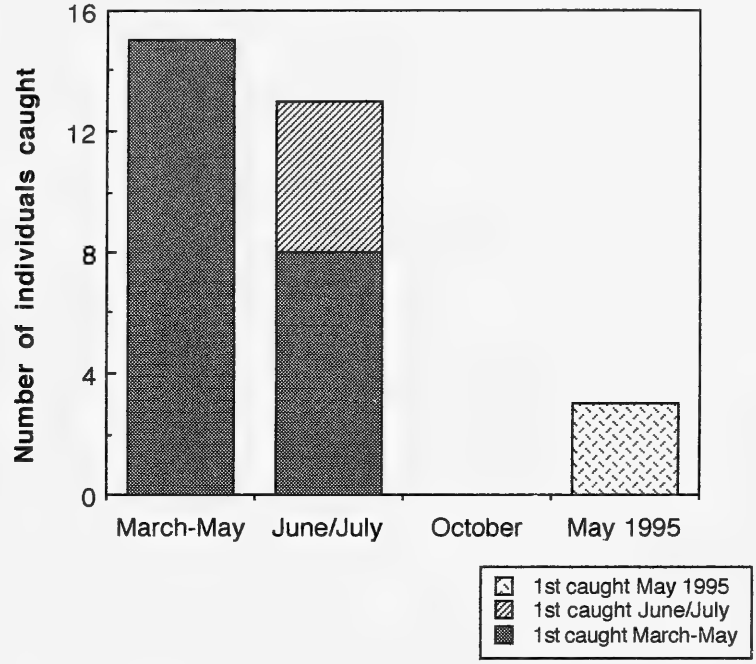
(a) Males



(b) Females

Fig. 2. Numbers of captures per 100 trap-nights for male (a) and female (b) *Antechinus stuartii* over 4 trapping periods at Royal National Park and two trapping periods at Cataract Catchment.

(a) Males



(b) Females

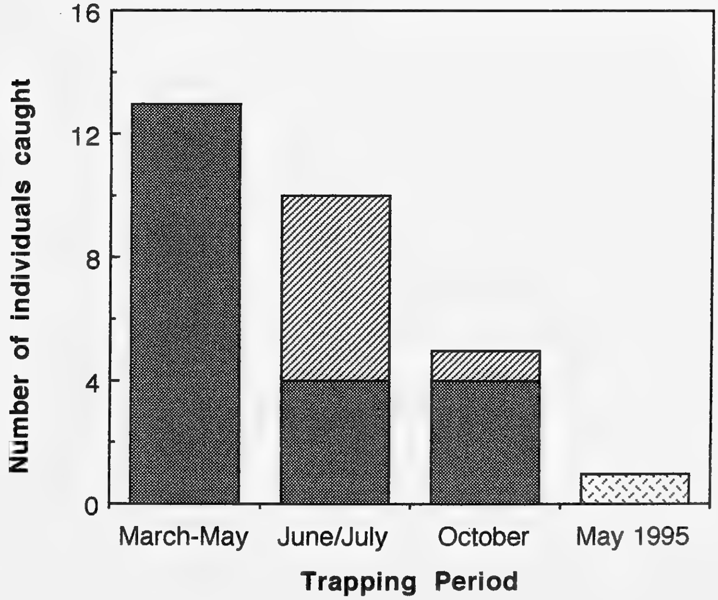
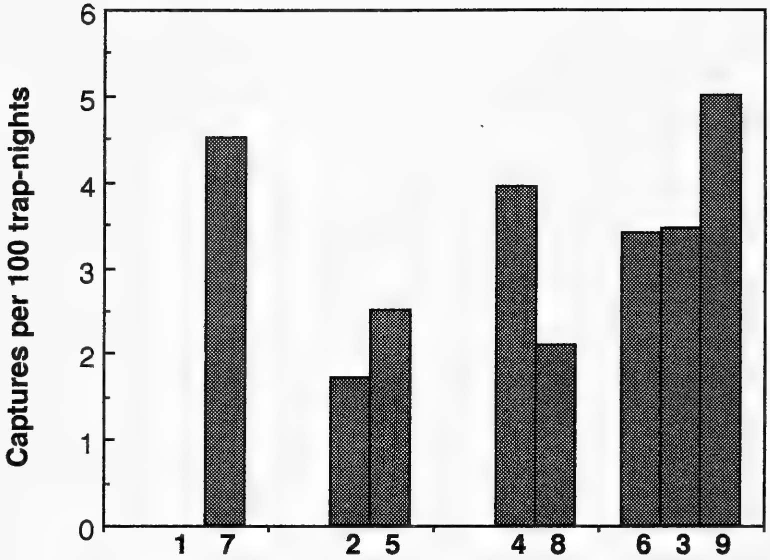


Fig. 3. Numbers of captures and recaptures of male (a) and female (b) *A. stuartii* at Royal National Park. Light hatching indicates the numbers of animals that were caught in June/July 1994 but not previously. Dark stippling in June/July and October 1994 indicates numbers of animals that had been caught in the March–May trapping period.

(a) Males



(b) Females

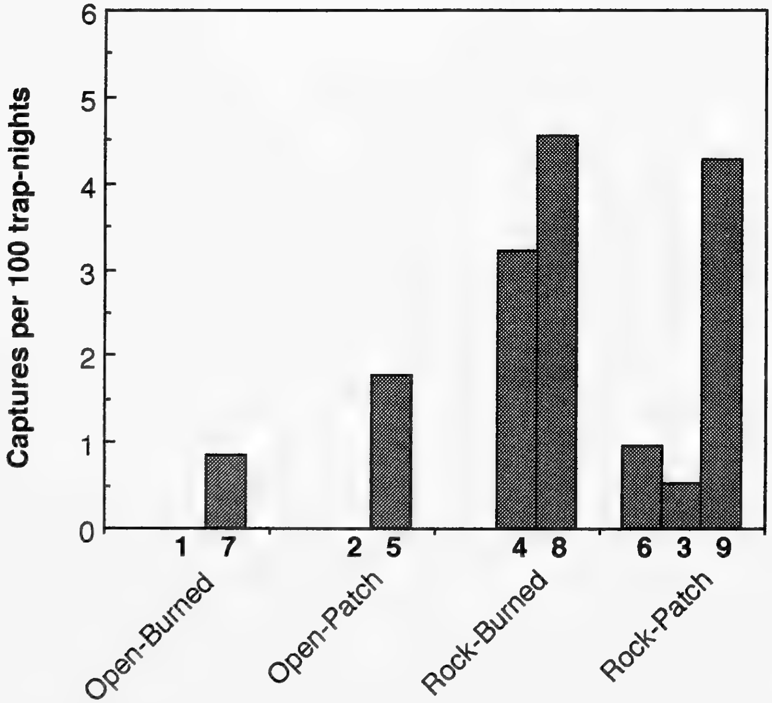


Fig. 4. Capture rates (captures per 100 trap-nights) for male (a) and female (b) *A. stuartii* caught in each of the 9 trapping grids at Royal National Park.

Movements of *A. stuartii*

The greatest distance between trap locations for a recaptured female *A. stuartii* was 260 m. Two male *A. stuartii* were trapped, in separate trapping periods, on different sides of the creek that runs between the trapping sites. These distances were sufficient to indicate that animals could move between most of the trap sites (Figure 1). However, most recaptures were within trapping grids, and spooling indicated that there was a substantial amount of movement of females along, or around, rock outcrops (Figure 5).

Use of floral resources

All 14 scat samples from animals captured in the Cataract Dam Catchment study area contained pollen of *Banksia* species, and none contained *Xanthorrhoea* pollen (Table 1): there was no *Xanthorrhoea* flowering in the Cataract area. In contrast, almost all scat samples from animals captured in both burned areas and unburned patches of vegetation at Royal National Park contained *Xanthorrhoea* pollen (during the time of *Xanthorrhoea* flowering), and most contained substantial pollen loads (Table 1). Many of the scat samples also contained *Banksia* pollen, even though there were few *Banksia* plants in flower and these were confined to the unburned patches of vegetation. It is notable that scat samples had *Banksia* and *Xanthorrhoea* pollen irrespective of whether they were from animals caught in burned areas (where *Xanthorrhoea* was flowering) or in the unburned patches (containing the only flowering *Banksia*).

The scurry marks on *Xanthorrhoea* flowering stalks were of a size and shape consistent with visits by *Antechinus* (Figure 6). A high proportion of flowering stalks showed evidence of visits by small mammals. For the ten 20 x 20m quadrats sampled, there was an average of 13.5 (±2.1 s.e.) flowering stalks. Of these, 11.2 (±1.7) had been visited. This amounts to about 85%.

TABLE 1

Banksia *and* Xanthorrhoea *pollen in scat samples from* Antechinus stuartii *at Royal National Park and Cataract Catchment. Pollen loads are classified as 0 (no grains), light (1–19 grains) and heavy (≥20 grains) in 10 scans at 100x of a faecal smear on a microscope slide.*

	Banksia pollen				*Xanthorrhoea* pollen			
	no. scats	% with: 0	1–19	≥20	no. scats	% with: 0	1–19	≥20
Royal NP unburned patches	15	33	40	27	12	0	17	83
Royal NP burned sites	20	50	40	10	10	10	50	40
Cataract Catchment	14	0	36	64	14	100	0	0

DISCUSSION

Few studies have examined in detail the population responses to fire of any animal species, though there is good evidence to suggest that (i) animals do die in fires, (ii) many animals survive the passage of a fire front, and (iii) there can be substantial post-fire mortality and/or emigration. Previous studies of mammals in Australian heathlands found that populations of several species decline to near zero soon after fire (see Fig. 3b of Fox 1982). In contrast, in this study we found that an *Antechinus* population survived well in sites that

5(a)

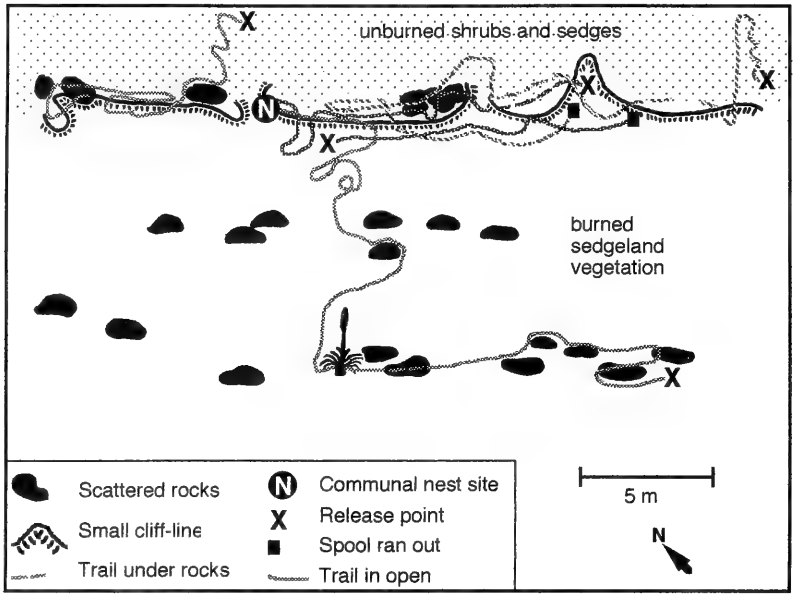


Fig. 5. (a) Map of movements of five *A. stuartii* individuals that were spooled in the area of the most extensive rock outcrop and unburned patch of vegetation — Site 9.

(b) Trail of thread (arrowed) along the edge of a sandstone outcrop in Site 9.

Fig. 6. Scurry marks, inferred to have been made by *A. stuartii*, in the powdery surface of the flowering stalks of *Xanthorrhoea media*.

were burned in the intense 1994 wildfire at Royal National Park. In the study by Newsome et al. (1975) at Nadgee Nature Reserve, there is a suggestion that *A. stuartii* survives well in some sites but not in others: in the trapping grids that were in forest or hind-dune shrubland (grids A, B, 3, 4 and 5) *A. stuartii* survived well throughout the year following the wildfire. In the swamp/heathland grids (grids 1 and 6), there was poor survival, though some animals were trapped during the year after the fire in both of these grids (Newsome et al. 1975).

Capture rates of both male and female *Antechinus stuartii* in our study were not particularly high (between 1 and 3.5 captures per 100 trap-nights) but they were comparable to the capture rates in the nearby, unburned study site of similar vegetation and fire history (Cataract Catchment). The population at Royal National Park appeared to be resident throughout 1994, as many animals captured first in March–May were recaptured in one or both of the subsequent trapping sessions. Moreover, all of the females captured in October either had young in the pouch or were pregnant. This reproduction was apparently successful, because both males and females of the next generation were captured during a limited trapping session in May 1995, although capture rates were low at this time. Perhaps this decline indicates that numbers will decline in the second year after fire, as was the case on grids 1 and 6 after the Nadgee wildfire (Newsome et al. 1975).

Although some long-distance movements occurred, identified by recapturing some animals in sites at some distance from the site of first capture, most recaptures were within trapping grids. Moreover, spooling of five *Antechinus* indicated that these animals were moving extensively along the sandstone outcrops and at least two of them were frequenting a communal nest under a ledge of sandstone.

The animals in this study appeared to be making substantial use of floral resources, presumably nectar, because pollen was present in almost all faecal samples examined. *Banksia* pollen predominated in samples from the Cataract Catchment study area: no *Xanthorrhoea* was flowering in this unburned vegetation. At Royal National Park, both *Xanthorrhoea* and *Banksia* pollen were evident in faeces, and nearly all *Xanthorrhoea* stems had scurry marks indicating visits by *Antechinus*.

We suggest that the presence of rock outcrops might have contributed to the unexpected maintenance of the *Antechinus* population in the Royal National Park heathland throughout 1994, following the wildfire. The rocky nature of the Hawkesbury Sandstone landscape may provide animals with cover from the heat of fire and also both a refuge from predators and nest sites following the fire. In other heathland and swamp sites, such as Nadgee Nature Reserve (Newsome et al. 1975) or Myall Lakes (Fox 1982), more uniform habitat may contain fewer refuges. In addition, the timing of the wildfire at Royal National Park was such that *Xanthorrhoea media* flowered in the winter after the fire, providing a high-energy food source (nectar). We speculate that a fire later in the year may have resulted in a 1-year delay in the burst of flowering, perhaps causing a more severe drop in *Antechinus* numbers. It remains to be seen what might happen in the second winter after the fire, if there is little flowering of *Xanthorrhoea* (Gill 1981, Whelan 1995).

In conclusion, we argue that experimental studies are badly needed to test the importance of cover, nest sites and a readily available winter energy supply, in the maintenance of *A. stuartii* populations in burned heathland. This study suggests that the timing of a fire may be crucial in determining the population dynamics of small-mammal populations indirectly, via the impact of fire season on the flora.

REFERENCES

Carthew, S.M. (1993). An assessment of pollinator visitation to *Banksia spinulosa*. *Australian Journal of Ecology* **18**, 257–268.

Cheal, D. (1983). The effects of fire on animal life. *Trees and Victoria's Resources*, **25**, 12–13.

Christensen, P.E.S. (1980). The Biology of *Bettongia penicillata* Gray 1937 and *Macropus eugenii* (Demarest 1917) in Relation to Fire. *Forests Department of Western Australia Bulletin* 91.

Christensen, P.E.S. and Kimber, P.C. (1975). Effect of prescribed burning on the flora and fauna of south-west Australian forests. *Proceedings of the Ecological Society of Australia* **9**, 85–106.

Cockburn, A. and Lazenby-Cohen, K.A. (1992). Use of nest-trees by *Antechinus stuartii*, a semelparous, lekking marsupial. *Journal of Zoology* **226**, 657–680.

Dickman, C.R. (1983). *Competition Between the Dasyurid Marsupials* Antechinus stuartii *and* Antechinus swainsonii. PhD Thesis, Australian National University.

Fox, B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath *Ecology* **63**, 1332–1341.

Fox, B.J. and McKay, G.M. (1981). Small mammal responses to pyric successional changes in eucalypt forest. *Australian Journal of Ecology* **6**, 29–41.

Gill, A.M. (1981). Adaptive responses of Australian vascular plant species to fires. In 'Fire and the Australian Biota'. (Eds. Gill, A.M., Groves, R.H., and Noble, I.) pp. 243–272 (Australian Academy of Science: Canberra).

Goldingay, R.L., Carthew, S.M. and Whelan, R.J. (1991). The importance of non-flying mammals in pollination. *Oikos* **61**, 79–87.

Green, K. (1989). Altitudinal and seasonal differences in the diets of *Antechinus swainsonii* and *A. stuartii* (Marsupialia: Dasyuridae) in relation to the availability of prey in the Snowy Mountains. *Australian Wildlife Research* **16**, 581–592.

Hall, S. (1980). The diets of two coexisting species of *Antechinus* (Marsupialia: Dasyuridae). *Australian Wildlife Research* **7**, 365–378.

Hemsley, J. (1967). 'Bushfire – S.E. Tasmania'. (National Parks and Wildlife Service: Tasmania).

Higgs, P. and Fox, B.J. (1993). Interspecific competition: a mechanism for rodent succession after fire in wet heathland. *Australian Journal of Ecology* **18**, 193–201.

Hyett, J. and Shaw, N. (1980). 'Australian Mammals: A Field Guide for New South Wales, Victoria, South Australia and Tasmania'. (Nelson: Melbourne).

Newsome, A.E., McIlroy, J. and Catling, P. (1975). The effects of an extensive wildfire on populations of twenty ground vertebrates in south-east Australia. *Proceedings of the Ecological Society of Australia* **9**, 107–123.

Recher, H. and Christensen, P.E.S. (1981). Fire and the evolution of the Australian biota. In 'Ecological Biogeography of Australia' (Ed. A. Keast) pp. 137–162 (Junk: Dordrecht).

Whelan, R.J. (1995). 'The Ecology of Fire'. (Cambridge University Press: Cambridge).

Disseminating Knowledge of Wildfire Using a Geographic Information System: Three Case Studies

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The Country Fire Authority of Victoria is developing a Wildfire Threat Assessment program which is specifically designed to provide CFA Operations management with access to databases that support strategic operational decision making by analysing information on wildfire behaviour, population and fire statistics.

Additional benefits have accrued from the program by using a number component databases in other forums. The utility of modern information systems lies in their ability to compress and integrate a number of varied and perhaps complex data sets such that the yields are understandable to a larger audience than would be the case if they were dealing with the raw data and mathematics.

In Victoria, many groups with an interest in wildfire are beginning to utilise the products of information systems to improve their comprehension of wildfire processes and understand how it may affect their own environment.

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INTRODUCTION

A Geographic Information System (GIS) is a computer system which is capable of combining several layers of geographical data to produce outputs in the form of summary statistics and maps. Geographic data is data which can be related to specific locations on the earth's surface. Roads, rivers, soils, vegetation and topography are examples of geographic data that are now capable of being analysed and integrated to produce value added information sets.

The utility of GIS technology lies with the fact that many scenarios can be viewed at the computer screen or as paper plots; each scenario altering a variable to determine the impact of that change on the overall output. When properly constructed and presented, outputs from the GIS (tables, reports and thematic maps) that summarise sometimes complex operations allow groups from varied backgrounds or levels of expertise to gauge the contribution that each component may have on an outcome.

In the past few years there has been an enormous growth in the availability of geographic data suitable for computer analysis at a price that is within the reach of most Government Departments. Examples in Victoria include statewide coverage of data such as topography, census data, road networks and cadastral boundaries. Data sets derived from satellite imagery and aerial photography such as vegetation, soils and built-up areas are also available.

There is presently a confluence of data availability, cost effective hardware and software in the GIS arena. It is enabling an increasing number of groups to analyse complex problems and allow for the results to be presented to a much wider audience.

THE COUNTRY FIRE AUTHORITY'S WILDFIRE THREAT MODEL

The CFA's interest in wildfire threat assessment using computer techniques began in the mid 1980's with the commissioning of a project to develop a threat assessment model for structural fires. During the development of this model it was acknowledged that a separate approach was necessary to model wildfire threat.

The analysis of threat is a precursor to more efficient application of resources resulting in a safer wildfire environment for Victorians. Once threat has been characterised and mapped, a number of moderating strategies such as deploying firefighting resources more effectively, identifying high threat areas where building construction practices can be modified and targeting education programs can be applied to increase survivability.

The need for improved information on the spatial distribution of wildfire threat has led to the development of the Wildfire Threat Model (WTM). A number of techniques already in use elsewhere in Australia were reviewed for their applicability to Victoria. However, they generally did not include life values or the built environment as their focus, features which are the legislated responsibility of the CFA.

The aim of the CFA's WTM is to develop an appropriate database and rationale for assessing the requirements for fire prevention and suppression resources throughout Victoria. It will provide CFA management with a profile of the wildfire threat across the state. As well as giving a generalised classification, the model will deliver specific information on population, dwellings, terrain, wildfire behaviour, and wildfire statistics. This will, in turn, enable objective analysis of the current wildfire brigade structure and identify areas which may require specific fire protection or fire prevention strategies.

The WTM reflects the CFA's view of wildfire threat and is thus inclined toward the protection of life and property. This view of threat may not necessarily coincide with that of other services or communities where other values vulnerable to fire, such as flora and fauna, may have precedence.

The WTM and the various products derived from the databases are to be used at a number of scales. At a statewide level, WTM will enable review of wildfire equipment levels and fire brigade structure and possibly assist in the designation of wildfire-prone areas. At a regional level the WTM provides input into short and long term regional planning processes and at its largest scale the WTM will assist in solving local issues such as the identification of areas unsuitable for development due to high loss potential and in providing an insight into the physical processes of wildfire at community group meetings.

The WTM is comprised of three modules :– Fire Behaviour, Damage Potential and Fire Statistics. The Fire Behaviour module combines vegetation data, litter weights, topography, low fuel areas and weather analysis in the GIS to produce a map of potential fire intensity. The Damage Potential module analyses the density of population and dwellings, and the agricultural productivity of a region whilst the Fire Statistics module examines wildfire statistics over a period of ten years. The three modules are then weighted and combined in a final layer — the Wildfire Threat Index.

Wildfire threat mapping — its use by CFA officers

CFA users of WTM maps analyse overall wildfire threat categories but also study fire intensity, population, housing and fire statistics maps to understand how each of the base maps contribute to the overall threat. For example, there may be a relatively high density of people or a large number of fires within a particular area and these can be studied and compared across a geographic area. The WTM is used as a planning tool both at the strategic or statewide level as well as at the local level. It will support management decisions regarding the formation of brigades, and the types and amounts of equipment.

At CFA Regional headquarters, fire threat maps are analysed along with the present fire brigade structure. This is undertaken to identify areas where the threat is high and coverage or performance is low. Strategic plans and annual plans would be adjusted to relieve shortcomings in the present structure.

OTHER USES OF GEOGRAPHIC INFORMATION SYSTEM-GENERATED MAPS

Plenty Gorge planning scheme amendment

The CFA often makes submissions at Planning Tribunals in high fire threat areas so that factors influencing the safety of residents and firefighters are reviewed by Tribunal members. Often CFA Officers present cases based on the intricacies of wildfire science such as the integration of meteorology, topography and vegetation and their contribution to fire behaviour to Panel members who are not familiar with basic wildfire behaviour principles.

Such a Planning Appeals Tribunal (Diamond Valley Planning Scheme Amendment L46) recently occurred reviewing development in the Plenty Gorge, approximately 40 kilometres to the north of Melbourne. Applications had been made to subdivide land within the gorge area. The CFA was of the view that because of the possibility of extreme wildfire behaviour consideration should be given to road widths and allotment size in the gorge.

A series of maps were produced to support a CFA case. The maps consisted of a base potential fire intensity map, and transparent overlays of slope, vegetation, aspect and current administrative boundaries. Fire Intensity is a main factor in increasing the wildfire threat. The greater the intensity, the more difficult it is to suppress a fire, the more damage it will inflict, and the more vulnerable a community in the path of that fire will be.

The following edited text is taken from the CFA's written submission to the Panel members by CFA Regional Officer Greg Flynn (Flynn 1994):

"(the Fire Intensity Maps) show diagrammatically the way in which the fire intensity map is compiled. Fuel weights that have been used for the calculations are 3 tonnes per hectare for grasslands and 20 tonnes per hectare for forest areas. They are representative of the growth, and resultant fuel weights likely to occur in this area in an average season. The Fire Danger Indices chosen for the calculations are 32.6 for grassland and 24.4 for forest. These FDI's have been chosen from statistical analysis of daily weather data for Melbourne from 1938 to (55 years) 1993 and then selecting the 95th percentile point for fire danger rating. ie It is likely that only five percent of days would experience higher fire danger ratings.

Fire Intensity is a measure of the degree of difficulty that firefighters would encounter in fire suppression activities. It is recognised that firefighters have the capability to mount a head on attack at a running wildfire up to 4000 kW/metre of energy. However, they are generally limited to an attack from the sides with fires generating between 4000 and 15000 kW/metre of energy. Fires generating more than 15,000 kW/metre are considered uncontrollable and other firefighting strategies are must be employed to protect life and property.

Looking at the map shows that the great majority of the sloping land in the vicinity of the gorge would carry a fire under the prescribed conditions of such an intensity that an effective control strategy could not be put in place until the fire came out of the gorge. Most of the sloping land has a fire intensity of 10000 kW/m or greater. Given the difficult access in much of this area I suggest that a fire of this intensity would be difficult to control here. This reinforces the need for the property owners to take the initiative and do the necessary fire prevention works to protect their own properties.

The map also indicates that most of the 'flat' land adjacent to the gorge will also carry a fire of significant intensity. This includes the great majority of land affected by Amendment L46 and again indicates the need for individual property protection. Obviously the amount of work required to achieve similar levels of protection in these flatter areas is not the same as that required to ensure the safety of similar houses in the gorge proper.

The Fire Intensity map is compiled of a series cells that represent an area on the ground of 100 metres by 100 metres. It defines clearly the areas of greatest hazard and may provide opportunity to review quite closely the potential effect that fire may have on any specific area. From the small on the ground cell size it can be seen that it is quite detailed, however it is only another tool to assist in planning our approach to fire prevention and suppression. It does not for example indicate any effects that fire spotting may have adjacent to the gorge. History indicates that this can be significant given the right conditions.'

Panel decision

The Panel handed down a decision which was in line with the CFA's submission i.e. subdivisions were restricted to 2 hectares in size and a number of fire prevention measures are to be included in the development. The Panel's written summary of the proceedings drew much from Flynn's (1994) written presentation.

The panel had first studied standard methodology for reviewing fire threat in the Gorge but found the GIS generated maps more reliable and understandable. To quote the Panel (Mitchell and Lewin 1994): '(we) found the Plenty Gorge Fire Intensity Map invaluable in assisting it in its deliberations on L46'.

Community fireguard

Community Fireguard is a community education program designed to reduce the loss of lives and homes in bushfires. The program is based on the fact that many people will have to face a wildfire without the support of the CFA, which cannot provide every person and home with individual protection during a major bushfire. It presumes that bushfires are survivable, provided communities take responsibility for their own safety.

Community Fireguard is made up of small groups. These may simply be a dozen or so neighbours living in an area where the threat of fire is high, or they may be an existing group such as Landcare or a conservation group which is interested in reducing the fire threat. Either way, with support from the CFA and by working together, these people find they can develop strategies which are simple, inexpensive and effective and can save lives and homes.

They also want to know what to expect from the emergency services and what the fire is going to look, sound and feel like if they are caught in the middle of it. Armed with this understanding, the groups can make decisions about the best way to protect themselves in a way that fits their lifestyle, environment, physical capabilities, finances and experiences.

To help groups find strategies for reconciling fire safety with other management objectives, Community Fireguard facilitators help groups to understand the experience of a major fire. Before deciding how best to tackle the fire threat, people need an understanding of how houses are destroyed by fire, how and why people die in fire and how a fire behaves.

A series of maps of potential fire behaviour has been generated for Community fireguard groups. People are most vulnerable to high intensity fire, and the potential fire intensity maps generated by the WTM are useful in identifying areas where the prerequisites for high intensity fires exist.

The maps are graphic, easily comprehended representations of potential fire behaviour. Because the map integrates slope, fuel and weather components, and presents the resulting fire intensity in a simple format it can be especially useful early in the program when the Community Fireguard participants have little understanding of the science behind fire behaviour.

The relatively large scale of the Fire Intensity maps is also advantageous as it allows residents to put their threat into context by comparison with other local geographic areas that they are familiar with. The similarities or differences in potential fire intensity can then be the starting point for discussing fire behaviour, e.g. Why is the potential for fire higher in this street than that one? Because one is on flat ground and the other is on the side of a hill.

Fire Intensity maps can become resources that residents can use when dealing with major land owners, such as government departments, who they may feel are not giving high enough priority to fire prevention works in their locality. Being able to use such tools helps them to be treated as stakeholders who have a substantial understanding of fire behaviour principles.

YarraCare

YarraCare is a community based program dealing with the management of the Yarra River catchment. It aims to identify priority land and waterway issues in the catchment and define the need for action. More than sixty community representatives participate in the formal YarraCare group meetings, forming a partnership with all key government agencies.

The Land Management series of papers addressed a number of issues that contribute to the decline in the water quality of the Yarra and its tributaries. The papers provided both the community and agencies with the opportunity to discuss the issues for future management of the catchment.

A paper describing the potential impact of bushfires on the environment and the people of the Yarra Catchment was prepared by Stephen Petris of the CFA (Petris et al. 1994). Wildfire threat is particularly high in parts of the Yarra Catchment due to a combination of relatively large population, rugged topography, poor road access and egress, high fuel loads and periodic extreme fire weather.

This is confirmed by the number of fires experienced in the Yarra Catchment. On Ash Wednesday 1983, for example, two major fires ravaged the catchment. The Cockatoo fire took six lives and destroyed 307 houses, whilst the Warburton fire burnt 40,000 hectares, destroying 27 homes. In 1962, fires at The Basin/Olinda, Christmas Hills, Chum Creek, Kinglake, St. Andrews, Hurstbridge, Warrandyte and Woori Yallock took 8 lives and destroyed 454 houses. Fires in the Basin/Olinda area burnt another 53 houses in 1968. In addition to the loss of human lives and assets, these fires also destroyed native and farm animals and their habitats, and caused pollution in water supplies.

Two topics were given particular attention. Firstly the paper developed a theme to assist the understanding of factors that contribute to fire threat by describing the concept of fire intensity, and secondly the paper described the effects of wildfires on both the natural environment and on communities, while discussing how communities can develop strategies to reduce the wildfire threat. A series of GIS-generated potential fire intensity maps were included in the report.

Petris developed the theme of fire intensity as contributing substantially to the wildfire threat faced by communities in the catchment. Part of the text (from Petris et al. 1994) follows:

‘Fire Intensity is an important factor in determining the impact of fire on human communities. Earlier in this report the intensities at which suppression forces can stop the forward spread of major fires was discussed. The Potential Fire Intensity map for the Yarra Catchment indicates that, for large parts of the catchment, on a day of very high fire danger, expected fire intensities are greater than that which can be controlled by suppression forces. On extreme fire days, when fire intensities are greater again, fire suppression agencies recognise that there is very little can be done to stop the forward spread of a major fire until weather conditions moderate, or until fire run into areas of low fuel e.g. areas recently fuel reduced.

On these days one of the most effective suppression strategies is to extinguish fires before they become large enough to threaten life and property. This was confirmed by the experience of the Ash Wednesday Fires in Victoria in 1983. Of the 180 fires that started on that day, suppression forces were able to extinguish 172 before they caused significant damage. However those fires that could not be quickly suppressed on these days rapidly reach intensities too high to be controlled.

Fortunately, there a many ways communities can reduce the threat to their lives and homes from major wildfires. A study by Wilson (1984) for example identified fire intensity as the most important factor in determining whether houses were destroyed by the Mount Macedon fire on Ash Wednesday. Residents can reduce the intensity of a fire as it passes by reducing the amount of available fuel. This can simply be achieved by reducing the amount of twigs, leaves, dry grass and bark around their homes and communities. Alternatively. the amount of available fuel may be reduced by keeping gardens and parks green during the fire danger period.'

Once again techniques first developed for the CFA's Wildfire Threat Mapping program substantially enhanced the notion and understanding of fire behaviour principles by providing a visual output of the combination of variables that contribute to wildfire threat.

CONCLUSION

The utility of Geographic Information Systems lies in their ability to compress and integrate a number of varied and perhaps complex data sets such that the yields are understandable to a larger audience than would be the case if they were dealing with the raw data and mathematics.

Many fire management groups across Australia are beginning to utilise GIS in the study of fire processes. Many more groups are beginning to see the products of GIS to improve their comprehension of wildfire and how it may effect them.

The CFA has established a wildfire threat analysis program that is providing a number of GIS based products facilitating more effective and responsible management of wildfire.

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REFERENCES

Flynn. G. (1995). Submission to Panel Report L46 Diamond Valley Planning Scheme, July, 1994 (Country Fire Authority of Victoria: Lilydale).

Mitchell K. & Lewin J. (1994). Planning and Environment Act 1987, Panel Report L46, Diamond Valley Planning Scheme. July, 1994, p. 23.

Petris. S., Garvey. M. and Finney. G (1994). 'Potential Bushfire Impacts in the Yarra Catchment' YarraCare Land Management Series Discussion Paper No. 7.

Wilson A. (1984). 'Assessing the Bushfire Hazard of Houses : A Quantitative Approach'. Rural Fire Research Centre, Technical Paper No. 6, December, 1984 (National Centre for Rural Fire Research: Monash University, Caulfield).

The Basis of Fuel Management on State Forest in NSW

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Fuel management has been practiced in NSW State forests since 1891 and forms an integral part of State Forests approach to fire management. State Forests believes the system of prioritised fuel management zones it has evolved, and continues to adapt as circumstances warrant, is the best combination of fuel management approaches needed to carry out its role within the community, meet its requirements under external legislation and fulfil its charter to the Forestry Act (1916).

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KEYWORDS: wildfire, hazard reduction, prescribed burning, fire management, fuel management

INTRODUCTION

State Forests, formerly known as the Forestry Commission of NSW, is a government trading enterprise that evolved as a result of restructuring, to fulfil the role of forest management in NSW.

State Forests is responsible for the management and protection of approximately 3.5 million hectares of dedicated State forest, and is also responsible for the management of timber on a further 3.7 million hectares of Crown-timber land (Table 1).

State Forests' corporate mission is to manage forests in an environmentally responsible manner, supplying products and services to meet customer expectations and achieve a commercial return.

Vital to the role of forest management is the protection of the community and forests from the adverse effects of uncontrolled wildfire.

TABLE 1

New South Wales Forest Area Statistics from 1993–94

Total area of NSW	80,000,000 ha
Forests in New South Wales	15,017,000 ha
Forests as percentage of State's area	18.7%
State forests	3,488,000 ha
Forests in National parks and Reserves	2,577,000 ha
Forests on other Crown land	3,696,000 ha
Forests on private land	5,256,000 ha

The protection of the community and forests from wildfire was first initiated by forest managers responding to the community and forest requirements from as far back as 1891 (Grant 1989). Since that time many lessons have been learned and recorded in regard to fuel management in NSW forests.

Legislation now documents the regulations guiding fuel management activities in NSW. Within this legislative framework there are some basic principles of fire management which should be acknowledged so that fuel management can be placed in perspective.

Implicit to fuel management, is an understanding of the link between fuel and fire behaviour. Fire is the result of the combination of three features, commonly referred to as the fire triangle. These feature are a source of fuel, a source of oxygen and a source of heat (ignition).

In a forest environment the fuel source is both the living and dead plant matter. The source of oxygen is the atmosphere and the source of ignition can be from deliberate or accidental ignition or a natural cause such as lightning.

If any one of these factors can be removed from the fire triangle, the fire will cease. Fuel is the only practical feature of the fire triangle that can be either removed or modified in a forest environment. Whilst natural causes of ignition cannot be prevented, concerted effort is placed on community education to reduce the risk of deliberate or accidental ignition.

Hazard reduction burning in rural NSW is the most practical and widely used method by which forest fuel is modified. Hazard reduction burning modifies the fuel in two ways. Firstly, it reduces the volume of fuel available to a wildfire, thereby reducing fire intensity (Luke and McArthur 1978). Secondly, it changes the fuel arrangement on the forest floor and just above the floor, which bears a strong influence on reducing the intensity of a wildfire (Chandler et al. 1983, Cheney 1981).

The reduction of intensity of a wildfire reduces the risk of injury to rural firefighters, the community, commercial forest products and sensitive forest environments.

Hazard reduction burning plans are carried out over broad forest areas, to account for the needs of protection for rural communities, parks and reserves, commercial forest products or particular forest features that require special attention in relation to fuel or fire management.

A case example of the planning procedure is used to examine the fuel management planning process and features accounted for when planning fuel management.

Genesis of Fuel Management in NSW

State forests in NSW have been managed by a government agency for more than 100 years. Prior to the initiation of the Forest Conservancy Branch in 1877, regulations governing forests were aimed at ensuring adequate amounts of timber were left for government purposes (Hannah 1986).

The agencies governing the forests between 1877 and 1909 were many and varied, but did not attempt to formulate or implement policy on forest management or protection (Hannah 1986). However, within that time period fuel and fire management began to take shape. The Forestry Act (1909) created the Department of Forestry but was superseded by the Forestry Act (1916) which promulgated the Forestry Commission of NSW. As recently as 1991 the Forestry Commission underwent a restructure to form a government trading enterprise and renamed the organisation State Forests.

State Forests of NSW, then the Forestry Commission, has had a long and extensive history of fuel and fire management in NSW and is a lead agency in this field. The Bushfires Act (1949) was first written by a Forestry Commission manager, and the more recent 1989 amendments to the Act were formulated from input and submissions by State Forests' predecessor.

Fire management techniques such as the use of fire breaks were being developed and implemented as early as 1912, by the then Department of Forestry, while the first use of prescribed burning was conducted in 1891 (Grant 1989). The first Fire Control Schools, began in 1947. These schools involved a seven day series of lectures and demonstrations on weather forecasting, fire control legislation, radio communications and methods of bushfire fighting (Grant 1989). The first fire control schools also taught the preparation and value of fire control plans. The fire control schools that began in 1947 have formed a strong basis for the more detailed fuel and fire management plans now used by land management agencies.

State Forests Role in Fuel Management

State Forests believes it is essential that the community be aware that fire is a constant and inevitable aspect of forest management. Mindful of the vital role of, and need for, community fire fighting, State Forests has assumed responsibility for significant aspects of community fire protection, particularly in country New South Wales.

State Forests operates to a charter as set out in the Forestry Act (1916). This charter puts forth the objective of State Forests to:

- conserve and utilise the timber on Crown-timber lands to the best advantage of the State
- provide adequate supplies of timber from Crown-lands for building, commercial, industrial, agricultural, mining and domestic purposes
- preserve and improve, in accordance with good forestry practice, the soil resources and water catchment capabilities of Crown-timber lands
- encourage the use of timber derived from trees grown in the State and consistent with the use of State forests for the purpose of forestry, flora reserves and the preservation of flora, promote and encourage State forests use for recreation and conservation of fauna.

In the attainment of these objectives, and in the exercise of its duties and functions, State Forests is required to take all practical steps which it considers necessary, or desirable, to ensure the preservation and enhancement of the quality of the environment.

Further, the Forestry Act (1916) also states that subject to the Bush Fires Act (1949), State Forests may carry out on Crown-timber lands measures for the protection from fire of timber and products on Crown-timber lands.

State Forests manages the forest estate under its control with the aim of serving a wide range of conservation, community and commercial needs. This aim requires that State Forests be committed to ecologically sustainable management and dedicated to the conservation of all aspects of the forest environment.

Underpinning the protection of the community, timber resources, water catchment, soil, flora and fauna is the development and maintenance of a successful fuel and fire management regime.

Role of Legislation in Fuel Management

State Forests fuel and fire management planning is guided by extensive legislation, including:

Bush Fires Act (1949)
Forestry Act (1916)
National Parks and Wildlife Act (1974)
Environment Planning and Assessment Act (1979)
Clean Air Act (1961)
Occupational Health and Safety Act (1983)
Endangered Fauna (Interim Protection) Act (1991)
Workers Compensation (Bush Fire Emergency and Rescue Services) Act (1987)
Crimes Act (1900)
Local Government Act (1918).

Meeting the functions of all of these Acts is a complex task. However, the long history of State Forests' role in fuel and fire management and its experience in both planning and fulfilling these tasks have provided State Forests with the capability to balance the objectives of impinging legislation.

The Bush Fires Act (1949) has been written to make provision for the prevention, control and suppression of bush fires, and for the mitigation of dangers resulting from bush fires. Further the act provides the primary impetus for conducting fuel management activities on rural lands, including State forest. The Forestry Act (1916) requires that timber and products on State Forests and Crown-timber lands are adequately protected from fire and that the measures undertaken to protect these values are consistent with good forestry practice.

The majority of the Acts prescribe a framework within which fuel management and fire suppression can be carried out. However, within the legislative framework the Bush Fires Act (1949) has primacy over nearly all other Acts, because the community places the value of protecting life and property very high.

FUEL MANAGEMENT

For the purposes of the Bush Fires Act (1949) New South Wales is divided into local government areas (LGA). Each LGA has a Bush Fire Management Committee comprising of members from the local community and land management agencies. This committee compiles a plan of operations and, a plan of fuel management for the LGA. The plan of operations outlines the method for suppressing bush fires, and the fuel management plan prescribes the measures by which fuel management shall be undertaken.

Objective of Fuel Management

The primary objective of fuel management is not to eliminate wildfire, which is impossible, but rather to create a mosaic of fire regimes and fuel such that the incidence and intensity of wildfire over the long term is reduced. Moderating the incidence and intensity of wildfire assists the protection of life and property while maintaining the integrity of the environment and helps protect commercial forest products.

It is widely recognised, both here and overseas, that fuel management — hazard reduction burning — makes it easier and safer to control fires (Chandler et al. 1983, Cheney 1981). Hazard reduction burning minimises the potential for severe wildfires, reduces fire management costs, and restricts wildfire damage on State forests and adjoining lands.

Further, State Forests rates hazard reduction burning as the best fire suppression training process available. It provides staff with important experience and awareness of fire behaviour, and the regular exposure to fire is a significant factor in maintaining fire readiness and a professionally developed fire culture.

State Forests specific fuel management objectives are:

- to protect life and property from wildfires
- to prevent the spread of wildfire onto neighbouring properties
- to protect assets on State Forest
- depending upon the assets to be protected, to provide a range of direct and indirect fire suppression options in the event of a wildfire
- to minimise damage to timber values on State Forests and other Crown-timber land
- to exclude fire from environmentally sensitive areas, for example a rainforest flora reserve
- to maintain biodiversity.

Fuel management — hazard reduction burning — reduces hazards in several ways:

- by reducing the total weight of fuels, the rate of spread and intensity of a fire is reduced, thereby reducing the impact of the fire upon forest values including soils, flora, fauna, water catchments and aesthetics.
- by reducing the height of the fuel bed, the flame height is reduced, thereby reducing the risk to firefighters and the impact on the forest
- by removing firebrand material, principally fibrous bark, the potential of wildfires to generate spot fires ahead of the main fire front is greatly reduced. (The reduction of spotting potential can reduce the overall rate of spread, and greatly increase the suppression capability and the safety of firefighters).

Several benefits follow from active fuel management, including:

- the opportunity to provide practical training for staff in fire behaviour, fire control techniques, fire safety measures and the use of a range of fire fighting equipment
- the establishment of good liaison and working relationships with forest neighbours, Bush Fire Brigades, councils and other authorities involved in co-operative hazard reduction burns along common boundaries for community and asset protection purposes
- to allow suppression resources, both firefighters and equipment, to be released from wildfires contained by effective hazard reduced areas.

Responsible fuel reduction does not aim to eliminate all readily flammable fuels. The correct timing of a hazard reduction burn, in conjunction with localised site variations in altitude and topography, moisture and vegetation cover, will commonly result in 30–50 per cent of the gross area being modified by the burn. The overall result is a reduction in fuel weight and arrangement on a proportion of the treated area, with a mosaic of burnt and unburnt areas.

Results of Fuel Management

Fuel management on a regional scale promotes a mosaic of fuel age, which maintains a lower average ‘fine fuel’ weight across the region. It also limits the vertical arrangement and continuity of fine fuel. These two effects combine to reduce the intensity of wildfire.

Fine fuel is the fuel that is less than six millimetres in diameter, and largely consists of leaves, twigs and bark. The coarser fuel, or heavy fuel, is modified slightly by hazard reduction burning.

The reason for targeting fine fuel in hazard reduction burning is because it is more volatile and the greatest contributor to a wildfire’s intensity, as compared to the heavy fuel. Modification of the fine fuel provides the greatest benefit in reducing a wildfire’s intensity, while minimising the impact on other values in the forest environment, such as timber, soil and water catchment values.

Low intensity hazard reduction burning generally reduces the fine fuel weight by up to 75 per cent over 30 to 60 per cent of the gross area being treated.

Following low intensity hazard reduction burning, the fine fuel weight will recover to 70–80 per cent of the pre burn weight in about 2–3 years. Whereas a high intensity wildfire will often reduce the fine fuel weight by more than 75 per cent, burn away heavier fuels and cover a higher proportion, approaching 100 per cent, of the area burnt over.

Fire Behaviour

The McArthur Forest Fire Danger Rating system provides a numerical fire danger index, ranging in scale from 0 to 100, as outlined in Table 2. The scale can be used to describe five classes of fire danger, ranging from low to extreme.

The fire danger index in conjunction with specific information about fuel weight, topography and forest type, allows predictions of fire behaviour to be made. Fire behaviour prediction will include features such as the rate of spread of the fire, flame height and possible spotting distance of a fire.

A prediction of fire behaviour is used during hazard reduction burning to ensure that the fire is a low intensity fire. Fire behaviour predictions are also used in wildfires to assist in the development of suppression strategies.

TABLE 2

Description of McArthur Forest Fire Danger Rating

Fire Danger Rating	Rating	Weather Description
Low	1–5	still wind, high humidity
Moderate	5–12	still to light wind, moderate humidity
High	12–24	moderate wind, moderate humidity
Very High	24–50	strong wind, low humidity
Extreme	50–100	strong and gusty wind, very low humidity

Planning Fuel Management

It would be impossible, and unacceptable, to conduct hazard reduction burning over the entire forest estate on an annual basis. Planning procedures have been developed to determine suitable priority zones which require fuel reduction. A number of factors which encompass the reasons for protection and fire behaviour are accounted for when determining priority zones, and include:

- value of asset to be protected
- wildfire history
- topography
- forest type
- weather — including temperature, relative humidity, drought factor and wind speed which provide a fire danger rating
- fuel loads (t/ha)
- fire spotting distance
- flame height
- rate of spread of fire.

Fuel management planning based on priority zones is a detailed method by which the forest manager can ensure that adequate protection is provided to neighbouring property, high value assets and forest values including timber, flora, fauna, soil and water catchments.

The case example uses these parameters to determine the objectives of fuel management related to the value of the asset to be protected and the fire behaviour that would be expected under the weather conditions generally experienced in the area.

Case Example of Fuel Management Planning

Experience has shown that five per cent of all wildfires account for 95 per cent of the damage incurred to assets (State Forests unpublished data). Also that this five per cent of fires tend to occur within 15 per cent of the highest fire danger rating days in an area.

Weather records for the case example area demonstrated that the 85th percentile (cut off point for the 15 per cent of highest fire danger rating days) recorded a Fire Danger Rating (FDR) of 30.

A FDR of 30 would typically combine weather parameters of 33°C temperature, 30 per cent relative humidity, and a 35 km/hr wind speed. Under these weather conditions a fire can be expected to behave quite differently for various fuel loads. Fuel load is a measure of the amount of fuel in a forest, expressed in t/ha.

Table 3a and 3b outline two different fire behaviour scenarios under different fuel loads comparing an FDR of 30 with a worst case scenario of a FDR of 100.

TABLES 3A AND 3B

Fire behaviour scenario using various fuel weights under an FDR of 30 and an FDR of 100.

Table 3a. FDR 30

Fuel load (t/ha)	Spotting Distance (km)	Flame Height (m)	Rate of Spread (km/hr)
5	0.3	2.5	0.17
10	0.8	5.5	0.34
15	1.5	9.5	0.51
20	2.2	13.3	0.72

Table 3b. FDR 100

Fuel load (t/ha)	Spotting Distance (km)	Flame Height (m)	Rate of Spread (km/hr)
5	1.9	6.0	0.56
10	3.8	14.0	1.11
15	6.0	Crown Fire	1.68
20	8.1	Crown Fire	2.39

These two tables illustrate the dangerous fire behaviour (flames up to 13 m or more, spotting distances more than 2 km and spreading forward at 700 m per hour) that is sustained at a FDR of 30. Significantly worse fire behaviour is apparent at a FDR of 100. Within the tables the dramatic reduction in fire behaviour as a result of fuel weight reduction is demonstrated at a FDR of 30. The flames are 5.5 m high at 10 t/ha and is unable to be directly attacked by firefighters. However, once the fuel weight is lowered to 5 t/ha the flame height is reduced to 2.5 m and is at the upper limit of direct attack by fire fighters.

The implications for protection of valuable assets are obvious and must involve the weight of fuel available to wildfires.

The case example determined five separate fuel management zones, of which each has a separate objective and fuel management regime. The five zones are:

- zone 1: community protection and protection of high value assets
- zone 2: strategic corridors
- zone 3: fuel management over broad areas of forest
- zone 4: burning for special or ecological purposes
- zone 5: fuels to be managed without burning or remain unmanaged.

Zone 1, Community Protection and Protection of High Value Assets

Purpose

To provide a high level of protection to life, property and other identified assets. This zone also includes post logging burning after harvesting where burning is necessary to reduce fuels and promote regeneration.

Aim

To maintain a fine fuel weight that is as low as possible

- to achieve up to 80% coverage in each burning unit in each operation
- to reduce fuel levels after harvesting by post logging burning
- to maximise fire suppression options, particularly direct fire suppression, this zone will generally absorb short distance spotting.

Zone Width

Based on a FDR of 30, the zone width should be approximately 300 metres to allow for a direct fire suppression effort. This zone will generally absorb burning embers from fires outside the zone. By maintaining low fuel loads, the flame height would be up to 3 m high and spotting distances of up to 300 m. The zone width would be adjusted to allow for slope and topography to take account of their effect on fire behaviour.

Burning Cycle

Burning cycle refers to how regular the same area will be hazard reduction burnt. The burning cycle in any one area will depend on the rate of fine fuel accumulation but will generally be considered in the range from 2–3 years or when fuel loads reach 5–8 t/ha. Post logging burning, will be conducted within 18 months after harvesting.

Applications

- community protection
- protection of adjoining plantations
- protection of adjacent rural land holdings
- protection along highway corridors.

Zone 2, Strategic Corridors

Purpose

To provide a strategic corridor which can act as a barrier to the spread of wildfire and assist in absorbing short distance spot fires. These corridors will complement zone 1 areas, particularly around community settlements, plantations and other high value assets.

Aim

- to provide a mosaic of fine fuel weights after burning of between 5–8 t/ha
- to achieve up to 60 per cent coverage in each burning unit in each operation
- burning under conditions when the lower layers of litter are moist to ensure that the nutrient rich litter and surface soil are not completely removed
- to maintain a thin layer of unburnt litter, preferably of 4–6 t/ha retained unburnt to minimise the effects on microfauna and flora
- to protect sheltered SE-aspects from fire in addition to gullies to provide refuge areas for fauna
- to maximise fire suppression options, but direct fire suppression as an option is not mandatory, this zone will generally absorb burning embers from fires outside the zone.

Zone Width

Based on a FDR of 30, the zone width should be approximately 800 m to allow some direct fire suppression effort in the event of a wildfire, however, indirect fire suppression methods such as backburning would be the main option. By maintaining a fuel load of 5–8 t/ha, flame height in the zone would be up to 5 m and spotting distance up to 800 m. In some instances, for example, adjacent to sensitive nature reserves or plantations, the zone width may be increased substantially (up to 3–4 km) to allow fire suppression within a crown fire free zone under a high FDR. The zone width would be adjusted to allow for slope and topography to take account of their effect on fire behaviour.

Burning Cycle

The burning cycle would depend on the rate of fine fuel accumulation but will generally be considered from 3–5 years or will be assessed when fuel loads reach 8–12 t/ha.

Applications

- corridor adjacent to zone 1 for protection of adjoining high value assets, such as plantations
- protection of adjacent rural land holdings with low density population
- corridor along highways
- provision of strategic corridors that will allow backburning in the event of a major wildfire.

Zone 3, Fuel Management Over Broad Areas of Forest

Purpose

Broad area fuel management is to act as a complement to other management objectives. In the broader forest area, where life and property are not directly at risk, fuel management will aim to provide a mosaic of burnt and unburnt areas that will still allow indirect fire suppression effort in the event of a wildfire, but also will maintain bio-diversity in the long term.

Aim

- to provide a mosaic of fine fuel weights after burning between 8–15 t/ha
- to maintain biodiversity
- to provide a mosaic of burnt and unburnt areas so there are no large contiguous areas of unmanaged fuel, this zone will complement the other zones as part of the protection over broad areas
- burning under conditions when the lower layers of litter are moist to ensure that the nutrient rich litter and surface soil are not completely removed
- to maintain a thin layer of unburnt litter, preferably of 4–6 t/ha, retained unburnt to minimise the effects on microfauna and flora
- to protect sheltered SE-aspects from fire in addition to gullies to provide refuge areas for fauna
- to achieve up to 60 per cent coverage in each burning unit in each operation.

Zone Width

Based on a FDR of 30, the fuels will be managed on a mosaic within a minimum zone width of 1.5 km and would still allow a range of indirect fire suppression options for fuel loads of up to 15 t/ha. The resulting flame height in wildfires under FDR 30 would be up to 9.5 m high and spotting distance up to 1.5 km.

Burning Cycle

The burning cycle will depend on the rate of fine fuel accumulation but will generally only be considered after a minimum of 6 years since the pervious burn or wildfire. Areas would be considered for burning in the 6–10 year time frame, or when fuel loads reach 12 t/ha. If the fire regime requires a burning cycle of longer than 10 years, fuel loads should not exceed 15t/ha.

Applications

- fuel reduction over broad areas, under conditions where mainly ridge top fuels will burn
- as a precursor to logging to assist in achieving post logging burning objectives.

Zone 4, Burning for Special or Ecological Purposes

Purpose

To provide specific burning and fuel management requirements for a number of purposes, such as research into the effects of fire on the environment, management strategies to provide specific fauna habitat, burning for specific flora protection or burning under young regrowth.

Aim

To provide the conditions and treatments or implement the regimes detailed in management or fauna and flora recovery plans.

Burning Cycle

This will depend on the specific requirements of the plans.

Burning under regrowth

This will commence when the dominant and co-dominant trees have reached an average diameter of 10 cm. Burning will aim to avoid damage to the dominant and co-dominant trees in the regrowth stand, and maintain an average of 5–6 t/ha over the area. Burning would be carried out when the weather conditions are suitable, and generally include:

- air temperature up to 25°C
- relative humidity between 50%–80%
- mean wind speed in the open up to 15 km/hr
- near surface fuel moisture between 12%–20%

These are guidelines and will be refined over time with careful records of burning results and fire behaviour at the time of burning.

Fauna Management

Fire regimes will be considered for the specific requirements of the management plan or recovery plan developed for particular fauna species.

Flora Management

Fire regimes will be considered for the specific requirements of the management plan or recovery plan developed for particular flora species.

Zone 5, Fuels to be Managed Without Burning or Remain Unmanaged

Purpose

These are fuels in areas where management priorities require that prescribed burning is to be excluded or areas where fuels are to remain unmanaged.

Aim

To exclude deliberate ignition, wildfires or fuel management, as appropriate from these areas.

Applications

Typical applications include:

- rainforest areas
- drainage and creek line filterstrips

- areas of significant historical, research or archaeological value
- rare or threatened plant species that are sensitive to fire
- most flora reserves.

In some cases the areas in this zone will need to be actively protected from fire and may be bound by zone 1. or zone 2.

CASE EXAMPLE AREA

The case example depicts a fire regime for an area of State forest just under 140,000 ha in size (Table 4). This State forest area like most in NSW is not isolated but is adjoined by other lands including national park, reserves, crown land and many hundreds of private land owners. There are many assets surrounding and within the forest area including community settlements, single dwellings and plantations, which all require protection from fire.

Several features of the case example need to be highlighted:

- the average repeat burning cycle over the total area is 12 years
- 2% of the total forest area has a repeat burning cycle of less than 3 years of which 60% of the area treated each year is burnt
- 28% of the total forest area has a repeat burning cycle of less than 7 years, of which 60%–80% is actually burnt
- 26% of the total forest area is not planned for burning or will be only burnt for ecological or special purposes.

TABLE 4

Annual area burnt within case example

Zone	(a) Total area within each forest zone (ha)	% of area in zone	(b) Burning cycle	% of total treated annually	(c) Planned burn coverage within each zone	(a/b) x (c) Annual area actually burnt (ha)
1. Community Protection	2,896	2%	1–3, av.2	1%	80%	1,158
2. Strategic Corridors	35,695	26%	3–5, av.4	6%	60%	5,354
3. Broad Area	48,953	35%	6–10, av.8	4%	60%	3,671
	16,060	11%	>10, av.12	1%	60%	803
4. Special or Ecological Burning	18,253	13%	Variable assume av.8	2%	Variable assume 50%	1,140
5. No Burning	17,961	13%				
Total	**139,818**					**12,126**

SUMMARY

State Forests believes that it consistently demonstrates a professional approach to fuel and fire management. The combination of a highly qualified and experienced staff, together with the operational, technical and managerial skills developed in fuel management, has created an effective and efficient fire culture to satisfy the imperatives of legislation, meet the objectives of State Forests' charter to the Forestry Act (1916) and carry out the vital role of community fire protection.

The fuel management planning zones developed by State Forests are a comprehensive method by which community protection, commercial forest products and the forest environment can be maintained and adapted as circumstances warrant.

REFERENCES

Chandler, C., Cheney, P. Thomas, P., Trabaud, L. and Williams, D. (1983). 'Fire in Forestry: Volume 1, Forest Fire Behaviour and Effects'. (John Wiley & Sons: New York).

Cheney, P. (1981). Fire Behaviour. In 'Fire and the Australian Biota' (Eds. A.M. Gill, R.H. Groves and I.R. Noble). (Australian Academy of Science: Canberra).

Grant, T.C. (1989). 'History of Forestry in NSW, 1788–1988'. (Star Printery: Erskineville, NSW).

Hannah, H. (1986). 'Forest Giants: Timbergetting in New South Wales Forests, 1800–1950'. (Forestry Commission of NSW: Sydney).

Luke, R.H. and McArthur, A.G. (1978). 'Bushfires in Australia'. (Australian Government Publishing Service: Canberra).

The Human Emotional Response to Bushfire Disasters

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Disasters can be viewed from the community, group or individual perspective, and from a variety of theoretical approaches. This paper details the clinical presentation of acute and chronic distress following disasters, where possible highlighting work following Australian bushfires. Preliminary findings from the Sutherland Bushfire Trauma Project are reported and service provision issues discussed.

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INTRODUCTION

The human emotional response to bushfires and other disasters is an area of great clinical and theoretical complexity. This complexity is reflected by contributions to the literature focused on the individual, group or administrative responses to disasters, by the traditional focus on the immediate post disaster phase as opposed to the more recent focus on long term sequelae, and by the various aetiological models advanced. Theoretical constructs include the medical 'disease model' with an emphasis on possible neurophysiological changes following trauma. Postulated psychological mechanisms include learnt responses following disasters, the individual's perception of threat during the stressful event and the presence of dysfunctional cognitions following a disaster, such as the individual's causal attribution's concerning the traumatic event. Lastly, sociological views have focused on altered community and family functioning following traumatic events.

This paper will focus on the extent to which disasters pose a threat to the emotional health of the individual, the clinical presentations typically seen after disasters such as bushfires and recent service provision innovations. For a more extensive discussion of the effect of trauma on adolescents and children see Terr (1991) and for adults Choy and De Bosset (1992). McFarlane and Raphael (1984) have reported specifically on the effects of the 1983 Ash Wednesday bushfires.

Much historical knowledge on this topic is anecdotal or descriptive. The application of scientific rigour to this research area has been impeded by the episodic, unpredictable nature of disasters and the decay of knowledge gained from one disaster to the next. Past research has been criticised because of the deficiency of sound methodology including the lack of standardised interviews and diagnostic criteria, comparison and control groups, and blind raters (Garmezy 1986). Further confounders such as premorbid individual vulnerability and protective factors, family variables and community factors have not been adequately accounted for. There is evidence that many of these deficiencies are being addressed in recent research with progress towards a more scientific model of description, identification of similarities, a codified classification system and subsequent hypothesis formation and experimentation — the 'experimental–theoretical' period described by Benedek (1985). Lastly ethical principles including the United Nations guidelines on research involving refugee populations is a major consideration in this area, and the use of control groups in disaster research requires close monitoring and adherence to rigorous approved ethical processes.

Disaster research has its antecedents in the literary report of the human experience of war. Adult psychological sequelae from involvement in war has been frequently recorded in fictional works and early medical writing, including the report of DaCosta's Syndrome following the American Civil War, 'Shell Shock' following World War I, and 'War Neurosis' after World War II. More recently emotional trauma incurred during the Vietnam War led to the inclusion of Post Traumatic Stress Disorder (PTSD) in the American Psychiatric Association's Diagnostic and Statistical Manual Third Edition (DSM III 1980), and its maintenance in DSM III-Revised and DSM IV (1994).

Children and adolescents are frequent victims in natural and man-made disasters. School-children, given they travel widely and often in groups, are at increased risk of trauma in car, coach, plane and shipping accidents and disasters. Despite the frequency of children and adolescents being involved in disasters, research concerning the emotional sequelae of trauma in the child and adolescent population significantly lags that in the adult population.

There is no longer doubt concerning the propensity of adults, children and adolescents to be emotionally traumatised after an event that was outside the range of usual human experience, and caused extreme fear and a perceived threat to life. Indeed examining evacuees from Cyclone Tracy, Parker (1977) found the latter to be the strongest predictor of initial psychiatric morbidity. Research in childhood that elucidate this point include Terr's descriptive reports (Terr 1979, 1983, 1991) after a school bus hostage situation, review of child survivors of a school sniper attack (Pynoos et al. 1987) and Yule's research on adolescent survivors of two shipping disasters (Yule 1990, 1992). In adults there is a large literature on PTSD in Vietnam and other war veterans and survivors of natural disasters. In a bushfire context, significant rates of distress were found in firefighters (McFarlane 1988).

ACUTE EMOTIONAL RESPONSE TO DISASTERS

Research and fictional accounts emphasise both post disaster emotional and behavioural symptoms, and concurrent impairment of functioning. The report of the individual appearing dazed, bewildered and confused is common, so too the afflicted denying their traumatic experience. Evidence of impairment includes the inability to complete the chores of daily living ie dressing, eating, washing, and the inability to complete expected tasks such as employment.

The American DSM IV classification (1994) states Acute Stress Disorder may last from 2 days to 4 weeks. Prominent symptoms include decreased emotional responsiveness, a reduced awareness of the environment, persistent re-experiencing of the event, avoidance of stimuli that may arouse recollections of the trauma and symptoms of arousal and anxiety (DSM IV 1994). Associated features include possible coexistent bereavement with symptoms of lowered mood, despair, hopelessness and anger. Survivors often experience a feeling of guilt that others were injured or killed. Finally, whilst broad categorical definitions attempt to be inclusive, the range of human feelings is such that any aroused or altered feeling state is possible following a disaster. Indeed excitement or a feeling of self efficacy in the face of extreme adversity is often witnessed in some individuals during the aftermath of a disaster.

PREVALENCE OF POST TRAUMATIC STRESS DISORDER (PTSD)

Most of the following comments will focus on PTSD, however comorbid depression or an anxiety disorder may predominate the clinical picture depending on the individual's experience during the disaster, their antecedent resilience and post disaster experiences. Comorbidity is an important treatment and prognostic consideration: after the Ash Wednesday fires the presence of multiple disorders was used to predict a worse outcome in distressed firefighters (McFarlane 1992).

The reported incidence of PTSD varies greatly, indeed uniform PTSD rates would be unexpected. Variations in the prevalence of PTSD following disasters are due to the characteristics of that particular event such as the extent of loss of life and property, community factors and infrastructure where it occurred, and the elapsed time from the disaster to when the subjects were investigated. Further the reported prevalence varies with research design; lower rates are seen with increasing study rigour and with semi-structured interviews rather than self report questionnaires (Rubonis & Bickman 1991).

The emotional toxicity of different traumatic experiences is often difficult to compare. Few studies have specifically looked at post bushfire distress, generalisations must be made from studies involving a range of natural disasters and man-made adversity. Following the kidnapping of 26 children from Chowchilla, California., and their subsequent period of captivity, Terr in a descriptive study reported that 100% of children experienced 'psychic trauma' (Terr 1979). Pynoos and Eth reported 94.3% of school children trapped in a school playground by sniper fire suffered PTSD symptoms. This rate decreased relative to the decreased proximity to the sniper and the direct threat to life (Pynoos & Eth 1987). Using self report questionnaires Yule found 41% of adolescent girl survivors of a shipping disaster were above standardised adult cut-off scores for post traumatic distress (Yule 1991). Recently Shannon and colleagues using a self report PTSD instrument surveyed 5,687 children 3 months after Hurricane Hugo. A post traumatic distress rate of 5% was reported (Shannon et al. 1994).

A battery of self report questionnaires assaying levels of distress, anxiety and depression were used in the Sutherland Bushfire Trauma Project (SBTP). On the Impact of Event Scale (Horowitz 1979) 10.4% of grade 4, 5 and 6 students (age 8–11 years) satisfied criteria for post disaster distress. Younger children were screened with a combination of projective tests and a child and parent questionnaire, 11.3% were identified. A smaller number of adolescents, 3.3% were identified on the IES. The latter is likely to be an under-estimate of the PTSD prevalence given the systematic bias that results from many adolescents knowing that high scores would lead to the offer of 'counselling'.

The issue of symptom chronicity is continuing to be clarified. Significant persisting symptom were found in adolescents 1 year after a shipping disaster by Yule (1992) and 14 months after a school sniper attack (Nader et al. 1990). MacFarlane in a cohort after the 1983 Ash Wednesday fires found that on parent report one third of children had persisting preoccupation with the fires 26 months later (MacFarlane 1987).

CLINICAL PRESENTATION OF PTSD

The clinical presentation of PTSD in the child and adolescent population is dependant upon the child's age and developmental stage. Non specific indications of distress may follow any trauma and include increased aggressive or withdrawn behaviour, clingy and dependant posturing, and sleep disturbance.

Infant and preschool children will communicate distress by behavioural change temporally linked to a given trauma. General signs include alterations in the ease of feeding, sleeping or settling the child. Regressed behaviour may include the child's unwillingness to explore the environment and increased stranger danger. Increased aggression or clingy behaviour is common.

Verbal preschool children display or voice broad emotions such as anger, sadness and excitement. Mixed or rapidly changing mood states are frequent. Separation anxiety is common, so too are specific trauma related fears. Post traumatic play (in Terr's terminology re-enactments, lack the fun element of play) is typical and re-enactments are compulsive, repetitive behavioural sequences that are unconsciously linked to the traumatic event (Terr 1991). Such re-enactments can be contagious — involving non traumatised children and can place children in danger. An example following bushfires would be playing with fire.

School age children: with increasing age, symptomatology is more typical of adult PTSD. Age related phenomena still exist such as behaviour disturbance, however, behaviour becomes more sophisticated. Fear of death, separation anxiety, or fear of the event recurring are common. Magical thinking and ascribing omen status to events before the trauma, variously termed 'omen formation' (Terr 1979) or 'cognitive reappraisal' is common, so too are phenomena such as nightmares and sleep disturbance. 'Flashbacks' are reported, however, the visual images and sounds reported in the Pynoos et al. (1987) sample have a more daydream quality than the sudden, intrusive adult phenomena. Symbolic associations occur and cause distress. Yule reports a fear generalisation gradient in the adolescent survivors of a shipping disaster. In this group, situations approaching the traumatic event evoked increasing distress. Some were distressed by any reference to water, such as water running from a tap (Yule 1990).

Denial and disavowal of the traumatic event is less often seen in childhood PTSD, except with trauma secondary to chronic sexual or physical abuse where adult coercion to remain silent and enforced secrecy is common. However, children often withhold the extent of their distressing experiences from their parents. In Yule's reports after shipping disasters the children's stated reason was that they did not want to make their parents even more anxious by the added burden of their feelings of distress (Yule 1991). Another distinction from adult PTSD is that numbing and restriction of emotional responsiveness is less frequently reported.

Time may diminish the emotional impact and symptoms of PTSD. However, late onset symptoms may develop. Anniversary reactions are common and may increase over time. Often their occurrence is not immediately attributed to the traumatic event (Terr 1991). Anniversary symptoms may include any in the PTSD spectrum. 'Future foreshortening' was reported in 23 of 25 Chowchilla children and included the view that their lives would not be full, long, nor their career or marriage successful (Terr 1983). Symptom chronicity emphasises the possibility that PTSD in the child will alter that child's developmental trajectory. Persistent symptoms and altered future aspirations are not the only impairments of this condition, in refugee groups PTSD is associated with deterioration in school performance (Kinzie 1986). In all student groups lower academic achievement is probable.

Adult diagnostic criteria for PTSD emphasise the presence of symptoms indicating (1) persistent re-experiencing of the trauma (intrusive recollections, dreams, distress following symbolic reminders of the event, and acting as if the event is recurring) (2)Persistent avoidance of stimuli associated with the event and emotional numbing (diminished interest in activities, feeling detached and estranged from others) and (3) symptoms of increased arousal (sleep and concentration difficulties, increased startle response) (DSM VI 1994). Impairment in adult populations includes relationship difficulties, inability to fulfil employment potential and comorbid drug and alcohol abuse and dependence.

THE SUTHERLAND BUSHFIRE TRAUMA PROJECT: A PUBLIC HEALTH INNOVATION

For many years post disaster critical incident debriefing has been advocated and undertaken by schools, volunteer and professional organisations and less frequently by adults in the broader community. However, despite the usefulness of this intervention it is unlikely that severe distress will be ameliorated, or a process of reintegration will be instituted by this procedure alone. Further, given the increasing literature on the chronic sequelae of trauma, it is clear that a second process of screening for morbidity, some time after the disaster is warranted. At this time individual's with persisting distress can be offered treatment before a chronic psychiatric condition is established.

Screening for PTSD would appear beneficial given the high prevalence of the disorder, its potential for chronicity and impairment, and the ability to distinguish distressed from non distressed individuals (after Fletcher & Fletcher 1988). Indeed Yule and Udwin (1991) found this process useful in adolescent survivors of a shipping disaster. Clearly screening may impose dangers to some; identification may expose the child and family to further anxiety, cost and inconvenience, it may encourage the assumption of the sick role and create stigma at school. As with any instrument or test, there is also an established false positive and negative illness identification rate.

Extensive screening (n = 4000 students) was utilised in the Sutherland Bushfire Trauma Project, an Australian program involving school children that is presently undergoing evaluation. The project assumptions were (1) a likely prevalence of Post Traumatic Stress Disorder of 5–10% in children and adolescents in an area that experienced significant morbidity, and home loss and damage following a bushfire disaster (86 houses were destroyed and 1 person killed in the Sutherland area of New South Wales). (2) The local health resources would not be able to provide psychological interventions for distressed children and adolescents. The project hypotheses were that it was possible to instigate extensive, school based, proactive screening for distress following the bushfire and to identify children and adolescents in most need of psychological care. Secondly, treatment innovations such as children using a therapeutic workbook ('The Bushfire and Me', Storm, McDermott, Finlayson 1994) supervised by a school or health psychologist and completed at home with the aid of parents, would be a cost effective means of providing a therapeutic intervention to large numbers of children. Similarly adolescent group therapy could cost effectively treat students in the school environment, allowing one practitioner to assist numbers of students at one time.

Future publications from the project will highlight epidemiological data including the prevalence of PTSD, depression and anxiety disorders in children in adolescents, and the relationship between bushfire exposure and proximity, separation experiences, accommodation displacement, and perception of threat to the reported prevalence rates. Risk factor analysis will include the above plus a separate module with data on parent distress, parent neuroticism and parent report of child neuroticism. Lastly the workbook and the adolescent group program are being evaluated in a randomised, controlled trial, one of the first studies of this type in the child and adolescent disaster literature.

SUMMARY

Natural disasters such as the 1994 New South Wales bushfire disaster are a cause of considerable immediate and longer term emotional distress in adults, children and adolescents. This paper has outlined the prevalence of Post Traumatic Stress Disorder reported after a range of disasters, and the specific rate found in children and adolescents 6 months after the bushfires in New South Wales. The clinical presentation of distressed adults and children has been detailed, emphasising the breath of possible reactions, the common finding of comorbid psychiatric conditions and the danger of secondary impairment in the interpersonal, academic or employment domains. The Sutherland Bushfire Trauma Project has been briefly described and based on its preliminary findings, it has been advised that routine review of disaster survivors, 6 months after the event, will identify individuals that are still distressed and will benefit from a mental health intervention.

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REFERENCES

Benedek, E.P. (1985). Children and psychic trauma: A brief review of contemporary thinking. In 'Post Traumatic Stress Disorder in Children' (Eds S. Eth and R. Pynoos) pp 1–16. (American Psychiatric Press Inc.: Washington).

Choy, T. and De Bosset, F. (1992). Post Traumatic Stress Disorder: An overview. *Canadian Journal of Psychiatry* **37**, 578–581.

'Diagnostic and Statistical Manual Third Edition' (1980). (American Psychiatric Association: Washington, DC).

'Diagnostic and Statistical Manual Fourth Edition' (1994). (American Psychiatric Association: Washington, DC).

Fletcher, R.H., Fletcher, S.W. and Wagner, E.H. (1988). 'Clinical Epidemiology, the Essentials'. Second edition. (Williams & Wilkins: Baltimore).

Garmezy, N. (1986). Children under severe stress: Critique and Commentary. *Journal of the American Academy of Child and Adolescent Psychiatry* **25**, 384–392.

Horowitz, M. (1979). Impact of Event Scale: A measure of Subjective Stress. *Psychosomatic Medicine* **41**, 209–213.

Kinzie, J.D., Sack, W.H., Angell, R.H. and Manson, S. (1986). The Psychological effects of massive trauma on Cambodian Children I. *J. Am. Acad. Child Adol. Psych.* **25**, 377–383.

McFarlane, S. (1987). Posttraumatic phenomena in a longitudinal study of children following a natural disaster. *Journal of the American Academy of Child and Adolescent Psychiatry* **26**, 764–769.

McFarlane, S. (1988). The Longitudinal Course of Post Traumatic Morbidity. *Journal of Nervous and Mental Disease* **176**, 30–39.

McFarlane, S. (1992). Multiple diagnosis in PTSD in victims of natural disaster. *Journal of Nervous and Mental Disease* **180**, 498–504.

McFarlane, S. and Raphael, B. (1984). Ash Wednesday: The effects of fire. *Australian and New Zealand Journal of Psychiatry* **18**, 341–351.

Nader, K., Pynoos, R., Fairbanks, L. and Frederick, K. (1990). Children's PTSD reactions one year after a sniper attack at their school. *American Journal of Psychiatry* **147**, 1526–1530.

Parker, G. (1977). Cyclone Tracy and Darwin Evacuees: On the Restoration of the Species. *British Journal of Psychiatry* 130, 548–55.

Pynoos, R.S., Frederick, C., Nader, K., Arroyo, W., Steinberg, A., Eth, S., Nunez, F. and Fairbanks, L. (1987). Life Threat and Post Traumatic Stress in School-age Children. *Archives of General Psychiatry* **44**, 1057–1063.

Rubonis, A.V. and Bickman, L. (1991). Psychological impairment in the wake of disaster:the disaster-psychopathology relationship. *Psychiatric Bulletin* **109**, 384–399.

Shannon, M.P., Lonigan, C.J., Finch, A.J. and Taylor, C.M. (1994). Children exposed to a disaster: 1. Epidemiology of post traumatic symptoms and symptom profiles. *Journal of the American Academy of Child and Adolescent Psychiatry* **33**, 80–93.

Storm, V. McDermott, B. Finlayson, D. (1994). 'The Bushfire and Me'. (New South Wales Department of Health: Sydney).

Terr, L. (1979). Children of Chowchilla: A study of psychic trauma. *Psychoanalytical Study of Children* **34**, 547–623.

Terr, L. (1983). Chowchilla Revisited: The effects of psychic trauma 4 years after a school bus kidnapping. *American Journal of Psychiatry* **140**, 1543–1550.

Terr, L. (1991). Childhood Traumas: an outline and overview. *American Journal of Psychiatry* **148**, 10–20.

Yule, W. (1990). The "Jupiter" sinking ; Effects on children's fears, anxiety and depression. *Journal of Child Psychology and Psychiatry* **31**, 1051–61.

Yule, W. (1992). Post traumatic Stress Disorder in Child Survivors of Shipping Disasters: The Sinking of the "Jupiter". *Psychotherapy and Psychosomatics* **57**, 200–205.

Yule, W. and Udwin, O. (1991). Screening child survivors for PTSD : Experiences from the "Jupiter". *British Journal of Clinical Psychology* **30**, 131–138.

Building in a Fire-Prone Environment: Research on Building Survival in Two Major Bushfires

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This paper discusses some eleven years of research by the authors into the reasons why houses are ignited and subsequently destroyed in bushfires in Australia. Particular reference is made to fires which occurred in February 1983 and January 1994. The effect on various aspects of building design and construction are discussed on the basis of statistical data obtained by surveying the fate of houses in the 1983 fires and comparisons made with survey data, obtained up to the date of writing, from the 1994 fires.

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KEYWORDS: Building design, bushfires, surveys, ignition

INTRODUCTION

In the twelve years since the major losses caused by the 'Ash Wednesday' fires of 16 February 1983 in Victoria and South Australia, much has been learnt about the mechanisms involved in the ignition and destruction of buildings by bushfires. This information forms the basis for Australian standards and advice on building design and construction in bushfire-prone areas as part of an integrated approach, involving vegetation management, subdivision and landscape design.

In the 'Ash Wednesday' fires 76 people died, and 2463 houses, more than 100 farm buildings, 30 000 stock, 20 000 km of fencing and 1.5 million bales of hay were destroyed. Monetary damage had been estimated to be in excess of A$440 million (Anon. 1983). Such bushfires are an inevitable part of living in the urban–rural interface in Australia and this has been highlighted by the recent January 1994 fires in New South Wales (NSW) where significant losses occurred. In these fires 4 people died, 206 houses were destroyed and the estimated damage was in excess of $100 million.

The challenge of providing adequate safety for buildings and their occupants is increasing in importance as more houses are being built in urban–rural interfaces throughout Australia and the bush itself is being preserved rather than cleared or replaced by exotic species. This paper summarises research carried out by the authors since the 1983 'Ash Wednesday' fires and details preliminary results of investigations of the 1994 NSW fires. Another survey of note was carried out by Wilson (1984) after the 1983 fires, but no attempt is made in this paper to compare the results.

SURVEYS OF BUILDING PERFORMANCE

Two extensive surveys of the performance of buildings in bushfires have been carried out by the authors. The first (Ramsay et al. 1986) was of 1148 buildings involved in the Otway Ranges (Victoria) fire which was one of the many fires which occurred on 'Ash Wednesday' 1983. The second survey is of buildings involved in three of the areas affected by the NSW 1994 fires in the Sydney metropolitan area: Como–Jannali, Cottage Point and Lane Cove. This survey is not complete, with 469 houses having been surveyed and some 50 still to be surveyed.

As indicated in Table 1, the proportions of houses in the two surveys which were threatened but 'not ignited', 'damaged' to varying degrees or 'destroyed' and not repairable, varied. The houses fared better in the NSW fires and various factors, some of which are discussed below, could explain these differences, even though their relative importance has not yet been evaluated.

The large number of houses involved in the Otway Ranges fire, the evenness of fire attack and the wide spread of building design and materials meant that statistical analysis (Ramsay et al. 1986) of the data collected was appropriate. However, the data from the NSW fires are small in terms of the three areas being surveyed and the construction of the houses were similar and did not give a wide spread of materials; it is thus not envisaged that statistical analysis will be appropriate. In both surveys, over 80 data elements were collected on each house and its surroundings. These data elements provided information on the various elements of the buildings and their surroundings, including roofs, walls, windows, floors, decks, colour, outbuildings, the site and the vegetation.

TABLE 1

Classification of damage

Classification	Otway Ranges survey		NSW survey	
	No.	%	No.	%
Not ignited	433	38	284	61
Damaged	92	8	56	12
Destroyed	623	54	119	25
Unknown	0	0	10	2
Total	**1148**	**100**	**469**	**100**

STASTICAL ANALYSIS OF OTWAY RANGES FIRE AND COMPARISON WITH THE NSW FIRES

In the following discussion, representative results of the Otway Ranges statistical analysis are discussed with appropriate preliminary comments on the NSW survey. The statistical analysis was carried out by fitting the data to a logistic model. A base model was developed using data elements selected on the basis of simple tabulations and additional data elements added individually to assess their significance (a 95% confidence level was used).

Wall Cladding

Previous surveys have come to conflicting conclusions regarding the role of wall cladding, e.g. the survey of the Beaumaris fires (Barrow 1944) indicated that cladding did not appear to play a role, whereas the Hobart–Blue Mountains survey (Anon. 1979) indicated that masonry cladding was best.

Table 2, based on the Otway Ranges survey, shows the results of the statistical analysis in terms of the relative risk of houses being destroyed (RRD) for houses with various claddings, with houses clad with timber taken as the base (i.e. relative risk for timber is assigned a value of 1.0). An RRD value of 0.5 would indicate that a house with a particular feature would be twice as likely to survive compared to a house with the 'base' feature. Generally, differences greater than 0.2 were considered to be significant. These data indicate that a house clad with masonry is less likely to be destroyed than one clad with fibre-cement sheet or timber which have similar although not identical RRD values. It may be argued that this may not only be a function of the actual material used but also related to the designs typical of houses with these cladding materials. For example, masonry-clad houses do not generally have an unenclosed subfloor space, whereas timber-clad houses do. However, the logistic model used for the statistical analysis takes the possibility of such interactions into account.

The results obtained for the NSW survey (Table 3) indicate that masonry-clad houses again fared best, but the data for the small number of houses (16%) with other than masonry walls have to be treated with caution.

There is a widely held belief that the colour of wall cladding plays a role in house survival and that white-coloured walls are beneficial in that they reflect the heat of the bushfire better than dark-coloured walls. The data from the Otway Ranges survey (see Table 4) do not support this view.

TABLE 2

Otway Ranges survey – effect of wall cladding

Cladding	Relative risk of destruction*
Masonry	0.4
Fibre cement	0.8
Timber	1.0

* 'Timber' assigned a reference value of 1.0.

TABLE 3

NSW survey — effect of wall cladding

Cladding	% for each material			
	Not ignited	Damaged	Destroyed	Unknown fate
Masonry	68	13	17	2
Fibre cement	52	15	31	2
Timber	35	8	58	0

TABLE 4

Otway Ranges survey – effect of wall cladding colour

Colour	Relative risk of destruction*
White	1.0
Light or pastel	0.8
Medium	0.9
Dark	0.9

* 'White' assigned a reference value of 1.0.

Roof Cladding

Several aspects of roofing were examined. In the Otway Ranges survey, houses with masonry tile or steel deck roofs survived more often than those with corrugated iron or fibre-reinforced cement roofs (Table 5), but the pitch of the roof did not appear to affect survival (Table 6). The latter finding is contrary to previously published advice (Barber and Morris 1983) which suggests that houses with high-pitched roofs are at greater risk than those with low-pitched roofs.

Table 7 shows data for the roof cladding material for the NSW survey. Tiled roofs again fared best; the relatively small numbers of steel deck (6%) and corrugated iron roofs (6%) makes differentiation of their behaviour difficult.

TABLE 5

Otway Ranges survey – effect of roof cladding

Cladding	Relative risk of destruction*
Tiles	0.4
Steel deck	0.7
Corrugated iron	0.9
Fibre cement	1.0

* 'Fibre cement' assigned a reference value of 1.0.

TABLE 6

Otway Ranges survey – effect of roof slope

Cladding	Relative risk of destruction*
Pitched (>12°)	0.8
Flat (<12°)	1.0

* 'Flat' assigned a reference value of 1.0.

TABLE 7

NSW survey – effect of roof cladding

Cladding	% for each material			
	Not ignited	Damaged	Destroyed	Unknown fate
Tiles	71	11	16	2
Corrugated iron	41	26	33	0
Steel deck	32	14	50	4

Degree of Elevation

The effect of the degree of elevation of the houses was examined as indicated in Table 8 for the Otway Ranges survey; houses on normal height stumps were elevated less than the 'low' category. It was found that houses on stumps were most likely to be destroyed, whereas houses built on concrete slabs were least likely; the other categories showed intermediate performance. The vulnerability of houses on stumps appeared to be due to factors such as the use of timber gap-boards to enclose the underfloor space of timber and fibre-reinforced-cement-clad houses, and the use of (timber) stumps at spacings closer than that used for other means of (greater) elevation.

TABLE 8

Otway Ranges survey — effect of degree of elevation

Elevation	Relative risk of destruction*
None (slab-on-ground)	0.2
High (>2 m)	0.4
Low (<2 m)	0.5
Stumps	1.0

* 'Stumps' assigned a reference value of 1.0.

Occupant Action

Two-thirds of the houses in the Otway Ranges survey were unoccupied on the day of the fire and very few of the remaining people actually stayed with their houses during the fire. However, those who returned to their houses after the fire front had passed were able to improve the chances of the survival of their houses and to diminish the damage sustained. Table 9 shows the beneficial effect of the presence of people and their fire-fighting activities and supports the information obtained by interview. People other than occupants also saved houses from destruction; the inclusion of these cases in the data of Table 9 would increase the statistical significance of the first two categories.

Personal interviews revealed that people were able to save their houses by extinguishing burning materials around the houses – woodheaps, fence posts, trees and other burning buildings – and by extinguishing small ignitions of the house itself before these small fires became uncontrollable. In many cases, residents carried out these salvage operations on their own houses and their neighbours' houses after the fire front had passed. Further houses were saved by fire brigade action, although because of the speed of the fire such actions were generally limited.

A similar picture is emerging from the NSW survey, but the amount of fire brigade activity was considerably greater, with the opportunity to minimise the attack on the housing and actually extinguish houses which had started to burn.

TABLE 9

Otway Ranges survey – effect of occupant action

Action	Relative risk of destruction*
Stayed	0.1
Left — returned within half an hour	0.4
Left — stayed away	0.6
Unoccupied — at time of fire	1.0

* 'Unoccupied' assigned a reference value of 1.0.

Vegetation

The amount and type of vegetation around the houses was found to be an important factor (see Table 10 for the Otway Ranges survey). Houses were more likely to be destroyed as the vegetation (no differentiation was made between 'natives' and 'exotics') around them became thicker and the proportion of trees to shrubs increased and presumably the fire intensity increased. This analysis did not take into account the 'housekeeping' on the property, i.e. the degree of clearing of undergrowth, grasses, leaf debris, etc., because in most cases the fire had destroyed the evidence. One would expect the amount of ground fuel would thus be a reflection of the density of vegetation and number of trees.

A similar picture emerges from the NSW survey, as shown in Table 11, and similar conclusions may be drawn.

TABLE 10

Otway Ranges survey – effect of surrounding vegetation

Vegetation type	Relative risk of destruction*
Grass	0.1
Shrubs	0.4
Trees	1.0

* 'Trees' assigned a reference value of 1.0.

TABLE 11

NSW survey – effect of surrounding vegetation

Vegetation type	% for each type			
	Not ignited	Damaged	Destroyed	Unknown fate
Grass	71	9	18	2
Shrubs	61	17	19	3
Tree	43	12	43	2

Area of Glazing

Windows are thought to be the most vulnerable part of a wall in that they may break and allow burning debris to ignite the interior of the house. The NSW survey has provided an opportunity to study the role of windows. Table 12 summarises data on the effect of glass area (in the wall with the greatest per cent of glass). There is a pronounced trend of increasing destruction with increasing per cent glass area, which is in accord with the perceived role of windows in house destruction.

TABLE 12

NSW survey – effect of area of glass (in wall with greatest % of glass)

Area of glass (%)	% for each category			
	Not ignited	Damaged	Destroyed	Unknown fate
<30	85	9	5	1
30–50	75	12	10	3
50–80	54	23	21	2
>80	36	14	50	0

MECHANISMS OF IGNITION AND DESTRUCTION

During the course of gathering data for the surveys, particular attention was given to gathering information on how the houses might have been ignited and thus ultimately destroyed. This was done by examining the houses themselves, particularly those which had been damaged but not destroyed, and interviewing occupants and fire brigade personnel. In the majority of cases the damaged houses had been saved by firefighting activities and the 'ignition points' were thus an indication of where the destroyed houses may have been ignited. The conclusions drawn are discussed in the following paragraphs.

'Exploding' Houses

In the 1983 'Ash Wednesday' and 1994 NSW fires as well as previous bushfires, there have been accounts of houses spontaneously exploding due to the heat of the fire front. However, examination of the remains of destroyed houses and interviews with people present during the fires did not substantiate these claims. From the theoretical viewpoint, such 'spontaneous explosions' are improbable. Because of the speed with which the fire front travels, a house is exposed to the heat of the fire front for only a few minutes and this would not appear to be sufficient to cause 'instantaneous' ignition and total involvement of a house in flames.

Modes of Ignition

There are three possible modes of ignition – burning debris lodging on combustible material, radiation from the fire and direct flame contact: all three modes appeared to play a part in house destruction.

Evidence for the modes of ignition in both surveys came mainly from surviving houses and interviews with eyewitnesses who had been in the area (but not necessarily occupying the houses). In the majority of cases, ignition appeared to have been caused by burning debris, although radiant heat and flame played a significant role in cases where the houses were directly abutting dense undeveloped vegetation. The burning debris attacked houses for some time before, and for many hours after, the fire front passed, whereas the fire front itself impinged upon the houses for only several minutes.

Burning debris can gain entry to a house through broken windows or gaps in and around the wall or roof cladding, and then ignite the contents. The burning debris lodges on and ignites horizontal timber in decks, steps and windowsills, or is blown up against and ignites timber used at ground level for stumps, gap-boards, posts and steps.

Thermal radiation may crack windows, allowing burning debris to enter; it can heat the building and its contents, facilitating ignition by embers or flame; and, in extreme cases, it can ignite external timber or combustible contents near broken windows.

Evidence for flame contact by the fire front was difficult to find and apparent evidence, such as charred wood, was ambiguous because it may have been the result of radiation or of the ignition of vegetation growing against a house.

The ignition and destruction of the houses was facilitated by the strong winds which accompanied the fires. The wind carried the burning debris as well as large objects capable of breaking windows. In some cases, the force of the wind 'opened-up' houses to burning debris by removing roofs and walls.

CONCLUSIONS

The results emerging from the survey of the performance of buildings in the NSW fires of January 1994 are similar to those obtained in previous surveys, especially that carried out on the Otway Ranges fire which occurred on 16 February, 1983.

Similar house design and material factors appear to be operating, and the fact that the majority of houses involved in the NSW fires were brick-clad with tiled roofs appears to account, at least in part, for the greater proportion of surviving houses. The significant firefighting effort appears to be another contributing factor.

The ignition agents – burning debris, radiant heat and flame – are also similar, with their relative importance varying according to the relationship of the house to areas of vegetation. However, burning debris appeared to play a role in all circumstances. Ignitions are aided by the wind carrying the burning debris and large objects capable of breaking windows.

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Surveys of the type described here are labour intensive and are not feasible without the active participation and cooperation of many people too numerous to list. However, particular acknowledgment is due to Colin Jolliffe, Justin Leonard and Alex Webb for their recent efforts in the NSW survey.

REFERENCES

Anon. (1979). 'Houses Exposed to Bushfires'. Notes on the Science of Building No. 154, Experimental Building Station. (Department of Housing and Construction: Australia).

Anon. (1983). *Australian and New Zealand Burn Association J.* **6**: 39.

Barber, J. and Morris, W. (1983). 'Design and Siting Guidelines: Bushfire Protection for Rural Houses'. (Department of Planning and Country Fire Authority of Victoria).

Barrow, G.J. (1944). A Survey of Houses Affected in the Beaumaris Fire, January 14, 1944. *J. CSIR* **18**: 27.

Ramsay, G.C., McArthur, N.A. and Dowling, V.P. (1986). Building survival in bushfires. *Proceedings of Fire Science '86, 4th Australian National Biennial Conference, 21–24 October*, The Institution of Fire Engineers.

Wilson, A.A.G. (1984). 'Assessing the bushfire hazard of houses: a quantitative approach'. Tech. Paper No. 6. (National Centre for Rural Fire Research, Chisholm Institute of Technology: Victoria).

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VOLUME 116

Quinkana babarra, a New Species of Ziphodont Mekosuchine Crocodile from the Early Pliocene Bluff Downs Local Fauna, Northern Australia with a Revision of the Genus

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WILLIS, P.M.A. AND MACKNESS, B.S. *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the Early Pliocene Bluff Downs Local Fauna, Northern Australia with a revision of the genus. Proc. Linn. Soc. N.S.W. 116, 143–151.

A new species of ziphodont mekosuchine crocodile, *Quinkana babarra* is described on the basis of a fragmentary right maxilla from the Early Pliocene Bluff Downs Local Fauna. This new crocodile differs from *Q. fortirostrum* and the recently described *Q. timara* in having: 1, a shorter snout; 2, palatal fenestrae only reaching to the level of the fifth and sixth maxillary alveoli and not the seventh as in *Q. fortirostrum*; 3, mild festooning and 4, teeth variously with or without serrations. Recognition of this new species necessitates the revision of the genus. Ingroup relationships of mekosuchines are obscure and the position of *Quinkana* within this subfamily cannot currently be determined.

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KEYWORDS: Bluff Downs, crocodile, mekosuchine, *Quinkana*.

INTRODUCTION

Recent investigations of fossil crocodiles from Australia have revealed many more taxa than previously recognised (e.g. Willis and Archer 1990; Willis et al. 1990; Willis and Molnar 1991a, 1991b; Megirian et al. 1991; Willis 1992, 1993; Megirian 1994). These appear to represent a monophyletic Australian clade (Willis et al. 1990, Willis and Molnar 1991a) now recognised as the Mekosuchinae (Willis et al. 1993). There are a variety of ecomorphs among the mekosuchines including generalised, broad-snouted crocodilians (*Pallimnarchus* and *Australosuchus*), semi-ziphodont forms (*Baru*), fully ziphodont forms (*Quinkana*) and small terrestrial crocodilians (*Trilophosuchus* and *Mekosuchus*). Two longirostrine taxa may also be mekosuchines (Willis and Molnar 1991b; Megirian et al. 1991).

Australasian ziphodont crocodilians were initially reported by Plane (1967) and Hecht and Archer (1977). These were assigned to either sebecosuchian or pristicampsine crocodilians. Molnar (1977, 1978a, 1978b, 1981) described and named the almost complete snout of *Quinkana fortirostrum*. Molnar (1981) also described the fragmentary maxilla from Texas Caves that had been a focus of the study by Hecht and Archer (1977), two maxillary fragments and three teeth from Croydon, north Queensland and isolated teeth from a number of localities in Queensland. Megirian (1994) described a second species, *Q. timara* from the Miocene deposits of Bullock Creek, Northern Territory. This new species is distinctive in having an elongate snout.

A new species of a *Quinkana*, is described here from northeastern Queensland. This necessitates revision of the generic diagnosis of *Quinkana* Molnar 1981. The new species of *Quinkana* is the third crocodilian reported from the Early Pliocene Allingham

Formation, northwest of Charters Towers, northeastern Queensland. Archer (1976) reported the presence of teeth of *Pallimnarchus* sp. (QM F7763, QM F7764). Molnar (1979) described an incomplete snout of *Crocodylus porosus* (QM F9229). A large quantity of additional crocodile material since recovered will be described (B.M) as part of a comprehensive study of the Bluff Downs Local Fauna in progress. The Allingham Formation appears to represent freshwater fluviatile and lacustrine deposits. A number of Early Pliocene taxa have been previously reported from the deposit including mammals, birds, reptiles and fish (Archer 1976, Bartholomai 1978, Archer and Dawson 1982, Archer 1982, Rich and Van Tets 1982, Vickers-Rich 1991, Mackness et al. 1993, Boles and Mackness 1994, Mackness 1995(a), Mackness 1995(b)). Collectively the Early Pliocene Allingham assemblage has been called the Bluff Downs Local Fauna (Archer 1976).

Osteological terminology follows Romer (1956) and Steel (1973). Abbreviations for specimen numbers: AM F, Australian Museum fossil collection; QM F, Queensland Museum fossil collection.

SYSTEMATICS

Order Crocodylia Gmelin, 1788
Suborder Eusuchia Huxley, 1875
Family Crocodylidae Cuvier, 1807
Subfamily Mekosuchinae Balouet and Buffetaut, 1987
Genus *Quinkana* Molnar, 1981

Molnar's (1981) original definition of *Quinkana* was based on the single species *Q. fortirostrum*. Molnar (1981) reported that no portion of the jugal extended anterior to the orbit and included this feature in the diagnosis of *Quinkana*. Re-examination of the type specimen of *Q. fortirostrum* (AM F57844) however, reveals that the jugal does extend anterior to the orbit. The anterior portion of the jugal can only be seen on the interior surfaces of the snout; the external surfaces are heavily sculptured, obscuring this and some other sutural contacts. Megirian (1994) claims that the external sutural contacts in this region can be traced but we have difficulty in recognising them. The jugal-maxillary contact in crocodiles, however, is diagonal in cross section such that the exterior expression of the jugal-maxillary contact is always anterior to the interior expression of the suture. Because the interior expression of the jugal-maxillary suture is anterior to the orbit, the exterior expression of this contact must be located even further towards the anterior.

Megirian (1994) revised the generic definition of *Quinkana* as part of his description of *Q. timara*. The following revision does not violate any of his generic determinations and extends the concept of *Quinkana* to accommodate the new species described here.

Revision of the genus *Quinkana*:

The following features were given by Molnar in his diagnosis of *Q. fortirostrum*: three knobs present on lacrimal and prefrontal dorsal to the anterior to the margin of the orbit; orbit rim superiorly adjacent or anterior to the margin of the palatal fenestrae.

The following revised generic features define *Quinkana*, apomorphies identified by (a): mekosuchine crocodilians with moderately deep snout; (a) alveoli elongate and arranged with the cross-sectional long axis aligned to the tooth row; palatal portion of the maxillary-premaxillary suture U-shaped with convexity directed posteriorly; maxillary alveoli subequal in size; (a) distinct alveolar process with a series of dentary tooth reception pits along the medial side; festooning suppressed; (a) snout trapezoid in cross section immediately anterior to the orbits; anterior process of palatine very short or absent.

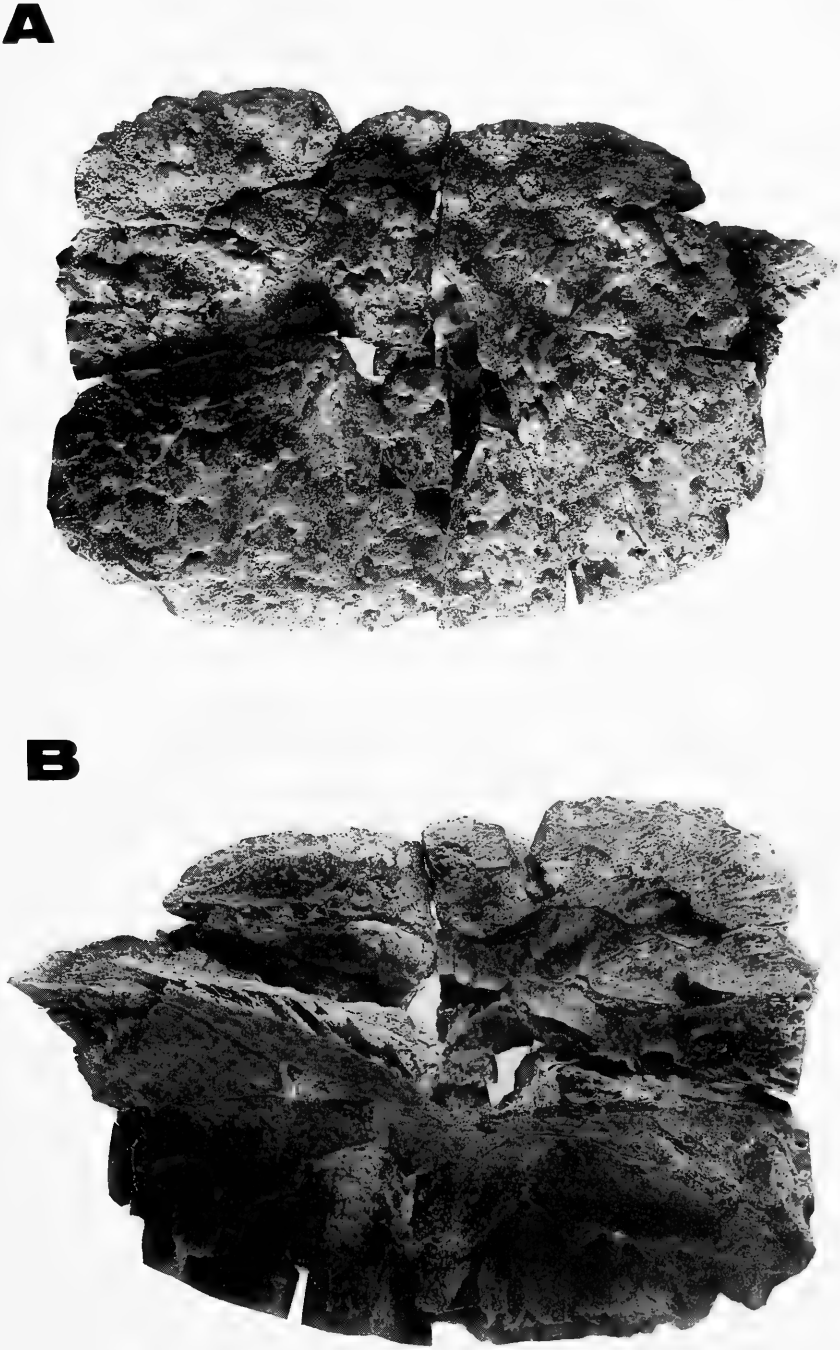

Fig. 1. Quinkana barbarra sp. nov. holotype QM F23220. Right maxilla. Actual size. A, buccal; B, lingual.

Crocodilans are remarkably conservative in form and regularly display convergence and parallel evolution. We have used a suite of characters including autapomorphies, generic synapomorphies and allometric characters to more clearly delineate a specific and generic diagnoses. Autapomorphies have been clearly marked in the diagnosis and the inclusion of the additional characters in the diagnosis is justified on the basis of clarification of our revised generic concept of *Quinkana*.

Knobs on the lacrimals and prefrontals, anterior shelves, suborbital jugal sulci and palatal buldges, as noted for *Q. fortirostrum* and *Q. timara*, are not known for *Q. babarra* and have been removed from the generic diagnosis.

Quinkana babarra n. sp. (Figs. 1–2)

Holotype

QM F23220, a partial right maxilla and associated fragments collected by Brian Mackness and colleagues in 1991.

Referred specimens

QM F23221–F23223, isolated ziphodont teeth. (Fig. 2).

Type locality

Dick's Mother Lode Quarry, Allingham Formation (Lat. 19°42′67″S, Long. 145°36′06″E), Bluff Downs Station, northeastern Queensland.

Age

Early Pliocene based on the interpreted age of the overlying Allensleigh basalt (Archer and Wade 1976).

Entmology

The specific name is from a Gugu-Yalanji dialect word *babarr*, meaning 'older sister' (Oates et al. 1964) and is used to denote the relationship of this crocodile to *Q. fortirostrum*.

Diagnosis

Quinkana babarra has a shorter, broader snout with mild festooning compared to *Q. fortirostrum* and *Q. timara* which have no festooning. *Quinkana babarra* is slightly smaller than the holotype (AM F57844) of *Q. fortirostrum* and NTM P895–19, the holotype maxilla of *Q. timara*. The palatal fenestrae in *Q. babarra* reach anteriorly to the level of the fifth and sixth maxillary alveoli but they only extend to the level of the seventh maxillary alveolus in *Q. fortirostrum* and the eighth maxillary alveolus in *Q. timara*. The lateral and upper surfaces of the maxilla are not as heavily sculptured as in *Q. fortirostrum* but are comparable to those of *Q. timara*. The sculpture on the lateral surface is less than on the dorsal surface where the bone rises into isolated small peaks. There is a larger peak in the antero-dorsal corner of the maxilla near the nasal-maxillary-premaxillary junction. In *Q. fortirostrum* this peak forms the postero-medial terminus of a low, rounded crest that extends obliquely across the maxilla onto the premaxilla above the fourth dentary tooth reception notch. This crest is poorly developed and only on the maxilla of *Q. timara*.

There is a pronounced trough on the posterior of the dorsal surface that extends anteriorly to the level of the fifth alveolus and posteriorly beyond the edge of the fragment as preserved. A similar but much less pronounced trough is present on *Q. fortirostrum*. *Quinkana babarra* is similar to *Q. fortirostrum* and *Q. timara* in having laterally compressed alveoli but these are arranged with the long axes in line with each other (in *Q. fortirostrum* and *Q. timara* each axis is slightly oblique). The alveoli are located on a narrow alveolar process with dentary tooth reception pits on the medial side. The alveoli indicate a degree of homodonty comparable to that of *Q. fortirostrum*. The total maxillary alveoli count is unknown in *Q. babarra* and *Q. timara* whereas in *Q. fortirostrum* it is twelve. The carinae of teeth in *Q. babarra* are variously with or without serrations in distinction from those of *Q. fortirostrum* and *Q. timara* which have serrate carinae.

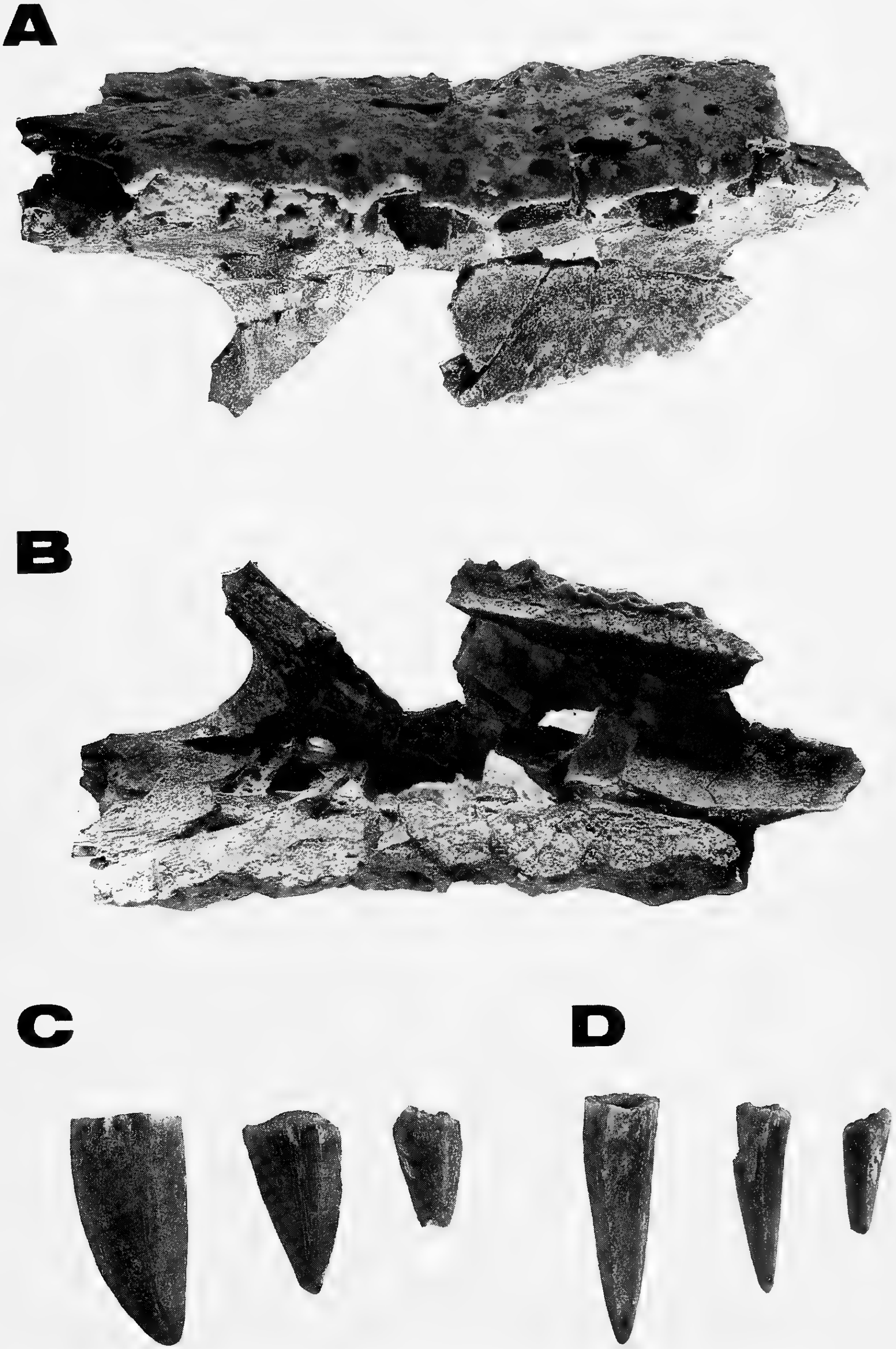

Fig. 2. Quinkana barbarra sp. nov. holotype QM F23220. Right maxilla. Actual size. A, ventral; B, dorsal. Isolated ziphodont crocodile teeth QM F23221–F23223 referred to *Q. babarra*. C, lateral; D, mesial.

Description

The holotype (Figs. 1, 2) is the only known specimen consisting of the anterior portion of the right maxilla and some associated fragments. The maxilla is reasonably complete, anterior to the fifth alveolus but the posterior extent is not preserved. There is almost a total suppression of festooning but the curvature of the tooth row in lateral view between the first and sixth alveoli is more pronounced than in *Q. fortirostrum* and *Q. timara*.

The palatal fenestra reaches anteriorly to a level between the fifth and sixth alveoli, almost to the level of the large nutrient foramina medial to the fifth alveolus. There is no indication of an anterior process of the palatine despite most of the palatal portion of the maxilla being preserved. The palatal junction with the premaxilla would have described a broad U-shaped suture similar to that of *Q. fortirostrum* and *Q. timara*.

Isolated ziphodont teeth from Bluff Downs (Fig. 2), are tentatively referred here to *Q. barbarra*. A single ziphodont tooth crown found as a fragment associated with the type specimen cannot be unambiguously shown to be part of that individual. As a consequence, it too is tentatively referred to *Q. babarra*. All ziphodont teeth from Bluff Downs exhibit lateral compression and anterior and posterior carinae. The carinae are serrate on some teeth but not on others. All teeth are mildly recurved such that the anterior carina is longer than the posterior carina. The posterior carina is mildly convex in profile.

COMPARISONS

Molnar (1981) referred a number of fragmentary maxillae and isolated teeth to *Quinkana* sp. because they were too incomplete to compare with the holotype of *Q. fortirostrum*. Similarly, an incomplete maxilla from Glen Garland Station, referred to in a note added in proof by Molnar (1981), could not be conclusively assigned by him to *Q. fortirostrum* but did show some differences in alveolar form and orientation. However, none of the fragmentary skull material referred to *Quinkana* sp. by Molnar (1981) exhibits the suite of diagnostic features that characterise *Q. babarra*.

The Glen Garland specimen does have an arrangement of alveoli similar to that seen in *Q. babarra*, a feature in which they both differ from *Q. fortirostrum* and *Q. timara*. This feature could represent intraspecific variation. Other characters, such as the anterior extent of palatal fenestrae cannot be determined on the Glen Garland specimen. For these reasons, we conclude that this specimen should be regarded as *Quinkana* sp. until better material is known.

PHYLOGENETIC AFFINITIES

Detailed phylogenetic analysis of the Mekosuchinae conducted by Willis (1995) and Salisbury and Willis (in press) confirm the mekosuchine affinites of *Quinkana* contrary to the possible pristichampsine affinites considered by Mergirian (1994). The phylogenetic affinities of the genus *Quinkana* are considered here with respect to other mekosuchines. Willis et al. (1990) recognised, but did not name, the clade of Australian Tertiary crocodiles that included *Baru*, *Pallimnarchus* and *Quinkana*. Willis and Molnar (1991a) expanded this concept to include the new genus *Australosuchus* and recognised additional synapomorphies for the clade. An unnamed Eocene crocodilian from south-eastern Queensland described by Willis and Molnar (1991b) appears to belong to the same clade but is represented by fragmentary material. Similarly, *Harpocochampsa*, a longirostrine crocodilian from Miocene sediments in the Northern Territory (Megirian et al. 1991) exhibits insufficient features to support or refute its assignment to the

Mekosuchinae. *Trilophosuchus*, from Miocene deposits at Riversleigh, northwestern Queensland (Willis 1993) is a small, terrestrial carnivore that also clearly belongs within the Australian clade.

It was not until the description of *Kambara*, a crocodilian from the early Eocene Murgon sediments of southeastern Queensland (Willis et al. 1993), that the Australian Tertiary crocodilian clade was formally named the Mekosuchinae. The small terrestrial Holocene crocodilian *Mekosuchus inexpectatus* from New Caledonia has also been included in the Mekosuchinae (Willis et al. 1993). There are now six genera within the Mekosuchinae. Unfortunately some genera are represented by fragmentary material and only two species are represented by almost complete skulls. This paucity of complete material has hampered efforts to identify characters that could resolve intergeneric relationships within the Mekosuchinae. Further, the species of *Quinkana* are the only truly ziphodont mekosuchines and their derived condition obscures the interpretation of character states that would otherwise be useful in determining their relationship to other members of the Australian clade.

Three mekosuchine genera (*Quinkana*, *Trilophosuchus* and *Mekosuchus*) are demonstrably terrestrial (Molnar 1981, Balouet and Buffetaut 1987, Willis 1993, Willis 1995, Salisbury and Willis in press), and these taxa appear to form a monophyletic clade. Both species of *Trilophosuchus* and *Mekosuchus* have short deep snouts reminiscent of atoposaurids, species of *Quinkana* have a longer snout that is more reminiscent of species of *Baru* than of the smaller mekosuchines. Species of *Baru* and *Quinkana* share a snout form that is trapezoid in cross section anterior to the orbits, a feature not characteristic of species of *Trilophosuchus* or *Mekosuchus*.

A fourth species of *Quinkana* from Miocene deposits at Riversleigh, along with other mekosuchines, is currently being described (P.W). Isolated teeth have been referred to *Quinkana* have been recorded from the mid Miocene Ongeva Local Fauna (Megirian et al. 1993, Murray et al. 1993) and the Pleistocene Wyandotte Local Fauna (McNamara 1990).

PALAEOECOLOGY

Ziphodont crocodiles have been found in South America, North America, Europe, Asia and Africa as well as in New Guinea and Australia (Langston 1956, Langston 1975, Plane 1967, Molnar 1981). Nearly complete skeletons of ziphodont crocodilians have been described from Europe (Kuhn 1938, Berg 1966). The hoof-like terminal phalanges and extensive development of armour in these species have been interpreted as a possible indication of terrestrial specialisation (see Kuhn 1938, Zappler 1960, Steel 1973). Molnar (1981) summarised the conditions of deposition of ziphodont fossils and all, except for a few cave fills, are near water environments. Molnar raised the problem of the association of ziphodont crocodiles with lacustrine or fluvial deposition and the notion of terrestriality but concluded that *Q. fortirostrum* was probably terrestrial. The palaeoecology of the Bluff Downs site has been interpreted as being a freshwater fluviatile and lacustrine deposit (Archer and Wade 1976).

Busbey (1986), while noting the depositional association problems raised by Molnar (1981), supported the notion of terrestriality using ziphodont cranial morphology which he interpreted to be convergent on terrestrial reptilian carnivores such as *Varanus komodoensis*. Several authors (Archer and Bartholomai 1978, Molnar 1981) have suggested an absence of very large terrestrial mammalian predators in Australian Tertiary and Pleistocene deposits as a possible reason for this niche being occupied by large reptiles such as species of *Quinkana* and *Megalania*. Remains of a large varanid have been recovered from the Bluff Downs site (Archer 1976) as well as several mammalian predators including *Thylacoleo crassidentatus* (Archer and Dawson 1982). *Quinkana babarra* is shown to be a large, terrestrial, reptilian, carnivore in the Bluff

Downs Fauna. Its presence, along with that of other large reptilian carnivores and the apparent absence of large mammalian carnivores, represents a fundamentally different structure to the large carnivore niches typical of modern faunas. The Bluff Downs Local Fauna is complete enough and demonstrates suitable diversity to allow a more thorough investigation of the structure and function of large terrestrial reptilian predators within a faunal context. The palaeoecology of the Bluff Downs Local fauna is the subject of ongoing study (B.M.).

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REFERENCES

Archer, M. (1976). Bluff Downs local fauna. *Memoirs of the Queensland Museum* **17**, 383–396.

Archer, M. (1982). Review of the dasyurid (Marsupialia) fossil record, integration of data on phylogenetic interpretation, and suprageneric classification. In 'Carnivorous marsupials' (Ed. M. Archer) pp. 397–443. (Royal Zoological Society of New South Wales, Sydney).

Archer, M. and Bartholomai, A. (1978). Tertiary mammals of Australia: a synoptic view. *Alcheringa* **2**, 1–19.

Archer, M. and Dawson, L. (1982). Revision of marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and Thylacoleonid evolution in the late Cainozoic. In 'Carnivorous marsupials' (Ed. M. Archer) pp. 477–494. (Royal Zoological Society of New South Wales, Sydney).

Archer, M. and Wade, M. (1976). Results of the Ray E. Lemley Expeditions, Part I. The Allingham Formation and a new Pliocene vertebrate fauna from northern Australia. *Memoirs of the Queensland Museum* **17**, 379–397.

Bartholomai, A. (1978). The Macropodidae (Marsupialia) from the Allingham Formation, Northern Queensland. Results of the Ray E. Lemley Expeditions, Part 2. *Memoirs of the Queensland Museum* **18**, 127–143.

Balouet, J.C. and Buffetaut, E. (1987). *Mekosuchus inexpactatus* n.g. n. sp. Crocodilien nouveau de l'Holocene de Nouvelle Caledonie. *Comptes Rendus des séances de l'Académie des Science, Paris* **304**, 853–857.

Berg, D.E. (1966). Die Krokodile, insbesondere *Asiatosuchus* ubd aff. *Sebecus*? aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **52**, 1–105.

Boles, W.E. and Mackness, B.S. (1994). Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Records of the South Australian Museum* **27**, 139–149.

Busbey, A.B. (1986). New material of *Sebecus* cf *huilensis* (Crocodilia: Sebecosuchidae) from the Miocene La Vanta Formation of Columbia. *Journal of Vertebrate Paleontology* **6**, 20–7.

Hecht, M.K. and Archer, M. (1977). Presence of xiphodont (sic) crocodiles in the Tertiary and Pleistocene of Australia. *Alcheringa* **1**, 383–85.

Kuhn, O. (1938). Die Crocodilier aus dem mittleren Eozän des Geiseltales bei Halle. *Nova Acta Leopoldina (N.F.)* **6**, 313–29.

Langston, W. (1956). The Sebecosuchia: cosmopolitan crocodiles? *American Journal of Science* **254**, 605–14.

Langston, W. (1975). Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. *Fieldiana: Geology*. **33**, 291–314.

Mackness, B.S. (1995)a. *Anhinga malagurala*, a new pygmy darter from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. *Emu*. **95**, 265–71.

Mackness, B.S. (1995)b. *Palorchestes selestiae*, a new species of palorchestid marsupial from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. *Memoirs of the Queensland Museum*. **38**, 603–609.

Mackness, B.S., Archer, M., and Muirhead, J. (1993). An enigmatic family of marsupials from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland. CAVEPS '93; Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics. Adelaide, 19–21 April 1993. Programme and Abstracts.

McNamara, G. (1990). The Wyandotte Local Fauna: a new, dated, Pleistocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum* **28**, 285–297.

Megirian, D. (1994). A new species of *Quinkana* Molnar (Eusuchia: Crocodylidae) from the Miocene Camfield Beds of Northern Australia. *The Beeagle, Records of the Norther Territory Museum of Arts and Science* **11**, 145–166.

Megirian, D., Murray, P.F. and Wells, R.T. (1993). The late Miocene Ongeva Local Fauna from the Waite Formation of Central Australia. CAVEPS '93; Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics. Adelaide, 19–21 April 1993. Programme and Abstracts.

Megirian, D., Murray, P.F. and Willis, P.M.A. (1991). A new crocodile of the gavial ecomorph morphology from the Miocene of northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **8**, 135–158.

Molnar, R.E. (1977). Crocodile with laterally compressed snout; first find in Australia. *Science* **197**, 62–4.

Molnar, R.E. (1978)a. The crocodile from Tea Tree Caves and ziphodont crocodiles in Australia. *Journal of the Sydney Speological Society* **22**, 3–10.

Molnar, R.E. (1978)b. Age of the Chillagoe crocodile. *Search* **9**, 156–8.

Molnar, R.E. (1979.) *Crocodylus porosus* from the Pliocene Allingham Formation of North Queensland. Results of the Ray E. Lemley Expeditions, Part 5. *Memoirs of the Queensland Museum* **19**, 357–65.

Molnar, R.E. (1981). Pleistocene ziphodont crocodilians of Queensland. *Records of the Australian Museum* **33**, 803–34.

Murray, P. and Megirian, D. (1992). Continuity and contrast in Middle and Late Miocene vertebrate communities from the Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **9**, 195–218.

Murray, P., Megirian, D. and Wells, R. (1993). *Kolopsis yperus* sp.nov. (Zygomaturinae, Marsupialia) from the Ongeva Local Fauna: New evidence for the age of the Alcoota fossil beds of Central Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **10**, 155–172.

Oates, W., Oates, L., Hershberger, H., Hershberger, R., Sayers, B, and Godfrey, M. (1964.) *Gugu-Yalangi and Wik-Munkan language studies*. Occasional Papers in Aboriginal Studies. Number Two. Australian Institute of Aboriginal Studies.

Plane, M.D. (1967). Stratigraphy and vertebrate fauna of the Otibanda Formation, New Guinea. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* **86**, 1–64.

Rich, P.V. and van Tets, G.F. (1982). Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. In 'The Fossil Vertebrate Record of Australasia' (Eds. P.V. Rich and E.M. Thompson, E.M.). pp. 235–384. (Monash University Offset Printing Unit: Clayton).

Romer, A.S. (1956). 'Osteology of the Reptiles'. (University of Chicago Press: Chicago).

Salisbury, S. and Willis, P.M.A. (in press). A new crocodylian from the early Eocene of southeastern Queensland and a primary investigation into the phylogenetic relationships of crocodyloids. *Alcheringa*.

Steel, R. (1973). Crocodylia. In 'Encyclopedia of Paleoherpetology' (Ed. O. Kuhn) Part 16. (Gustav Fisher Verlag: Stuttgart).

Vickers-Rich, P. (1991). The Mesozoic and Tertiary History of Birds on the Australian Plate. In 'Vertebrate Palaeontology of Australasia' (eds. P. Vickers-Rich, J.M. Monaghan, R.F. Baird, R.F. and T.H. Rich) pp. 721–808. (Pioneer Design Studio: Lilydale).

Willis, P.M.A. (1992). Four new crocodilians from early Miocene sites at Riversleigh Station, northwestern Queensland. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **9**, 269.

Willis, P.M.A. (1993). *Trilophosuchus rackhami gen. et sp. nov.*, a new crocodilian from the early Miocene limestones of Riversleigh, northwestern Queensland. *Journal of Vertebrate Paleontology* **13**, 90–8.

Willis, P.M.A. (1995). The phylogenetic systematics of Australian crocodilians. PhD thesis, University of New South Wales, Sydney.

Willis, P.M.A. and Archer, M. (1990). A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. *Memoirs of the Queensland Museum* **28**, 159–63.

Willis, P.M.A., Murray, P.F. and Megirian, D. (1990). *Baru darrowi gen. et sp. nov.*, a large, broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in northern Australia. *Memoirs of the Queensland Museum* **29**, 521–40.

Willis, P.M.A. and Molnar, R.E. (1991)a. A new middle Tertiary crocodile from Lake Palankarinna, South Australia. *Records of the South Australian Museum* **25**, 39–55.

Willis, P.M.A. and Molnar, R.E. (1991)b. A longirostrine crocodile from the early Tertiary of southeastern Queensland. *Alcheringa* **15**, 229–33.

Willis, P.M.A., Molnar, R.E. and Scanlon, J.D. (1993). An early Eocene crocodilian from Murgon, southeastern Queensland. *Kaupia: Darmstädter Beitrage zur Naturgeschichte* **3**, 25–32.

Zappler, G. 1960. Fossil bonanza. *Natural History* **69**, 18–31.

New Species of *Calandrinia* (Portulacaceae) from Queensland, Australia

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SYEDA, S.T. (1996). New species of Calandrinia (Portulacaceae) from Queensland, Australia. Proc. Linn. Soc. N.S.W. 116, 153–159

Two species of Calandrinia Kunth. (Portulacaceae), C. arenicola and C. tumida are described here as new. Pollen and seed morphology are described. Distribution maps of both species are provided. S.E.M. micrographs of seed and pollen are given. The affinities of the new species are discussed. Keys are also provided to distinguish these species from their close relatives.

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INTRODUCTION

The genus *Calandrinia* comprises ca. 100 species. Thirty four species grow in Australia, and the remainder in America. The Australian species were first reviewed by Bentham (1863) and were last reviewed by Syeda (1979).

The new species *C. tumida* belongs to section *Basales* von Poellnitz, and *C. arenicola* belongs to sect. *Pseudodianthoideae* von Poellnitz. These sections were recognized by von Poellnitz (1934), Syeda (1979) and Syeda and Carolin (1989).

In the review of *Calandrinia* by Syeda (1979) based on a detailed study of general morphology, seed type and pollen type, it was found that several collections from Queensland did not agree with any of the species previously described. These specimens are here assigned to two new species.

C. arenicola Syeda sp. nov.

Herba prostrata carnosa scapis pluribus 5–55 cm longis. Folia basalia caulinaque oblanceolata usque lanceolata petiolata. Flores in pedicellis patulis, bracteis scariosis vel herbaceis. Petala 6 oblanceolata vel anguste spathulata. Stamina ca. 12. Stigmata tria libra usque ad basim. Capsula valvis tribus. Semina nigra subreniformia granulata hebetata.

Prostrate succulent reddish herb with a short stem. Scapes several, arising from the axils of the basal leaves, 5–55 cm long. Leaves several at the base as well as on the scapes, petiolate, lanceolate to oblanceolate, 2.5–5.5 cm long, 2–5 mm broad; petiole 5–12 mm long; upper leaves smaller. Flowers many in monochasia; bracts scarious as well as leafy, alternating, 0.7–1.3 mm long; pedicel spreading, 3–13 mm long. Sepals ovate, acuminate-mucronate, 4–5.5 mm long, 3.5–4.5 mm broad. Petals 6, white to pink, oblanceolate to narrow spathulate, 5–7 mm long, 1.5–2.5 mm broad. Stamens 12 or 13, filaments of unequal length, flat, connate at the base to form a membranous cup around the base of the ovary, 2–4 mm long; anther oblong, versatile, 0.4–0.6 mm long, ca. 0.3 mm broad. Ovary globular, 2.5–3.5 mm long; stigmas 3, free to the base,

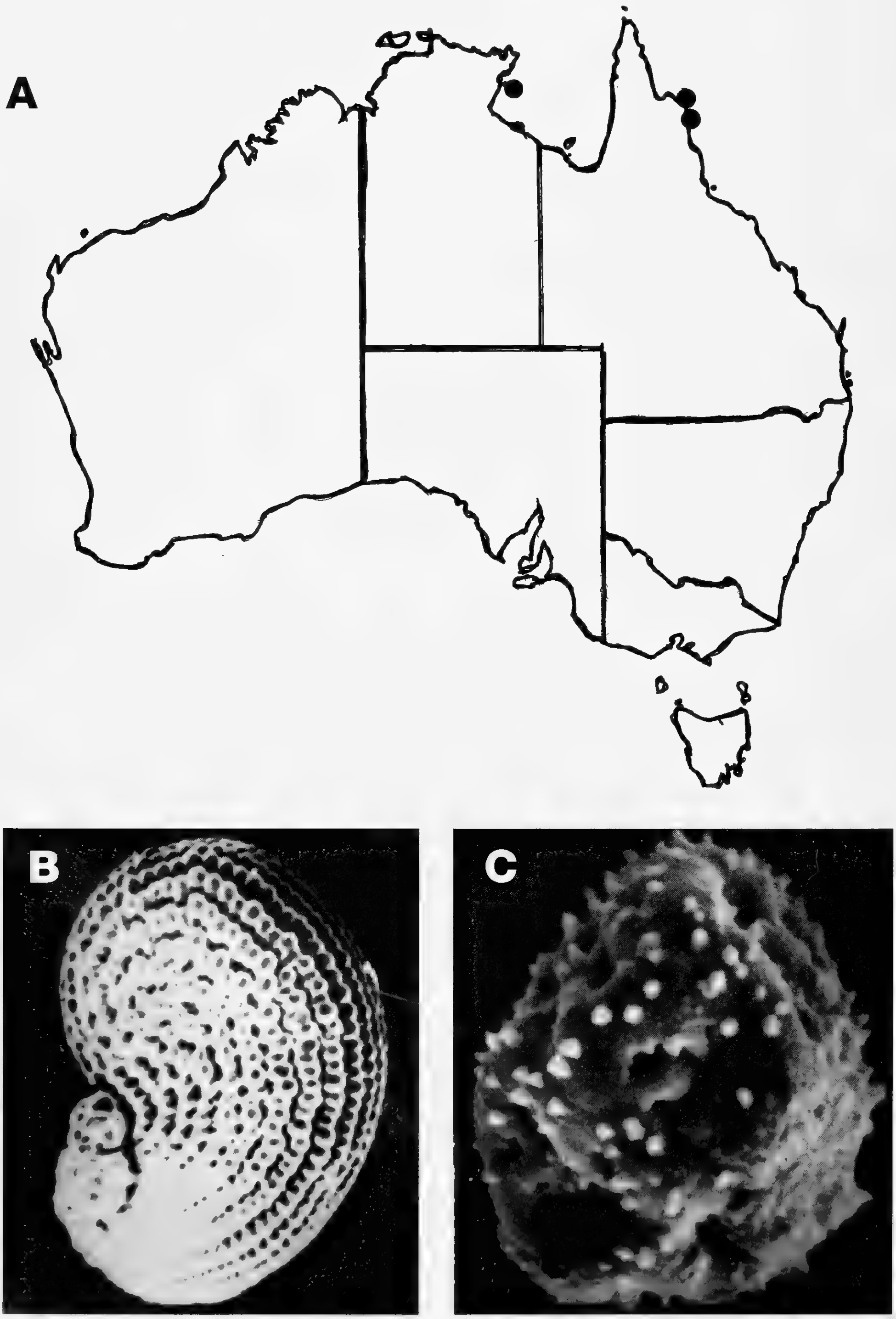

Fig. 1. Calandrinia arnicola Syeda, sp. nov. A- distribution map; B- Seed 60X; C-Pollen grain 3000X

whitish, sparsely hairy, 1–1.5 mm long; ovules many, ca. 0.20 mm broad, reniform, attached to a basal placenta. Fruit a capsule, ovoid-globular, 3-valved from the summit, usually as long as the sepals.

Holotype

Cooktown, mouth of Endeavour River, north bank, S.T. Blake 23295, 16-5-1970 (BRI 172485). Isotypes: NSW, CANB.

Pollen morphology

Pollen grains irregular in shape, irregularly angled in outline, 20.0–21.2 µm in diameter. Apertures not distinct; notches present all over the pollen surface, variable in size and shape, (Fig.1C). Sexine tectate 1.6–2.0 µm thick, usually more thickened in the convex part. Tectum papillate, non-punctate; the papillae small, broad, closely to irregularly distributed, usually of uniform size. Bacula sparsely standing, thin. Nexine half of the sexine thickness or thinner.

Voucher specimen

Cooktown, mouth of Endeavour River, S.T. Blake 23295, 16-5-1970 (NSW) type material.

Seed morphology

Seed black, broadly reniform, dull glossy, surface pattern aligned-papillate, numerous in each capsule, ca. 1.2 mm long, ca. 1 mm broad, (Fig. 1B).

Voucher specimen

Cooktown, mouth of Endeavour River, S.T. Blake 23295, 16-5-1970 (BRI 172485).

Distribution and ecology

Cape York and Carpentaria region of Queensland (Fig. 1A). Coastal sand dunes.

Discussion

The seeds of *C. arenicola* show some superficial resemblance to those of *C. balonensis* Lindl. but in other characters it is very different from *C. balonensis. C. arenicola* has oblanceolate to narrow spathulate petals, petiolate leaves, stigmas free to the base, few stamens, and one leafy and one scarious bract at each node.

Morphologically *C.arenicola* is very close to *C. eremaea* Ewart, but differs in bract and seed characters. The following key is provided to assist in separating these related species.

1 Bracts all scarious; pedicel reflexed in fruit; seeds colliculate, papillate, usually with coppery lustre .... *C. eremaea*
1* One leafy and one scarious bract in each pair; pedicel not reflexed in fruit; seeds, aligned papillate, without coppery lustre...................................... *C. arenicola*

The pollen characters of *C. arenicola* distinguish it from all other species of *Calandrinia*. This species has the smallest pollen grains of irregular shape with deep notches and no distinct apertures. Further detailed investigation of the pollen of this species is needed.

Syeda and Carolin (1988), while discussing the phylogeny and origin of Australian *Calandrinia*, indicated that *C. arenicola* shares characters with both sect. *Pseudodianthoideae* von Poellnitz and sect. *Basales* von Poellnitz.

C. arenicola has the characteristic stigma and capsule valve number of sect. *Pseudodianthoideae*, but is unique in its seed surface pattern, and in having inaperturate pollen. It appears that this might be a connecting species between sect. *Pseudodianthoideae* and sect. *Basales*. The reason for suggesting *C. arenicola* as a connecting species is based on the phylogenetic study (Syeda and Carolin 1990) which reveals that *C.arenicola* is very close to the members of sect. *Basales* and, more importantly, it shares equally the primitive and advanced characters. In a cladistic analysis of *Calandrinia* (Syeda and Ashton 1989) using PHYSYS the result led to questioning the placement of *C. arenicola* and *C. strophiolata* F. Muell. in sect. *Basales*.

Specimens examined

Little Lagoon, Groote Eylandt, in the Gulf of Carpentaria, R.L. Specht 233, 13–4–1948 (AD, BRI, CANB and NSW); Lizard Island, N. Byrnes 3191, 7-5-1975 (BRI); Lizard Island (Great Barrier Reef), F.R. Fosberg 55017, 26-6-1973 (BRI); Cape Flattery, 53 km. NNE. of Cooktown, T.J. McDonald 1577, 15-4-1975 (BRI).

C. tumida Syeda sp. nov.

Herba erecta annua 7–35 cm alta. Scapis pluribus. Folia linearia plerumque basalia. Flores in pedicellis patulis. Sepala interdum decidua. Petala 8–10, lanceolata. Stamina numerosa. Stigmata 4–5 libra usque ad basin. Capsula indurata circumscissa ad basim, decidua. Semina numerosa orbiculario-reniformia atrofusca vel nigra in centro tumida.

Erect annual herb with a very short stem. Scapes several, arising from the axils of the few basal leaves, 7–35 cm high. Leaves several, mostly at the base, rarely on the scapes, sessile, linear, obtuse, 10–40 mm long, 0.75–1.0 mm broad. Flowers arranged in monochasia; pedicel spreading-erect, 3–16 mm long. Bracts scarious, acute, alternate to opposite, 0.5–1.0 mm long. Sepals broad-ovate, obtuse, thin, 4–4.5 mm long, 4.5–5.5 mm broad. Petals lanceolate, purple, 4.5–6.0 mm long, 1.5–3.0 mm broad. Stamens numerous; filaments of unequal length, united at the base in a ring around the ovary, slightly adnate to the base of the petals, hairy at the base, 1.7–3.5 mm long; anther oblong, versatile, 0.5–0.6 mm long, 0.2–0.3 mm broad. Ovary globular, pale, thick, 1.8–2.2 mm long; stigmas 4–5 free to the base, hairy, 1.5–2.0 mm long; ovules numerous, red-brown, reniform, ca. 0.16 mm long and 0.14 mm broad, attached to an unbranched free central placenta. Fruit a capsule, globular, circumsciss at the base to half of its length in the form of a cup, deciduous with or without sepals, as long as or little longer than sepals.

Holotype

19.2 km north of Esmeralda station, Queensland, N.H. Speck 4732A, 18-7-1957 (CANB). Isotypes: BRI007376, AD961032031, MEL.

Pollen morphology

Pollen grains spheroidal in shape, circular in outline, 35.0–39.2 µm in diameter, 18 or more pantoporate nonoperculate (Fig. 2C). Pori ± sunken, circular or sometimes elongated, 2.8–4.5 µm in length, 2.5–3.5 µm in breadth. Apertural membrane with closely spaced and irregularly distributed spinules, the spinules small, rather broad, varying in size.

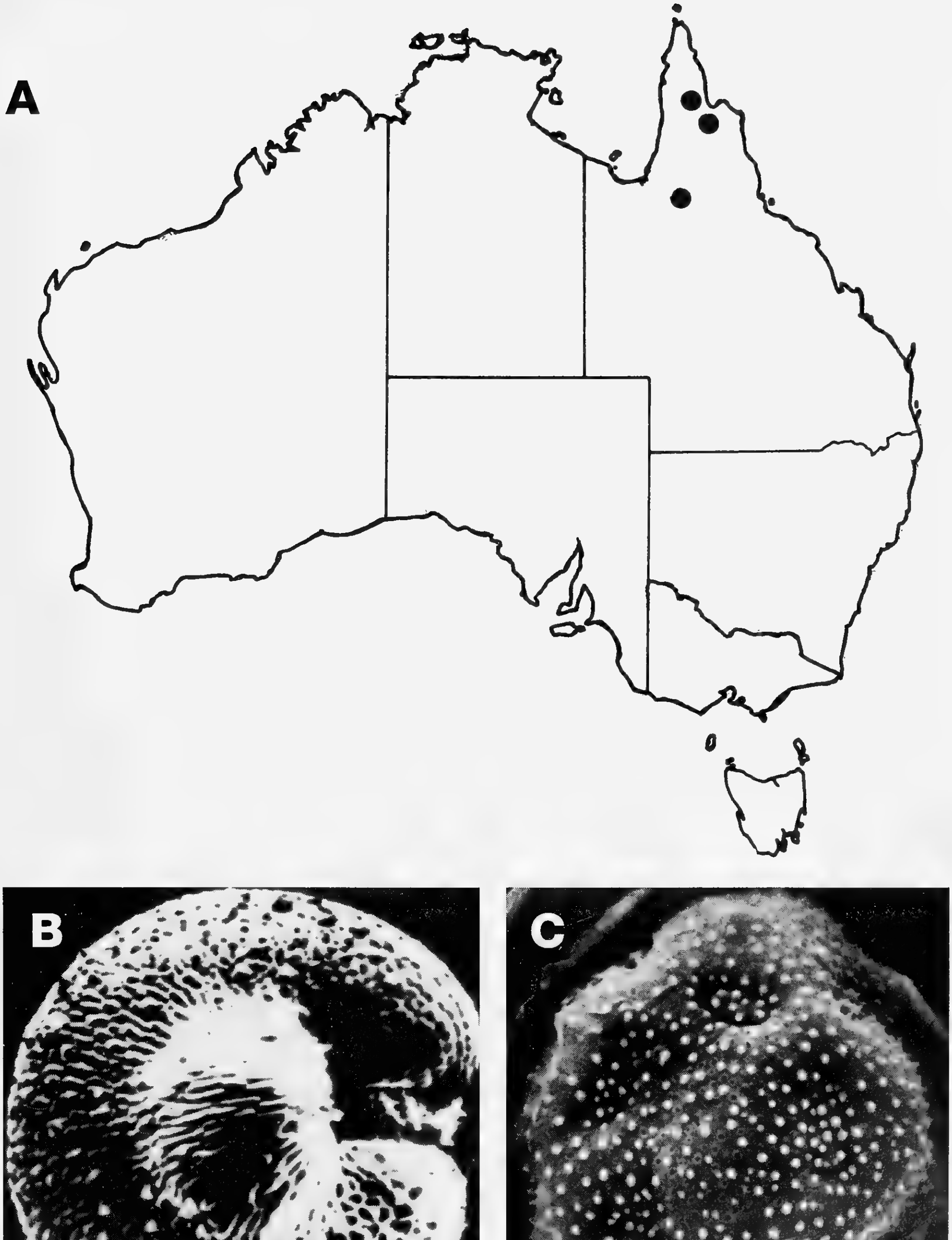

Fig. 2. Calandrinia tumida Syeda, sp. nov. A- distribution map; B- Seed 100X; C-Pollen grain 2000X

Sexine tectate, ca. 2.4 µm thick in the centre of mesoporium, gradually thinner towards the apertures. Tectum spinulose and punctate; the spinules small, broad, closely to irregularly distributed, varying in size. Punctae distinct, more numerous, wide in the centre of mesoporium, rather closely spaced, a few longish, mostly of same diameter. Bacula distinct, standing evenly to sparsely. Nexine ca. 0.6–1.0 µm thick.

Voucher specimen

19.2 km north of Esmeralda Station, Queensland, N. H. Speck 4732A, 18-07-1957 (AD 961032031).

Seed morphology

Seeds black or dark brown, reniform to orbicular, with a bulging centre, glossy, colliculate-tuberculate, numerous in each capsule, 0.35–0.45 mm in diameter (Fig. 2B).

Voucher specimen

19.2 km north of Esmeralda Station, Queensland, N. H. Speck 4732A, 18-07-1957 (AD 961032031).

Distribution and ecology

Southern Cape York, Queensland, Australia, (Fig. 2A). An erect herb on sandy soil in open forest.

Discussion

C. tumida is morphologically close to *C. spergularina* F. Muell. in the dehiscence of the capsule and to some extent its distribution, but it is distinguished from *C. spergularina* in having 8–9 petals, numerous stamens, and most clearly in its seeds which are reniform-orbicular with bulging centres that have a colliculate-tuberculate pattern. A key is provided to help in separating these closely related species.

1. Stamens 5–13; petals 6, white; seed ovate without bulging centres, colliculate ....*C. spergularina*
1* Stamens more then 20; petals 8–10, purple; seed reniform-orbicular with bulging centres, colliculate-tuberculate ....*C. tumida*

The seeds of *C. tumida* are reniform-orbicular with a bulging centre, a characteristic found only in this species. Moreover, some of the diagnostic morphological characters show it to be a very distinct species of *Calandrinia*. The capsule is circumscissile in its upper half, a feature showing resemblance to *Portulaca*, but the superior ovary is a characteristic feature of *Calandrinia*.

C. tumida has pollen with irregular apertures in depressions or notches acquiring mostly circular to somewhat elongated shapes. Hence, pollen type may be considered as pantoporate.

Specimens examined

Yarraden Station, ca. 24 km S. of Coen, J. Wright 153, July 1967 (BRI 236857); Kennedy Rd., 72 km beyond Laura, C.H. Gittins 977, July 1965 (BRI 077429).

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REFERENCES

Bentham, G. (1863). 'Flora Australiensis, Vol.I' (Lovell Reeve and Co., London).

Carolin, R.C. (1987). A review of the family Portulacaceae, *Australian Journal of Botany* **35**, 383–412.

Syeda, S.T. (1990). Three new species of *Calandrinia* (Portulacaceae) from inland Australia. *Telopea* **2**, 59–61.

Syeda, S.T. and Carolin, R.C. (1990). Phylogeny and origin of Australian *Calandrinia* (Portulacaceae). *Pakistan Journal of Botany* **22**, 75–78.

Syeda, S.T. (1979). The genus *Calandrinia* H. B. et K. in Australia, University of Sydney, M.Sc. Thesis.

Syeda, S.T. and Carolin, R.C. (1988). Seed type and seed surface pattern in *Calandrinia* sens. lat. (Portulacaceae). *Proceedings of the Linnean Society of N.S.W., Australia* **110:**307–316.

Syeda, S.T. and Ashton, P.S. (1989). A cladistic analysis of *Calandrinia* (Portulacaceae). *Pakistan Journal of Botany* **21**, 158–169.

von Poellnitz, K. (1934). Die Calandrinien-Arten Australiens. Fedde Rep. **35**:161–173.

Placoderm (Pisces: Placodermi) Remains from Lower Devonian Rocks at Taemas, New South Wales

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FINDLAY, C. S. (1996). Placoderm (Pisces: Placodermi) remains from Lower Devonian rocks at Taemas, New South Wales. Proc. Linn. Soc. N.S.W. 116, 161–186

This paper describes six new specimens of placoderm fish from the Early Devonian limestone sequence of Taemas in southeast New South Wales. All these specimens contribute to our understanding of the morphology of taxa at this time of early evolution of the group. They include: a paranuchal plate of *Errolosteus* which suggests a sliding neck joint for this genus; an incomplete head shield of a brachythoracid including the left and right central, right preorbital, postorbital and marginal plates with a portion of the endocranium attached showing a dorsal ossification; two specimens of *Arenipiscis*, an incomplete head shield including left and right centrals, anterior of nuchal, left and right paranuchals, right preorbital, postorbital and marginal and a small piece of the left preorbital plate, with the second specimen a nuchal plate with a complete posterior margin; a brachythoracid with a more extensive right marginal plate than previously known and an incomplete postorbital plate; and a brachythoracid skull with palate and endocranial ossification showing a unique parasphenoid, a new condition for the pituitary vein on the palate, a double hyomandibular articulation, a previously undescribed myodome in the orbital cavity, a distinctive buccohypophysial foramen, anterior supragnathals and a dorsal articulation on the autopalatine of the palatoquadrate.

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INTRODUCTION

Some Early Devonian limestones in southeast Australia contain a rich fauna of placoderm fish. The placoderm remains discussed in this paper were collected by Prof. K.S.W. Campbell and C.S. Findlay of the Geology Department, Australian National University (ANU), and Dr G.C. Young of the Australian Geological Survey Organisation (AGSO). The material was found in the Warroo and Crinoidal limestones of the Taemas Formation (Fig. 1), approximately 12 kilometres south of Yass in southern New South Wales. Five of the specimens were found on the north shore of Warroo Creek at the junction with Burrinjuck Dam, Yass Sheet 1:100 000, grid reference 8628-667303. The seventh specimen, ANU 49125, was found on the shore of Burrinjuck Dam, Yass Sheet 1:100 000, grid reference 8628-654319.

To avoid confusion about stratigraphic nomenclature, I have used the term Taemas Formation, and I refer to constituent units recognised by Browne and subsequent workers by an informal nomenclature that uses lower case descriptive names, eg. Currajong limestone.

The stratigraphy of this and the nearby Wee Jasper area has been described by Browne (1959) and Pedder, Jackson and Philip (1970). The Warroo limestone has a rich marine invertebrate fauna including ostracods, nautiloids, brachiopods, bivalves, gastropods and rugose corals. It has been interpreted as a quiet marine deposit formed below

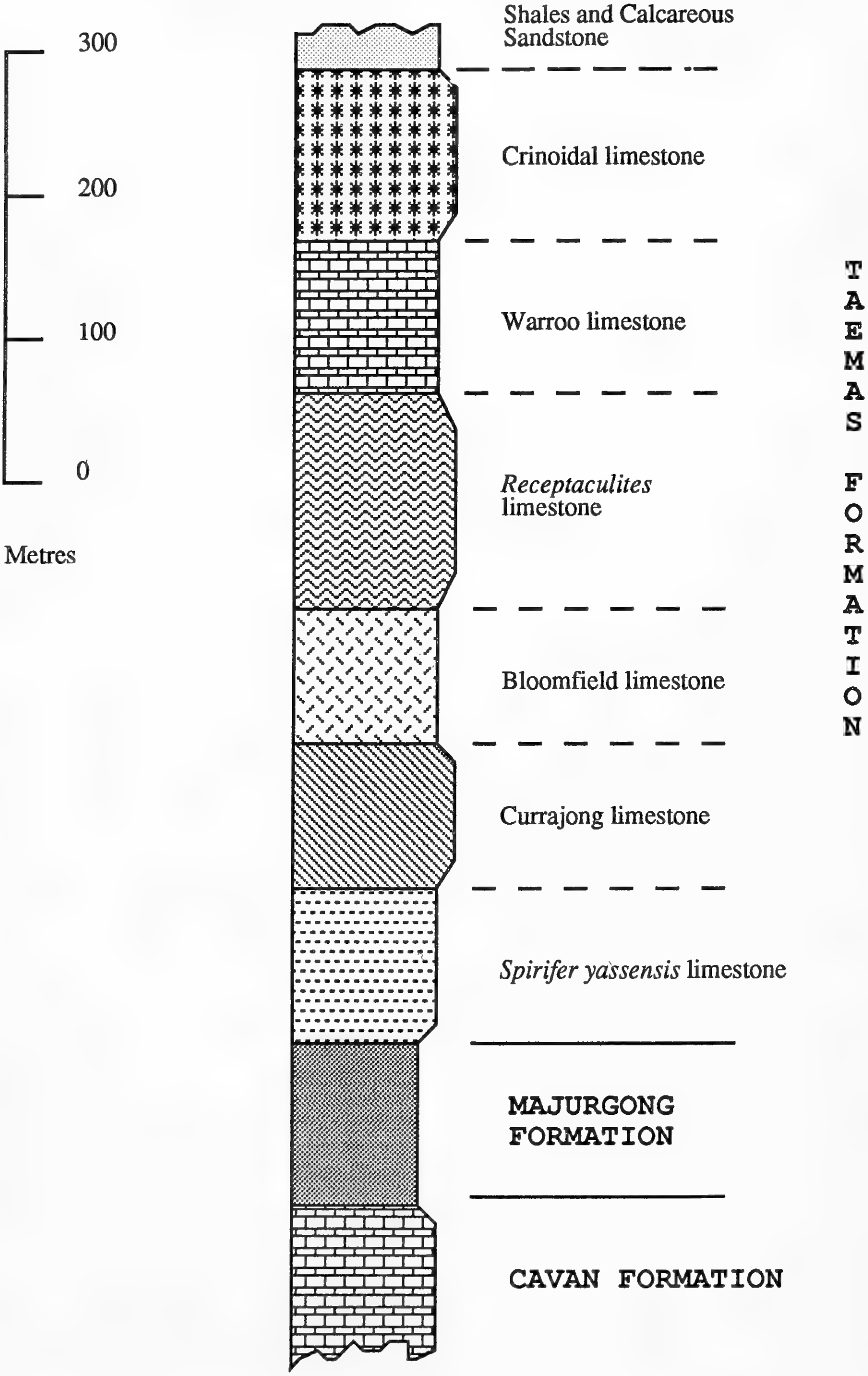

Fig. 1. Stratigraphic column of the Murrumbidgee Group showing the subdivisions of the Taemas Formation overlying the Majurgong and Cavan Formation.

wave base. The overlying Crinoidal limestone is considered to have been deposited on a more shallow marine bank which was periodically covered with crinoids.

The dating of these two units presents a problem because they have as yet yielded no conodonts or other zonal fossils of value for inter-regional correlation. However, conodonts have been described from the western outcrop at Wee Jasper by Pedder et. al., and it is possible to use local fossil assemblages to make a correlation between the Taemas and the Wee Jasper sequences. The basal two units, the Cavan and the Majurgong Formations can be recognised in both areas. Within the overlying Taemas Formation previous workers have recognised the *Spirifer yassensis*, Currajong, Bloomfield and *Receptaculites* limestones. However, the Warroo and Crinoidal limestones are unique to the Taemas area. In the western outcrop at Wee Jasper, the post-*Receptaculites* rocks consist of massive limestones containing many mound-like constructions. It is presently assumed that these represent facies equivalents of the Warroo and Crinoidal limestones.

The currently accepted international division of the Lower Devonian into Stages and their associated conodont zones are shown in Figure 2 which is part of a figure prepared by Oliver and Chulpác (1991), Mawson et. al. (1992) have provisionally placed the Pragian-

SERIES	STAGE		CONDONT ZONE
	W. EUROPEAN	BOHEMIAN	
LOWER DEVONIAN	EMSIAN	DALEJAN	*P. cost. patulus*
			P. serotinus
		ZLICHOVIAN	*P. inversus*
			P. gronbergi
			P. dehiscens
	SIEGENIAN	PRAGIAN	*P. pireneae*
			Eogn. s. kindlei
	GEDINNIAN		*Eogn. sulcatus*
		LOCHKOVIAN	*Ped. pesavis*
			Anc. delta
			O. eurekanensis
			I. w. woschmidti

Fig. 2. Subdivision of the Lower Devonian based on Oliver and Chulpác (1991) and Ziegler (1979).

CATALOGUE NO.	LOCATION	HORIZON	DESCRIPTION
CPC 31618	Warroo Creek	Crinoidal lst.	left paranuchal plate cf. *Errolosteus goodradigbeensis*
CPC 31619	Warroo Creek	Crinoidal lst.	skull roof cf. *Parabuchanosteus murrumbidgeensis*
CPC 31620	Burrinjuck Dam	Warroo lst.	skull roof Gen. indet. sp. indet.
CPC 31621	Burrinjuck Dam	Warroo lst.	nuchal plate cf. *Arenipiscis westolli*
CPC 31622	Burrinjuck Dam	Warroo lst.	marginal and postorbital plates Gen. indet. sp. indet.
ANU 49215	Burrinjuck Dam	Crinoidal lst.	skull roof cf. *Arenipiscis westolli*

Fig. 3. Specimens described in this paper.

Emsian boundary at the first appearance of *P. dehiscens dehiscens* in the Cavan Formation. The *dehiscens* Zone is known from the Cavan Formation in both the Taemas and the Wee Jasper areas (Philip et. al. 1967). The Taemas Formation therefore is unequivocally younger than basal Emsian. Pedder et. al. recognised *Polygnathus linguiformis foveolatus* from ca. 230 metres above the base up to the top of the Taemas Formation at Wee Jasper. Klapper and Johnson (1975) assigned this subspecies to *P. perbonus*, whose appearance ushers in Mawson's *perbonus* Zone. This zone is correlated with the *gronbergi* Zone overseas (Klapper and Johnson 1980). The appearance of this form occurs well below the *Receptaculites* limestone equivalents. The Warroo and Crinoidal limestones cannot therefore be older than the *gronbergi* Zone. The upper limit can be fixed according to Mawson (1987) by the occurrence near the top of the Taemas Formation of some members of the group assigned to *Polygnathus linguiformis linguiformis* by Pedder et. al. (1970, Plate 40, Figs 6 & 8). These Mawson considers to belong to 'delta morphotype' of *Polygnathus serotinus*, characteristic of the *serotinus* Zone.

Consequently, the post-*Receptaculites* units must lie between the upper part of the *gronbergi* Zone and the *serotinus* Zone. In terms of the Bohemian sequence, this means they cross the Zlichovian-Dalejian boundary. Zeigler (1979) considered these zones to cross from the early to the late Emsian.

The six placoderm specimens which are listed below (Fig. 3) add to the information given in previous studies. This paper deals only with new information and subsequent reinterpretation of previous descriptions where applicable.

The preparation of the material was carried out using acetic acid of 5% or 10% strength to dissolve the limestone matrix, depending upon the strength of the bone (Toombs 1948). The exposed bone was strengthened with polyvinyl butyral (sold under the trade name Mowital) diluted with alcohol.

Five of the specimens collected and described for this paper are registered with the Australian Geological Survey Organisation, within the Commonwealth Palaeontological Collection and have the prefix 'CPC'. Associated material referred to from the same source has the same prefix. One specimen has the prefix ANU and is located in the Geology Department of the Australian National University. Another specimen referred to, from the Australian Museum, Sydney, has the prefix AMF.

The stratigraphy of the Crinoidal limestone was originally desribed by Browne (1959). It is now considered (Findlay 1991) to have been deposited on a carbonate platform at the base of which there are channels which have yielded rich placoderm material. Above the Crinoidal limestone are interbedded shales and calcareous sandstone formed in a somewhat different environment. They will be the subject of a subsequent paper by the author.

SYSTEMATIC DESCRIPTIONS

Order EUARTHRODIRA Gross 1932

Suborder INCERTAE SEDIS

Infraorder INCERTAE SEDIS

Genus ERROLOSTEUS Young 1981

Type Species: *Errolosteus goodradigbeensis* Young 1981, from the Taemas Formation, Emsian.

Remarks

CPC 31618 has been compared with the genus *Errolosteus* on the basis of the dermal ornamentation of parallel ridges with tubercules on them as described for the holotype. The allocation of *Errolosteus* to the Infraorder Brachythoraci Gross 1932 assumes that the genus has a ball-and-socket neck joint consisting of thick bone. The neck joint for the type species is unknown. Specimen CPC 31618 suggests a sliding neck joint and shows a unique pattern for the overlap areas of the paranuchal, nuchal and central plates. Long (1984) assigned an anterior dorsolateral plate with a short rounded condyle from the Buchan fauna to this genus on the basis of surface ornamentation of "..concentric ridges bearing small tubercles" (Long 1984, p. 178), and the compatible shape of the plate with the dorsal margin of the anterior lateral plate of *Errolosteus* described by Young (1981). However, the pattern of these parallel ridges on the Buchan specimen does not show the longitudinal direction of the rows which diverge at sharp angles between groups of ridges across single plates, as can be seen on the holotype and CPC 31618. The dorsal margin of the anterior lateral plate of *Errolosteus* (Young 1981) is not preserved, preventing comparison with the Buchan specimen. As CPC 31618 is a topotype, it is possible Long's material from Buchan may belong to a different genus. The identification of this genus on the parallel ornamentation alone should be approached with caution.

cf. *Errolosteus goodradigbeensis* Young 1981

Figs 4, 5

Material

CPC 31618, an almost complete left paranuchal plate.

Horizon

Warroo limestone.

Discussion

The dermal ornamentation is comparable with the description given for the holotype. Both specimens show parallel ridges with tubercles of approximately the same spacing on the paranuchal plates. The distinctive pattern of ridges meeting at sharp angles on single plates can be clearly seen on CPC 31618 (Fig. 4A, 5A) and the holotype.

The posterior section of this bone is very thin for a paranuchal. Normally this plate in a brachythoracid has a thickening of the bone at its posterior end to incorporate the ball-and-socket joint of the neck. The possibility that CPC 31618 was weathered has been considered and rejected because such weathering would have had to be intense and localised at the point of the joint. However, the small notch at the posterior of the plate where the sensory groove passes off the plate shows no sign of weathering and the posterior margin is complete. This, coupled with the absence of thickening, suggests the neck joint was a sliding one.

Compared with *Taemasosteus* White (1952) and *Parabuchanosteus* White and Toombs (1972), the overlap areas of this paranuchal plate are distinctive. As is normal, the nuchal plate overlaps the paranuchal, but is overlapped by an unusual protuberance forming a notch (*no*, Fig. 4A) on the paranuchal. A similar notch pattern has been found between different plates on *Buchanosteus confertituberculatus*, where the marginal plate carries a notch onto the central plate (Young 1979, Fig. 1). This notch on the marginal and central plates is also found on a placoderm specimen described by Lelièvre (1989, Fig. 2). These are the only other occurrences of this feature in Early Devonian arthrodires known to me.

Suborder PHLYCTAENIOIDEI Miles 1973

Remarks

The higher classification for the following specimens is based on that proposed by Young (1979). This system is applied by other authors (eg. Long 1984) for the fauna from southeastern Australia. Alternative classification systems have been proposed eg. Denison 1978.

Infraorder BRACHYTHORACI Gross 1932

Family BUCHANOSTEIDAE White 1952

Genus PARABUCHANOSTEUS White and Toombs 1972

Type species

Buchanosteus murrumbidgeensis White 1952, from the Taemas Formation, Emsian.

Remarks

This specimen has been allocated to the buchanosteid group as the surface ornamentation of tubercles, the pattern of the skull roof plates and the lateral line pattern represent the general pattern found in that group. The parasphenoid of CPC 31619 most closely resembles that described for *Parabuchanosteus*.

Parabuchanosteus was differentiated by White and Toombs (1972) from *Buchanosteus* by the different shapes of the parasphenoids. That bone in *Parabuchanosteus* is described as "...spade-shaped...as wide as long...largest medially in front and crossed towards rear with a deep groove...pierced by a pair of foramina in centre". Young (1979) disputed this and concluded that *Parabuchanosteus* is a junior synonym of *Buchanosteus*. He proposed an allometric growth pattern for the parasphenoid based on the examination of three new specimens, ANU 21805, 21818 and 21807, from the Taemas fauna, and comparison with previously described material, and attempted to show that *B. confertituberculatus* fell within the allometric growth range. In my opinion the bones of the three new specimens do not "...provide evidence that parasphenoid shape varied with size" (Young 1979) as they are not attached to specimens that allow an unequivocal identification of genus or species. Therefore, though the argument may be valid, it requires support from more complete material. Further, the three specimens from Taemas referred to by Young (1979) are not topotypes and it has not been established that the species in the two locations are identical in other characters; hence, in view of the fact that the three new parasphenoids in question are not associated with other skeletal material that can be compared with the types of *Buchanosteus*, they must be interpreted with caution. The new specimen described here, CPC 31619, has a parasphenoid that most closely resembles that of the type of *Parabuchanosteus* figured by White and Toombs (1972, Fig. 5). Meanwhile it is noted that the new material has a myodome within the orbit which is not found in previously described buchanosteid material. Although Young (1979) has described myodomes within the orbital cavity of species he has described as *B. confertituberculatus* (Chapman), this specimen, CPC 31619, shows a myodome of different shape, size and position. This may be grounds for further consideration of the validity of two genera.

CPC 31619 agrees with the general pattern of sensory canals and plate boundaries described in previous literature for buchanosteids, in particular the description given by Young (1979). A number of new features previously undescribed contribute to a better understanding of the buchanosteid group. These include a different parasphenoid shape, anterior supragnathals, articulation facets on the dorsal and ventral surface of the endocranium, a different pattern for the pituitary vein on the palate, and a large myodome within the orbital cavity.

cf. *Parabuchanosteus murrumbidgeensis* White and Toombs 1972

Figs 6, 7, 8, 9

Material

CPC 31619, an incomplete skull roof including the palate, parasphenoid and endocranium.

Horizon

Crinoidal limestone.

Discussion

Skull roof

This specimen is represented by two pieces. These have been kept separate to facilitate analysis of the endocranium but are restored in Fig. 6A to show the pattern of the lateral line canals. The smaller piece has most of the lateral line canal pattern which indicates the extent of the skull roof and the individual plates. The large piece has a considerable amount of endocranium attached.

The posterior pitline on this specimen is long and continuous forming a deep channel. This has not been described previously for buchanosteids. The taxonomic significance of continuity of the lateral line canal system is not well understood. However, it is worth noting that Ørvig (1971) illustrated different lateral line patterns in arthrodires with varying degrees of representation of the posterior pitline. Each genus has a distinctive position or degree of representation for the posterior pitline. There does not appear to be significant variability within a genus.

The indentation half way down the infraorbital sensory canal (*ioc*, Fig. 6A) is interpreted as a post-depositional artefact.

Parasphenoid

The parasphenoid on this specimen most closely resembles the description given for *Parabuchanosteus*. Its left side has been slightly distorted and compressed in a medial direction with a deep groove containing a single buccohypophysial foramen. Previous workers described the buccohypophysial foramina as paired (White and Toombs 1972) or bilobed (Young 1979, Hills 1936). This suggests that the opening may be variable on the ventral surface of the bone and the actual division may take place within the bone. Central to the posterior half of the parasphenoid is a deep, regular cruciform furrow, previously undescribed. The denticles associated with this furrow are larger and more pointed than those on the rest of the parasphenoid, and are orientated towards the centre of the furrow.

External surface of endocranium

The anterior section of the endocranium is visible in dorsal view as a bilobed convex structure in an anterolateral position to the parasphenoid. This area on CPC 31619 (Fig. 6A) has been displaced in a lateral direction and, as this area is poorly known in primitive arthrodires, it is difficult to determine how much of the endocranium has been displaced. This entire bilobed structure is not endocranial, as on its ventral surface there is ornamentation interpreted as denticles. The area covered in denticles appears to be a separate bone and is interpreted as a pair of anterior supragnathals (*ASG*, Fig. 6B). Like advanced arthrodires, primitive arthrodires have been assumed to have had two pairs of supragnathals, a posterior pair associated with the autopalatine section of the palatoquadrate, and a previously unknown anterior pair, lying in an anterolateral position on the ethmoid region of the endocranium. If the above interpretation is correct, this will be the first known occurrence of anterior supragnathals in a primitive arthrodire.

Articulation facets, art_1 and art_2 (Fig. 6A) identified on the dorsal and ventral surface of the endocranium are considered to be the counterparts to the articular facets found on the palatoquadrate, as described for *Buchanosteus confertituberculatus* (Young 1979, Fig. 15). A third articulation surface, art_3, can be seen on this specimen (Fig. 6B), but does not correspond with the art_3 of Young (1979).

No groove or canal for the pituitary vein (i.e. the subpituitary fenestra) on the ventral surface of the endocranium, such as is normal for buchanosteids, has been observed on this specimen. There is a series of foramina in approximately the correct position (*f. pv*, Fig. 6B) where blood vessels from the roof of the mouth could have drained into the pituitary vein which must have been located internally to the palate.

The anterior postorbital process has an open end which is divided into two by a strut of dermal bone, with the more posterior one being triangular and the anterior one oval (*apo*, Fig. 6B). White and Toombs (1972) noted that the end of the anterior postorbital process is always unossified and presumably bore a cartilaginous area for articulation of the hyomandibular. This specimen suggests a double articulation on the hyomandibular (*art. hm*, Fig. 8), previously unknown.

The hyomandibular nerve foramen is clearly shown adjacent to the two hyomandibular articulations (*VII hm*, Fig. 8). The foramen found exiting the palate in a position posterior to the hyomandibular foramen (*IX*, Fig. 6B) has not been described previously in the buchanosteid group. When viewed from the posterior end of the specimen, a canal with ossified walls is seen running from this foramen into the endocranium above the palate. It is interpreted as the glossopharyngeal nerve canal.

Endocranial cavity

A previously undescribed myodome, not present on *Buchanosteus confertituberculatus* Young (1979), can be seen within the right orbital cavity above the opening for the jugular vein on CPC 31619 (*my*, Fig. 6B). Myodome structures do not normally vary significantly within placoderm species, particularly in the orbital cavity; this suggests CPC 31619 belongs to a different species from *Buchanosteus confertituberculatus*. The separate ossification of the jugular canal and the facialis canal found on CPC 31619 is in contrast to the description given for *Buchanosteus confertituberculatus* by Young (1979), where the two vessels are described as having occupied a single ossified canal, again suggesting a specific difference.

Perichondrial ossification associated with the Nerve VIII complex can be seen to run up to the skull roof (*cn*, Fig. 8) directly under the central sensory canal. This appears to be a canal in cross-section which suggests the lateral line system may, in part, be innervated by Nerve VIII.

Family INCERTAE SEDIS
Genus and Species INCERTAE SEDIS

Remarks

This material has been allocated to the brachythoracid group because the surface ornamentation, position of the roof plates and associated lateral line canals follow the standard pattern found in the following three representatives of that group: *Buchanosteus confertituberculatus* Chapman 1916, *Parabuchanosteus murrumbidgeensis* White and Toombs 1972, and *Taemasosteus novaustrocambricus* White 1952. It is described here as it shows an ossified dorsal roof to the endocranium, previously unknown in this group.

Gen. indet. sp. indet.

Figs 10, 11

Material

CPC 31620, a portion of skull roof which includes incomplete left and right central plates, and incomplete right preorbital, postorbital and marginal plates.

Horizon

Warroo limestone.

Discussion

The ossified braincase is partly preserved on this specimen. The shape and location of the perichondrial ossification directly under the junction of the lateral line canals on the central plate suggest part of the inner ear system which has this position in other forms (Miles 1971, Young 1979). The large lateral tube (*sem. c*, Fig. 10B) is interpreted as the horizontal semicircular canal joined to the anterior ampulla. The anterior ampulla is connected to a larger structure interpreted as the sacculus which has been displaced. The adjacent perichondrial ossification is interpreted as the roof of the brain cavity (*r. cv*, Fig. 10B). There is no previous record of an ossified dorsal roof to the endocranium in placoderms. However, CPC 31619 described elsewhere in this paper, shows the same thin ossification.

Ossified canal walls are apparent on the ventral surface of the skull (*c. oss*, Fig. 10B), and appear to be incorporated into the endocranium, suggesting a new interpretation for the ossified canals incorporated with the ventral surface of the skull roof. This canal system has been referred to by Ørvig (1957, p. 307) as "...surely vascular, forming a wide-spread plexus, the *subcutaneous vascular plexus*...". These canals are very similar to those described by Campbell and Barwick (1982) for *Chirodipterus australis*, a Late Devonian lungfish, and *Dipnorhynchus kiandrensis,* a lungfish from the Early Devonian at Kiandra, N.S.W. These two lungfish show ossified canal walls between the dermal roofing bones and the endocranium which Campbell and Barwick have interpreted as part of the sensory system. Similar structures occur in *Eusthenopteron foordi* (Jarvik 1942) from the Upper Devonian in Canada. The concentration of these canals around the inner ear complex in the specimen under description, may indicate a relationship with the acoustic nerve which would be consistent with the view that the lateral line canals are in part innervated by this nerve.

Family INCERTAE SEDIS

Genus ARENIPISCIS Young 1981

Type species

Arenipiscis westolli Young 1981, from the Taemas Formation, Emsian.

Remarks

This genus was erected by Young (1981) on a number of criteria including the following which can be seen on the new material: fine dermal ornamentation, elongated skull roof, trapezoidal nuchal with a distinctive median ventral depression.

CPC 31621 is more complete than previously described nuchal plates (Long 1984, Young 1981) and differs in the dimensions of the plate, the central depression area and the ventral foramina. The dorsal surface of ANU 49215 differs from that of the holotype in that it shows a more extensive lateral line system and well defined sutures between plates.

ANU 49215 has been slightly distorted causing minor buckling at the anterior end of the central plates and minor separation of the plates. It is considered that the right preorbital, postorbital and marginal are not distorted, apart from being displaced in a ventral direction from the central plates.

The only other possible generic assignment of this material would be to *Burrinjucosteus asymmetricus* White 1978, which shows a number of similarities including the anterior shape of the nuchal plate; the shape and position of the paranuchals; the sinuous line and direction of the suture between the two centrals where the base runs from the right side of the nuchal plate to the left of the central line at the top; the anterior shape of the central plate; the possible asymmetrical shape of the centrals; ridges of thickened bone on the ventral surface; and very fine surface ornamentation. However, the proportions of the head shield, microscopic features of the dermal surface and the structures on the ventral surface more closely resemble *Arenipiscis*.

cf. *Arenipiscis westolli* Young 1981

Figs 12, 13, 14, 15, 16

Material

CPC 31621, a nuchal plate; ANU 49215, skull roof plates including left and right central plates, right preorbital, postorbital, marginal, anterior of left and right paranuchals and nuchal, and small piece of left preorbital.

Horizon

Warroo limestone (CPC 31621); Crinoidal limestone (ANU 49215)

Discussion

CPC 31621 is almost complete with only a small section of the posterior margin and left edge broken (Figs 12, 13). This permits an interpretation of the posterior margin, which is different from that reconstructed from the incomplete holotype and paratype (CPC 16972) by Young (1981, Fig. 5). The thickening of the nuchal on the ventral surface along the posterior margin is well preserved, resulting in a straight posterior margin with no apparent embayment. The posterolateral corner of the nuchal plate is more complete on CPC 31621 than on previously described material and shows this to be much broader than the thin tapering corners described for the holotype and paratype.

The foramina for the nutritive vessels associated with the median depression described for the holotype differ from those found on CPC 31621 which shows one large foramen at the posterior end of the depression, and a few smaller ones at the anterior end of the plate adjacent to the overlap areas. The central depression (*m. dep*, Fig. 12B) also differs considerably from previous descriptions. There is no “elevated crest of bone” (Young 1981) delineating the depression. Only the posterior end is well defined where it sinks into the ventral surface, rather than being raised as previously described. The anterior end of the depression is not defined on CPC 31621.

The dorsal surface shows an indentation on the right side (*?scar*, Fig. 12A), which x-radiographs show to be a surficial mark. This has been interpreted as a wound, possibly a tooth mark, as it does not resemble boring of an invertebrate.

The sutures between the plates are well defined on ANU 49215 (Figs 14, 15) and differ from those of the holotype (Young 1981, Fig. 5) in a number of ways. The anterior edges of the paranuchal plates terminate posterior to the anterior end of the nuchal plate, which in turn differs from the holotype in its width and shape at the anterior end. The right postorbital plate is complete and does not show an elongated posterior margin as suggested for the incomplete bone on the holotype. The suture between the central plates is well defined on both the dorsal and ventral surfaces. The posterior pitline and the middle pitline, clearly seen on this specimen, are not present on previously described material.

The fine dermal ornamentation found on ANU 49215 (and the holotype) has not been described before. Figure 16 shows it to be unique, differing from that illustrated for *Burrinjucosteus asymmetricus* (White 1978, Plate VII). The individual tubercles do not show the standard pattern of small domes with surrounding rosette structures; rather, they are pinnacle-like. In places the tubercles form parallel rows, with some sections of the skull roof showing pits at the base between the tubercles and other sections showing areas of tubercles orientated in one direction. Although the data are too sparse to allow a firm interpretation, this linear orientation of the tubercles and the arrangement of the pits suggest the possibility that they had some sensory function.

The ventral surface of ANU 49215 shows the same ridges (*cr. so*, Fig. 14B) as those described for the holotype, but unlike the latter they do not follow the lateral line canal. The ridge running in a rostrocaudal direction is much larger than on the holotype and has a prominent bulbous swelling, whereas the adjoining ridge (also larger) runs in a mesial direction and then curves gently in a posterior direction. The latter ridge is so oriented that it leaves a deep depression posterior to the so-called supraorbital crista (Young 1981, Fig. 6). The supraorbital crista is not directed ventrolaterally as described for the holotype, but rather is vertical.

The thickening on the ventral surface of the holotype, said to be for the semicircular canal, is not apparent on ANU 49215 (Fig. 14B), which shows a circular structure with a lateral projection to the centre on the right central plate in the same position. The remnants of a similar structure can be seen on the left central plate in the same position. From a functional perspective, it is difficult to imagine the inner ear projecting up into the dermal skull roof as suggested by Young (1981). This structure is more likely to have been a brace for the endocranium against the skull (also proposed by Young).

At the posterior end of the central plates towards the midline on the ventral surface, directly beneath the junction of the three lateral lines on the dorsal surface, ANU 49215 clearly shows a network of grooves in the surface of the dermal bone (*cn*, Fig. 14B). Branches of this network run in a posterior direction to lie under the boundary of the nuchal and paranuchal plates. One branch can be seen to run in a continuous line in an anterior direction and curve to the lateral margin along the crest of the arcuate ridge described above. Where these canals terminate, and in some cases at their junctions, pits run into the dermal roof. These canals are interpreted as part of the sensory system.

The groove illustrated by Young (1981, Fig. 6) as carrying the vagus nerve, is not evident on the holotype. In vertebrates this large visceral nerve exits the posterior portion of the brain behind the inner ear complex and always runs in a ventral direction. In fish, small branches supply the gills and taste sensation, with the main trunk running backward to the visceral region (Romer 1962). The description for the holotype would have the vagus nerve with an improbable orientation posterolaterally and dorsal into the ventral surface of the dermal roof bone. Further, it is considered the distance between the postulated vagus nerve and the position of the postulated labyrinth cavity as illustrated by Young (1981, Fig. 6), is not sufficient to allow room for the otic complex.

Gen. indet. sp. indet.

Figs 17, 18

Material

CPC 31622, an almost complete right marginal and an incomplete right postorbital plate.

Horizon

Warroo limestone.

Remarks

These two plates are referred to the brachythoracid group as the surface ornamentation closely resembles the pattern found on *Parabuchanosteus murrumbidgeensis*, *Buchanosteus confertituberculatus* and *Taemasosteus novaustrocambricus*.

The only known postmarginal plates from the Taemas-Wee Jasper fauna are figured for *Buchanosteus confertituberculatus* (Young 1979, Plate 1D) a poorly preserved plate, and for *Parabuchanosteus murrumbidgeensis* (White and Toombs 1972, Plate 1, Plate 2, Fig. 3, Plate 4) two incomplete postmarginal plates. Therefore, relationships between the marginal and the postmarginal plates are not well known in the brachythoracid group.

Discussion

The posterior section of the lateral line canal, the postmarginal canal (*pmc*, Fig. 17A), is as long as the anterior section, previously undescribed. This can be interpreted as either a long marginal plate, or part of the postmarginal plate attached. The ventral side of the marginal plate clearly shows an overlap area at the posterior end for the postmarginal plate (*oPM*, Fig. 17 B), indicating a long and narrow marginal plate ending in a point. This differs from previously described marginal plates in the brachythoracid group.

SUMMARY

The information given in this paper is useful for the further understanding of the placoderm fauna from the Taemas-Wee Jasper area. Several previously unknown features have been suggested: a double hyomandibular articulation on the anterior postorbital process of a brachythoracid; a dorsal articulation on the autopalatine section of the palatoquadrate in the same group; and, possible anterior supragnathals. The two specimens of *Arenipiscis* sp. differ from the previously described material and may represent a new species.

After comparison with specimens held within the Commonwealth Palaeontological Collection at the Australian Geological Survey Organisation, and those in the literature, it was determined that on the basis of ornamentation alone accurate identification of genera within the brachythoracid group is not possible for the Taemas–Wee Jasper fauna. A possible exception to this could be *Errolosteus* (if this is in fact a brachythoracid). Tubercles vary in density and size from plate to plate on the same individual. It is clear that individual specimens show considerable variation from almost smooth to highly tuberculate on different parts of the dermal plates. By some authors the smoothness has been attributed to wear in some instances but I consider that it may be variation between individuals of the same species, or within the genus.

In this work difficulty has been encountered in allocating specimens to species and genera because the current knowledge of the limits of the described taxa is inadequate. As a result, several specimens have been referred to as Incertae Sedis. This situation is exacerbated by the attempts of previous workers to assign new material from different areas to already defined taxa, without knowing the range of variation in such taxa at the type localities. It would not be surprising if, when larger topotypic collections are available, the ranges of variation of these early placoderm species were found to be wider than at present appreciated. Until this is done the contribution of the Taemas-Wee Jasper material to the understanding of the higher classification of placoderms is in question.

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Geological Survey Organisation for granting me access to material, considerable assistance and extensive discussions during the preparation of my thesis, though it should be noted that we disagree on several points of interpretation.

REFERENCES

Browne, I.A. (1959). Stratigraphy and structures of the Devonian rocks of the Taemas and Cavan areas, Murrumbidgee River, south of Yass, New South Wales. *Journal and Proceedings of the Royal Society of New South Wales* **92**, 115–128.

Campbell, K.S.W. (1976). Excursion Guide No. 9B. 25th International Geological Conference.

Campbell, K.S.W. and Barwick, R.E. (1982). A new species of the lungfish *Dipnorhynchus* from New South Wales. *Palaeontology* **25**, 509–527.

Chapman, F. (1916). On the generic position of "*Asterolepis ornata*, var. *australis*," McCoy: with description of a new variety. *Proceedings of the Royal Society of Victoria* **28**, 211–215.

Denison, R.H. (1978). Placodermi. In 'Handbook of Paleoichthyology, Volume 2' (Ed. H. -P. Schultze). (Gustav Fischer Verlag: Stuttgart).

Findlay, C. (1991). Vertebrate fossils, facies and palaeoenvironment of the Upper Taemas Subgroup, Yass, New South Wales. Honours Thesis, Geology Department, Australian National University.

Gross, W. (1932). Die Arthrodira Wildungens. *Geologische und Palaeontologische Abhandlungen* **19**, 5–61.

Hills, E.S. (1936). On certain endocranial structures in *Coccosteus*. *Geological Magazine* **73**, 213–226.

Jarvik, E. (1942). On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zool. Bidr. Upps* **21**, 235–675

Klapper, G. and Johnson, G.J. (1975). Sequence in conodont genus *Polygnathus* in Lower Devonian at Lone Mountain, Nevada. *Geologica et Palaeontologica* **9**, 65–83.

Klapper, G. and Johnson, G.J. (1980). Endemism and dispersal of Devonian conodonts. *Journal of Paleontology* **54**, 400–455.

Lelièvre, H. (1989). Les Vertébrés de la Formation de Jawf du Dévonien inférieur D'Abrabie Saoudite. *Bulletin of the Museum of Natural History, Paris* **11**, 123–130.

Long, J.A. (1984). New placoderm fishes from the Early Devonian Buchan Group, eastern Victoria. *Proceedings of the Royal Society of Victoria* **96**, 173–186.

Mawson, R. (1987). Early Devonian conodont faunas from Buchan and Bindi, Victoria, Australia. *Palaeontology* **30**, 251–297.

Mawson, R., Talent, J.A., Brock, G.A. and Engelbretsen, M.J. (1992). Conodont data in relation to sequences about the Pragian-Emsian boundary (Early Devonian) in south-eastern Australia. *Proceedings of the Royal Society of Victoria* **104**, 23–56.

Miles, R.S. (1971). The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of Edinburgh* **65**, 179–210.

Miles, R.S. (1973). An actinolepid arthrodire from the Lower Devonian Peel Sound formation, Prince of Wales Island. *Palaeontographica* **143A**, 109–118.

Oliver, W.A. and Chulpác, I. (1991). Defining the Devonian. *Lethaia* **24**, 119–122.

Ørvig, T. (1957). Notes on some Lower Paleozoic vertebrates from Spitsbergen and North America. *Norsk Geoloogisk Tidsskriff* **37**, 285–353.

Ørvig, T. (1971. Comments on the lateral line system of some brachythoracid and ptyctodontid arthrodires. *Zoologica Scripta* **1**, 5–35.

Pedder, A.E.H., Jackson, J.H. and Philip, G.M. (1970). Lower Devonian biostratigraphy of the Wee Jasper region, New South Wales. *Journal of Paleontology* **44**, 206–251.

Philip, G.M. and Pedder, A.E.H. (1967). A correlation of some Devonian limestones of New South Wales and Victora. *Geological Magazine* **104**, 232–239.

Romer, A.S. (1962). 'The Vertebrate Body. Third edition'. (W. B. Saunders Co.: London).

Toombs, H.A. (1948). The use of acetic acid in the development of vertebrate fossils. *Museums Journal* **48**, 54–55.

White, E.I. (1952). Australian arthrodires. *Bulletin of the British Museum (Natural History) (Geology)* **1**, 249–304.

White, E.I. (1978). The larger arthrodiran fishes from the area of the Burrinjuck Dam, N.S.W. *Transactions of the Zoological Society of London* **34**, 149–262.

White, E.I. and Toombs, H.A. (1972). The buchanosteid arthrodires of Australia. *Bulletin of the British Museum (Natural History) (Geology)* **22**, 379–419.

Young, G.C. (1979). New information on the structure and relationships of *Buchanosteus* (Placodermi, Euarthrodira) from the Early Devonian of New South Wales. *Zoological Journal of the Linnean Society* **66**: 309–352.

Young, G.C. (1981). New Early Devonian brachythoracids (placoderm fishes) from the Taemas–Wee Jasper region of New South Wales. *Alcheringa* **5**, 245–271.

Ziegler, W. (1979). Historical Subdivisions of the Devonian. In 'The Devonian System' (Eds. M.R. House, C.T. Scrutton and M.G. Bassett). pp. 23–47 (Palaeontological Association Special Papers in Palaeontology 23).

TABLE 1

List of abbreviations used in Figs. 4–18.

III	nervus oculomotorius III
Vpf	nervus profundus V
VI	nervus abducens VI
VII	nervus facialis VII
VII hm	hyomandibular branch of facial nerve
VII pal	palatine branch of facial nerve
VIII	nervus acousticus VIII
IX	nervus glossopharyngeus IX
ASG	anterior supragnathal
a. amp	anterior ampulla
a. orb	orbital artery
apo	anterior postorbital process of endocranium
art_{1-3}	articulation facets
art. hm	articular facets for hyomandibular
b. lat	nervus buccalis lateralis
C	central plate
cn	canal
c. oss	ossified canals
cr. so	supraorbital crista
csc	central sensory canal
d. end	external opening of endolymphatic duct
d. endi	internal opening of endolymphatic duct
f. bhy	buccohypophysial foramen
fla	flange
f. pv	foramina associated with pituitary gland
if. pt	infranuchal pit
if. r	infranuchal ridge
ioc	infraorbital sensory canal
M	marginal plate
m. dep	median depression
ml	median line
mlc	main lateral line sensory canal
mp	middle pitline
my	myodome
Nu	nuchal plate
no	notch
oC	area overlapping or overlapped by central plate
oM	area overlapping marginal plate
oNu	area overlapped by nuchal plate
oPM	area overlapping postmarginal plate
oPNu	area overlapping or overlapped by paranuchal plate
oPtO	area overlapping postorbital plate
oSO	area overlapped by suborbital plate
orb	orbit
PNu	paranuchal plate
PrO	preorbital plate
Psp	parasphenoid
PtO	postorbital plate
plp. C	posterior process of central plate
pmc	postmarginal sensory groove
pp	posterior pitline
r. cv	perichondral roof of cranial cavity
reV	trigeminus recess
sac	sacculus
sem. c	semicircular canal
soc	supraorbital sensory canal
v. pit	pituitary vein

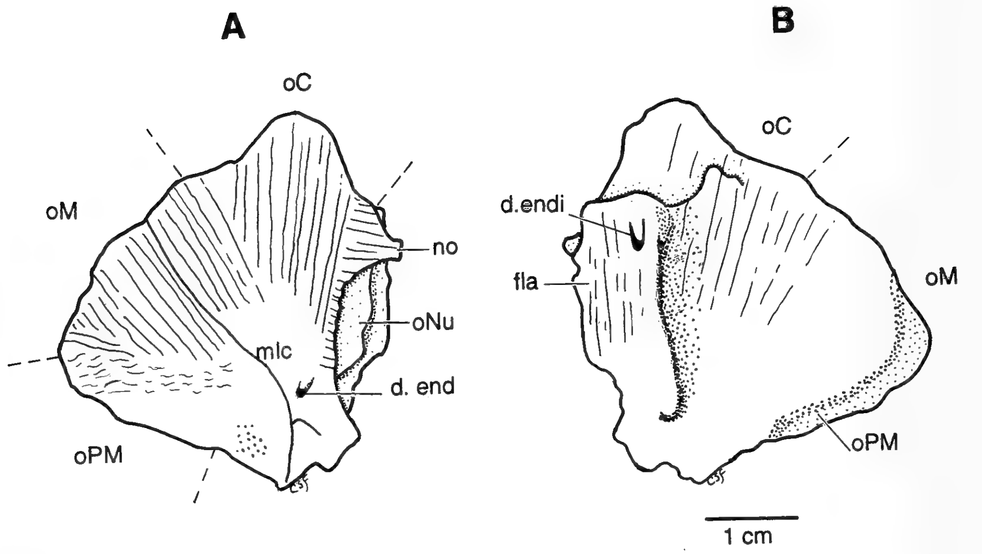

Fig. 4. cf. *Errolosteus goodradigbeensis*. Drawings of left paranuchal plate, CPC 31618. **A**, dorsal view; **B**, ventral view.

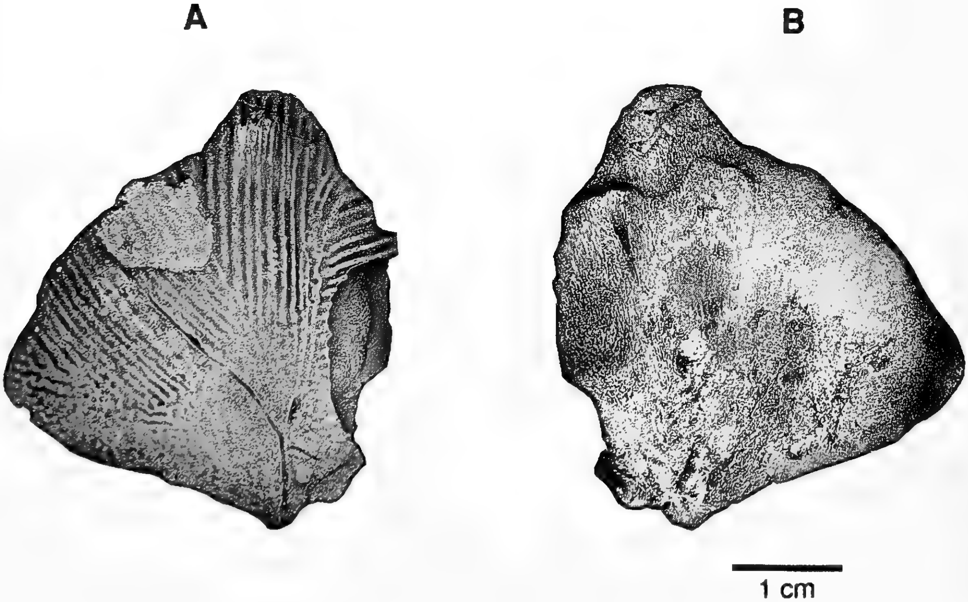

Fig. 5. cf. *Errolosteus goodradigbeensis*. Left paranuchal plate, CPC 31618. **A**, dorsal view; **B**, ventral view.

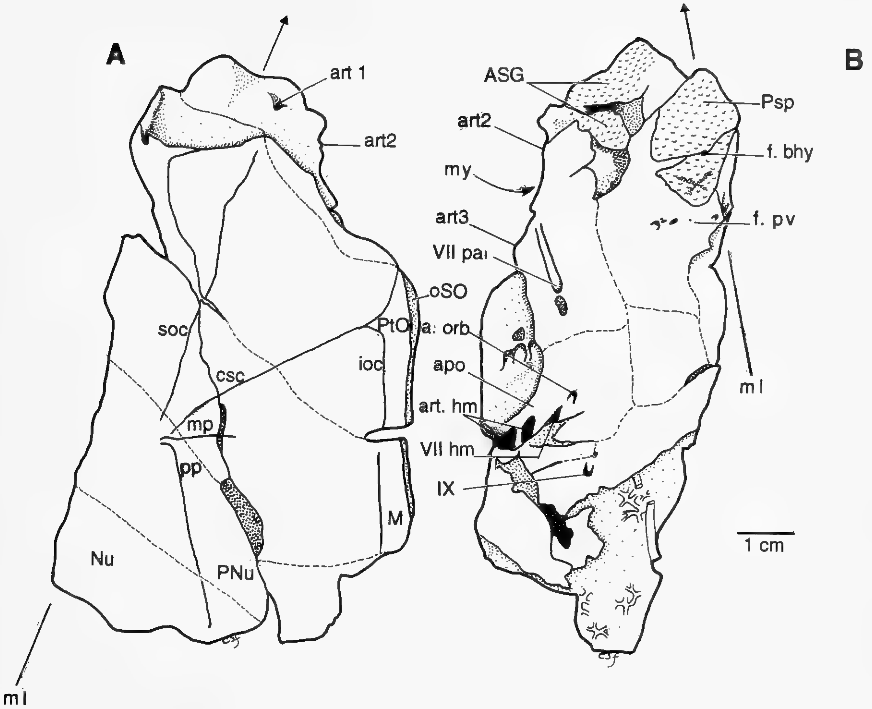

Fig. 6. cf. *Parabuchanosteus murrumbidgeensis*. Drawings of portion of skull, CPC 31619. **A**, dorsal view with both pieces together; **B**, ventral view of larger piece.

Fig. 7. cf. *Parabuchanosteus murrumbidgeensis*. Portion of skull, CPC 31619. **A**, dorsal view with both pieces together; **B**, ventral view of larger piece.

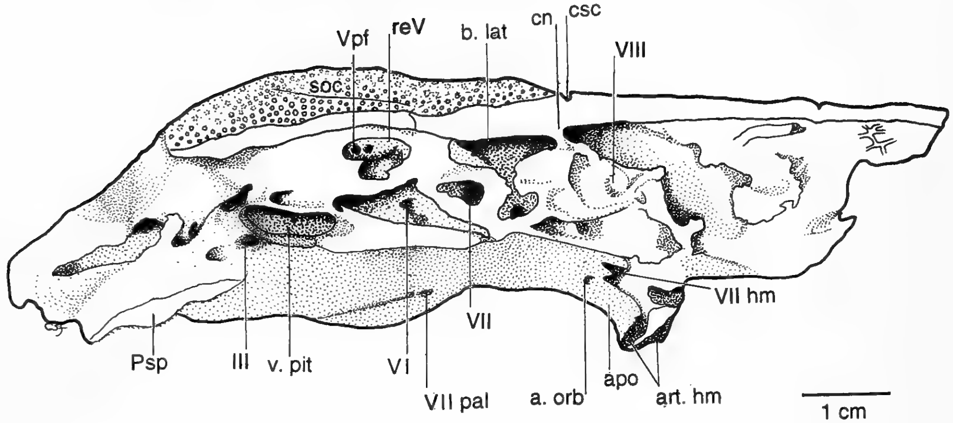

Fig. 8. cf. *Parabuchanosteus murrumbidgeensis*. Drawing of portion of skull, CPC 31619. Medial view of larger piece showing internal features.

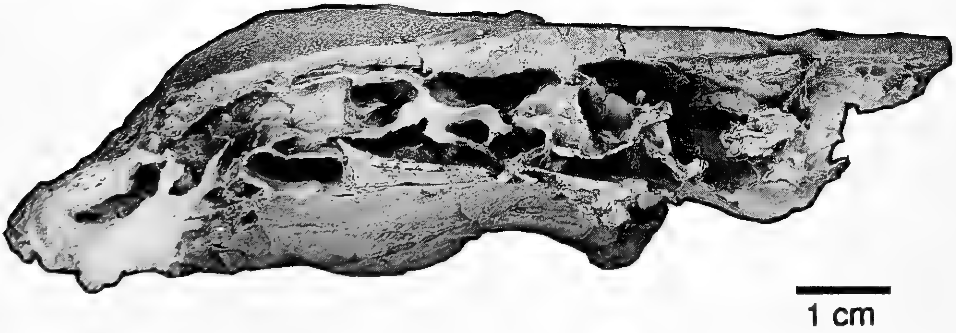

Fig. 9. cf. *Parabuchanosteus murrumbidgeensis*. Portion of skull, CPC 31619. Medial view of larger piece showing internal features.

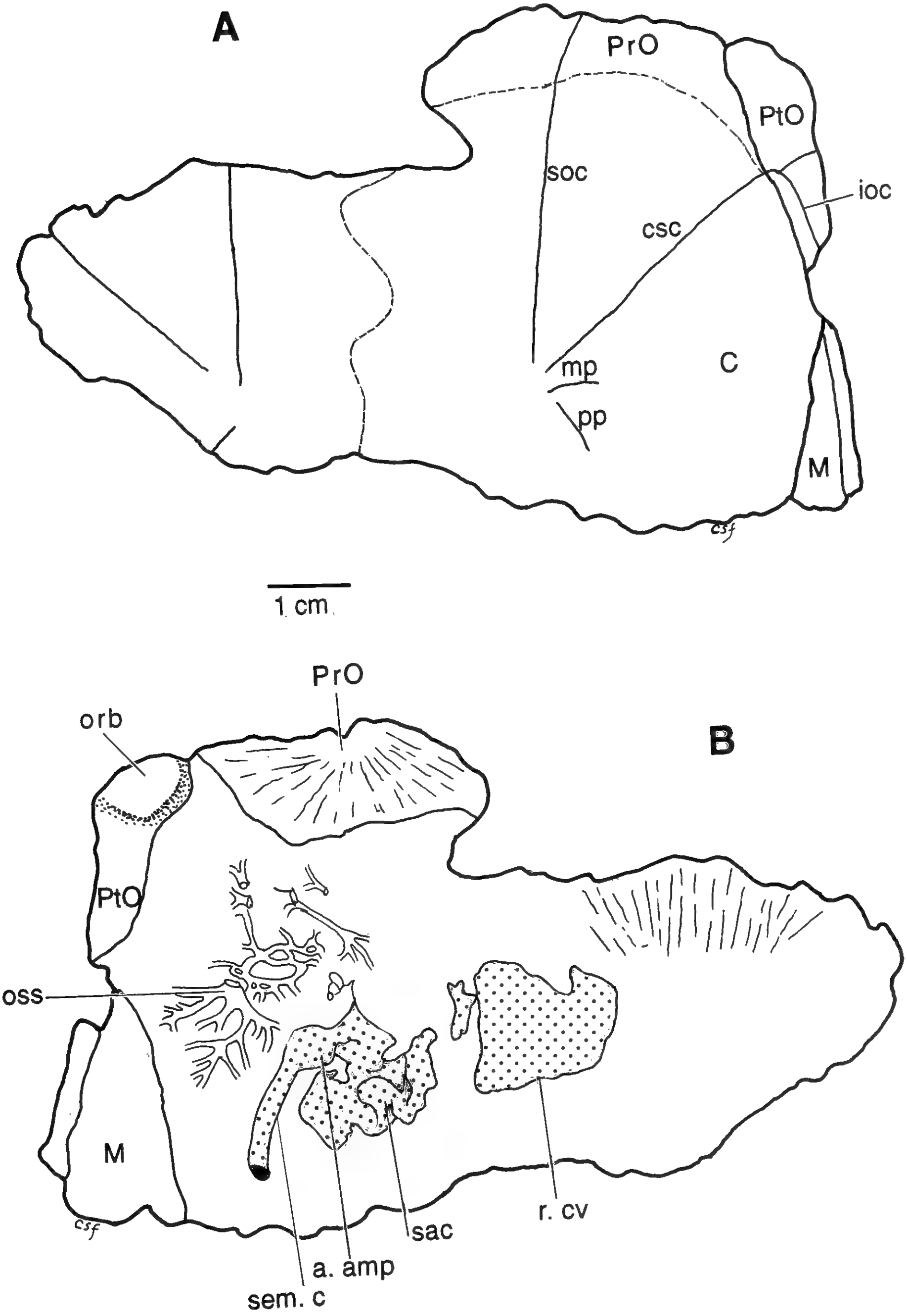

Fig. 10. Gen. indet. sp. indet. Drawings of portion of skull roof, CPC 31620. **A,** dorsal view; **B**, ventral view.

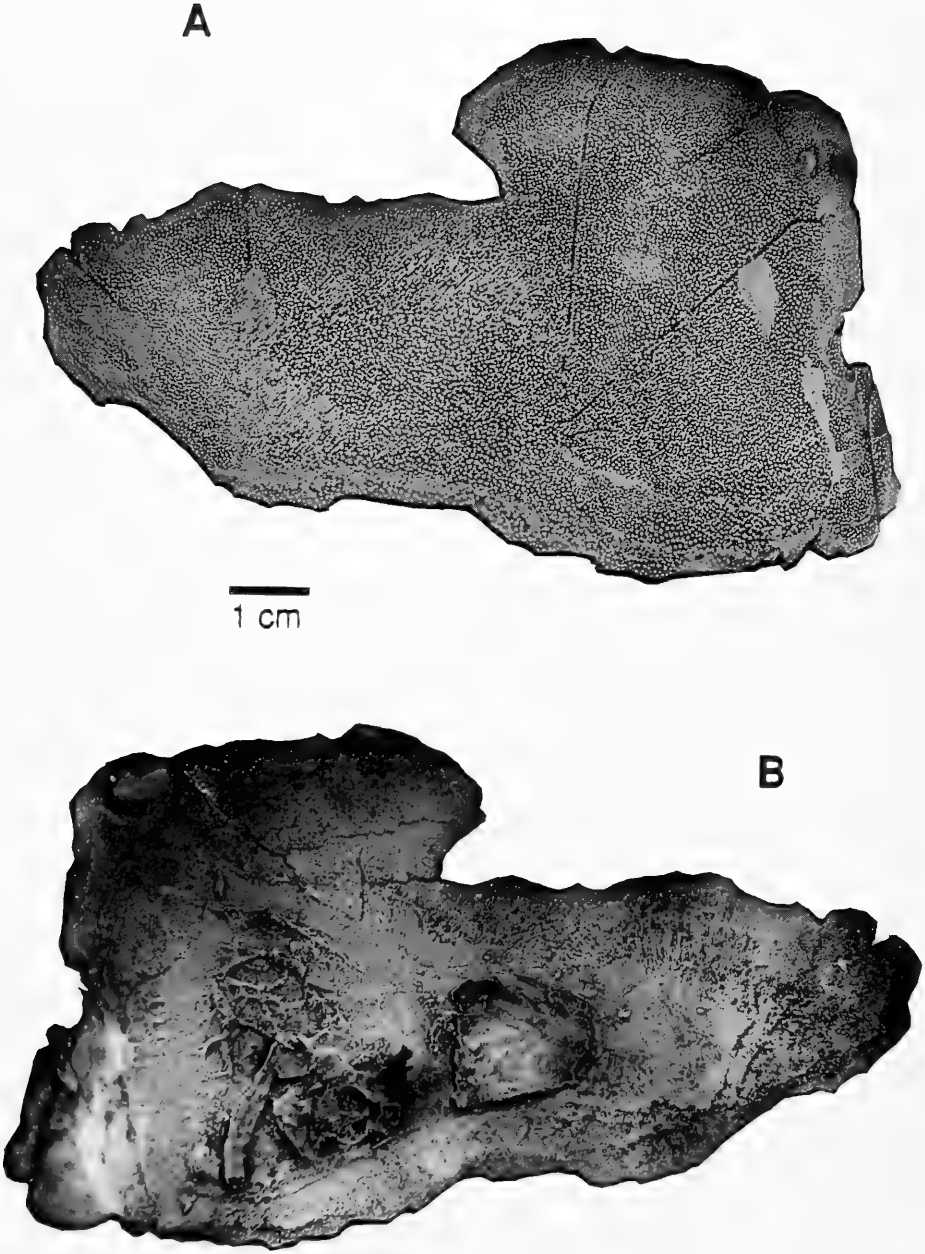

Fig. 11. Gen. indet. sp. indet. Portion of skull roof, CPC 31620. **A,** dorsal view; **B**, ventral view.

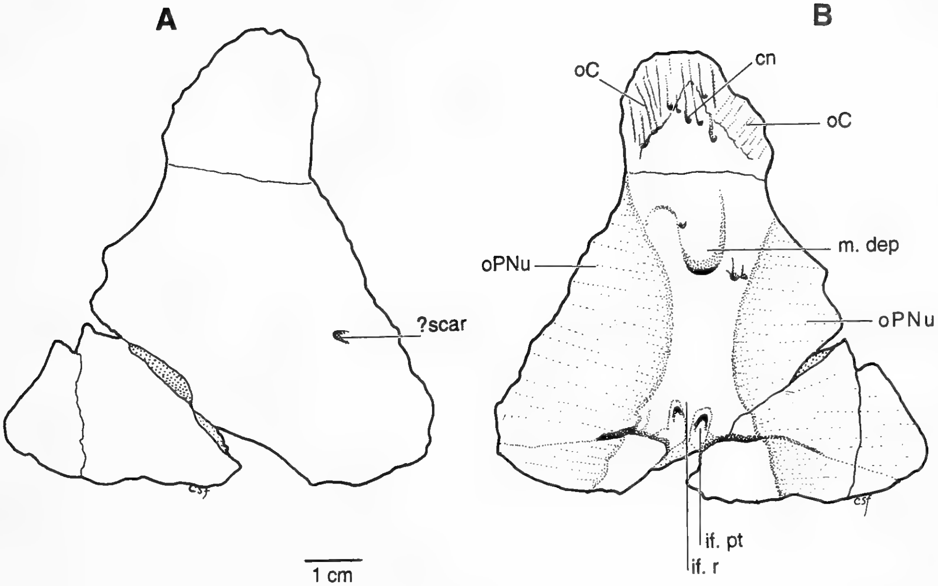

Fig. 12. cf. *Arenipiscis westolli.* Drawings of nuchal plate, CPC 31621. **A**, dorsal view; **B**, ventral view.

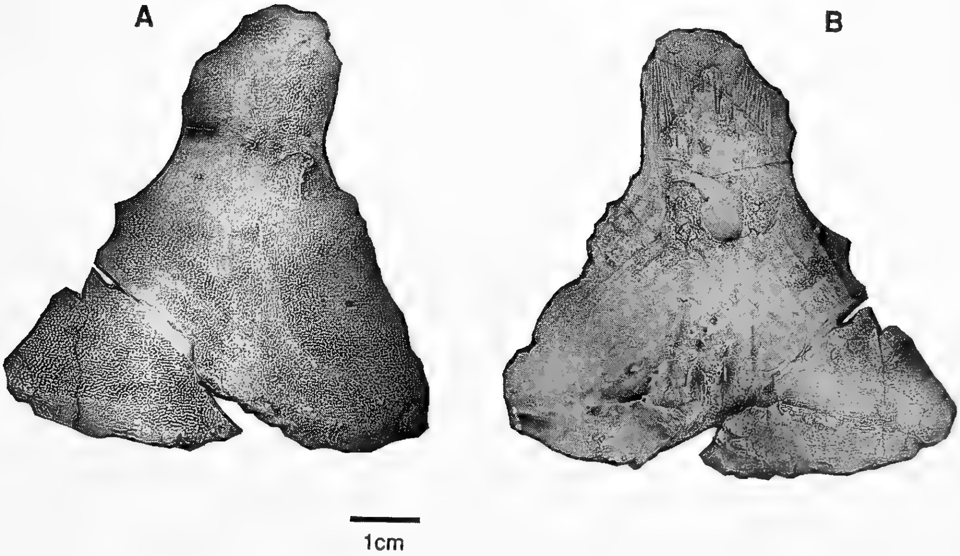

Fig. 13. cf. *Arenipiscis westolli.* Nuchal plate, CPC 31621. **A**, dorsal view; **B**, ventral view.

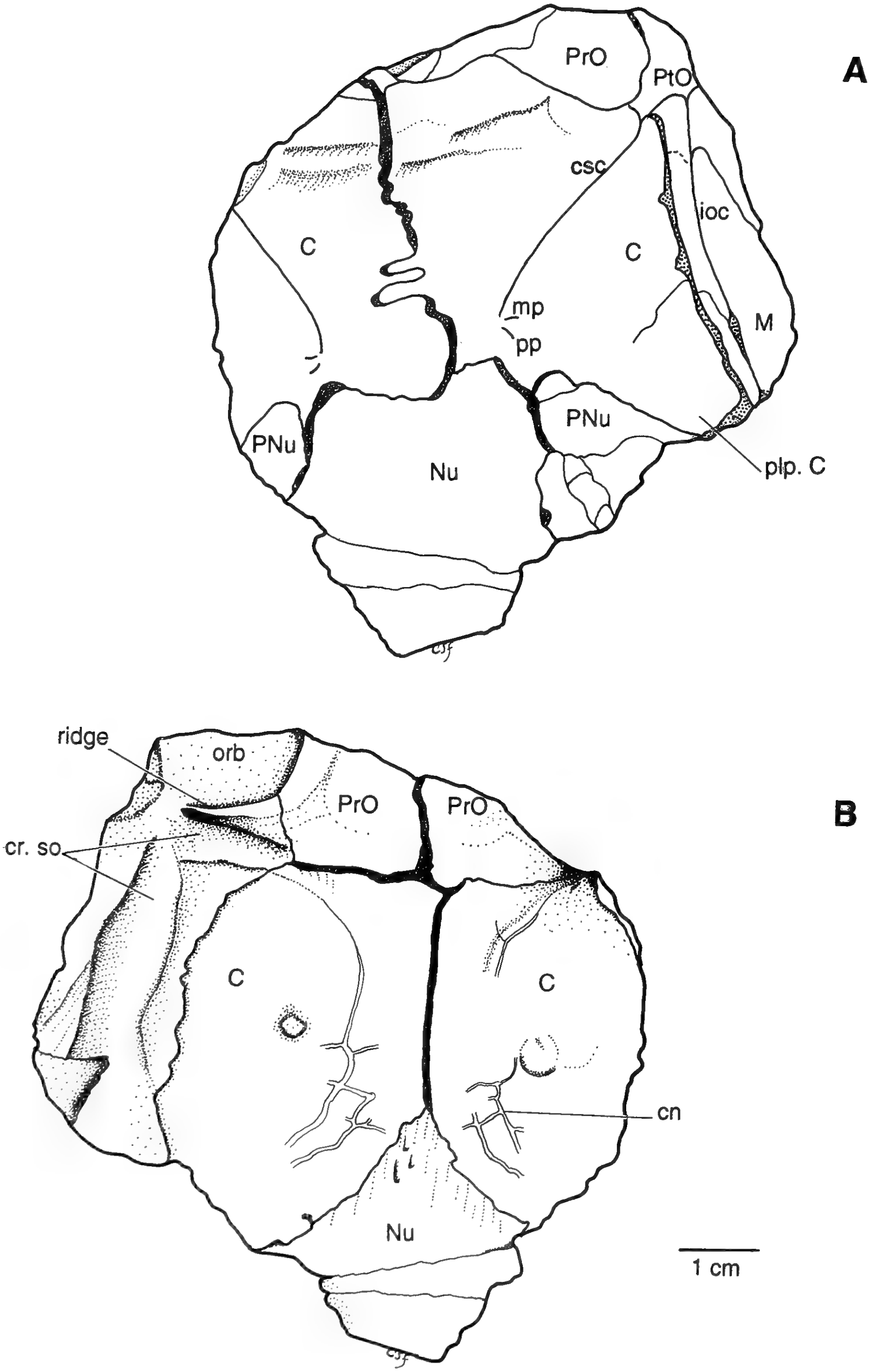

Fig. 14. cf. *Arenipiscis westolli.* Drawings of portion of skull, ANU 49215. **A**, dorsal view; **B**, ventral view.

Fig. 15. cf. *Arenipiscis westolli*. Portion of skull, ANU 49215. **A**, dorsal view; **B**, ventral view.

Fig. 16. cf. *Arenipiscis westolli.* ANU 49215. (**A**) Junction of central, marginal and postorbital plates showing the structure of the tubercles and (**B**) Junction of nuchal, central and paranuchal plates showing the linear pattern of tubercles. Scale bar represents 5mm.

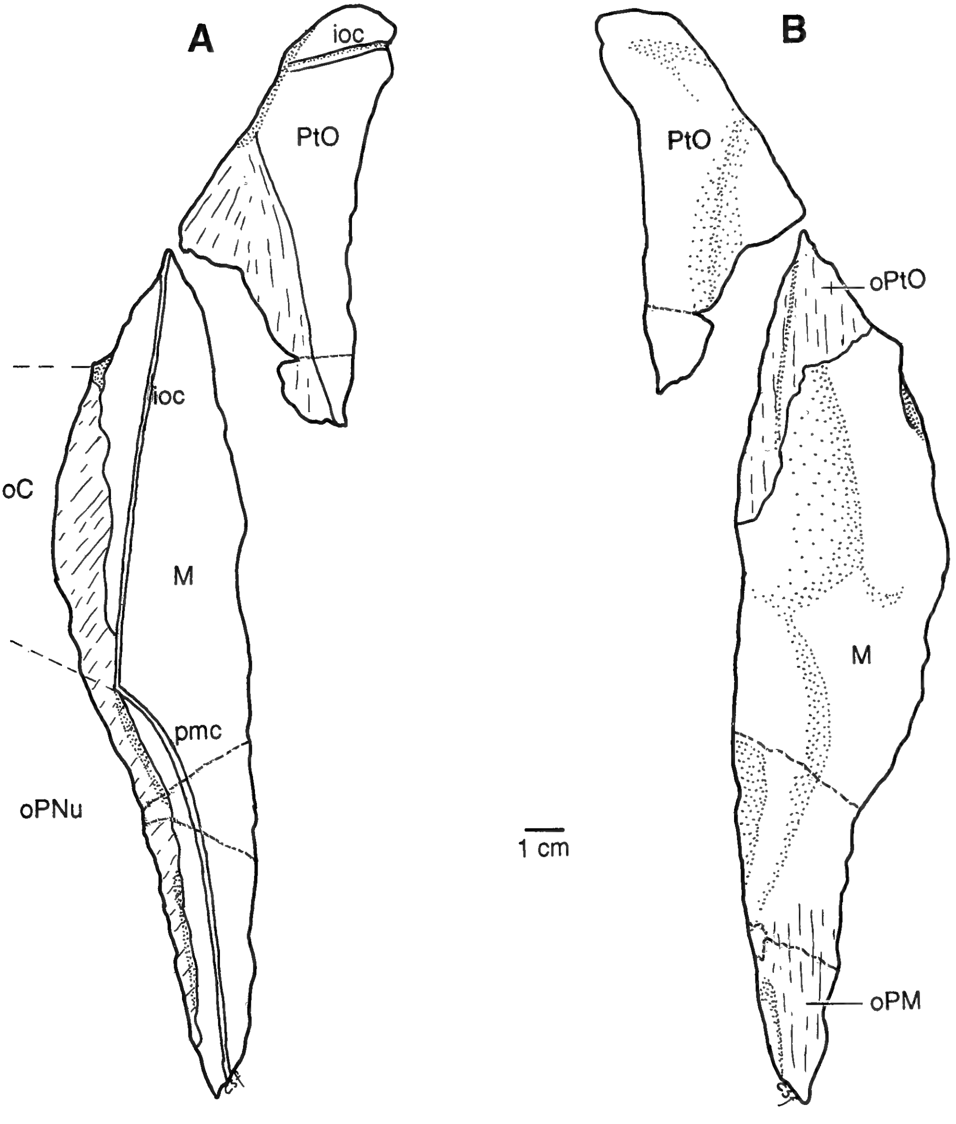

Fig. 17. Gen. indet. sp. indet. Drawings of incomplete right postorbital and marginal plates from the skull, CPC 31622. **A**, dorsal view; **B** ventral view.

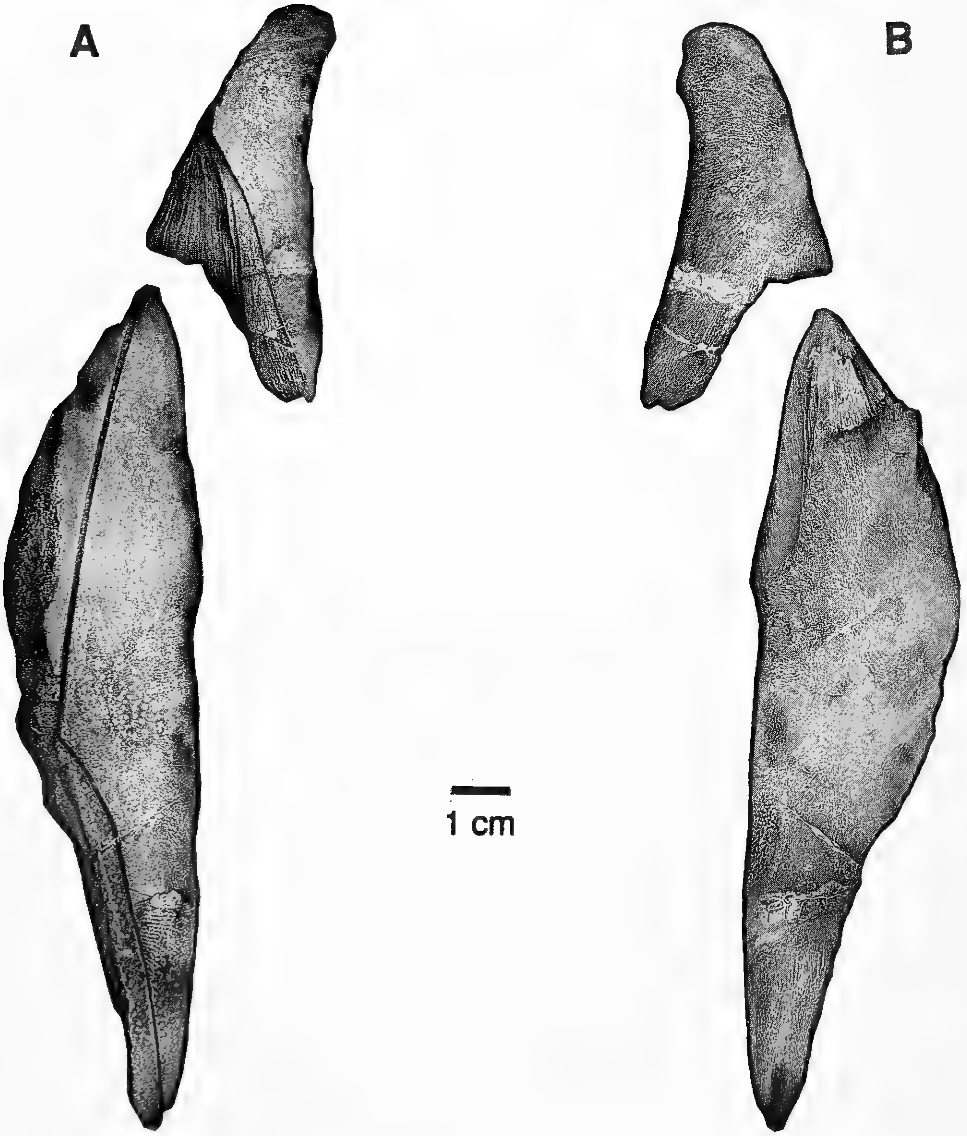

Fig. 18. Gen. indet. sp. indet. Incomplete right postorbital and marginal plates from the skull, CPC 31622. **A**, dorsal view; **B** ventral view.

The Australian Longicorn Beetle Genus *Coleocoptus* Aurivillius(Coleoptera: Cerambycidae)

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WANG, Q. (1996). The Australian longicorn beetle genus Coleocoptus Aurivillius (Coleoptera: Cerambycidae). Proc. Linn. Soc. N.S.W. 116, 187–192

The monotypic phoracanthine genus Coleocoptus is reviewed and redescribed. C. senio (Newman) is redescribed and illustrated. The distribution and biology of C. senio are noted.

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KEYWORDS: Cerambycidae, Phoracanthini, *Coleocoptus senio*, taxonomy, distribution, biology.

INTRODUCTION

Coleocoptus Aurivillius 1893 is a monotypic phoracanthine genus of exclusively Australian-New Guinean distribution. Aurivillius (1893) proposed the genus based on *Coptocercus sexmaculatus* Hope 1844. In 1912, Aurivillius synonymised *Coleocoptus sexmaculatus* (Hope) with *C. senio* (Newman) (= *Phoracantha senio* Newman 1840). The synonymy was confirmed when the types of these two species were examined.

Coleocoptus is most closely related to *Phoracantha* Newman, and according to Wang's (1994b) cladistic analysis, they are in fact sister genera. *Coleocoptus* differs from *Phoracantha* in having the prothorax distinctly longer than wide, and the elytra with truncate apices. Although *Coleocoptus* is monotypic, its distribution is almost as extensive as that of *Phoracantha* which includes at least forty species, many of which have very localised distributions (Wang 1995b). The adult of *C. senio* has never been well described and illustrated but the immature stages were well described by Duffy (1953, 1963) based on specimens obtained from *Syncarpia* in New South Wales.

Taxonomic terminology follows Wang (1993a,b; 1994a,b; 1995a,b; 1996) and Wang et al. (1994). Specimens for this study were borrowed from the following: Australian Museum, Sydney (AM), Australian National Insect Collection, Canberra (ANIC), Natural History Museum, London (BMNH), Museum of Victoria, Melbourne (MV), Northern Territory Museum, Darwin (NTM), Oxford University Museum, Oxford (OUM), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM), and University of Queensland Insect Collection, Brisbane (UQIC). The author's collection has been deposited in MV. Distribution data were obtained from specimens examined.

GENUS *COLEOCOPTUS* AURIVILLIUS

Coleocoptus Aurivillius 1893:160. Type species: *Coptocercus sexmaculatus* Hope 1844:195, by monotypy; Carter 1929:119, McKeown 1947:33.

Diagnosis

Distinguished by combination of head, pronotum, thoracic sterna and abdomen with depressed hairs; segments 3–7 of antennae with sharp apical unispines; prothorax longer than wide, with small spine at each side; 5 feebly raised nodules on pronotal disc; densely and heavily punctate throughout entire disc except medial nodule and anterior pair of nodules; elytra with pale unraised fascia(e); a cylindrical hair arising from each puncture on elytral disc; apex obliquely truncate without spines or processes; femora lineate or gradually thickened, with depressed hairs. Tegmen of male terminalia with 2 parameres; spined region of internal sac of aedeagus with 3 sections; styli of ovipositor arising terminally.

Comments

This genus is closely related to *Phoracantha* (Wang 1995b) but differs in having the prothorax distinctly longer than wide and the elytral apices truncate. It is also similar to *Phytrocaria* Wang (Wang 1996) but differs in having prothorax distinctly longer than wide, each puncture on head and basal half of elytral disc with only 1 cylindrical depressed hair, and styli of ovipositor arising terminally.

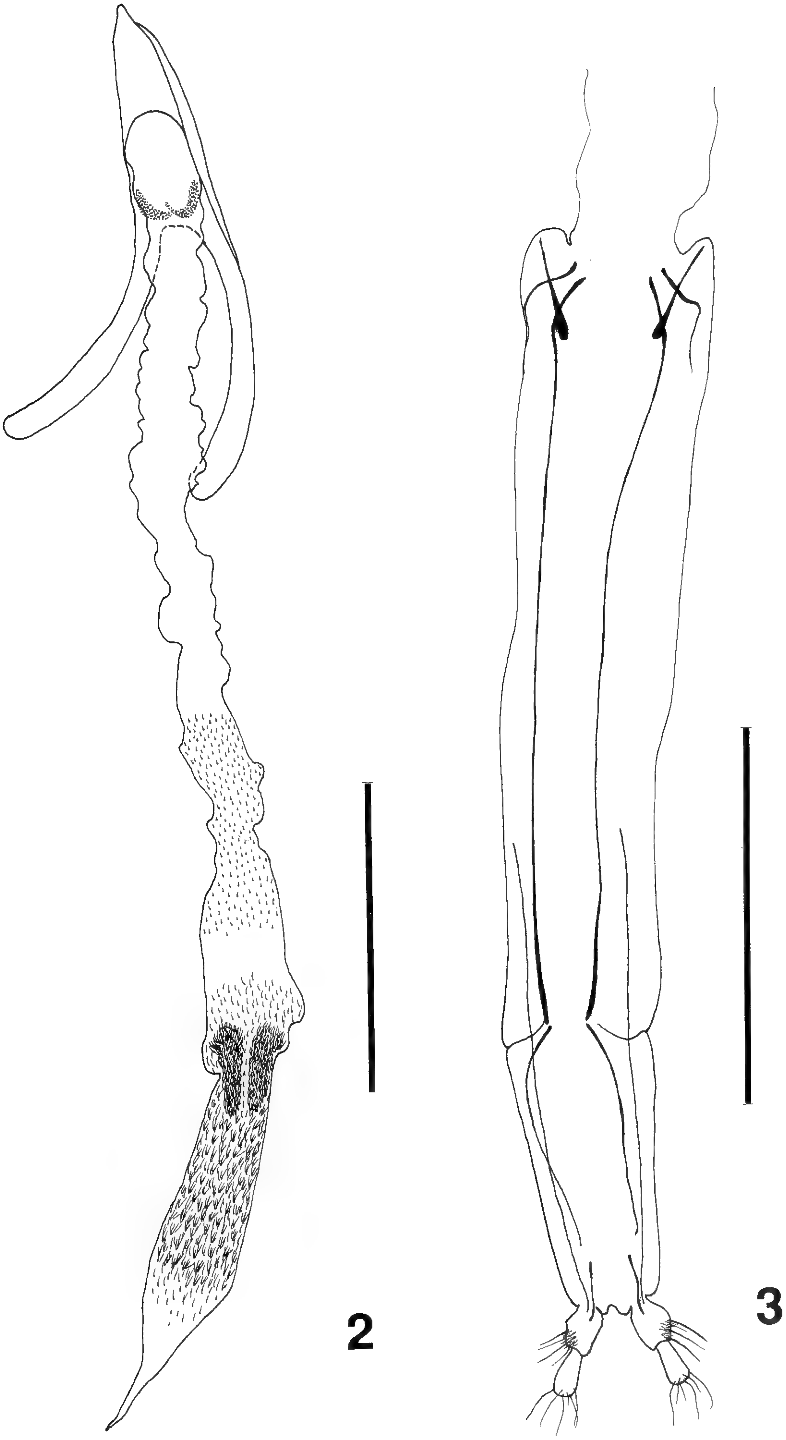
COLEOCOPTUS SENIO (NEWMAN)
(FIGS 1–3)

Phoracantha senio Newman 1840:4. — Newman 1842:352; Erichson 1842:247; Gahan 1893:172; Lea 1917:617; Lever 1946:10.

Coleocoptus senio. — Aurivillius 1917:5; McKeown 1947:33; Gressitt 1959:95; Duffy 1953:179, 1963:75.

Coptocercus sexmaculatus Hope 1841a:51. — Hope 1841b:63, 1844:195; Aurivillius 1893:160, 1912:93 (synonymy).

Fig. 1. Dorsal view of *C. senio*.



Figs. 2–3. Genitalia of *C. senio*: 2, median lobe and internal sac of male genitalia; 3, ovipositor.

Material examined

Types

P. senio. Holotype, female, SOUTH AUSTRALIA: Adelaide (BMNH, Ent Club 44–12).

C. sexmaculatus. Holotype, female, AUSTRALIA: no locality (OUM, Col 1786).

Other material, 235 males, 298 females [10 males, 8 females (AM); 12 males, 15 females (ANIC); 14 males, 18 females (BMNH); 46 males, 69 females, terminalia slides Nos Coleocoptus m-920613-1 and f-920613-1 (MV); 2 males, 1 female (NTM); 32 males, 36 females (QM); 86 males, 101 females (SAM); 33 males, 50 females (UQIC)]. NORTHERN TERRITORY: Casuarina, 19.x.1976; Victoria River, 11.xi.1984; Barrow Ck (21°32'S, 133°53'E); McArthur River, 1.vi.1967; Port Darwin; Daly River (14°10'S, 131°20'E); Tennant Ck (19°39'S, 134°11'E); Cockatoo Ck (15°56'S, 129°03'E); Ranken Store, 65 km SE of Alexandria, 23.ix.1977; Alice Springs; Flora River, Sept.1912; Katherine River; QUEENSLAND: Springbrook, 26.iii.1966; Kedron, 5.iv.1958; South Percy Island (21°45'S, 150°18'E), 23–29.xi.1992; Flora (21°56'S, 148°33'E), Sept.1912; Lake Broadwater, via Dalby, 26–28.i.1985; Mornington Island (16°36'S, 139°21'E), 29.v.1960, at light; Fulham Vale, Jan.1892; Mt Spec, 7.xi.1969; Normanton, 25.v.1972; Birdsville, 17.ix.1977; Riversleigh HS, nr. Gregory River, 26–30.iv.1986, malaise trap; Lawes, 6.ii.1952; Wulguru, 12.x.1962; Mt. Nebo, 7.v.1959; Stanthorpe, 7.xii.1923; Toowoomba, 7.xii.1964; Cunnamulla; Augathella, 4.i.1974; Charleville, under bark of *Eucalyptus camaldulensis*, 8.i.1974; Mutchilba, Dec.1933; Brisbane, Nov.1909; Warwick, 1948; Blackburn, 10.iii.1940; NEW SOUTH WALES: Broken Hill, 10.xii.1966; Acacia Plateau, via Legume, 9.i.1967; Walgett, 30.xii.1971; Grafton, 26.ii.1967; Forest Reefs; Bourke, 26.xii.1973, at light; Merrimbula, 23.ii.1950; Mullaley, Nov.1957; Canowindra, 10.i.1955; Sydney; Glen Roy, 25.xii.1953; Red Cliffs, 28.xii.1954; AUSTRALIAN CAPITAL TERRITORY: Canberra; VICTORIA: Mitchell Gorge, Jan.1929; Mildura, Jan.1937; Kiata, 27.xii.1918; Caulfield, 26.ii.1918; Benetook, 25.xi.1951; Rosanna, 17.iii.1953; Gippsland; Officer, 20.vii.1924; Ararat, 8.ii.1937; SOUTH AUSTRALIA: Leigh Ck (30°29'S, 138°25'E); Whyalla, 10.xi.1947; Scorpion Springs C.P., Nanam's Well, 17.xii.1983, at light; Blackwood, 18.xii.1960, at light; Devon Downs; Roxby Downs, 23.x.1976, at light, in *Acacia sowdenii* woodland; Ooldea; Athelstone, 1.iii.1986, at light; Kimba; Kangaroo Island, Feb.1888; Tumby Bay; Ardrossan; Yumbarra National Park, 11.xi.1975, at light; Emu Junction, Great Victoria Desert, 11.x.1976; Sturt Vale Station, 17.xi.1975, at light; Sandplain (29°09'S, 134°06'E), 25.x.1984, at light; Aldinga Sellicks, 2.iv.1987, at light; Olary, 19.xi.1975, under bark of red gum (*Angophora costata*); WESTERN AUSTRALIA: Swan River; Derby, 29.viii.1953; Gill Pinnacle, 10.xi.1963, at light; Meekatharra-Billiluna Pool, April 1930–Aug.1931; Esperance (33°52'S, 121°54'E), 5.i.1944; Kimberley; PAPUA NEW GUINEA: Port Moresby, Nov.-Dec.1958.

Description

Body length

male, 10–16.2 mm; female, 10.2–19.5 mm.

Colour

Antennae, legs and ventrites reddish brown with apical half of femora dark reddish brown; head, pronotum and elytra dark reddish brown to blackish brown. Elytra with following pale yellow markings: 1 narrow incomplete fascia at sub-base, 1 wider, more or less complete fascia at middle, and apices (Fig.1).

Head

Head with very dense large punctures of irregular form, each bearing a pale depressed hair. Distance between lower lobes of eyes 1.2–1.4 times distance between antennal socket and lateral angle of postclypeus, and 1.7–2 times distance between upper lobes of eyes. Antennae 1.3–1.5 times length of body in male and just slightly longer than body in female; segment 3 distinctly longer than segment 4 or 5, and 3–4 times length of its apical spine.

Thorax and abdomen

Nodules on pronotal disc: median one and anterior pair obvious and nitid but posterior pair vague and punctate; each puncture on pronotal disc with a long pale erect hair; sparse pale depressed hairs on disc; very small spine or process at each side. Elytra nitid, about 2.8–3 times length of prothorax in male but about 3–3.3 times length of prothorax in female; dense, large and deep punctures on basal half of disc, more than 50% of punctures with short pale depressed hair each, at most as long as diameter of punctures, and remaining punctures bearing long erect or sub-erect hair each; dense but small punctures on apical half of disc, more than 50% of punctures with very short pale depressed hair each, and remaining punctures with long erect hair each; punctures on basal half of disc aligned in rows. Abdomen nitid with dense pale depressed hairs.

Male terminalia

Apex of median lobe sharply pointed (Fig.2). Spined region of internal sac slightly longer than unspined region; spined region divided into 3 sections: first section about 1.5 times as long as second section, with fairly dense simple small and long spines; second section with fairly dense simple large and long spines in basal 2/5 and with mixture of dense multi-branched spines and sparse simple small and long spines in apical 3/5; 2 longitudinal dark areas, composed of very dense multi-branched spines in apical 3/5; third section about twice as long as second section, with mixture of dense multi-branched spines and sparse basally forked spines; a wide unspined gap between first and second sections (Fig.2). Eighth sternite obliquely truncate at terminal sides; dense long setae arising from it laterally and terminally; setae present in mid-terminal area; dense microspines on ventral surface. Apex of eighth tergite more or less rounded.

Ovipositor

As in Fig.3.

Variation

The two pale fasciae of the elytra may be widened and connected with each other to form a broad fascia.

Biology

Hosts are *Syncarpia laurifolia* (Duffy 1953 and 1963), *Acacia leiocalyx* (Hockey and Baar 1988), *A. sowdenii* (?), *Eucalyptus botryoides, E. crebra* (Webb 1987), *E. camaldulensis* and *Angophora costata*. Larvae feed under the bark of the hosts. Adults were collected at light and under the bark of their hosts during all months except June and July.

Distribution

Northern, southern, eastern and central Northern Territory, northern, eastern and southern Queensland, eastern, northern, southern and western New South Wales, Australian Capital Territory, Victoria, southern and south-eastern South Australia, south-western, northern and far south-eastern Western Australia, south-eastern Papua New Guinea; introduced into New Zealand and Fiji.

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REFERENCES

Aurivillius, P.O.C. (1893). Verzeichniss der von Herren C. Lumhltz und C. Frestedt im nördlichen Queensland gesammelten Cerambyciden. *Entomologisk Tidskrift* **14**, 153–169.

Aurivillius, P.O.C. (1912). Cerambycidae: Cerambycinae. In 'Coleopterorum Catalogus, Vol. XXII. Cerambycidae I' (Ed. S. Schenkling) pp 1–574 (Junk: Berlin).

Aurivillius, P.O.C. (1917). Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910–1913. Part 12, Cerambycidae. *Arkiv foer Zoologi* **10**, 1–50.

Carter, H.J. (1929). Revision of the Australian Phoracanthini (Cerambycidae), with notes and descriptions of new species of this group and allied genera. *Proceedings of the Linnean Society of N. S. W.* **54**,118–136.

Duffy, E.A.J. (1953). 'A Monograph of the Immature Stages of British and Imported Timber Beetles (Cerambycidae)'. (British Museum, Natural History: London).

Duffy, E.A.J. (1963). 'A Monograph of the Immature Stages of Australasian Timber Beetles (Cerambycidae). (British Museum, Natural History: London).

Erichson, W.F. (1842). Beitrag zur fauna von vandiemensland mit besonderer rucksicht auf die geographiche verbreitung der insecten. *Archiv fur Naturgeschichte* **8**, 83–287.

Gahan, C.J. (1893). Notes on the longicornia of Australia and Tasmania, Part I., with a list of the species collected by Mr. J.J. Walker and descriptions of new forms. *Transactions of the Entomological Society of London* **2,** 165–197.

Gressitt, J.L. (1959). Longicorn beetles from New Guinea, I (Cerambycidae). *Pacific Insects* **1**, 59–171.

Hockey, M.J., and de Baar, M. (1988). New larval food plants and notes for some Australian Cerambycidae (Coleoptera). *Australian Entomological Magazine* **15**, 59–66.

Hope, F.W. (1841)a. An extract of observations on the Stenochoridae of New Holland, with descriptions of new genera and species of that family. *Proceedings of the Zoolological Society of London* **8**, 46–55. [Note: this is an extract of Hope's (1844) paper. See below]

Hope, F.P. (1841)b. Observations on the Stenochoridae of New Holland. *Annals and Magazine of Natural History* **7,** 58–67.

Hope, F.W. (1844). Observations on the Stenochoridae of New Holland, with descriptions of new genera and species of that family. *Transactions of the Zoological Society of London* **3,** 187–202.

Lea, A.M. (1917). Results of the South Australian Museum expedition to Strzelecki and Cooper Creeks September and October 1916: Insecta. *Transactions of the Royal Society of South Australia* **41**, 489–630.

Lever, R.J.A.W. (1946). Entomological notes. *Agricultural Journal of Fiji* **17,** 9–15.

McKeown, K.C. (1947). Catalogue of the Cerambycidae of Australia. *Memoirs of the Australian Museum* **10,** 1–190.

Newman, E. (1840). Entomological notes: Coleoptera, Cerambycites. *The Entomologist* **1**, 1–16.

Newman, E. (1842). List of longicorns collected at Port Philip, South Australia, by Edmund Higgins. *The Entomologist* **22,** 351–354.

Wang, Q. (1993)a. A revision of *Atesta* Pascoe (Coleoptera: Cerambycidae, Phoracanthini) from Australia, with descriptions of eighteen new species. *Invertebrate Taxonomy* **7**, 961–1024.

Wang, Q. (1993)b. *Paratesta* gen.n. (Coleoptera: Cerambycidae) from Australia. *Journal of the Austalian Entomological Society* **32**, 369–377.

Wang, Q. (1994)a. The monotypic genus *Epithora* Pascoe (Coleoptera: Cerambycidae: Phoracanthini) from Australia: taxonomic review and ecological notes. *Giornale Italiano di Entomologia* **7,** 79–86.

Wang, Q. (1994)b. 'Systematics, Biogeography and Ecology of Australian Phoracanthine Borers (Coleoptera: Cerambycidae)'. PhD thesis, La Trobe University, Melbourne.

Wang, Q. (1995)a. The Australian longicorn beetle genus *Skeletodes* Newman (Coleoptera: Cerambycidae). *The Coleopterists Bulletin* **49**, 109–118.

Wang, Q. (1995)b. A taxonomic revision of the Australian genus *Phoracantha* Newman (Coleoptera: Cerambycidae), *Invertebrate Taxonomy* **9**, 865–958.

Wang, Q. (1996). *Phytrocaria* Wang, a new genus of Phoracanthini, with a new species from Australia (Coleoptera: Cerambycidae: Cerambycinae). *The Coleopterists Bulletin* **50** in press

Wang, Q., Thornton, I.W.B. and New, T.R. (1994). Systematics and biogeography of the Australian-New Guinean genus *Thoris* Pascoe (Coleoptera: Cerambycidae: Phoracanthini). *Invertebrate Taxonomy* **8,** 839–860.

Webb, G.A. (1987). Larval host plants of Australian Cerambycidae (Coleoptera) held in some Australian insect collections. *Forestry Commission of New South Wales Technical Paper* **8**, 1–19.

Benthic Foraminiferal Assemblages in the Clyde River Estuary, Batemans Bay, N.S.W.

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COTTER, K.L. Benthic foraminiferal assemblages in the Clyde River Estuary, Batemans Bay, N.S.W. Proc. Linn. Soc. N.S.W. 116, 193–208

The Clyde River Estuary was sampled to determine the distribution of foraminiferal assemblages. The River was sampled (34 localities) from its tidal limit at Shallow Crossing to the bridge at Batemans Bay, a distance of 41.25 kilometres. Thirty-six species (belonging to 21 genera) of foraminiferids were identified. The benthic populations of foraminifera were examined using Q-mode cluster analysis, the Fisher α Index and the constancy or presence of species. Three Assemblages were distinguished. These were the Upper Estuary Assemblage characterised by Textulariina and two assemblages from the Lower Estuary: Group A characterised by *Ammonia beccarii* and *Elphidium craticulatus*; and Group B which has these species but also a large Miliolidae content. The controlling factors on foraminiferal distribution are salinity, substrate and nutrient supply. Salinity controls the dominance of arenaceous foraminifera in the Upper Estuary and the limit to which calcareous forms can penetrate into lower salinity levels; the miliolinids are also constrained by salinity; nutrient supply appears to control the abundance of some species. The grain size of the substrate can be linked to the distribution of some species.

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KEYWORDS: estuary, foraminifera

INTRODUCTION

Previous studies of foraminifera in Australia include examinations of collections from Victoria, South Australia and Tasmania (Chapman, 1907, 1941; Parr, 1932, 1945). Later studies of estuarine environments include those in Western Australia from Oyster Harbour, near Albany (McKenzie, 1962) and the Hardy Inlet (Quilty, 1977). In Victoria foraminiferal distribution in Port Phillip Bay (Collins, 1974) and the Gippsland Lakes System (Apthorpe, 1980) have been studied.

Along the south-east coast of New South Wales, foraminiferal assemblages are known in Port Hacking (Albani, 1968), Broken Bay (Albani, 1978) including Pittwater (Johnson and Albani, 1973; Albani and Johnson, 1975), the Minnamurra River (Michie, 1975; 1982) and Lake Illawarra (Yassini and jones, 1989).

The Clyde River Estuary at Batemans Bay, located 285 kilometres south of Sydney, was sampled in September of 1979 and these findings have now been reviewed. The study concentrated on the tidal limit of the river from the bridge at Batemans Bay to Shallow Crossing, a distance of 41.25 kilometres (Fig. 1). The Clyde River was chosen for this study because foraminiferal distribution patterns had been documented further north in the Minnamurra River, NSW (Mitchie, 1975), and in the Gippsland Lakes System, Victoria (Apthorpe, 1980) to the south; the intervening area of coastal New South Wales had not been studied. The Clyde River is situated approximately midway between these two study areas. The only studies completed since 1979 in this region have been a comprehensive study of Lake Illawarra, NSW (Yassini and jones, 1989) which is again further to the north and the Malacoota Inlet, Victoria (Bell and Drury, 1992) to the south. The study aimed to define the benthic foraminiferal assemblages in the Clyde River Estuary and so provide a more comprehensive analysis of the south-east coast of Australia.

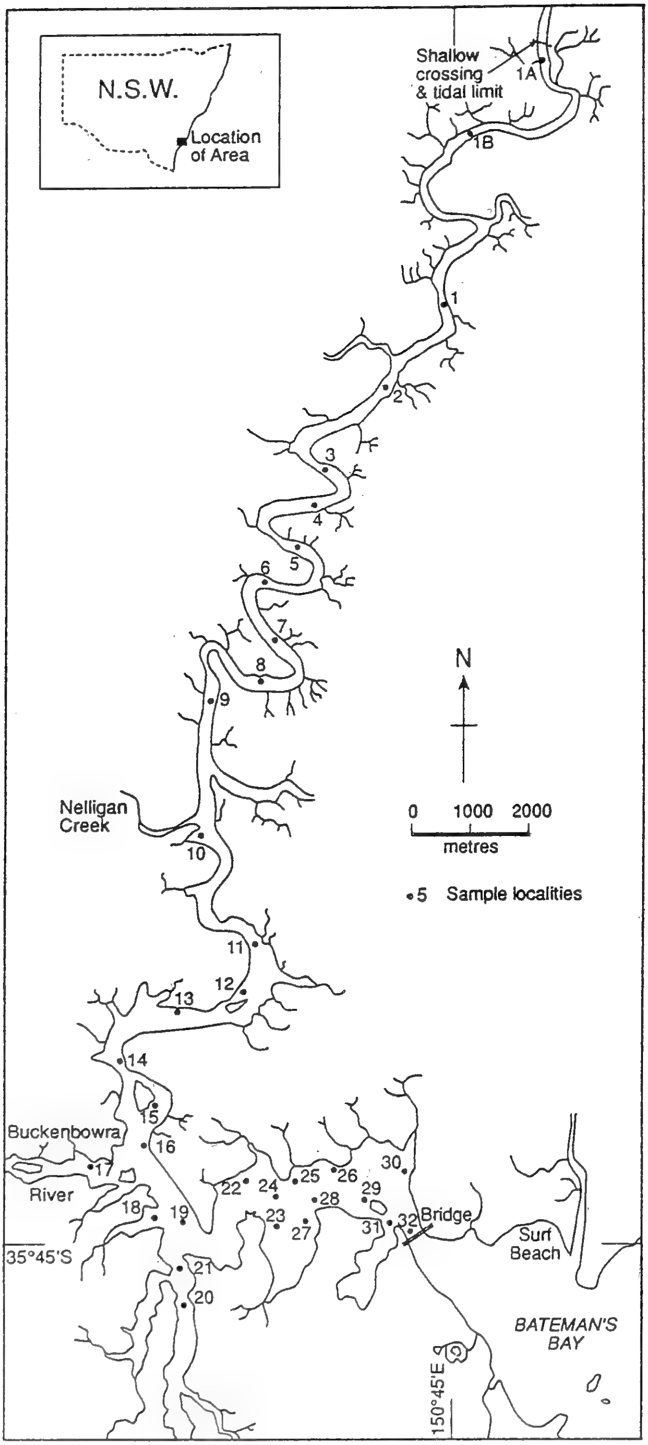

Fig. 1. Map of the Clyde River Estuary showing sample localities.

PARAMETERS OF THE CLYDE RIVER ESTUARY

The Clyde River rises in the Sassafras Tableland north of the Buddawang Range and travels southeast approximately parallel to the coast. At latitude 35°45´S the River turns east and broadens and slows leading to an increase in mangroves before emptying into Batemans Bay. Shallow Crossing marks the tidal limit of the river (Fig. 1). Lag gravel deposits extend downstream to a point between localities 4 and 5 where mud becomes an important part of the sediment. Sand-sized grains, and sediments of a larger grain-size, are found in the midstream along the length of the river while mud and silt sized particles occupy the areas near the banks. localities 9, 13, 16, 19, 21, 24 and 32 are located in central positions in the channel with grain sizes from gravel to coarse and fine sand.

The bathymetry of the Clyde River estuary is unknown and depth is only known for the sample localities. Most localities averaged 1–2m in depth the exceptions being those localities situated midstream in the tidal channel: 9 (6.4m), 13 (7.0m), 16 (4.5m), 19 (4.5m), 21 (7.0m), 24 (4.5m), and 32 (7.25m) Turbidity readings proved to be very variable from clear to 3m to turbid from the surface. The southeast coast of N.S.W. has a warm temperate climate with a seasonal distribution of rainfall with maximum precipitation in Autumn resulting in an average annual rainfall of 1000mm. Water temperature at a depth of one metre ranged from 10.5°C to 15°C in September. There was little difference between surface and bottom water temperatures.

There is a small tidal range in the Clyde River and all sampling was completed on a falling tide of 1 .6m in September. Salinity readings were taken at the time of sampling and ranged from 0‰ at locality lA (Shallow Crossing) to 32‰ at locality 32.

The river drains a State forest in its upper reaches. Down stream there is grazing activity around the small settlement of Nelligen and the expanding tourist industry in Batemans Bay has brought recreation to the river in the form of water skiing, fishing and recreational boating. A thriving oyster industry is located around the mangrove areas in the lower estuary.

METHODS

Sampling was completed from a small boat using a Phleger Corer. Once retrieved, the sample was placed in a plastic bag, labelled and a solution of 50:50 formaldahyde and distilled water was added. During the collection of samples readings of depth were taken using an echo sounder, a Y.S.I Model 33 S.C.T Meter was used to measure salinity and temperature with a Martek Mark V Water Quality Analyser used to measure pH. In the laboratory samples were washed through a set of three sieves 420µm, 125µm, 75µm and residue from each wash dried at approximately 35°C and allowed to cool. Foraminifera were picked using a fine brush under a binocular microscope. The 75µm fraction was found to contain only a few juveniles (which are a problem to identify as features are indistinct) so this fraction was not examined fully. A coarse fraction (>420µm) of 100cm^3 and a fine fraction (<420µm but >1 25µm) of 50cm were picked, identified and counted from each sample locality. Species classification (Appendix) conforms with Loeblich and Tappan (1988), and with Collins (1974), Parr (1945) and Albani (1968, 1978, 1979) as additional Australian references. Nine of the 34 sample localities were barren of foraminifera.

The foraminiferal population was studied as a total population because the staining of living tissue using Rose Bengal proved to be unreliable, as found by others (Arnold, 1974; Erskian and Lipps, 1977; Quilty, 1977). It has been found that in marginal marine environments dead assemblages closely resemble living ones (Nichols and Ellison, 1967; Nichols and Norton, 1969; Apthorpe, 1980) and these assemblages are considered to be stable over time (Scott and Medioli, 1980). The Clyde River Estuary is a microtidal environment, where vertical mixing is caused by cellular circulation, and little reworking is

Locality

	4	5	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	25	26	27	28	29	30	31	32
Millammina fusca	6	2	35	6	1	6	1	2	13	1	4	14	1	11										1	
Leptohalysis								2	1																
Protoschista findens	13	6	46	2	2	2		2	6		1	9		1		4	1		1						
Haplophragmoides australensis	6				1				3			3	1	2											
Haplophragmoides canariensis	2	1	1						2																
Trochamminita irregularis	1	1							1																
Ammobaculites agglutinans										1		2			3										
Ammobaculites barwonensis														1	5									1	
Tritaxis conica												2													
Trochammina inflata	2								4	1				1					1						
Spiroloculina lucida																		9				1		10	
Massilina secans tropicalis																								1	1
Quinqueloculina poeyana																		2	19				7	22	2
Quinqueloculina pseudoreticulata																								6	
Quinqueloculina seminula																		5	7					57	1
Quinqueloculina subpolygona																		5	3				2	2	1
Flintina ?sp.																		9	4				2	2	2
Triloculina oblonga																2	1	23	16				3	11	4
Triloculina sp. cf. *T. trigonula*																							3	1	2
Discorbis australis															5				1		4				
Rosalina australis																		1	10		1		9	1	
Cibicides phillipensis																4	3							5	
Cibicides refulgens																		2	3						7
Nonion depressulus																18	5								
Nonionella auris														4	4	30	13	2	24	6			7	11	1
Ammonia beccarii									1	1				261	621	638	222	43	54	1551	1472	20	190	178	42
Ammonia tepida																5	3		3	57	14			9	
Cribrononion simplex														3	3	64	9		5				1	3	
Elphidium advenum														21	143	112	47	15	10	39	54		9	30	16
Elphidium craticulatus														113	148	654	246		4	87	122	1	1	17	2
Elphidium crispum															5	14		5	6					8	11
Elhidium depressulum														1	6	30	9				8			1	1
Elphidium jenseni																4							10	36	10
Elphidium limbatum																10	3								
Elphidium macellum																	1	1					3	7	3

TABLE 1

Distribution of benthic foraminifera in the Clyde River Estuary expected. The cellular circulation also prevents the formation of a salt wedge penetrating upstream. The benthic foraminifera were treated as a total population and indeed a sampling in January illustrated this point, as very little change was found in the distribution of benthic foraminifera between January and September.

DISTRIBUTION OF FORAMINIFERIDS

A total of 36 benthic species were recovered from the Clyde River Estuary. The distribution of these foraminiferids is indicated in Table 1. Samples from localities 1A to 19 contained varying numbers of foraminifera. These ranged from zero specimens per 10cm^3 of sediment (localities: 1A, 1B, 1, 2, 3, 6, 9, 13) to 5.7 per 10cm^3 of sediment (locality 7). The agglutinated foraminiferids are represented by a total of eleven species and form the only component in localities 4 to 16 (salinity readings 1‰ to 25.5‰). Dominant species include: *Protoschista findens, Miliammina fusca* and *Eggerella australis*. This distribution is common in marginal marine areas and has been found where similar estuarine conditions prevail (Albani, 1968; Murray, 1973; Erskian and Lipps, 1977; Quilty, 1977).

Foraminiferal numbers increase rapidly from locality 20 downstream, especially in the mangrove areas, with 25 species represented. This increase ranged from 1.5 specimens per 10cm^3 of sediment (locality 29) to 116.7 and 116.0 per 10cm^3 of sediment (locality 27 and 22 respectively). The Rotaliina dominate this section of the river with *Ammonia beccarii, Elphidium craticulatus* and *Elphidium advenum* the dominant species. *Ammonia beccarii* a widespread euryhaline species inhabiting a broad range of temperature and salinity conditions (Murray, 1991) and often constitutes the dominant species of foraminifera in estuarine environments (Cann and De Deckker, 1981). Maximum abundance of *Ammonia beccarii* occurs in the mangrove areas where oyster leases are also located (localities 20, 21, 22, 23, 25, 26, 27, 28). These areas have a substrate of fine mud and this species has been found in similar conditions elsewhere in Australia (Johnson and Albani, 1973; Apthorpe, 1980; Yassini and Jones, 1989) and on other continents (Murray, 1976; 1991).

Seven *Elphidium* spp. are confined to localities 20 to 32 (salinities range from to 27‰ to 32‰) and identification is often difficult because of extreme intraspecific variation. This group is found on mud and sand substrates with an increase in numbers of *Elphidium craticulatus, E. advenum* and *E. depressulum* on the mud of the mangrove area (localities 20–32, 27 and 28). The miliolina were found in appreciable numbers (6 species) from locality 25 downstream. Miliolina generally prefer marine conditions (Murray, 1973; 1991) and this was reflected in their distribution with salinity readings from 30‰ to 32‰ In the present study the dominant species are represented by *Quinqueloculina seminula, Q poeyana, Flintina* ?sp. and *T. oblonga* and these were found in localities with sand-sized grains.

DISTRIBUTION OF ASSEMBLAGES

Several methods of analysis were used to determine the foraminiferal assemblages in the Clyde River Estuary: Q-mode cluster analysis, the Fisher α Index and the constancy or presence of species. Q-mode cluster analysis (Fig. 2) identified three distinct foraminiferal assemblages. Only benthic foraminifera were used as is the custom in previous analysis of this type (Howarth and Murray, 1969; Johnson and Albani, 1973; Albani and Johnson, 1975; Erskian and Lipps, 1977). Planktonic foraminifera live in the water column and are always transported and then deposited representing an allochthonous population (Murray, 1991; Swanberg and Bjørklund, 1992); whereas benthic species from a microtidal environment, such as the Clyde River Estuary, are accumulated

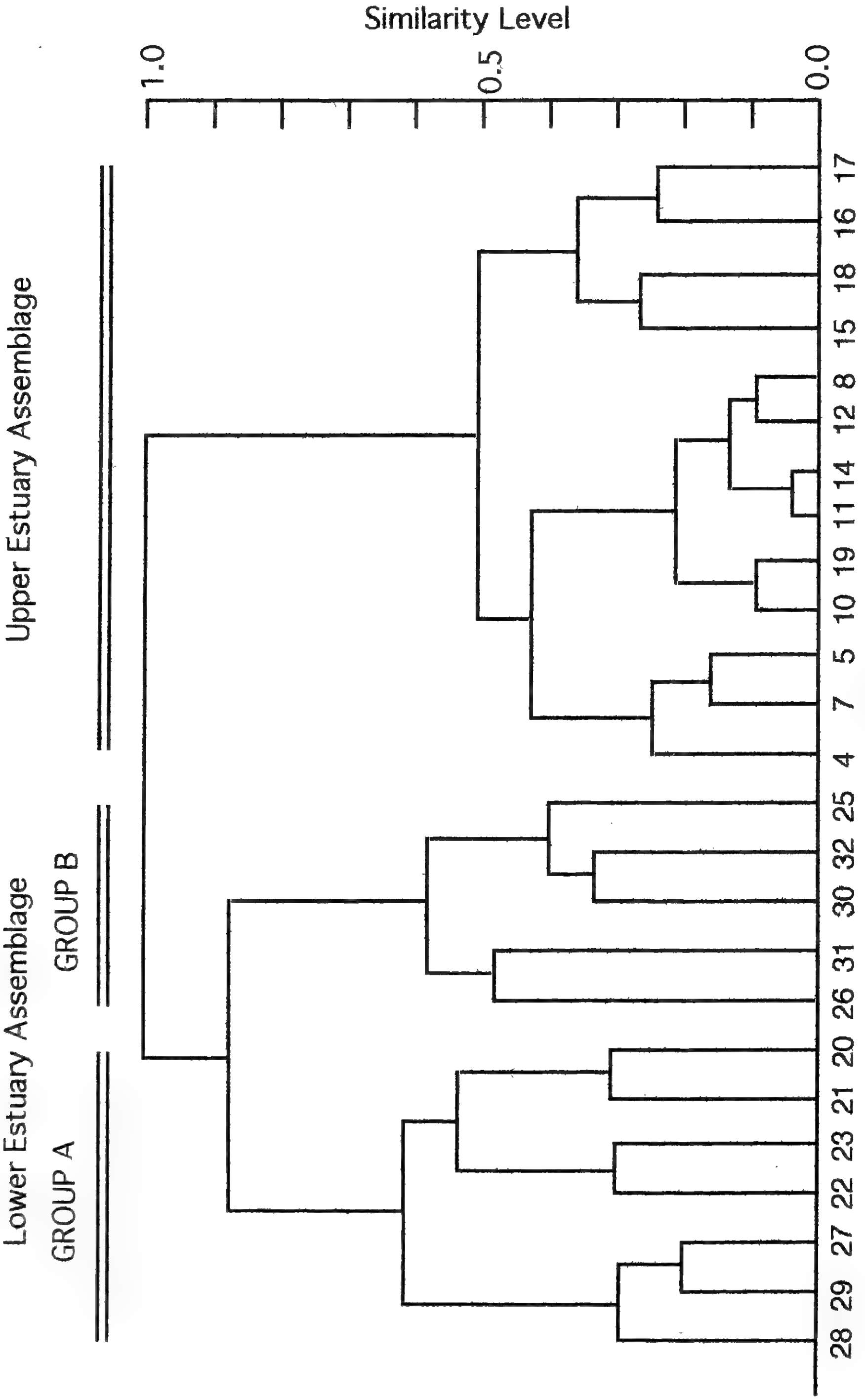

Fig. 2. Q-mode cluster analysis dendrogram of those localities producing benthic foraminifera.

in bottom sediments close to where they live. All 36 benthic species were selected for analysis by Q-mode cluster analysis. When rare species from only a limited number of sites, representing 1% or less of the population (Michie, 1978), were qualitatively analysed a similar distribution of asssemblages was found.

The Fisher α Index (Michie, 1987; Murray, 1991) compares numbers of species and gives a numerical measure of diversity. The benthic foraminifera were examined using this Index to provide a further quantitative analysis of the data. The Fisher α Index revealed that for localities 4 to 19 the diversity was very low in the range of $\alpha <1.0$ to α 1.0. Localities 20 to 32 showed diversities of between α 3.0 and α 4.5. Diversities of α 4.5 to α 11.0 are found in normal marine conditions (Murray, 1973).

The constancy or presence of species was calculated as a percentage using the expression $C = 100p/P$, where p is the number of samples containing the species and P is the total number of samples studied (Sanchez Ariza, 1983; Bell and Drury, 1992). This expression identifies constant species (>50% of sample locality) accessory species (25–50%) and accidental species (<25%) and was calculated for each Assemblage deliniated by the Q-mode cluster analysis.

The Fisher α Index and the calculation of species constancy confirmed the Assemblages delineated using Q-mode cluster analysis. The three foraminiferal assemblages (Fig. 3) in the Clyde River Estuary are: the Upper Estuary Assemblage (localities 4 to 19), and two assemblages in the Lower Estuary — Group A (localities 20, 21, 22, 23, 27, 28, 29) and Group B (localities 25, 26, 30, 31, 32).

Upper Estuary Assemblage

This Assemblage has a low diversity of foraminifera with a textulariid fauna dominating this part of the river. An example of this distribution is represented by locality 10 where *Miliammina fusca, Protoschista findens* and *Eggerella australis* represented 86% of the fauna and at locality 18 these three species represent 89%. These species are the most abundant taxa in all localities in the Upper Estuary with two accessory species (25–50% of sample localities) *Haplophragmoides canariensis* and *H. australiensis*

Lower Estuary Assemblage

This Assemblage (localities 20 to 32) has a more complicated pattern and diversity is higher than in the Upper Estuary Assemblage. These localities are dominated by *Ammonia beccarii, Elphidium craticulatus, Elphidium advenum, Cribronion simplex,* and *Nonionella auris.*

The Group A Assemblage is confined to the southern shore of the river. Apart from the dominant species above, *Elphidium Depressulum* and *Ammonia tepida* were present in over 50% of the sample localities. A small number of accessory species (25–50% of the sample) *Protoschista findens*, *Eggerella australis*, *Ammobaculities rostratus*, *Triloculina oblonga*, *Discorbis australis*, *Elphidium crispum*, *E. limbatum* and *Nonion depressulum* are present in this Assemblage. The textulariids that extend into this Assemblage are represented by at most four specimens and are dominated by the Rotaliina.

The Group B Assemblage spreads from the channel under the bridge (locality 32) and along the northern shore of the estuary and has a large miliolina component (9 species) which is absent in localities further upstream. locality 25 contained 44% milolinid species with 30% at locality 31. The dominant species, present in over 50% of the sample localities, are *Quinqueloculina seminula*, *Q. poeyana, Flintina* ?sp., *Triloculina oblonga*, *T.* sp. cf. *T. trigonula*, *Rosalina australus*, *Cibicides reflugens*, *Elphidium crispum*, and *E. macellum*. This assemblage contains very few accessary species (25–50% of samples) with only *Elphidium jenseni* and *Spiroloculina lucida* represented.

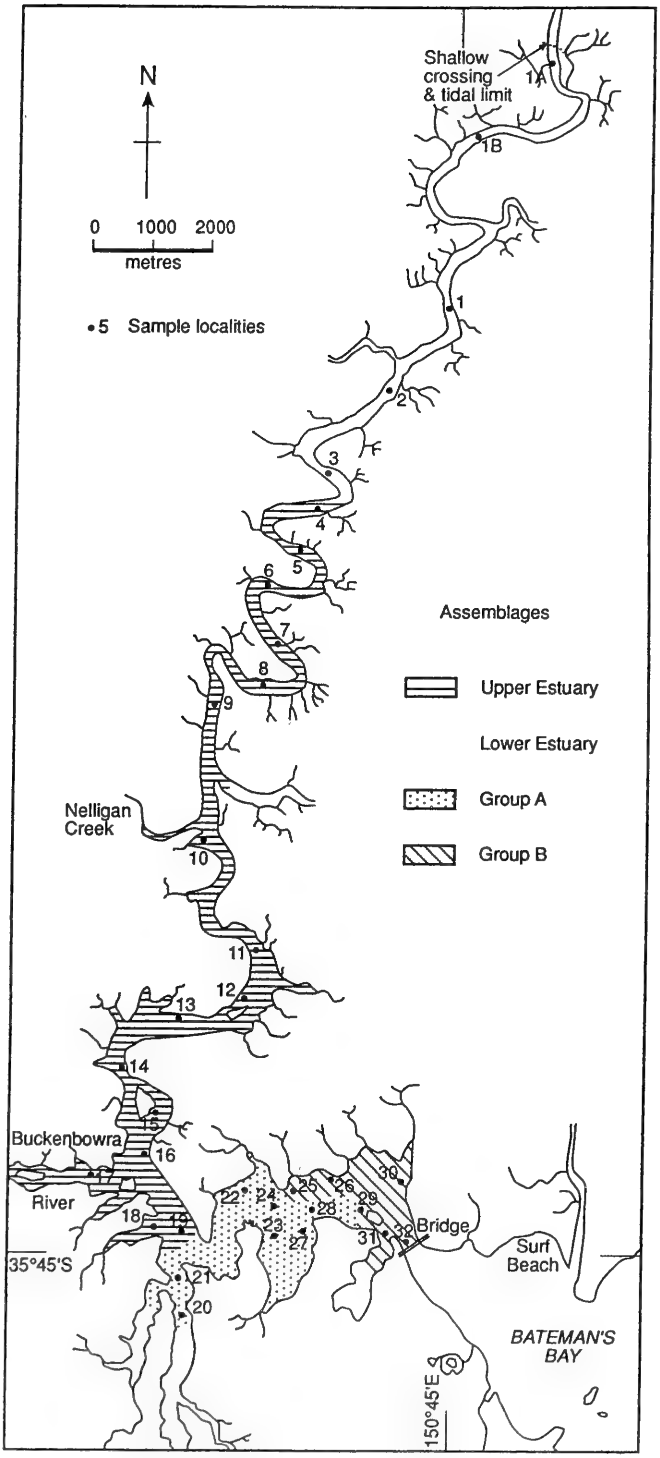

Fig. 3. Benthic foraminiferal assemblages in the Clyde River Estuary.

DISCUSSION

The factors which control distribution of foraminifera in the Clyde River Estuary include salinity, substrate and nutrient supply. Salinity controls the dominance of arenaceous foraminifera in the Upper Estuary and the limit to which calcareous forms can penetrate into lower salinity levels; the miliolina are also constrained by salinity; nutrient supply appears to control the abundance of some species. The association of some species with a particular substrate grain size is discussed below.

Salinity was found to be an important limiting factor of species distribution in the Estuary. The species of foraminifera found are known to be euryhaline; however, the miliolina in the lower Estuary Assemblage are found in a minimum salinity of 30‰ (32‰ marine conditions). Further spot sampling out into the Bay showed that the Lower Estuary Assemblage Group B extends further in that direction. The agglutinated foraminifera are restricted to salinities lower than 28‰ and it is only at higher salinities that calcareous forms begin to appear in large numbers. The two examples of Rotaliina *(Ammonia beccarii)* found in localities 17 and 18 have thinner tests than those found further downstream and this may be the result of lower calcium levels.

Substrate types are known to be a factor in the distribution of invertebrates and it has been shown that sediments rich in clays and muds support a higher density microfauna than larger sediments (Carricker, 1967). With an increase in silt and clay sized particles the number of microfaunal species increases, as does the population density. A sediment analysis revealed that sediment type is associated with the distribution of some foraminifera. In the Clyde River Estuary *Ammonia beccarii* is found in areas with a smaller grain size, the *Elphidium* spp. are found associated with a range of grain sizes while miliolina are only found in areas of larger grain size. Similar findings in the Western Pacific margin have been discussed by Murray (1991). As the population of foraminifera in the river are treated as a total population it is difficult to determine whether the tests are responding to the sedimentary environment, or to the nutrient supplies at that particular locality, or some other unidentified factor. Swanberg and Bjørklund (1992) present evidence which suggests that various sedimentary environments tend to selectively preserve different types of tests. If this is the case then there is a direct response of shell, size and form to the substrate. Several localities did not yield any specimens. The ones present upstream may have been the result of low salinity (localities 1A–3, 6, 9 and 13) the one further downstream (locality 24) is in the tidal channel and the Phleger Corer does not always penetrate coarser sediments (Murray, 1991). locality 29, however, situated in the channel, did yield a small number of tests.

Ammonia spp. and *Elphidium* spp. are known to be herbivores or detritus feeders on mud substrates as these contain an abundance of organic detritus, bacteria and epiphytes (Lipps and Valentine, 1970; Murray, 1991). The largest numbers of these foraminifera in the Clyde River are found in the mangrove areas which have a small sediment size and oyster leases are also present which may contribute to an increased nutrient supply. A similar distribution of foraminiferids has been found in a mangrove environment in other studies (Ludbrook, 1961; Nichols and Norton, 1969).

The benthic foraminiferal assemblages in the Clyde River Estuary can be compared with other studies on the south-east coast of Australia. In Broken Bay NSW, (Albani, 1978) seven biotopes are recognised. The Fluviomarine (B5) Biotope identified by Albani (1978), situated at the entrance to Broken Bay and penetrating upstream, can be compared with the Clyde River Lower Estuary-Group B Assemblage. The species in common are *Quinqueloculina subpolygona. Triloculina oblonga, Elphidium crispum, E. depressulum* and *Cibicides refulgens*. Broken Bay and the Clyde River Estuary appear to have a similar distribution of foraminifera, although Broken Bay has a large wide opening to the open ocean. In comparison the Clyde River has a more restricted opening which does not allow the penetration of the miliolina upstream as in Broken Bay. The Upper Estuary Assemblage of the Clyde River Estuary is absent from Broken Bay which does not have a long meandering river system like the Clyde and the arenaceous fauna are therefore absent. However, further sampling in the Hawkesbury River may reveal this fauna further upstream.

In the Gippsland Lakes system (Apthorpe, 1980) salinity was found to be the most important controlling factor influencing the distribution of foraminifera. A Semi marine Fauna produced ten different miliolina, the most common being *Quinqueloculina seminulum*, and *Triloculina trigonula*, with *Elphidium advenum, E. macellum* and *Ammonia aoteanus* (which Apthorpe (1980) considers is a possible cool temperate water morphotype of *A. beccarii),* all of which are also found in the Clyde River Estuary in a similar environmental and areal distribution. The extent of the Gippsland Lakes System makes comparison difficult and only general statements are possible. The arenaceous fauna is controlled by salinity in both systems with *Elphidium* spp. represented on both sandy and muddy substrates as in the Clyde River.

The coastal lagoon of Lake Illawarra NSW (Yassini and Jones, 1989) has four distinct assemblages. Although both this area and the Clyde River Estuary have a restricted tidal circulation the areal extent of each is very different and comparison is not a simple matter. The long meandering nature of the Clyde River for much of its length confines the textulariids to this low salinity region regardless of the substrate. Both show a dominant Miliolidae assemblage in areas of marine salinity and sandy substrate.

Definition of the benthic foraminiferal assemblages in the Clyde River Estuary provides a more detailed analysis of the south-east coast of Australia. Comparison with other studies described above, which are to the north and south of the Clyde River Estuary, allow a comprehensive understanding of not only foraminiferal distribution but also the factors which control that distribution. There is an association between salinity levels and the distribution of Textulariina, Miliolina and Rotaliina foraminifera. The grain size of the substrate and nutrient supply appear to be linked to the distribution of some foraminifera in the Clyde River Estuary.

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REFERENCES

Albani, A.D. (1968). Recent Foraminiferida from Port Hacking, NSW. *Contributions to the Cushman Foundation for Foraminiferal.Research* **19**, 85–119.

Albani, A.D. (1978). Recent Foraminifera of an estuarine environment in Broken Bay, NSW. *Australian Journal of Marine and Freshwater Research* **29**, 355–398.

Albani, A.D. (1979). Recent Foraminifera from New South Wales. *Australian Marine Sciences Association Handbook* **3**, 1–57.

Albani, A.D. and Johnson, K.R. (1975). Resolution of foraminiferal biotopes in Broken Bay, NSW. *Journal of the Geological Society of Australia* **22**, 435–446.

Apthorpe, M. (1980). Foraminiferal distribution in the estuarine Gippsland Lakes System, Victoria. *Proceedings of the Royal Society of Victoria* **91**, 207–232.

Arnold, Z. M. (1974). Field and laboratory techniques for the study of living foraminifera. In 'Foraminifera Vol. 1' (Eds. R.H. Hedley and C.G. Adams) pp. 153–206. (Academic Press: London).

Bell, K.N. and Drury, S.R. (1992). The foraminiferal fauna of Mallacoota Inlet, East Gippsland, Victoria. *The VictorianNaturalist* **109**, 7–16.

Cann, J. H. and De Deckker, P. 1981. Fossil Quaternary and living foraminifera from Athalassic (non-marine) saline lakes, southern Australia. *Journal of Paleontology.* **55**, 660–670.

Carricker, M.R. (1967). Ecology of estuarine benthic invertebrates: A Perspective. In 'Estuaries' (Ed. C.H. Lauf) pp. 442–487 (American Association for the Advancement of Science Publication No.83).

Chapman, F. (1907). Recent foraminifera of Victoria: some littoral gatherings. *Journal. Quekett Microscopical Club* **10**, 117–146.

Chapman. F. (1941). Report on foraminifera soundings and dredgings of the F.I.S. Endeavour along the continental shelf of S.E. coast of Australia. *Transactions of the Royal Society of South Australia* **65**, 145–211.

Collins, A.C. 1974. Port Phillip Bay Survey 1957–63: Foraminiferida. *Memoirs of the National Museum of Victoria* **35**, 1–61.

Erskian, M.G. and Lipps, J.H. (1977). Distribution of foraminifera in the Russian River estuary, northern California. *Micropaleontology* **23**, 453–469.

Howarth, R.J. and Murray, J.W. (1969). The foraminiferida of Christchurch Harbour, England: a reappraisal using multivariate techniques. *Journal of Paleontology* **43**, 660–675.

Johnson, K.R. and Albani, A.D. (1973). Biotopes of benthonic foraminifera in Pittwater, Broken Bay, NSW (Australia). *Paleogeography, Palaeoclimatology, Palaeoecology* **14**, 265–276.

Lipps, J.H. and Valentine, J.W. (1970). The role of Foraminifera in the trophic structure of marine communities. *Lethaia* **3**, 279–286.

Leoblich, A.R. and Tappan, H. (1984). Some new Proteinaceous and Agglutinated Genera of Foraminifera. *Journal of Paleontology* **58**, 1158–1163.

Leoblich, A.R. and Tappan,H. (1988). 'Foraminiferal Genera and their Classification'. (van Nostrand Reinhold: New York).

Ludbrook, N.H. (1961). Stratigraphy of the Murray Basin in South Australia. *Geological Survey of South Australia Bulletin* **36**, 1–96.

McKenzie, K.G. (1962). A record of Foraminifera from Oyster Harbour near Albany, Western Australia. *Journal of the Royal Society of Western Australia* **45**, 117–132.

Michie, M.G. (1975). Biotopes of benthic Foraminifera in the Minnamurra River, N.S.W. B.Sc. (Hons) thesis, University of Woolongong.

Michie, M.G. (1978). Data manipulation in cluster analysis and the concept of zero presence. *Mathematical Geology* **10**, 335–345.

Michie, M.G. (1982). Use of the Bray-Curtis similarity measure in cluster analysis of foraminiferal data. *Mathematical Geology* **14**, 661–667.

Michie, M.G. (1987). Distribution of Foraminifera in a macrotidal tropical estuary: Port Darwin, Northern Territory of Australia. *Australian Journal of Marine and Freshwater Research* **38**, 249–259.

Murray, J.W. (1973). 'Distribution and Ecology of Living Benthic Foraminiferids'. (Heinemann Educational Books: London).

Murray, J.W. (1976). Comparative studies of living and dead benthic foraminiferal distributions. In 'Foraminifera Vol. 2' (Eds. R.H. Hedley and C.G. Adams) pp. 45–109. (Academic Press: London).

Murray, J.W. (1991). 'Ecology and Palaeoecology of Benthic Foraminifera'. (Longman Scientific and Technical: London).

Nichols, M.M. and Ellison, R.L. (1967). Sedimentary patterns of microfauna in a coastal plain estuary. In 'Estuaries' (Ed. G.H. Lauff) pp. 283–288. (American Association Advancement of Science Special Publication 83).

Nichols, M.M. and Norton, W. (1969). Foraminiferal populations in a coastal plain estuary. *Paleogeography, Paleoclimatology, Paleoecology* **6**, 197–213.

Parr, W.J. (1932). Victoria and South Australian shallow-water foraminifera. *Proceedings of the Royal Society of Victoria* **44**, 218–234.

Parr, W.J. (1945). Recent foraminifera from Barwon Heads, Victoria. *Proceedings of the Royal Society of Victoria* **56**, 189–218.

Quilty, P.G. (1977). Foraminifera of Hardy Inlet, south-western Australia. *Journal of the Proceedings of the Royal Society of Western Australia* **59**, 79–90.

Sanchez Ariza, M.C. (1983). Specific thanatocoenoses of Recent planktonic foraminifera of the neritic zone in the Motril-Nerja area, Spain, as a function of depth diversity and constancy. *Journal of Foraminiferal Research* **13**, 277–282.

Scott, G.H. and Medioli, F.S. (1980). Living vs total foraminiferal populations: their relative usefulness in paleoecology. *Journal of Paleontology* **54**, 814–832.

Swanberg, N.R. and Bjørklund, K.R. (1992). The radiolarian fauna of western Norwegian fjords: a multivariate comparison of the sediment and plankton assemblages. *Micropaleontology* **38**, 57–74.

Yassini, I. and Jones, B.G. (1989). Estuarine foraminiferal communities in Lake Illawarra, N. S. W. *Proceedings of the Linnean Society of New South Wales* **110**, 229–266.

APPENDIX

Taxonomic Notes

Brief notes on selected species are presented below either because their identification presented problems or their presence is of note.

Order: FORAMIMFERIDA Eichwald, 1830
Suborder: TEXTULARIINA Delage and Hérouard, 1896
Family: HORMOSINIDAE Haeckel, 1894
    Genus: *Leptohalysis* Loeblich and Tappan, 1984
        Leptohalysis sp.
        (Figure 4., No. 5.)
        Remarks: This is a small delicate species described by Collins (1974) as *Reophax* sp. A from Port Phillip Bay. Victoria. It is similiar to *R. catella* Höglund, 1947 but is smaller with a larger number of chambers. The species has also been described by Bell and Drury (1992) as *Leptohalysis* sp. occurring in Western Port and the Mallacoota Inlet, Victoria. Leoblich and Tappan (1984) transferred the *R. scotti* group to which this species is related to the Genus *Leptohalysis*. Three specimens are present at localities 14 and 15 in the Clyde River Estuary and these resemble *Leptohalysis* sp. (Bell, 1994, pers. comm.)

Suborder: MILIOLINA Delage and Hérouard, 1896
Family: HAUERINIDAE Schwager, 1876
    Genus: Flintina Cushman, 1921
        Flintina ?sp.
        (Figure 5., No.4.)
        Remarks: This is a very distinctive species with rounded inflated chambers and a broadly rounded periphery. It appears to have a triloculine arrangement of chambers. The porcelaneous, imperforate wall has many fine striae running longitudinally. The aperture is large with a bifed tooth and is flush with the surface. This individual may represent an early stage of this (Loeblich and Tappan, 1988). It is present in localities 25, 26, 30–32 and represented by 19 specimens.
    Genus: *Triloculina* d'Orbigny, 1826
        Triloculina sp. cf. *T. trigonula* Lamarck, 1804
        (Figure 5., No.1.)
        Remarks: This species resembles *T. trigonula* in every respect except that the apertural lip projects in onto the stem of the bifed tooth. It is present in localities 30–32 and represented by six specimens.

The following is a list of the remaining species of benthic foraminifera recovered from the Clyde River Estuary at Bateman's Bay. Classification follows that of Loeblich and Tappan (1988).

Suborder: TEXTULARIINA Delage and Hérouard, 1896
Family: RZEHAKINIDAE Cushman, 1933
    Genus: *Miliammina* Heron-Allen and Earland, 1930
        Miliammina fusca Brady, 1870

Family: THOMASINELLIDAE Loeblich and Tappan. 1984
    Genus: *Protoschista* Eimer and Fickert, 1899
        Protoschista findens Paker, 1870

Family: HAPLOPHRAGMOIDIDAE Maync,1952
    Genus: *Haplophragmoides* Cushman, 1910
        Haplophragmoides australensis Albani, 1978
        Haplophragmoides canariensis d'Orbigny, 1839
    Genus: *Trochamminita* Cushman, Cushman and Brönnimann, 1948
        Trochamminita irregularis Cushman and Brönnimann, 1948

Family: LITUOLIDAE de Blainville, 1827
    Genus: *Ammobaculites* Cushman, 1910
        Ammobaculites agglutinans d 'Orbigny, 1846
        Ammobaculites barwonensis Collins, 1974

Family: TROCHAMMINIDAE Scwager, 1877
    Genus: *Tritaxis* Schubert, 1921
        Tritaxis conica Parker and Jones, 1865
    Genus: *Trochammina* Parker and Jones, 1859
        Trochammina inflata Montagu, 1808

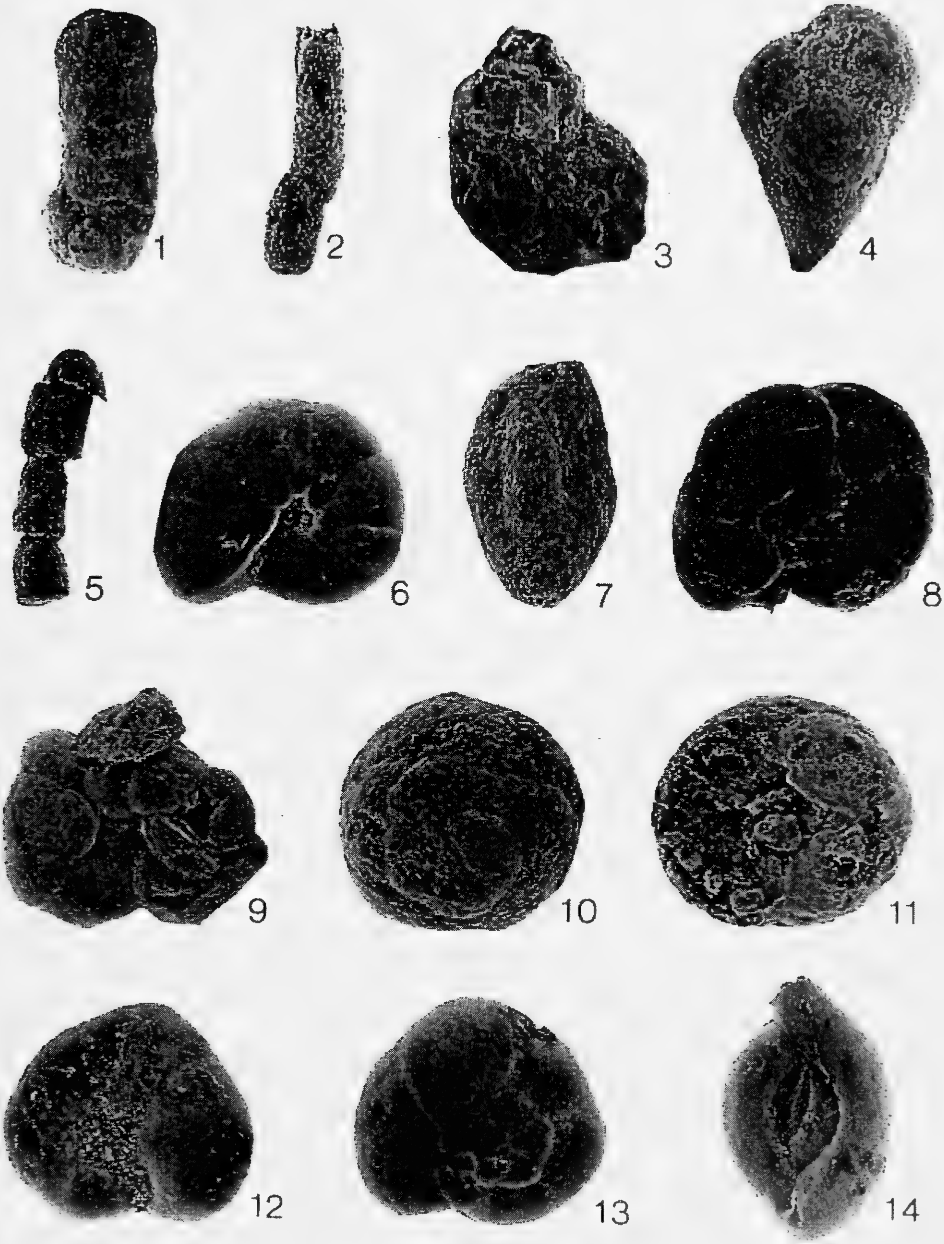

Fig. 4. **1.** *Ammobaculites agglutinans*, x55; **2.** *Protoschista findens*, x45, deformed specimen; **3.** *Ammobaculites barwonensis*, x56; **4.** *Miliammina fusca*, x60; **5.** *Leptohalysis* sp., x100, top chamber broken; **6.** *Haplophragmoides canariensis*, x50; **7.** *Eggerella australis*, x71; **8.** *Haplophragmoides australensis*, x32; **9.** *Trochamminita irregularis*, x50; **10,11.** *Tritaxis conica*, x68, spiral and umbilical views; **12,13.** *Trochammina inflata*, *x55*, umbilical and spiral views; **14.** *Spiroloculina lucida*, x31.

Family: EGGERELLIDAE Cushman, 1937
Genus: *Eggerella* Cushman, 1935
Eggerella australis Collins, 1958

Suborder: MILIOLINA Delage and Hérouard, 1896
Family: SPIROLOCULINIDAE Wiesner, 1920
Genus: *Spiroloculina* d'Orbiguy, 1826
Spiroloculina lucida Cushman and Todd, 1944

Family: HAUERINIDAE Schwager, 1876
Genus: *Massilina* Schlumberger, 1893
Massilina secans tropicalis Collins, 1958
Genus: *Quinqueloculina* d'Orbiguy, 1826
Quinqueloculina poeyana d'Orbigny. 1939
Quinqueloculina pseudoreticulata Parr, 1941
Quinqueloculina seminula Linné, 1758
Quinqueloculina subpolygona Parr, 1945
Genus: *Triloculina* d'Orbiguy, 1826
Triloculina oblonga Montagu, 1803

Suborder: ROTALIINA Delage and Hérouard, 1896
Family: PEGIDIIDAE Heron-Allen and Earland, 1928
Genus: *Discorbis* Lamarck, 1804
Discorbis australis Parr, 1932

Family: ROSALINIDAE Reiss, 1963
Genus: *Rosalina* d'Orbigny, 1826
Rosalina australis Parr, 1932

Family: CIBICIDINAE Cushman, 1927
Genus: *Cibicides* de Montfort, 1808
Cibicides phillipensis Collins, 1974
Cibicides reflugens de Montfort, 1808

Family: NONIONIDAE Schultze, 1854
Genus: *Nonion* de Montfort, 1808
Nonion depressulus Walker and Jacob, 1798
Genus: *Nonionella* Cushman, 1926
Nonionella auris d'Orbigny, 1839

Family: ROTALIIDAE Ehrenberg. 1839
Genus: *Ammonia* Brünnich, 1772
Ammonia beccarii Linné, 1758
Ammonia tepida Cushman. 1926

Family: ELPHIDIIDAE Galloway, 1933
Genus: *Cribrononion* Thalmann, 1947
Cribrononion simplex Cushman, 1933
Genus: *Elphidium* de Montfort, 1808
Elphidium advenum Cushman, 1922
Elphidium craticulatus Fichtel and Moll, 1798
Elphidium crispum Linné, 1758
Elphidium depressulum Cushman, 1933
Elphidium jenseni Cushman. 1924
Elphidium limbatum Chapman, 1909
Elphidium macellum Fichtel and Moll, 1738

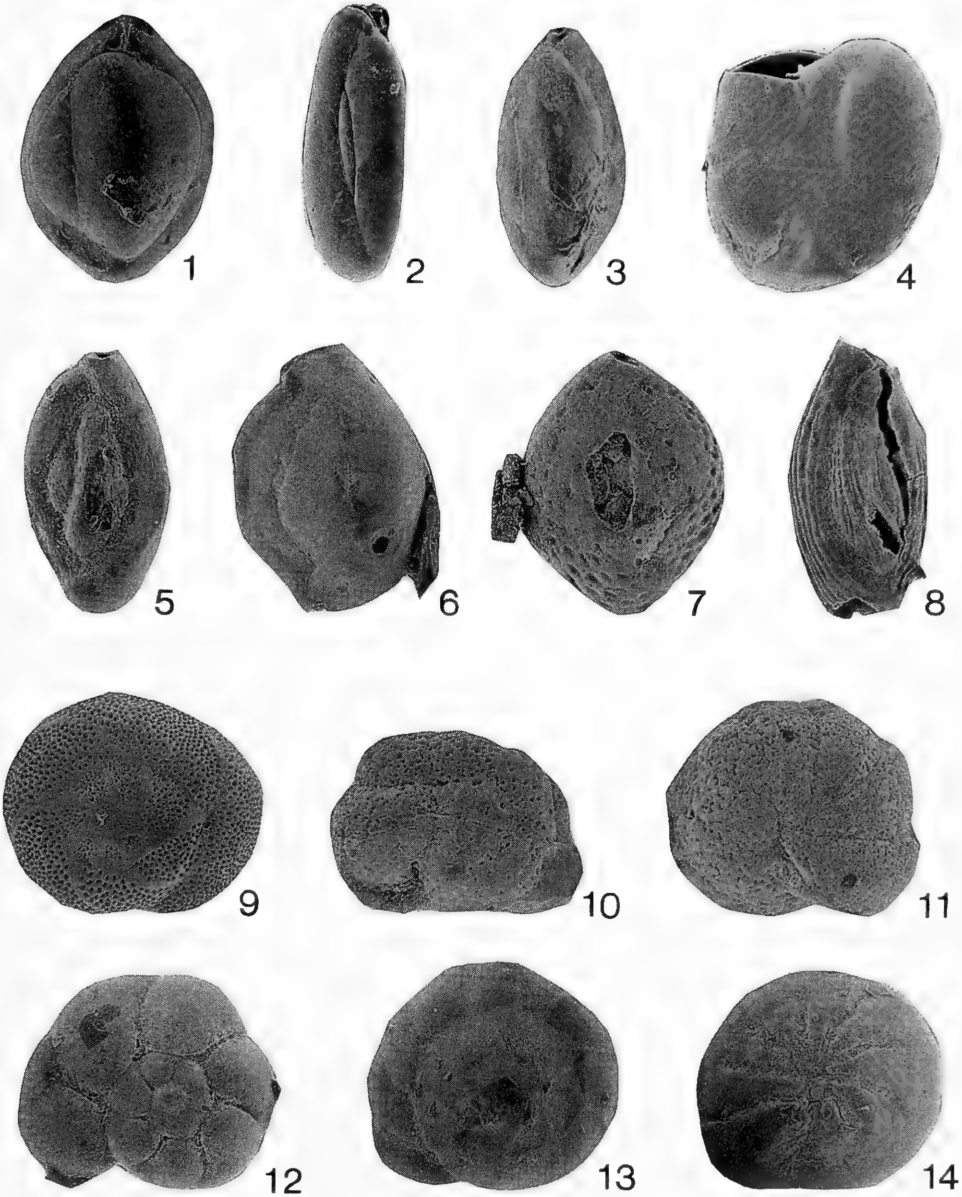

Fig. 5. **1.** *Triloculina* sp. cf. *trigonula*, x58, showing aperture; **2.** *Triloculina oblonga* x68; **3.** *Quinqueloculina seminula* x35; **4.** *Flintina* ?sp., x33. showing aperture; **5.** *Quinqueloculina subpolygona* x30; **6.** *Massilina secans tropicalis* x70; **7.** *Quinqueloculina pseudoreticulata* x28, damaged specimen; **8.** *Quinqueloculina poeyana* x55, damaged specimen; **9.** *Discorbis australis*, x46; **10.** *Rosalina australis*, x52; **11.** *Cibicides phillipensis*, x47; **12.** *Cibicides reflugens*, x48; **13,14.** *Ammonia beccarii*, x45, spiral and umbilical views.

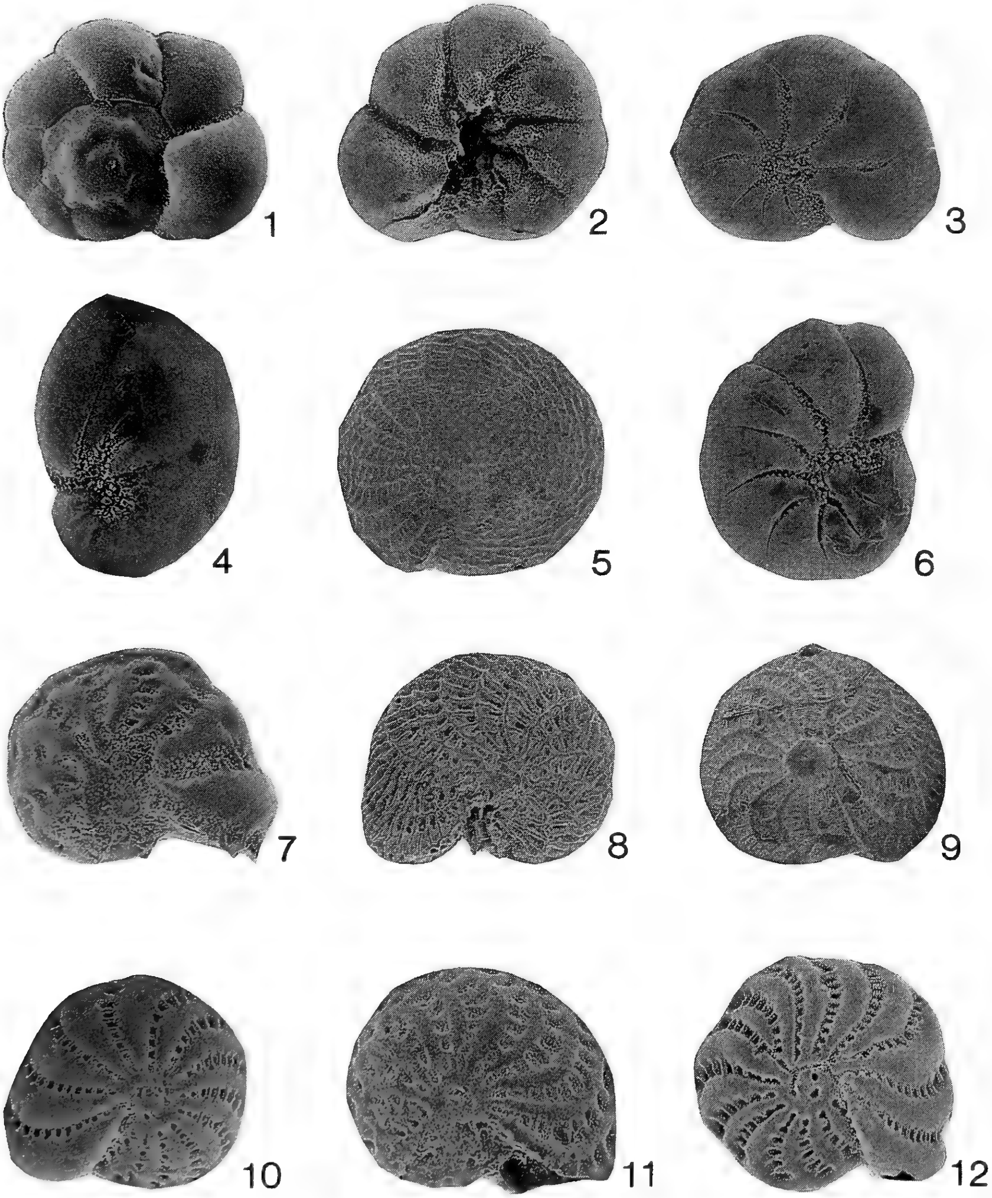

Fig. 6. **1,2.** *Ammonia tepida* x83, spiral and umbilical views; **3.** *Nonionella depressulus,* x85; **4.** *Nonionella auris* x78; **5.** *Elphidium craticulatus*, x22; **6.** *Cribrononion simplex*, x76; **7.** *Elphidium limbatum*, x41; **8.** *Elphidium jenseni,* x33; **9.** *Elphidium macellum* x60; **10.** *Elphidium advenum* x84; **11.** *Elphidium crispum* x38; **12.** *Elphidium depressulum* x78.

The Effects of Spatial Constraints on Fish Shoal Cohesion

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Using shoals of four individuals, the effects of different experimental treatments on the movement behaviour and group cohesion of mullet were examined. Mean swimming speeds significantly increased with the presence of a patch of weed, whilst mean turning frequencies significantly increased as tank size decreased. Mean interfish distances and separation angles did not vary significantly between different treatments.

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KEYWORDS: mullet, shoaling behaviour, group cohesion, tank size.

INTRODUCTION

Although many aspects of fish schooling and shoaling behaviour have been previously investigated through controlled laboratory experiments (see review by Pitcher and Parrish 1993), there is limited information available concerning the effects of housing conditions on shoaling behaviour. The aim of the present study was to examine the effects of tank size and structural complexity (the presence or absence of vegetation), on the swimming behaviour of individuals and overall group cohesion. Kleerekoper et al. (1970) reported that as tank size decreased, swimming speeds of individuals decreased and turning rates increased. Tank size has also been shown by other workers to affect swimming speed and group polarity (Inagaki et al. 1976, Sakamoto et al. 1976, Aoki 1980). Andorfer (1980) found that structural complexity, in the form of a centrally located cylinder, had a concentrating effect on groups. However, no study to date has examined the behaviour of identified group members. This study differed from previous studies by concentrating on known focal individuals within groups over a range of different treatments.

MATERIALS AND METHODS

Juvenile mullet, *Mugil cephalus,* (mean fork lengths 68 to 82mm) were caught by seine net in a freshwater creek at Karana Downs, southeast Queensland. Fish were transported to the laboratory and placed in filtered aquaria. A total of 24 fish were used in a six block experiment conducted over a period of 14 days. Each block consisted of a shoal of four individuals, which were subjected to three treatments: control tank (110 x 110 x 30cm), reduced tank (55 x 55 x 30cm), and structured tank (110 x 110 x 30cm with a centrally located 30 x 30 x 10cm patch of artificial weed). The tanks were filled to a depth of 15cm. The order of the trials was randomised, with no shoal being subjected to more than one trial per day. All individuals remained identifiable by slight differences in size and body patterns. Home tanks housed four fish (all from a given block) between trials. Trials were carried out between 1000 and 1400h under conditions of natural light, water temperature remained constant at 22 ± 2°C. The bottom of both tanks was opaque white to provide maximum contrast for video analysis. At the beginning of each trial, fish were removed from the home tank, placed in the test tank, and left undisturbed for 50 minutes prior to video recording. Each group was filmed for 10 minutes using a National Panasonic video camera suspended above the centre of the tank. A sequence of 100 frames (1 frame = 1 sec) was chosen at random from a 10 minute recording. A Dapple II-GS Image Analyser was used to digitise the co-ordinates of each fish's head and tail. A BASIC program was used to calculate mean swimming speeds (body lengths s^{-1}), mean direction of movement (degrees) from headings of individual fish using circular statistics, and mean interfish distances (body lengths). Separation angle (degrees) was calculated from mean direction of movement, and represented a measurement of the polarisation of individuals within the group. Mean turning frequencies were obtained from plots of swimming trails, and log-transformed prior to analysis to stabilise the variance. A two-way ANOVA with Tukey's multiple range test was used to analyse significant differences between treatments. All analyses were performed using generalised linear procedures (SAS Institute 1986).

RESULTS

Tank size and the presence of 3-D structure had a significant effect on mean swimming speeds and turning frequencies ($F = 8.59$, $p < 0.005$; $F = 239. 12$, $p < 0.0001$ respectively). Multiple range testing indicated that mean swimming speeds were significantly higher when a structure was present. Mean swimming speeds did not differ significantly between groups in the reduced tank and control treatments (Fig. 1). Mean turning frequencies were significantly higher in the reduced tank compared to the control and structured treatments (by factors of 2.6 times and 2.0 times respectively).

Mean interfish distances and separation angles did not vary significantly between treatments according to the two-way ANOVA ($p > 0.05$) (Fig. 1). Separation angle, a measure of the polarisation of the individuals within the group, was highest in the smaller tank and lowest in the structured tank. Individuals within each treatment maintained an interfish distance of approximately 0.95 body lengths.

DISCUSSION

Previous studies have recorded the schooling and shoaling behaviour of fish within tanks without taking into consideration tank size or structure. This study found that swimming speeds and turning frequencies were significantly influenced by both tank size and structural complexity. Swimming speeds decreased and turning frequencies increased with a reduction in tank size. Individuals in the smaller tank performed slow moving circles covering only short distances, which may have been due to the limited swimming area available to the fish, as observed by Kleerekoper et al. (1970).

Fish within the smaller tank performed more turns compared to those in the control and structured tanks, probably because they had a higher chance of encountering the walls of the tank. Inagaki et al. (1976), suggested that the polarity of fish in schools would be affected by tank size, due to fish depolarising when they encountered a wall, and then repolarising as they moved away. Results obtained in this study suggested that tank size and the presence of a structure had a definite, although not statistically significant, effect on the behaviour of individuals, as well as on the abilities of the individuals to co-ordinate their movements in a cohesive manner. Tank size and structural complexity should be considered when analysing interactive fish behaviour so that analysis of movement behaviour (swimming speeds and turning frequencies) and group cohesion (interfish distances and separation angles) is not biased by these conditions.

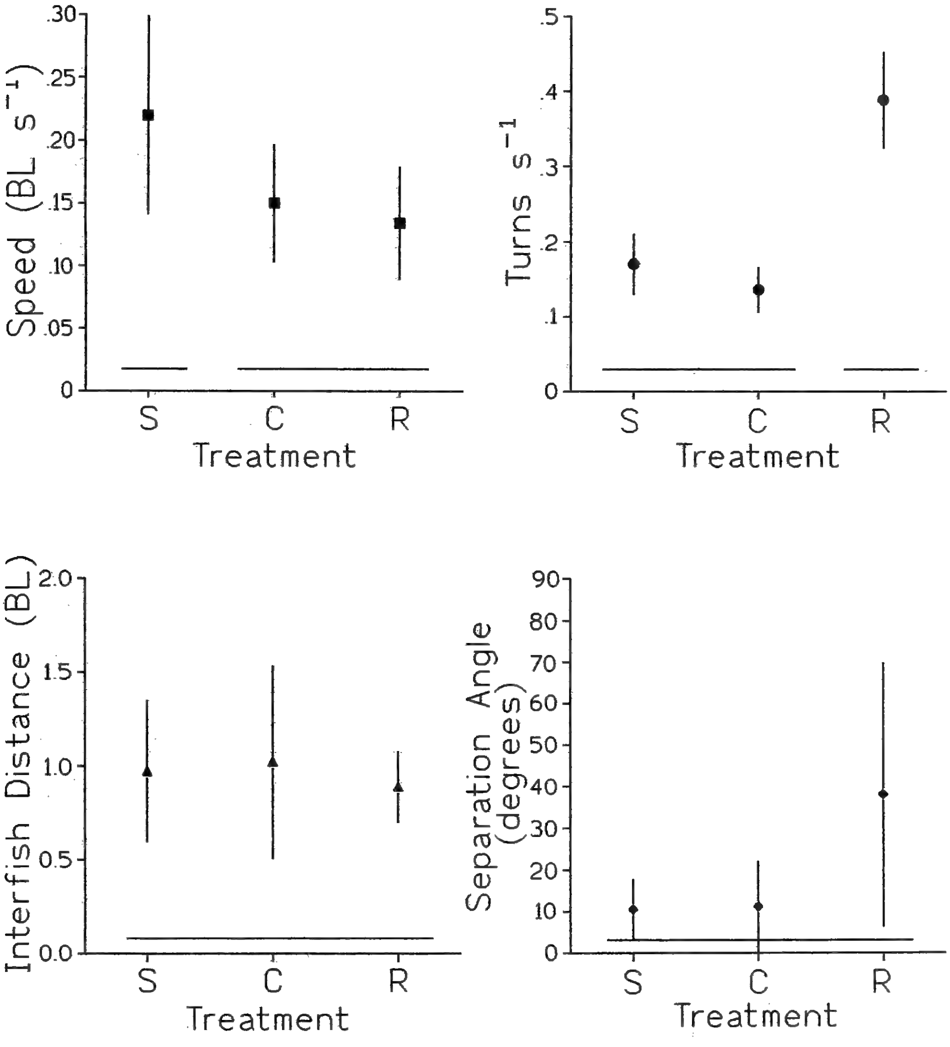

Fig. 1. The effects of treatment on mean swimming speed (body length s^{-1}), mean turning frequency (turns s^{-1}), interfish distance (BL) and separation angle (degrees). S = Structured Tank, C = Control Tank, R = Reduced Tank. Filled symbols and vertical lines indicate means and standard errors for pairs of fish, and horizontal lines connect treatments which did not differ significantly at the 5% level according to the two-way ANOVA.

REFERENCES

Andorfer, B. (1980). The schooling behaviour of *Leucaspius delineatus* (Heckel) in relation to ambient space, and the presence of a pike *(Esox lucius). Oecologica* **47**, 137–140.

Aoki, I. (1980). An analysis of the schooling behaviour of fish: internal organization and communication process. *Bulletin of the Ocean Research Institute, University of Tokyo* **12**, 1–64.

Inagaki, T. Sakamoto, W. and Aoki, I. (1976). Studies on the schooling behaviour of fish III. — Mutual relationship between speed and form in schooling behaviour. *Bulletin of the Japanese Society of Scientific Fisheries* **42**, 629–635.

Kleerekoper, H., Timm, A.M., Westlake, G.F., Davy, F.B., Malar, T. and Anderson, V.M. (1970). An analysis of locomotor behaviour of goldfish *(Carassius auratus). Animal Behaviour* **18**, 317–330.

Pitcher, T.J. and Parrish, J.K. (1993). Functions of Shoaling Behaviour in Teleosts. In 'Behaviour of Teleost Fish 2nd Edition' (Ed. T.J.Pitcher) (Chapman and Hall: London).

Sakamoto, W., Inagaki, T. and Kuroki, T. (1976). Studies on the schooling behaviour of fish IV. — Some discussions concerning continuity of swimming speed and response time of individuals. *Bulletin of the Japanese Society of Scientific Fisheries* **43**, 1083–1091.

SAS Institute (1986). 'SAS User's Guide: Statistics'. (SAS Institute: Cary, North Carolina).

Amino Acid Racemisation Dating of a Last Interglacial Estuarine Deposit at Largs, New South Wales

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A Late Pleistocene age of 103 ± 15.5 ka BP is assigned to an estuarine shell bed at Largs in the lower Hunter Valley, New South Wales. The numeric age is based on the extent of leucine racemisation in the arcoid bivalve *Anadara trapezia* and a model of apparent parabolic racemisation kinetics. Although characterized by contrasting racemisation rates within and between genera, the relative extent of racemisation for the amino acids alanine, aspartic acid, glutamic acid, lysine, phenylalanine and proline are in accord with values previously reported for fossil molluscs from last interglacial coastal deposits in southern Australia. The amino acid racemisation data reported here provide a firmer basis with which to correlate the Largs estuarine deposit to the last interglacial maximum (ca. 134 to 118 ka BP; substage 5e of the marine $\delta^{18}O$ record).

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KEYWORDS: amino acid racemisation; last interglacial; New South Wales; Quaternary Period.

INTRODUCTION

Since the early observations of Abelson (1954, 1956) that protein residues may remain in fossils for considerable intervals of time, an extensive literature has emerged on the application of time-dependent amino acid racemisation reactions to Quaternary dating (Miller and Brigham-Grette 1989; Murray-Wallace 1993; Wehmiller 1993). Earlier reviews of the method are provided by numerous workers (Kvenvolden 1975; Schroeder and Bada 1976; Williams and Smith 1977; Davies and Treloar 1977; Wehmiller 1984). In this paper we apply the amino acid racemisation method to assess the age of an estuarine shell bed at Largs, near the town of Maitland in the lower Hunter Valley, New South Wales.

In the protein of living organisms, amino acids are bound in peptides as left-handed molecules (L-amino acid: *laevorotatory*), a phenomenon that has been related to enzymic reactions (Williams and Smith 1977). With death, the enzymic reactions that formerly maintained the disequilibrium condition cease (i.e. exclusively L-amino acids) and amino acids then slowly and progressively interconvert from a left-handed to a right-handed counterpart (D-amino acid: *dextrorotatory*). This process is termed amino acid racemisation. The interconversion of L- to D-amino acids continues until an equilibrium mixture is attained (i.e. D/L = 1). Depending on the nature of the materials and the diagenetic temperature history, this process can take several hundred thousand years.

The Largs deposit was first described by David and Etheridge in 1890 and in view of the importance of this site for reconstructions of the Late Quaternary environmental history of eastern Australia, has been the subject of other investigations (Iredale 1951;

Murray-Wallace et al. 1988; Thom and Murray-Wallace 1988; Leary 1992). Host to a diverse assemblage of intertidal to shallow subtidal molluscs, the deposit provides a rare opportunity in eastern Australia to quantify sea-level during the last interglacial maximum (substage 5*e* of the marine oxygen isotope record). Despite earlier attempts (Murray-Wallace et al. 1988; Thom and Murray-Wallace 1988), reliable numeric ages for this deposit have remained elusive. This work presents the results of amino acid racemisation analyses for a wider range of mollusc genera than previously reported from this site (Murray-Wallace et al. 1988), as well as a numeric age for the deposit based on a model of apparent parabolic racemisation kinetics (Mitterer and Kriausakul 1989; Murray-Wallace and Kimber 1993). The age assigned to the Largs deposit based on the extent of leucine racemisation, represents the first numeric age assigned to a Late Quaternary deposit in eastern Australia, using the amino acid racemisation method.

METHODS

A trench 4 m in length and 1.5 m deep was excavated in the embankment of a Late Pleistocene river terrace of the Hunter River, near the town of Largs (Grid Reference 693805 Maitland Sheet 1:25 000; Fig. 1). The surfaces of the pit were cleaned with a brush and samples were collected for analysis of the molluscan fossil assemblage and for amino acid racemisation and radiocarbon dating. Sediment samples were also collected for description using a binocular microscope. X-ray diffraction analysis was undertaken to determine aragonite-calcite content of molluscs and to assess sample integrity for dating. Amino acid racemisation analyses followed established methods (Kimber and Griffin 1987; Murray-Wallace 1993) and were undertaken for the total acid hydrolysate for several amino acids. Measurement of the amino acid residues was performed on a Hewlett-Packard 5890A gas chromatograph using a 25m coiled, fused silica capillary column with the stationary phase Chirasil-L-Val. Analyses were generally performed on the hinge region of bivalve molluscs using 1g of shell calcium carbonate. The present day mean annual temperature for the site, a relevant consideration for amino acid racemisation studies, is 17.9°C (Australian Climatic Averages).

THE LARGE SHELL BED

Stratigraphy and sedimentology

A shallow excavation on the footslope of a large embankment revealed four lithologically-distinct units, as previously noted for this site (Iredale 1951; Thom and Murray-Wallace 1988; Figs. 2 and 3). A summary of the stratigraphic and sedimentologic characteristics of the deposit is given here. The basal unit (unit A) consists of 2 m of light grey, fine- to very fine-grained well sorted muddy sand, as revealed through augering in the floor of the pit. Binocular microscope analysis revealed a subangular grain morphology dominated by quartz and lithic fragments. A gradational contact separates unit A from an overlying unit (unit B) of well-sorted fine-grained, mottled quartzose sands that is 1.2 m thick. Whole shells and shell fragments do not occur within this unit. The main shell bed (unit C) overlies mottled quartzose sands, and contains a diverse assemblage of mollusc genera. The unit is of variable thickness ranging between 50 to 65 cm. The sediments comprise well-sorted, predominantly fine-grained, yellowish brown quartz sands. Both articulated and disarticulated bivalve molluscs are common, with the assemblage dominated by the estuarine species *Anadara trapezia.* Calcium carbonate accounts for 60% of the total sediment on a dry weight basis. Thin section analysis revealed that the non-carbonate fraction consisted of 40% quartz, 30% lithic fragments, 25% clay and 5% heavy

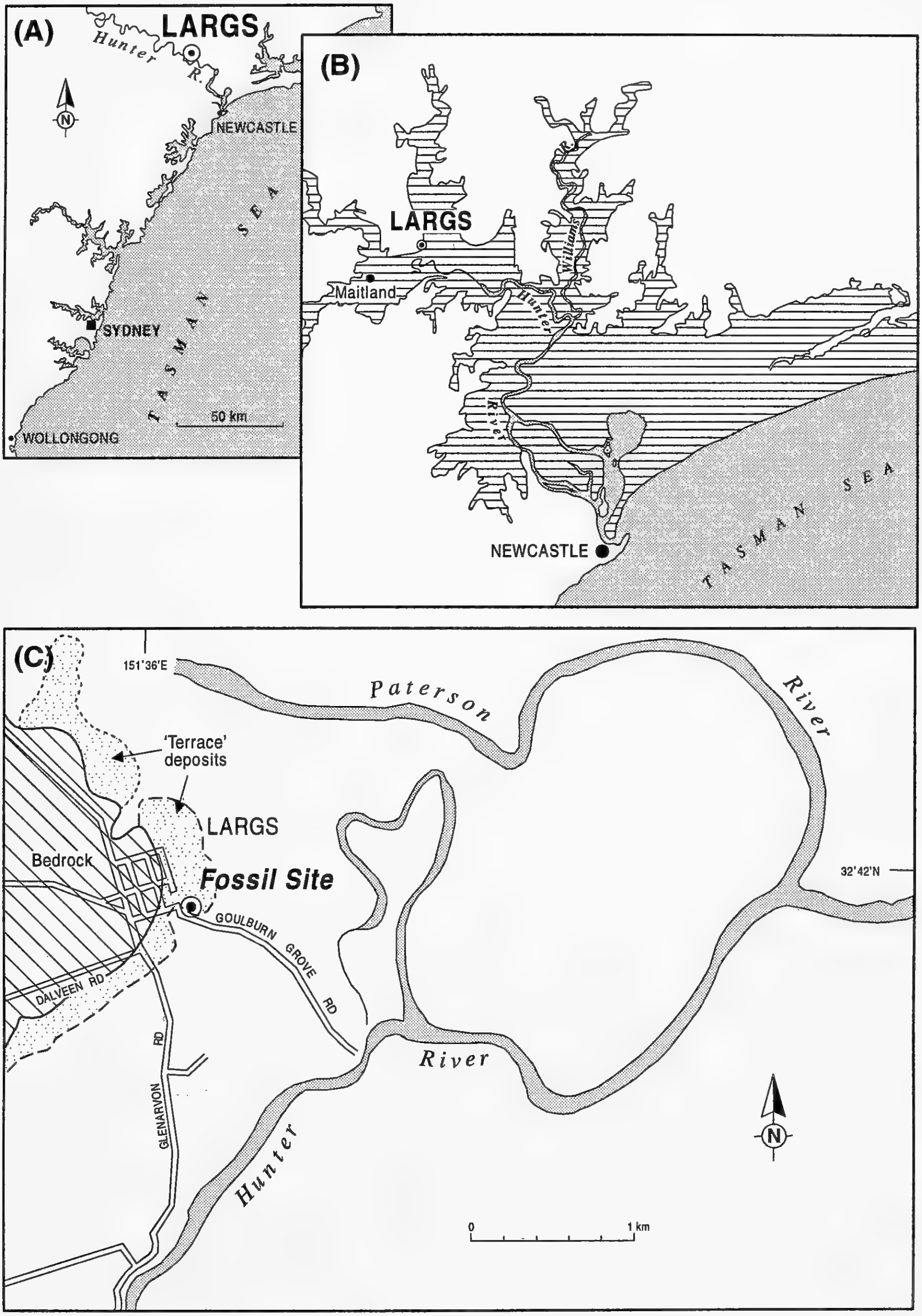

Fig. 1. Location maps showing the general setting of the last interglacial estuarine shell bed at Largs, New South Wales. (a) New South Wales central coast; (b) extent of Late Quaternary deposits in the lower Hunter Valley–Newcastle region, and (c) location of the Largs fossil site (source: Gregory's Newcastle Street Directory, 17th Edition, 1989).

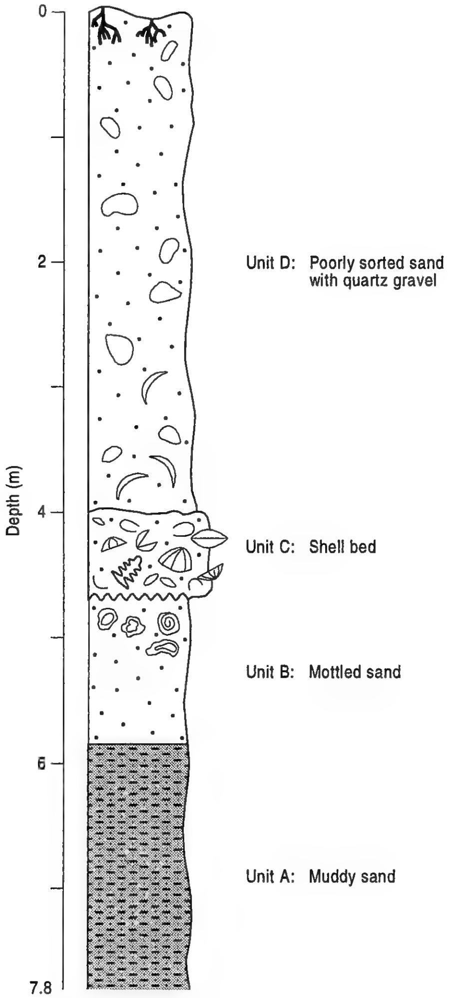

Fig. 2. Measured section of the last interglacial estuarine shell bed at Largs, New South Wales.

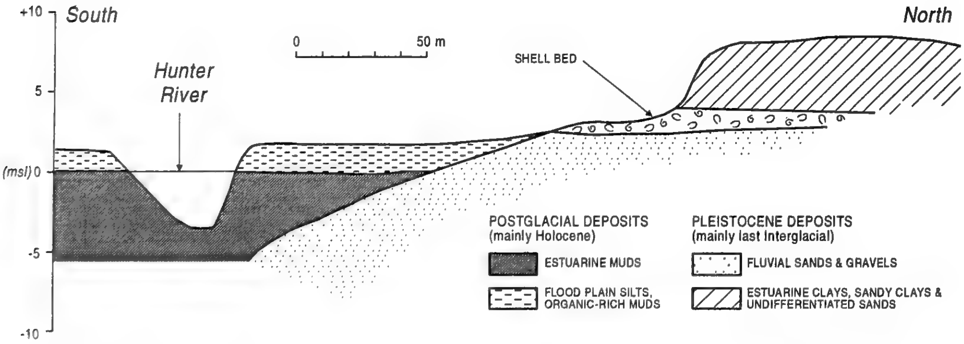

Fig. 3. General stratigraphic relationships of the Largs estuarine deposit (after Roy et al. 1995).

minerals. The quartz component consisted of two distinct populations on the basis of surface morphology; a fine-grained, subrounded to rounded quartz population and a subangular population of very fine to fine-grained size, reflecting windblown marine and fluvial provenances respectively. The shell-rich horizon is interpreted as an estuarine sand with a strong marine influence. Unit C is overlain by up to 4 m of very poorly sorted, greyish brown sand (unit D; Fig. 2). As the excavation was located on the footslope of a large embankment, only 30 cm of this unit was revealed. Shell fragments account for less than 1% of the sediment in unit C. Large angular pebbles of quartz are common.

Fossil molluscs

The shell-rich unit contains an abundant and diverse assemblage of fossil molluscs. The estuarine bivalve *Anadara trapezia* is by far the dominant species (Table 1). The bivalve *Notospisula trigonella* and the gastropod *Nassarius jonasi* also occur abundantly within the deposit. Twenty-six species of molluscs were recovered from the shell bed, although up to 40 species have previously been identified (Iredale 1951; Thom and Murray-Wallace 1988). For the majority of species, the number of individuals identified at any given depth generally did not exceed twenty (Table 1). Articulated bivalves are common in all species from the fragile *Tellina deltoidalis* and *Notospisula trigonella* to the more robust *A. trapezia.* The molluscs represent a death assemblage with *in situ* reworking of the upper portion of the shell bed resulting from wave action. Separate measurements of the length and height of left and right valves of *A. trapezia* ($n = 310$) and *Trichomya hirsuta* ($n = 40$) revealed a bimodal size distribution indicating that the assemblage had not undergone preferential transportation (Leary 1992).

Collectively the species indicate that deposition occurred in an estuarine environment under conditions of moderate to low wave energy. Equal numbers of left and right valves were noted, providing further evidence for quiet water deposition. The species *Anadara trapezia, Scaeochlamys livida* and *Mimichlamys gloriosa* are common on present-day estuarine mudflats. A maximum water cover of 2 m over the shell-rich unit was inferred (Thom and Murray-Wallace 1988), suggestive of a higher sea level of *ca.* 4 ± 1 m during the last interglacial maximum. Members of the genus *Cymatium* are presently found only in warmer water conditions than prevail around the Newcastle region today, indicating warmer temperatures at the time of deposition of the Largs shell bed. The presence of corals of last interglacial age at Grahamstown (Marshall and Thom 1976) is consistent with warmer ocean surface waters by as much as 2°C during this interval (Murray-Wallace and Belperio 1991).

RESULTS AND DISCUSSION

Radiocarbon dating

Six valves of *A. trapezia* collected from the Largs shell bed yielded an uncorrected radiocarbon age of 34,390 ± 370 yr BP (SUA-3008). This result is regarded as a minimum age, reflecting the incorporation during diagenesis of approximately 2% radiocarbon, with a modern activity, which could not be isolated during sample pretreatment. The result is significant, however, for it precludes a Holocene age being assigned to the Largs deposit. A previously reported measurement on a single valve of *A. trapezia* yielded an age of > 37,000 yr BP (Lab. Code: O-1843; Langford-Smith and Thom 1969).

Amino acid racemisation dating

Where possible, well-buried molluscs (i.e. > 1 m) were collected for amino acid racemisation analysis so as to minimize diurnal and seasonal temperature fluctuations,

TABLE 1

Species diversity of fossil molluscs in the last interglacial estuarine deposit, Largs, New South Wales. Depth within the shell bed is taken from the upper-bounding surface of Unit C (see Fig. 2).

Species/depth (cm)	0–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	61–65
Anadara trapezia	a	a	a	e	e	e	e	e	e	e	e	e	e
Antetrichomya problematica		a	a	b	b	b	b	b	a	a			
Barnacle sp.								a	a	a			
Bedeva hanleyi					b			b	b				
Cabestana spengleri										a	a	a	
Corbula sp.				b	b	b	b	b	b	b	b	b	b
Cymatium parthenopeum					a								
Dentalium sp.							a						
Herpetopoma aspersa				a	a	a	b	a	a				
Mactridae sp.					a								
Mimachlamys gloriosa				a	a	a	a	a	a	a	a	a	
Monilea lentiginosa				b	b	b	b	b	b	b	b	b	
Nassarius dorsatus				a	a	a	a	a	a				
Nassarius jonasi				d	d	d	d	d	b	b			
Notospisula trigonella				d	d	e	e	d	d	d	d		
Ostrea angasi								a	a	a	b	b	
Pecten fumatus							a	a	b	b			
Pinna bicolor						a							
Pitar sp.						b	b	b	b	b	b		
Polinicies conicus				a	a	b	b	b	a	a	a		
Polinicies sordidus				a	a	c	b	b	b	b			
Protholathia contessi					b	b	b						
Pyrazus ebeninus							a	a	a				
Scaeochlamys livida				a	a	a	a	a	a	a			
Tellina deltoidalis						a	a	a					
Trichomya hirsuta												b	b

Number of shells: a: 1–9; b: 10–19; c: 20–29; d: 30–39; e: >40 such that longer-term temperature variations associated with climate change were the dominant influence on diagenetic racemisation. To avoid intra-shell amino acid D/L ratio variation, analyses were performed on the hinge region of bivalve molluscs.

Despite some variation related to genus, the extent of racemisation of amino acids in the fossils from the Largs shell bed is representative of values typically obtained for Late Pleistocene fossils from southern Australia (cf., Murray-Wallace et al. 1991; Table 2). The relative extent of racemisation of the different amino acids in each mollusc genus is also in accord with previously published results (Kimber and Milnes 1984). In *Chlamys gloriosa*, the lower extent of racemisation for glutamic acid, leucine and lysine may relate to a genus-effect (Miller and Brigham-Grette 1989). Collectively, however, the extent of racemisation for all amino acids in molluscs from the Largs shell bed is greater than in radiocarbon calibrated specimens of Holocene age from Tom Thumb Lagoon, near Wollongong, New South Wales (Table 2). Comparable extents of racemisation to the specimens of *A. trapezia* from Largs have been noted in *A. trapezia* and the cockle *Katelysia* sp. from other last interglacial coastal deposits in southern Australia (Murray-Wallace et al. 1991; Table 2). An assumption implicit in these correlations is that sites with equivalent current mean annual temperatures are likely to have experienced similar diagenetic temperature histories (Wehmiller 1984).

X-ray diffraction revealed trace quantities of calcite inverted from metastable aragonite in the molluscs dated by radiocarbon and amino acid racemisation. Although this may have influenced the incorporation of younger carbon resulting in the apparent radiocarbon age, the comparable extent of racemisation of amino acids in *A. trapezia* from Largs to those from Port Wakefield in South Australia (Table 2) suggests that the younger carbon introduced to these individuals was not in the form of amino acids. The absence of serine and threonine, two unstable amino acids lost from fossils during early diagenesis supports the integrity of the amino acid racemisation data and indicates that the results are based on indigenous amino acids.

A numeric age for the deposit was derived using the model of apparent parabolic racemisation kinetics of Mitterer and Kriausakul (1989). Accordingly, age is determined by the equation:

$$t = [\ (\mathrm{D/L})_{\mathrm{S}}\ /\ \mathrm{M_c}\ ]^2$$

where t is the calculated age, $(\mathrm{D/L})_{\mathrm{S}}$ is the extent of racemisation in a fossil sample of unknown age and $\mathrm{M_c}$ is the slope of the line defined as $[\ = (\mathrm{D/L})_{\mathrm{cal}}/t^{1/2}]$. In the latter equation, the term $\mathrm{D/L_{cal}}$ refers to the extent of racemisation in a fossil of known age, used to determine the slope ($\mathrm{M_c}$) and $t^{1/2}$ is the square root of fossil age of the calibration sample. An age of 103,000 ± 15,500 yr BP was determined based on the extent of leucine racemisation in *Anadara trapezia* from the Largs shell bed. The error term accounts for a 1°C uncertainty in the diagenetic temperature history. Molluscs of interstadial age (40 ka BP; oxygen isotope stage 3) and also dated by amino acid racemisation and radiocarbon from Gulf St Vincent, South Australia (Murray-Wallace et al. 1993) were used to calibrate this numeric age assessment. The calculated age represents a minimum age estimate and we correlate the deposit with the last interglacial maximum, which based on oxygen isotope chronologies from marine cores and uranium-series dating of emergent coral terraces occurred some 134 to 118 ka BP (Martinson et al. 1987; Stein et al. 1993; Zhu et al. 1993). This is the only time in the Late Quaternary, apart from the Holocene, when sea level was sufficiently high to flood the palaeo Hunter Valley. Given that the Largs estuarine shell bed occurs 2 m above present sea level and that a maximum palaeo water cover of 2 m is inferred (Thom and Murray-Wallace 1988), much of the lower Hunter Valley is likely to have been flooded during the last interglacial maximum.

TABLE 2

Extent of amino acid racemisation (total acid hydrolysate) in molluscs from the last interglacial shell bed at Largs, NSW and in Holocene and modern specimens.

Locality	Species and number of analyses	Age	Amino acid D/L ratio*						
			ALA	ASP	LEU	PHE	GLU	PRO	LYS
Quarantine Bay, NSW	*Anadara trapezia* (n=2)	modern	—	0.11	0.03 ±0.001				
Tom Thumb Lagoon, NSW	*A. trapezia* (n=4)	6750±140 yr cal BP (SUA-3058)	0.32 ±0.001	—	—	0.31 ±0.02	0.18 ±0.004	0.38 ±0.003	—
Largs, NSW	*A. trapezia* (n=4)	~125 ka	0.60 ±0.15	0.55 ±0.07	0.46 ±0.02	0.57 ±0.03	0.36 ±0.02	0.61 ±0.09	0.47 ±0.08
Largs, NSW	*Antetrichomya problematica* (n=2)	~125 ka	0.56 ±0.02	0.70 ±0.06	0.54 ±0.03	0.58 ±0.02	0.40 ±0.02	0.56 ±0.05	0.54 ±0.04
Largs, NSW	*Chlamys gloriosa* (n=l)	~125 ka	0.58	0.69	0.25	0.41	0.26	0.53	0.37
Largs, NSW	*Pinna bicolor* (n=l)	~125 ka	—	0.66	0.45	0.47	0.34	0.70	0.58
Largs, NSW	*Pyrazus ebeninus* (n=l)	~125 ka	0.49	0.69	0.29	0.37	0.47	0.45	—
Largs, NSW	*Trichomya hirsuta* (n=l)	~125 ka	0.64	0.71	0.46	0.56	0.38	0.53	0.53
Port Wakefield, Gulf St. Vincent, SA	*A. trapezia* (n=12)	~125 ka	0.67 ±0.02	0.54 ±0.03	0.51 ±0.02	0.73 ±0.06	0.43 ±0.01	—	—
Port Wakefield, Gulf St. Vincent, SA	*Katelysia rhytiphora* (n=6)	~125 ka	0.72 ±0.03	0.46 ±0.02	0.51 ±0.07	0.67 ±0.04	0.38 ±0.04	—	—

* Amino acids: ALA – alanine; ASP – aspartic acid; LEU – leucine; PHE – phenylalanine; GLU – glutamic acid; PRO – proline and LYS – lysine. ± represents 1 σ standard deviation for between-shell D/L ratio variation.

Few mollusc-rich coastal deposits of last interglacial age are known to crop out or occur in shallow subcrop along the New South Wales coast (Thom et al. 1992). Thus, the Largs estuarine shell bed represents an important reference section for the last interglacial maximum in eastern Australia and from a geochronological perspective, the deposit represents an important benchmark from which to correlate future possible finds of last interglacial strata, and for terrestrial-marine correlations.

CONCLUSIONS

A numeric age of 103 ± 15.5 ka BP is derived for the Largs estuarine shell bed based on the extent of leucine racemisation in *Anadara trapezia* and a racemisation kinetic model of apparent parabolic kinetics. The Largs shell deposit is here correlated with the last interglacial maximum (substage 5*e* of the marine oxygen isotope record) which occurred some 134 to 118 ka BP. The amino acid racemisation data reported for the last interglacial molluscs in this study represents a contribution to the growing body of data that will permit future researchers to correlate Late Quaternary coastal deposits in southeastern Australia.

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REFERENCES

Abelson, P. H. (1954). Organic constituents of fossils. *Carnegie Institution of Washington, Yearbook.* **53**, 97–101.

Abelson, P. H. (1956). Paleobiochemistry. *Scientific American* (July), 2–7.

Davies, W. D., and Treloar, F. E. (1977). The application of racemisation dating in archaeology: a critical review. *The Artefact* **2**, 63–94.

David, T. W. E., and Etheridge, W. R. (1890). ‘Geology of the Commonwealth of Australia’. (Edward Arnold: London).

Iredale, T. (1951). Recent palaeontology. *Australian Zoologist* **11**, 347–350.

Kimber, R. W. L., and Milnes, A. R. (1984). The extent of racemization of amino acids in Holocene and Pleistocene marine molluscs in southern South Australia: Preliminary data on a time-framework for calcrete formation. *Australian Journal of Earth Sciences* **31**, 279–286.

Kimber, R. W. L., and Griffin, C. V. (1987). Further evidence of the complexity of the racemization process in fossil shells with implications for amino acid racemization dating. *Geochimica et Cosmochimica Acta* **50**, 1159–1161.

Kvenvolden, K. A. (1975). Advances in the geochemistry of amino acids. *Annual Review of Earth and Planetary Sciences* **3**, 183–212.

Langford-Smith, T., and Thom, B. G. (1969). New South Wales coastal morphology. *Journal of the Geological Society of Australia* **16**, 572–580.

Leary, S. (1992). Aminostratigraphy of the Newcastle Bight embayment, with particular reference to a Late Pleistocene deposit at Largs. Unpubl. BSc (Hons) thesis, University of Newcastle, Australia.

Marshall, J. F., and Thom, B. G. (1976). The sea level in the last interglacial. *Nature* **263**, 120–121.

Martinson, D. G., Pisas, N. G., Hays, J. D., Imbrie, J., Moore, T. C., and Shackleton, N. J. (1987). Age dating and the orbital theory of the ice ages: Development of a high-resolution 0 to 300000-year chronostratigraphy. *Quaternary Research* **27**, 1–29.

Miller, G. H., and Brigham-Grette, J. (1989). Amino acid geochronology: resolution and precision in carbonate fossils. *Quaternary International* **1**, 111–128.

Mitterer, R. M., and Kriausakul, N. (1989). Calculation of amino acid racemization ages based on apparent parabolic kinetics. *Quaternary Science Reviews* **8**, 353–357.

Murray-Wallace, C. V. (1993). A review of the application of the amino acid racemisation reaction to archaeological dating. *The Artefact* **16**, 19–26.

Murray-Wallace, C.V., and Belperio, A.P. (1991). The last interglacial shoreline in Australia — A review. *Quaternary Science Reviews* **10**, 441–461.

Murray-Wallace, C.V. and Kimber, R.W.L. (1993). Further evidence for apparent `parabolic' racemization kinetics in Quaternary molluscs. *Australian Journal of Earth Sciences* **40**, 313–317.

Murray-Wallace, C.V., Kimber, R.W.L., Belperio, A.P. and Gostin, V.A. (1988). Aminostratigraphy of the last interglacial in southern Australia. *Search* **19**, 33–36.

Murray-Wallace, C.V., Belperio, A.P., Picker, K., and Kimber, R.W.L. (1991). Coastal aminostratigraphy of the last interglaciation in southern Australia. *Quaternary Research* **35**, 63–71.

Murray-Wallace, C.V., Belperio, A.P., Gostin, V.A. and Cann, J.H. (1993). Amino acid racemization and radiocarbon dating of interstadial marine strata (oxygen isotope stage 3), Gulf St. Vincent, South Australia. *Marine Geology* **110**, 83–92.

Roy, P. S., Hudson, J.P. and Boyd, R.L. (1995). Quaternary geology of the Hunter Delta — an estuarine valley-fill case study. In 'Conference on Engineering Geology of the Newcastle–Gosford Region' (Eds. S.W. Sloan and M.A. Allman) pp. 64–84 (Australian Geomechanics Society: Newcastle).

Schroeder, R.A., and Bada, J.L. (1976). A review of the geochemical applications of the amino acid racemization reaction. *Earth Science Reviews* **12**, 347–391.

Stein, M., Wasserburg, G.J., Aharon, P., Chen, J.H., Zhu, Z.R., Bloom, A. and Chappell, J. (1993). TIMS U-series dating and stable isotopes of the last interglacial event in Papua New Guinea. *Geochimica et Cosmochimica Acta* **57**, 2541–2554.

Thom, B.G., and Murray-Wallace, C.V. (1988). Last interglacial (Stage 5e) estuarine sediments at Largs, New South Wales. *Australian Journal of Earth Sciences* **35**, 571–574.

Thom, B.G., Shepherd, M., Ly, C.K., Roy, P.S., Bowman, G.M., and Hesp, P.A. (1992). 'Coastal Geomorphology and Quaternary Geology of the Port Stephens–Myall Lakes Area'. (Department of Biogeography and Geomorphology, A.N.U., monograph 6: Canberra).

Wehmiller, J.F. (1984). Relative and absolute dating of Quaternary mollusks with amino acid racemization: evaluation, applications and questions. In 'Quaternary Dating Methods' (Ed. W.C. Mahaney) pp. 171–193 (Elsevier: Amsterdam).

Wehmiller, J.F., (1993). Applications of organic geochemistry for Quaternary research: aminostratigraphy and aminochronology. In 'Organic Geochemistry' (Eds. M.H. Engel and S. Macko) pp. 755–783 (Plenum Press: New York).

Williams, K.M., and Smith, G. G. (1977). A critical evaluation of the application of amino acid racemisation to geochronology and geothermometry. *Origins of Life* **8**, 91–144.

Zhu, Z.R., Wyrwoll, K.-H., Collins, L.B., Wasserburg, G.J. and Eisenhauer, A. (1993). High-precision U-series dating of last interglacial events by mass spectrometry: Houtman Abrolhos Islands, Western Australia. *Earth and Planetary Science Letters* **118**, 281–293.

Relationships and Classification of the Pseudopomyzidae (Diptera: Nerioidea)

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Some groundplan character states of the Nerioidea are examined with special reference to the morphology of the Pseudopomyzidae. The Heleomyzidae are interpreted as a closely related outgroup to the Nerioidea. The Neriidae are possibly the sister group to the Pseudopomyzidae. Groundplan characters of the Pseudopomyzidae are reviewed. Although of small morphological diversity, there are few apparent autapomorphies for the family. The seven recognized pseudopomyzid genera are placed in three informal groups, though the monophyly of these is imperfectly demonstrated.

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INTRODUCTION

The aim of this paper is not to present a taxonomic revision of the Pseudopomyzidae, but to look at their principal morphological features, in order to establish family limits and relationships and to contribute to an understanding of the nerioid groundplan. Because the pseudopomyzids appear to be particularly primitive representatives of the Nerioidea, this study has the potential to throw some light on the origin and phylogeny of the superfamily.

This group has been given family status by D. McAlpine (1966, 1994), Hennig (1969 and elsewhere), and Krivosheina (1979). I initially pointed out significant resemblances to the Cypselosomatidae and therefore referred the Pseudopomyzidae to the superfamily Micropezoidea (now termed Nerioidea on grounds of priority). Griffiths (1972) merged the Pseudopomyzidae with the Cypselosomatidae and was followed by others, notably J. McAlpine (1989). As there are some impressive and consistent differences between Cypselosomatidae s.str. and Pseudopomyzidae, and because I question the validity of their supposed synapomorphies, I retain family status for Pseudopomyzidae.

The living Pseudopomyzidae are distributed in the Palaearctic Region (*Pseudopomyza* Strobl and *Polypathomyia* Krivosheina), Oriental Region (*Tenuia* Malloch — Philippines), Australasian Region (*Pseudopomyza*), and the Neotropical Region (*Latheticomyia* Wheeler, *Heloclusia* Malloch, *Pseudopomyzella* Hennig, *Pseudopomyza*, the first extending into the United States). A satisfactory key to living genera has been given by Krivosheina (1979).

The biology of the Pseudopomyzidae is very little known. Krivosheina (1979, 1984) recorded the larvae of *Polypathomyia stackelbergi* Krivosheina living under the bark of rotting logs of several tree species. Frey (1952) stated that the adults of *Pseudopomyza atrimana* (Meigen) gather in the afternoon over rotting logs in Finland, a habit which suggests a similar larval habitat to that of *P. stackelbergi*.

VALUE OF CLADISTIC INVESTIGATION

The basic philosophy of Hennig's phylogenetic systematics is now so widely recognized as based on simple logic that it influences most current systematic research. But the cladistic methodology which grew out of Hennigian thinking is often treated as an arbitrary formula to be applied to every problem in taxonomy, without consideration of the relevance of the data. Some of my taxonomist colleagues reject cladistic method as incapable of revealing facts of any significance or as too difficult to apply in their own research fields.

To me, the value of cladistic research must depend on the answers to certain fundamental questions. Question 1: Will evolutionary processes leave us with one or more identifiable apomorphies to indicate each internode of the evolutionary tree? The answer depends on the answer to two further questions. Question 2: Will one or more distinctive apomorphies be produced for most internodes? Question 3: If such apomorphies are produced, will they be retained in a recognizable form in sufficient descendent taxa to be recorded by taxonomists? A negative answer to question 2 may result from evolutionary conservatism, or brevity of internodal time, or a combination of these two factors. A negative answer to question 3 may result from masking of particular apomorphies by subsequent evolutionary modification. The general answer to questions 2 and 3 therefore is: 'Sometimes', or 'In a proportion of cases'. The answer to question 1 therefore must be: 'In a proportion of a certain proportion of internodes', with no certain method of generalising as to the value of the final proportion of internodes. All post-Hennigian cladistic methodology depends on the answer to question 1 being rather strongly positive (though not necessarily absolutely so). As the general answer is not very positive, we can only expect the resolution of nodes in a cladogram to be sometimes right, sometimes wrong. The assertion, that use of a large number of characters in cladistic programs tends to neutralise homoplasic errors, is unconvincing. If the evidence for monophyly at a node is not preserved in the study specimens no amount of loading morphological noise into a computer program will resolve the problem.

I therefore believe that the indiscriminate use of morphological data without very careful and informed evaluation is unlikely to produce a cladogram of any complexity which accurately indicates the phylogenetic tree, and it may not necessarily indicate an approximation to the true tree.

I incline to accept some strongly characterised taxa, even though not supported by identifiable autapomorphies, for the reason that lack of obvious autapomorphies is not proof of polyphyletic (or paraphyletic) status. Their likelihood of being monophyletic may be greater than that of some taxa based only on weakly hypothetical autapomorphies. The family Pseudopomyzidae, the monophyly of which is only weakly evidenced by apparent autapomorphies, is therefore retained.

A problem in cladistic method is multiple character convergence between taxa, which can be difficult to distinguish from multiple synapomorphy. This has led to such unjustified taxa as 'Micropezoidea s.str.' and the 'indubitably monophyletic' Megamerinidae of Hennig (1958, 1965), both re-evaluated in my current research.

Selection-directed multiple convergence is, however, only one of the possible causes of error through reliance on statistical parsimony. Some kinds of characters are inherently unstable (e.g. characters commonly involved in niche divergence following speciation, and characters involved in sexual selection), so that lack of change in these, through a series of speciation events, is relatively improbable.

I believe that Hennigian logic can produce some viable theories about phylogenetic relationships when the data are carefully considered with due regard to major stable outgroups (rather than minor unstable ones), to overall stability of character states, and to likelihood of simple reversals with reversal of selection pressure. My experience suggests that some groups are far more amenable to cladistic treatment than others.

On firmer ground than generation of cladograms, can be some attempts to determine monophyletic taxa and their sister groups. In his many papers dealing with phylogeny of Diptera, Hennig often limited himself to the latter kinds of conclusion and only rarely produced detailed cladograms.

RELATIONSHIPS

The Pseudopomyzidae have been consistently placed in the Nerioidea (Micropezoidea) in modern phylogenetically based classifications. Other generally included families are Cypselosomatidae, Neriidae, Micropezidae s.l., and I now confirm the inclusion of the Megamerinidae, but the evidence for this will be published elsewhere.

The family Pseudopomyzidae possesses the following features which are distinctive groundplan conditions for the superfamily and are, to a certain extent, also diagnostic features for it. They are apomorphic in relation to the groundplan of Schizophora and are probably autapomorphies for Nerioidea.

1). Face desclerotized on lower part medially. Despite the statement of Hennig (1971b: 5) to the contrary, a desclerotized zone of variable extent and often of triangular shape on the lower part of the face is the general condition of the Nerioidea, occurring as the predominant condition in all five families, though there is some apparently secondary sclerotization in *Cypselosoma* s.str. and the majority of the micropezid subfamily Taeniapterinae. Even in these latter categories there is often clear differentiation between a lightly sclerotized median zone and heavily sclerotized lateral parts of the face.

2). Male postabdomen with elongate, ventrally channelled epandrium having a pair of terminal surstyli and cerci; also elongate basiphallus supported by usually two pairs of longitudinal sclerotized rods, with a pair of preapical processes and a terminal, anteriorly directed elongate distiphallus, with flexible apex (see Hennig 1969).

3). Female postabdomen: segment 7 longer than preceding segments, with fused tergite and sternite, forming an ovipositor sheath or oviscape; segment 8 with tergite and sternite desclerotized. This set of characters (3) is not present in Megamerinidae.

A further possible groundplan apomorphy for Nerioidea is: accessory glands of female reproductive system absent. This is suggested by my dissections of *Pseudopomyza collessi* McAlpine, *Clisa australis* (McAlpine) (Cypselosomatidae), *Telostylinus angusticollis* (Enderlein) (Neriidae), and of *Metopochetus* sp. (Micropezidae, Eurybatinae) by M.A. Schneider in my laboratory.

Outgroups of the Nerioidea

In order better to understand character polarities and their significance for classification in the families of Nerioidea, knowledge of the sister group or, at least, one or more closely related outgroups of the Nerioidea would be helpful.

J. McAlpine (1989) has indicated in a cladogram (his fig. 116.2) a sister group relationship between the Nerioidea and Diopsoidea, but gave no supporting discussion in the text. The synapomorphies supporting this alliance given on the cladogram are: body form slender; Sc and R_1 approximated; pterostigma lost; A_2 reduced. These are character states so widely present and of such frequent arisal among acalyptrate schizophorans as to carry almost no conviction for supporting monophyly in this case. I have seen certain representatives of the Heleomyzidae, Clusiidae, Chloropidae, Teratomyzidae, Asteiidae, and other families that combine these character states.

Furthermore, some nerioids, such as *Cypselosoma* and certain pseudopomyzids, are not particularly slender in habitus (probably primarily robust), and some forms placed in Diopsoidea (e.g. the Tanypezidae and *Gobrya*) and in the Nerioidea (megamerinids and numerous micropezids) have as great distal divergence between Sc and vein 1 (R_1) as do many of the Sciomyzoidea. In the apparent groundplan of the Micropezidae vein 7(A_2) is not greatly reduced. For these reasons I consider that no acceptable evidence has been produced to demonstrate the probability of a close relationship between the Nerioidea and Diopsoidea.

J. McAlpine (1989) considers that the Nerioidea have retained more plesiomorphic conditions in their groundplan than any other acalyptrate superfamily. However, I regard some of these character states as not demonstrably plesiomorphic or probably not present in the groundplan of the Nerioidea. The large 'relatively unmodified' male sternite 6 present in many Nerioidea may not be the groundplan condition of the Schizophora. My studies of both Heleomyzidae (McAlpine 1985) and Neurochaetidae (McAlpine 1988) seem to indicate that what is effectively a large median ventral sternite 6 in a few representatives of these families is an apomorphic effect and that sternite 6 is primarily very asymmetrical in both families. It may well be asymmetrical both in position and shape in the groundplan of Schizophora, judging both from comparative morphology within the Schizophora and comparison with the outgroup Syrphoidea. Furthermore the conditions of undeveloped vibrissa, apical to subapical arista, unbroken costa, and long, acute cell cup I do not consider to be in the groundplan of the Nerioidea, for reasons given below.

The families Pseudopomyzidae and Cypselosomatidae include those nerioids with habitus most like that of numerous conventional schizophorans which are probably of more or less plesiomorphic habitus for the Schizophora. They also possess such normal attributes of other acalyptrate superfamilies (outgroups in the broad sense) as a series of postocular setulae, a strongly differentiated vibrissa, a presutural bristle, two notopleural bristles (anterior and posterior), and an apical ventral spur on the mid tibia. I consider these attributes most likely to represent groundplan states for the Nerioidea, in addition to the more generally accepted ones given above. Because the costal break near the end of the subcosta is characteristic of these families (often occurring as a trace also in the Neriidae) and contributes to overall resemblance to possibly related outgroups (see below), I regard its presence as a groundplan character state for the Nerioidea, and the closing of the break as an apomorphy, where it occurs in this superfamily.

Before the significant attributes of pseudopomyzids and cypselosomatids were understood, their component genera were placed by competent dipterists in or near several other schizophoran families. I consider that it may be profitable to explore similarities of these nerioid taxa to the Clusiidae (where Hennig, 1948, provisionally placed the cypselosomatid taxa) and to the Heleomyzidae (in or near which pseudopomyzid taxa have been placed by Malloch 1933, Hennig 1958, and Harrison 1959).

Cypselosomatids show some clusiid-like features, including the following: postvertical bristles usually divergent; vibrissa distinct; face more or less desclerotized; fronto-orbital bristles in a well developed series, reaching well forward on postfrons; costa broken only near end of subcosta; vein 7 (A_2) not extending beyond alula. In addition the aedeagus of *Clusia lateralis* (Walker) as shown by Soós (1987, fig. 70.9) is remarkably similar to that of *Clisa* (D. McAlpine 1966, fig. 1d, as *Cypselosoma*), and to that of some other nerioid flies. Other clusiid genera have diverse and often very different aedeagi, but in *Tetrameringia* (see D. McAlpine 1960, fig. 26) the aedeagus approaches that of *Clusia* to some extent. Possibly, then, the resemblance between the aedeagi of *Clusia* and cypselosomatids is coincidental convergence. I also think that the other above points of resemblance may not be adequate to support a theory of close relationships between the Nerioidea and the Clusiidae.

The general characters of the Pseudopomyzidae which resemble those of the Heleomyzidae (or many heleomyzids) include the following: postvertical bristles convergent; fronto-orbital bristles in a simple series, reclinate; vibrissa distinct; arista inserted dorsally; costa broken near end of subcosta, with one or two differentiated bristles before break; costa with spaced anterior to anteroventral spines or spinules on section bordering marginal cell (r_1) (e.g. *Heloclusia*, *Latheticomyia*, *Polypathomyia*); anal cell (cup) relatively short, not acute; fore femur with seriate dorsal and posteroventral bristles; mid tibia with large apical ventral spur; fore basitarsus with male-restricted terminal ventral process (in *Polypathomyia stackelbergi* Krivosheina, *Latheticomyia tricolor* Wheeler, and *Heloclusia imperfecta* Malloch); mid basitarsus longer than fore basitarsus.

The modification of the male fore basistarsus has been previously mentioned (D. McAlpine 1991) as occurring in certain taxa of Heleomyzidae, Sphaeroceridae (both Heleomyzoidea), Dryomyzidae, Helcomyzidae, and Coelopidae (Sciomyzoidea), but its presence in the Nerioidea has been overlooked, except by Wheeler (1956). I have not seen the modification in nerioid genera other than *Heloclusia*, *Latheticomyia*, and *Polypathomyia* (Pseudopomyzidae), and perhaps *Cliobata raptimanus* (Bezzi) (Micropezidae, Taeniapterinae). The modification in the male of *C. raptimanus* (see Aczél 1951: fig. 15) looks so different that it may not be homologous. Otherwise, it is probable that this male basitarsal modification is a single origin structure present only in the superfamilies Sciomyzoidea, Heleomyzoidea (or Sphaeroceroidea), and Nerioidea. However, evolutionary loss of the modification must have occurred in many lineages, and its presence in some taxa may be due to reactivation of old genetic material. It therefore has limited usefulness as an indicator of relationships. The wideness of occurrence of the modification seems to indicate that the trait was acquired in an ancient common ancestor of the three superfamilies, and this ancestor may also have been ancestral to certain other at present unidentified taxa of Schizophora.

Because of the above points of resemblance between the Pseudopomyzidae, as a somewhat primitive nerioid group, and the Heleomyzidae, I regard the Heleomyzoidea as probably a closely related outgroup of the Nerioidea, perhaps its sister group. For this reason comparison of nerioid taxa with the Heleomyzidae appears to have some validity for determining character polarities in the Nerioidea, and my interpretations therefore often differ from those of Hennig (1958), Aczél (1959), J. McAlpine (1989).

Relationships to other nerioid groups

A relationship between Pseudopomyzidae and Cypselosomatidae has often been postulated and some have suggested that the two families should be merged (see above). The latest argument for combining these groups (as two subfamilies of Cypselosomatidae) gives the following autapomorphies for Cypselosomatidae s.l. (J. McAlpine 1989): (1) vibrissa developed; (2) arista arising dorsobasally; (3) costa with subcostal break; (4) costagial bristle very strong; (5) male with strong paired bristles on sternite 8 and epandrium; (6) female with two spermathecae. In accordance with my theory of the Heleomyzoidea as an outgroup for the Nerioidea, characters 1–4 are likely to be groundplan plesiomorphies for the Nerioidea and not autapomorphies of any of its component groups. Condition 4 occurs in many taxa of Micropezidae and Neriidae and is probably a groundplan plesiomorphy in each family. The paired bristles on male sternite 8 and the epandrium (character 5) possibly represent a homologous groundplan condition for both Pseudopomyzidae and Cypselosomatidae s.str., but this does not necessarily place the condition as a synapomorphy (autapomorphy for Cypselosomatidae s.l. in J. McAlpine's terminology). There is really no evidence that this condition does not date from an earlier stage in nerioid evolution, perhaps even in the groundplan of the Nerioidea. It would, then, have been secondarily lost in other nerioid lineages, a not improbable event in view of the inherent instability in male postabdominal characters and the fact of the absence of these bristles in some pseudopomyzids.

The number of spermathecae (character 6) is often unstable within the more morphologically diverse schizophoran families (e.g. Heleomyzidae, Carnidae, Coelopidae, Tephritidae). Hennig's (1969) descriptions of pseudopomyzid spermathecae suggest instability in the family (two of similar size present in *Pseudopomyza* (*Rhinopomyzella*) *nigrimana* (Hennig), two, of which one appears to be vestigial, in *P.* (*R.*) *albimana* (Hennig), 'Spermatheken habe ich nicht gefunden' in *Latheticomyia longiterebra* (Hennig). *Pseudopomyza collessi* and the cypselosomatid *Clisa australis* each have two similar spermathecae with lightly sclerotized vesicles (D. McAlpine 1993, 1994). In the Micropezidae three spermathecae are reported for *Compsobata univitta* (Walker) (Sturtevant 1925), *Calobata petronella* (Linné) (Hennig 1958, as *Trepidaria* sp.), *Calycopteryx mosleyi* Eaton, and for *Metopochetus* sp. (author's observations). According to Freidberg (1984), *Micropeza* (three species examined) has three normal spermathecae and a fourth of unusual structure. Dufour (1851) has reported two spermathecae for '*Calobata cothurnata*' (perhaps *Compsobata cibaria* (Linné)), a count that has been queried, but not refuted, by Sturtevant. In the Neriidae, *Telostylinus angusticollis* (Enderlein) perhaps has only two spermathecae (author's dissection of an immature female), but Steyskal (1987) gives in the family description of Neriidae 'two pairs of colorless spermathecae present.' Perhaps this statement is based on *Odontoloxozus longicornis* (Coquillett), the best known nearctic species. In view of the frequency of arisal of a spermathecal count of two in the Schizophora, the very few recorded spermathecal counts in the Nerioidea, and the apparent variability in the three nerioid families for which more than one species has been investigated, it is not reasonable to regard the spermathecal count of two as necessarily a synapomorphy for Pseudopomyzidae + Cypselosomatidae.

Griffiths (1972) gives a further three 'apomorphous conditions' for Cypselosomatidae s.l. (including Pseudopomyzidae), all characters of reduction in wing venation, two of which are excluded by J. McAlpine (1989) on account of further evidence of the probable groundplan condition of the 'Pseudopomyzinae' (the family Pseudopomyzidae as here delimited). The third character state, 'Subcosta reduced, failing to reach wing margin as distinct vein,' applies to most species of both Pseudopomyzidae and Cypselosomatidae s.str., but not so clearly to *Polypathomyia stackelbergi*, in which the termination of the subcosta differs only slightly from that of some Neriidae. There is thus considerable variation in the extent of subcostal reduction in the Pseudopomyzidae, and reduction of the subcosta is one of the most frequently derived apomorphies known in the Schizophora. One should not therefore found a theory of monophyly of Pseudopomyzidae + Cypselosomatidae on this character alone.

From the above it is clear that evidence for synapomorphy between the Pseudopomyzidae and Cypselosomatidae is at best quite weak, and, as has been shown by Andersson (1976) and Krivosheina (1979), the two groups are strongly differentiated. The resemblance between these families is largely or entirely due to a combination of symplesiomorphy and convergence.

Some groundplan character states of the Pseudopomyzidae

I. Characters retained from groundplan of Nerioidea.

- (a) Postvertical bristles convergent.
- (b) Fronto-orbital bristles in a simple reclinate series.
- (c) Vibrissa well differentiated.
- (d) Seriate postocular setulae present.
- (e) Face desclerotized on lower median part.
- (f) Arista (antennal segment 6) with extensive non-seriate short hairs.
- (g) Dorsocentral bristles in a complete series.
- (h) Propleural (proepisternal) bristle distinct.

(i) Upper anterior and posterior sternopleural bristles present.
(j) Anterior intra-alar bristle (close behind transverse suture) absent.
(k) Membranous cleft of mesopleuron meeting anterior section of sternopleural (anapleural) suture at a right angle or acute angle.
(l) Fore femur with elongate dorsal and posteroventral bristles.
(m) Mid tibia with large apical ventral spur.
(n) Tarsi cylindrical, not depressed distally.
(o) Fore basitarsus with male-restricted terminal ventral process.
(p) Mid basitarsus more elongate than fore basitarsus.
(q) Costa with subcostal break and pair of bristles at basal side of break.
(r) Anterodorsal and anteroventral costagial bristles large, latter not basad of former.
(s) Costa with spaced anterior to anteroventral spines among the hairs.
(t) Posterodistal angle of discal cell not obtuse, with vein 4 (CuA_1 or M_4) extending well beyond angle.
(u) Basal crossvein (bm-cu or base of M_{3+4}) separating second basal (bm) and discal cells.
(v) Anal crossvein (transverse section of CuA_2) recurved.
(w) Alula forming a prominent lobe.

This set of characters includes those used above as evidence for a relationship between Nerioidea and Heleomyzoidea together with other groundplan characters which are plesiomorphic relative to those of certain other nerioid taxa.

II. Characters apomorphic in relation to groundplan of Nerioidea.
(a) Antenna porrect.
(b) Arista inserted mid-dorsally to subapically on antennal segment 3.
(c) Subcosta reaching costa very close to vein 1 (R_1), the intervening membrane distally indistinct.
(d) Distal section of vein 7 (A_2), beyond alular incision, absent without trace.

The shortness of this list is in accordance with the theory that the Pseudopomyzidae are morphologically closer than other families to the groundplan of the Nerioidea. Although there are numerous differences between the Pseudopomyzidae and Neriidae, these mostly concern the well developed autapomorphies of the Neriidae as compared with the Pseudopomyzidae. Characters II(a) and II(b) above possibly represent intermediate states in their respective character sequences between the nerioid groundplan condition (probably close to that of *Cypselosoma* species) and the more advanced condition seen in the Neriidae. The most plausible autapomorphy for the Pseudopomyzidae is still the reduction of the subcosta. In the Neriidae the subcosta is complete, well sclerotized throughout, and terminates separately in the costa. It seems possible on this evidence that the Pseudopomyzidae and Neriidae are sister groups. Further points of resemblance such as the presence of convergent postvertical bristles and the retention in certain Neriidae of a small but unambiguous vibrissa render this relationship plausible, but, as probable plesiomorphic states for the Nerioidea, they do not provide positive evidence. An alternative hypothesis of a sister group relationship between Neriidae and Micropezidae was supported provisionally by Griffiths (1972), and Hennig (1958) also favoured a close relationship between Neriidae and Micropezidae s.l., without regarding them as sister groups.

MONOPHYLETIC GROUPS IN PSEUDOPOMYZIDAE

Most authors dealing with classification in the Pseudopomyzidae have been concerned with defining species and genera. Hennig (1969) and Krivosheina (1979) each gave a key to the genera. Krivosheina considered the genera *Pseudopomyzella* and *Heloclusia* to be each isolated within the family by its unusual morphology, and proposed grouping the rest of the genera into the two subfamilies Pseudopomyzinae (for *Pseudopomyza* and *Rhinopomyzella*) and Latheticomyiinae (for *Latheticomyia*, *Polypathomyia*, and, possibly, *Tenuia*). The relationships of *Eopseudopomyza* were not mentioned, and the system was not claimed to be phylogenetic.

In attempting to define groups of pseudopomyzid genera which may be monophyletic, a number of character sequences have been considered, but polarities are often difficult to determine because of the remoteness or independent specialisation of outgroups. The following characters do not appear to be sufficiently stable for group characterisation: development of spaced costal spines, development of vein closing cell bm (second basal), development of prescutellar acrostichal bristles, and, to some extent, development of discal setulae on the scutellum. The position of the preabdominal spiracles is not recorded in all genera, though usually it is within the lateral margin of each tergite. In *Latheticomyia* the lateral margins of some abdominal tergites appear to have undergone desclerotization, a process which leaves the spiracles in an extended pleural membrane. I have not seen specimens of the genera *Eospeudopomyza* and *Tenuia*, and their morphology is known to me only from published descriptions. I do not consider that character sequences in the family are sufficiently understood for production of a cladogram.

The following three informal groups are suggested as being possibly monophyletic, but their status needs further study.

Group 1

Fronto-orbital bristles three; setulae near middle of postfrons little developed; cheek with a linear series of setulae; dorsocentral bristles five; anterior intra-alar bristle absent; subcosta distinct to well beyond mid-length of cell c (second costal); cell cup (anal cell) moderately small; distal section of CuA_2+A_1 (vein 6) strong, rather abruptly discontinued well before margin. Included genera: *Latheticomyia* Wheeler (Americas), *Tenuia* Malloch (Philippines).

The group is perhaps characterised mainly by plesiomorphies. The condition of vein CuA_2+A_1 is probably apomorphic in relation to that in group 2, but is not absolutely distinct from that in group 3. The absence of the anterior intra-alar bristle and the less reduced cell cup may be plesiomorphic states relative to those of the other two groups. Hence the group, if monophyletic, may be a sister group to the other two groups combined.

Group 2

Fronto-orbital bristles two or three; setulae near middle of postfrons little developed; setulae of cheek not forming a linear series; dorsocentral bristles four; anterior intra-alar bristle usually present; subcosta variable in length; cell cup very small (often incomplete); distal section of vein CuA_2+A_1 gradually fading distally (except in *Polypathomyia*). Included genera: *Heloclusia* Malloch (Neotropical Region), *Polypathomyia* Krivosheina (eastern Palaearctic Region), *Pseudopomyza* Strobl (Palaearctic, Neotropical, and Australasian Regions).

The group includes all those pseudopomyzids with four pairs of long dorsocentral bristles, not intergrading with setulae anteriorly. This is perhaps an apomorphic conditon, as the groundplan condition of the outgroup Cypselosomatidae probably includes the presence of five or more dorsocentrals. (The alternative outgroup Neriidae is regarded as too specialised in thoracic morphology, including chaetotaxy, for comparison).

The delimitation and subgeneric classification of *Pseudopomyza* have been treated by D. McAlpine (1994).

Group 3

Fronto-orbital bristles four; setulae near middle of postfrons well developed and medially inclined; setulae of cheek not forming a long linear series; dorsocentral bristles five, or becoming indefinite anteriorly; anterior intra-alar bristle developed; subcosta distinct only on about basal half of cell c (second costal); cell cup very small; distal section of CuA_2+A_1 (vein 6) abruptly discontinued (*Pseudopomyzella*) or apparently more distally prolonged (*Eopseudopomyza*). Included genera: *Pseudopomyzella* Hennig (Neotropical Region), *Eopseudopomyza* Hennig (Palaearctic, Tertiary).

This group includes all known pseudopomyzids with four fronto-orbital bristles, with coarse medially inclined setulae near the middle of the postfrons just in front of the ocelli, and all those with three well developed series of anterior intradorsocentral setulae (including acrostichals). These three conditions could be autapomorphies as they contrast with those in all possible outgroups to the Pseudopomyzidae, or at least with their groundplans. The reduced cell cup and presence of an anterior intra-alar bristle suggest a relationship to group 2.

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P.S. Cranston, D.H. Colless, N.P. Krivosheina, L. Papp, and J.R. Vockeroth supplied material of pseudopomyzids. D.J. Bickel critically read the manuscript.

REFERENCES

Aczél, M.L. (1951). Morfologia externa y division sistematica de las Tanypezidiformes con sinopsis de las especies Argentinas de Tylidae (Micropezidae) y Neriidae (Dipt.) *Acta Zoologica Lilloana* **11**, 483–589, pl. I-IV.

Aczél, M.L. (1959). Diptera: Neriidae and Micropezidae (Tylidae). *Insects of Micronesia* **14**, 47–90.

Andersson, H. (1976). Revision of the genus *Formicosepsis* de Meijere (Diptera; Cypselosomatidae). *Entomologica Scandinavica* **7**, 175–185.

Dufour, L. (1851). Recherches anatomique et physiologiques sur les diptères. *Mémoires de l'Académie des Sciences de France* **11**, 171–360.

Freidberg, A. (1984). Acalyptratae of Israel: the family Micropezidae (Diptera). *Israel Journal of Entomology* **18**, 11–20.

Frey, R. (1952). Über *Chiropteromyza* n.gen. und *Pseudopomyza* Strobl (Diptera, Halpostomata). *Notulae Entomologicae* **32**, 5–8.

Griffiths, G.C.D. (1972). 'The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen'. Series entomologica 8. W. Junk, The Hague.

Harrison, R.A. (1959). Acalyptrate Diptera of New Zealand. *N.Z. Department of Scientific and Industrial Research Bulletin* **128**, 382 + vii pp.

Harrison, R.A. (1964). Insects of Campbell Island. Diptera. *Pacific Insects Monographs* **7**, 304–324.

Hennig, W. (1948). Über einige verkannte Dipteren-Gattungen. *Acta Zoologica Lilloana* **6**, 169–170.

Hennig, W. (1958). Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. *Beiträge zur Entomologie* **8**, 505–688.

Hennig, W. (1965). Die Acalyptratae des Baltischen Bernsteins und ihre Bedeutung für Erforschung der phylogenetischen Entwicklung diesen Dipteren-Gruppe. *Stuttgarter Beiträge zur Naturkunde* **145**, 215 pp.

Hennig, W. (1969). Neue Gattungen und Arten der Acalypteratae. *The Canadian Entomologist* **101**, 589–633.

Hennig, W. (1971a). Neue Untersuchungen über die Familien der Diptera Schizophora (Diptera: Cyclorrhapha). *Stuttgarter Beiträge zur Naturkunde* **226**, 76 pp.

Hennig, W. (1971b). Die Familien Pseudopomyzidae und Milichiidae im Baltischen Bernstein (Diptera: Cyclorrhapha). *Stuttgarter Beiträge zur Naturkunde* **233**, 16 pp.

Krivosheina, N.P. (1979). A new representative of the family Pseudopomyzidae from the Palaearctic Fauna and the taxonomic position of this family in the system of Diptera. *Revue de l'Entomologie de l'URSS* **58**, 179–189. (In Russian).

Krivosheina, N.P. (1984). Family Pseudopomyzidae. In 'Catalogue of Palaearctic Diptera 10' (Eds. Á. Soós and L. Papp) p. 49. (Elsevier: Amsterdam).

Malloch, J.R. (1933). Acalyptrata (Helomyzidae, Trypetidae, Sciomyzidae, Sapromyzidae, etc.). *Diptera of Patagonia and South Chile* **6**, 177–391, pl. 2–6.

McAlpine, D.K. (1960). A review of the Australian species of Clusiidae (Diptera, Acalyptrata). *Records of the Australian Museum* **25**, 63–94.

McAlpine, D.K. (1966). Description and biology of an Australian species of Cypselosomatidae (Diptera), with a discussion of family relationships. *Australian Journal of Zoology* **14**, 673–685.

McAlpine, D.K. (1985). The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. *Records of the Australian Museum* **36**, 203–251.

McAlpine, D.K. (1988). Studies in upside-down flies (Diptera: Neurochaetidae). Part II. Biology, adaptions, and specific mating mechanisms. *Proceedings of the Linnean Society of New South Wales* **110**, 59–82.

McAlpine, D.K. (1991). Review of the Australian kelp flies (Diptera: Coelopidae). *Systematic Entomology* **16**, 29–84.

McAlpine, D.K. (1993). A new genus of Australian cypselosomatid flies (Diptera: Nerioidea). *General and Applied Entomology* **25**, 2–4.

McAlpine, D.K. (1994). A new Australian species of pseudopomyzid fly (Diptera: Nerioidea) and the subgenera of *Pseudopomyza*. *Proceedings of the Linnean Society of New South Wales* **114**, 181–187.

McAlpine, J.F. (1989). 116. Phylogeny and classification of the Muscomorpha. In 'Manual of Nearctic Diptera' (Ed. J.F. McAlpine) 3, 1397–1518. (Canadian Government Publishing Centre: Hull, Quebec).

Soós, A. (1987). 70. Clusiidae. In 'Manual of Nearctic Diptera' (Ed. J.F. McAlpine) 2, 853–857. (Canadian Government Publishing Centre: Hull, Quebec).

Steyskal, G.C. (1987). 57. Neriidae. In 'Manual of Nearctic Diptera' (Ed. J.F. McAlpine) 2, 769–771. (Canadian Government Publishing Centre: Hull, Quebec).

Sturtevant, A.H. (1925). The seminal receptacles and accessory glands of the Diptera, with special reference to the Acalypterae (part). *Journal of the New York Entomological Society* **33**, 195–215.

Wheeler, M.R. (1956). *Latheticomyia*, a new genus of acalyptrate flies of uncertain family relationship. *Proceedings of the United States National Museum* **106**, 305–314.

New Species and New Records of Pseudocaeciliidae, Philotarsidae and Elipsocidae (Insecta: Psocoptera) from the Mount Royal Area, Hunter Valley, New South Wales

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Smithers, C.N. (1996). New species and new records of Pseudocaeciliidae, Philotarsidae and Elipsocidae (Insecta: Psocoptera) from the Mount Royal area, Hunter Valley, New South Wales. Proc. Linn. Soc. N.S.W. 116: 233–243

Sixteen species of Pseudocaeciliidae, including *Heterocaecilius mouldsi* sp.n., *H. rotundus* sp.n. and *Pseudoscottiella alettae* sp.n., five species of Philotarsidae and four species of Elipsocidae (Insecta: Psocoptera) are recorded from Tuglo Wildlife Refuge, near Mount Royal, New South Wales.

Manuscript received 20 Jun 95, accepted for publication 13 Dec 95.

KEYWORDS: Psocoptera, Hunter Valley, New South Wales, Pseudocaeciliidae, Philotarsidae, Elipsocidae.

INTRODUCTION

This paper records the results of the study of nearly 500 specimens of Psocoptera (Insecta) collected as part of a faunal survey of Tuglo Wildlife Refuge (32°.14'S, 151°.16E'), near Mount Royal, New South Wales. Sixteen species of Pseudocaeciliidae are represented (including *Heterocaecilius mouldsi* sp.n., *H. rotundus* sp.n., *Pseudoscottiella alettae* sp.n. and the previously unknown male of *Pseudoscottiella papillosa* Schmidt and Thornton) as well as five species of Philotarsidae and four of Elipsocidae. Results for other families of Psocoptera collected during the survey have been dealt with elsewhere (Smithers 1989, 1993b, 1994). The survey is intended to provide a species inventory as a precursor to more detailed studies on the biology and ecology of the group. Survey locality and collecting methods have been briefly described by Smithers (1993a). The survey area (at and near 750 m) lies between the higher altitudes of Barrington Tops and the lower altitudes of the Hunter Valley and so provides a series of habitats between the altitudinal extremes found in the region. The plant associations of the Refuge include several of those found in nearby Mount Royal State Forest (Shields et al. 1992) and most of the Psocoptera mentioned can be expected to occur there. Months in which each species was collected are given in brackets after the species name. The material is deposited in the Australian Museum.

PSEUDOCAECILIIDAE RECORDED FROM TUGLO WILDLIFE REFUGE

Previously known species

Austropsocus antennalis Thornton and New (December, January)

Austropsocus costalis Thornton and New (April, November)

Austropsocus omega Thornton and New (June, December)

Austropsocus sinuosus (Banks) (January, May, June, December)

Austropsocus tibialis Thornton and New (January, May, June, August, September, October)

Austropsocus viridis (Enderlein) (January, March, May, June, August, October, December)

Heterocaecilius brunellus (Tillyard) (June)

Heterocaecilius lachlani (Enderlein) (January, April, May, June, July, August, October, November)

Lobocaecilius monicus Lee and Thornton (January, February, May, June, October, December)

Pseudoscottiella crenulata New (February, March, April, May, June, September, October, December)

Pseudoscottiella papillosa Schmidt and Thornton (January, June, December)

Pseudoscottiella rotundata New (April, May, June, October)

Pseudoscottiella yenoides Schmidt and Thornton (June)

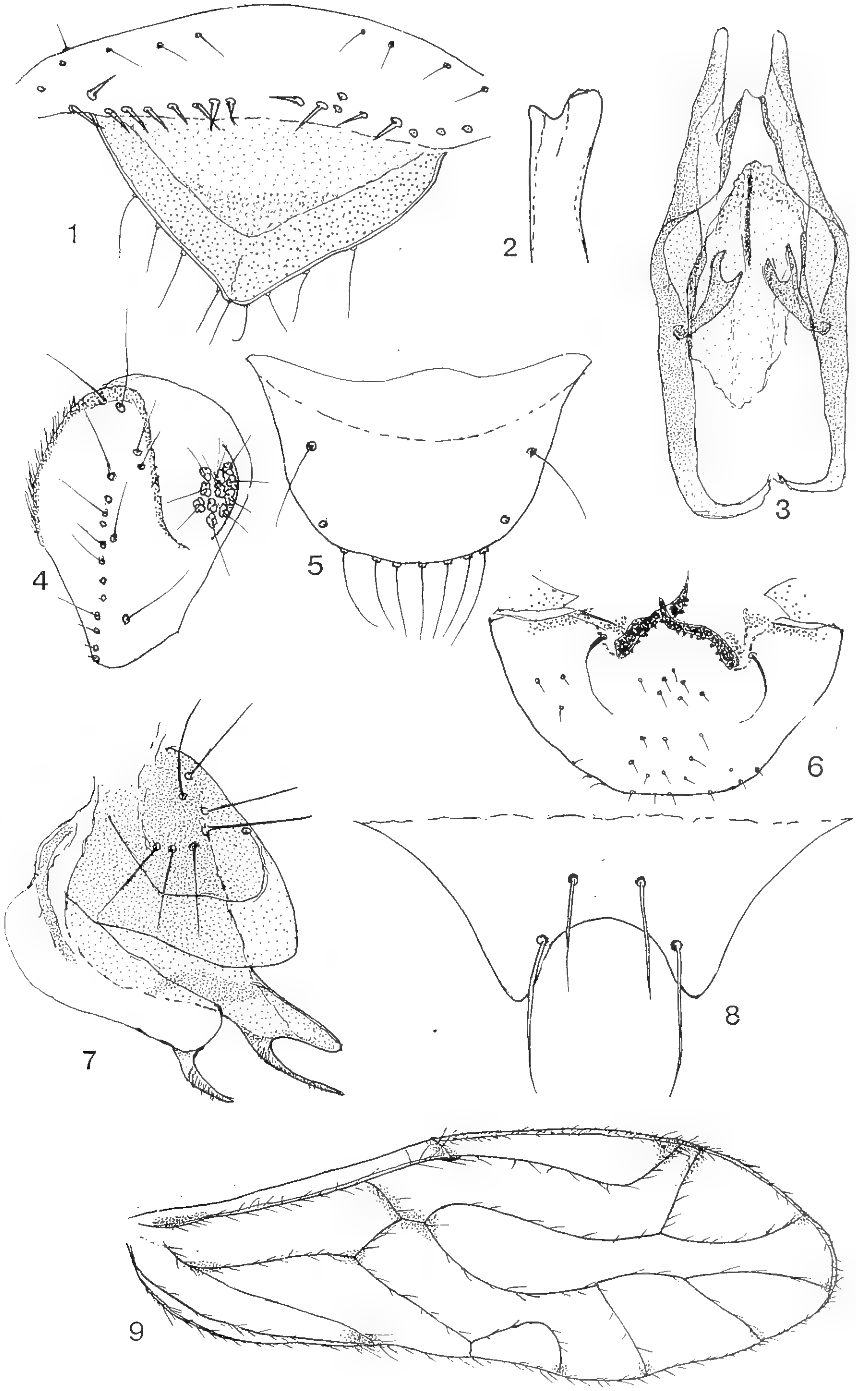
New species

Heterocaecilius mouldsi sp. n.

Male

Colouration (in alcohol). Head dark cream with purplish W-shaped mark between eyes, middle of the W coinciding with ocellar triangle. Vertex brown, a little paler in middle of each epicranial plate. Postclypeus and labrum dark cream. Genae brownish adjacent to epistomial suture anterior to antennal socket, paler posteriorly. Antennae dark cream, a little paler than postclypeus, scape and pedicel little darker than flagellar segments. Eyes black. Ocellar tubercle black. Maxillary palp as flagellar segments of antennae. Prothorax pale. Meso- and metathorax variously brown above; pleura pale. Legs pale. Fore wings hyaline, faintly marked with brown at end of pterostigma, stigmapophysis, ends of main veins and of Rs and basal section of Rs-M fusion. Veins brown. Hind wings hyaline, veins brown. Abdomen pale.

Morphology. Length of body: 2.6 mm. Median epicranial suture not very obvious. Vertex rounded, setose, with at least one large seta near each eye. Postclypeus with fine, short setae. Length of flagellar segments: f1: 0.70 mm.; f2: 0.52 mm. Antennae clothed with long setae, many of which are several times longer than flagellar diameter. Two small trichoid sensilla on first flagellar segment in basal quarter. Eyes moderately large, just reaching level of vertex. IO/D: 1.6; PO: 0.78. Ocelli large. Lacinia (Fig. 2). Measurements of hind leg: F: 0.65 mm.; T: 1.19 mm.; t1: 0.34 mm.; t2: 0.11 mm.; rt: 3:1; ct: 20,0. Claws with small preapical tooth. Fore wing length: 3.9 mm. Fore wing costa broadened in pterostigma and to wing apex. Stigmapophysis small. Pterostigma gradually broadening distally with a smoothly rounded posterior margin. Pterostigmal area glabrous. Rs and M fusion short but variable. Rs sinuous but not exceptionally so. Areola postica fairly tall, semicircular, smoothly arched. Anal cell without sensilla. Anal margin thickened at hind angle of wing. Hind wing without special features, a few setae on branches of Rs and M. Ninth tergite (Fig. 1) well sclerotised, sparely setose with a posterior transverse row of about 18 very short, stout setae, the row shortly interrupted medially. Epiproct (Fig. 1) triangular with posterior angle rounded, basally shaped to fit posterior lobe of ninth tergite; a few setae near posterior margin. Hypandrium (Fig. 6) with two sinuous, pointed, papillose apophyses, each with a basal lobe and smaller apophysis. Phallosome (Fig. 3) (slightly tilted in preparation illustrated) symmetrical, a median sclerite on penial bulb, some rugosity and two short curved, forked sclerites; anterior end of phallosome transverse, very narrow in midline.



Figs. 1–9. Heterocaecilius mouldsi sp.n. (1) Ninth tergite and epiproct of male; (2) Lacinia; (3) Phallosome; (4) Female paraproct; (5) Female epiproct: (6) Hypandrium: (7) Gonapophyses; (8) Posterior lobes of subgenital plate; (9) Female fore wing.

Female

Colouration (in alcohol). As male but paler areas on vertex more extensive and with paler area adjacent to median epicranial suture. Fore wing (Fig. 9).

Morphology. Length of body: 2.6 mm. Length of flagellar segments: f1: 0.39 mm; f2: 0.27 mm. Antennae finer than in male, but also strongly setose. Eyes smaller than in male, not reaching level of vertex. IO/D: 3.1; PO: 0.67. Ocelli small. Lacinia as in male. Measurements of hind leg: F: 0.57 mm; T: 0.97 mm; t1: 0.26 mm; t2: 0.09 mm; rt: 2.9:1; ct: 14,0. Preapical tooth on claws not obvious. Fore wing length: 3.0 mm; width: 1.1 mm. Fore wings (Fig. 9). Epiproct (Fig. 5) very large, held vertically with small scattered setae and much stronger marginal setae. Paraproct (Fig. 4) weakly sclerotised with field of closely packed trichobothria with "rosette" bases. Subgenital plate (Fig. 8) with two posterior lobes, each with two strong setae. Gonapophyses (Fig. 7). Ventral valve broad-based, membranous, with strong spiculate distal apophysis. Dorsal valve broad basally, tapering posteriorly with strong preapical, spiculate apophysis. External valve large, lightly sclerotised, divided into two lobes, the smaller lobe setose.

Material examined

1 male (holotype), Tuglo Wildlife Refuge, 48 km N. Singleton, New South Wales, 6.i.1979, A. S. Smithers. 1 female (allotype), as holotype, 13–14.vii.1976, M. S. Moulds. Other paratypes, locality as holotype: 1 male, 1.ix.1976, 1 male, 1.x.1976, 1 female, 9.ii.1984, 1 female, 3.iii.1984, A. S. Smithers. Holotype and paratypes in Australian Museum. This species is named for Max Moulds, in appreciation of his donation of specimens of Psocoptera to the Australian Museum over many years.

Discussion

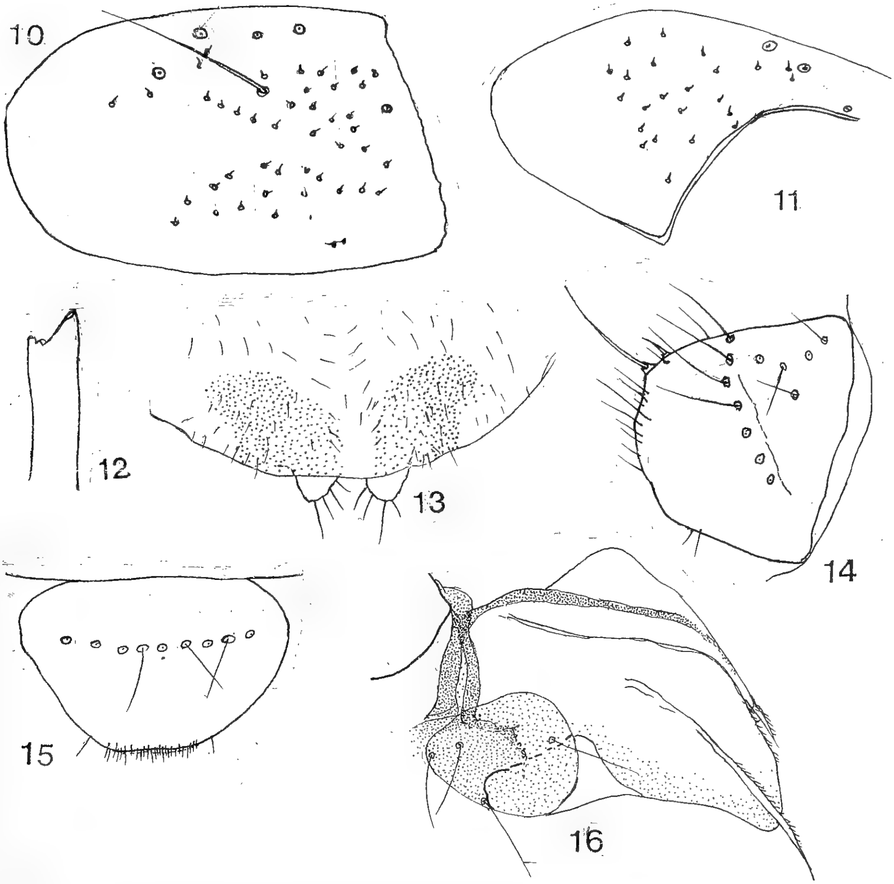
Heterocaecilius mouldsi falls well within the definition of the genus as erected by Lee and Thornton (1967). The male phallosome sclerites are characteristic as is the roughened area in the middle of the epiproct. A row of short, stout setae along the hind margin of the ninth tergite is also found in *H. dardanus* Lee and Thornton, from Fiji, but there are fewer setae in the row in *H. mouldsi* than in *H. dardanus*. In the female the double lobes of the external valve of the gonapophyses with the small part alone bearing setae is distinctive and unusual in the genus.

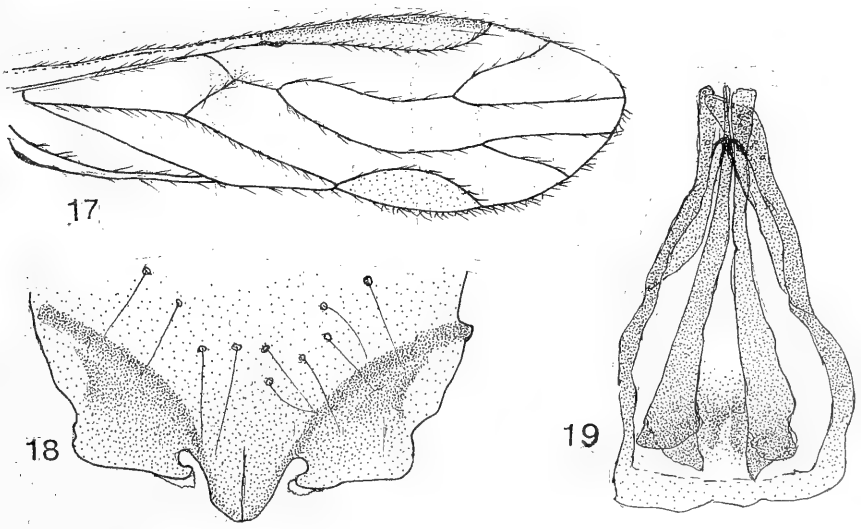
Heterocaecilius rotundus sp. n.

Female

Colouration (in alcohol). Head dark brown, shining, darker near median epicranial suture and adjacent to compound eyes, the darker areas irregular in shape. Postclypeus very dark brown, almost black along anterior margin. Genae almost black as is the labrum. Antennae pale brown. Eyes black. Thoracic nota and pleura dark brown. Legs brown. Maxillary palps with first segment pale, other segments dark brown. Strongly reduced wings dark brown (Fig. 10). Abdomen brown, dorsally dark brown because of heavy sclerotisation, ventrally membranous areas almost colourless, a few small brown areas where cuticle is more heavily sclerotised.

Morphology. Length of body: 1.8–2.2 mm. Head setose, with some long setae and a fairly dense clothing of finer setae. Median epicranial suture very distinct on vertex but evanescent anteriorly, ending at about level of hind margin of eyes. Vertex sharp, posteriorly overlying prothorax; postclypeus fairly flat so that head appears somewhat prognathous. Length of flagellar segments: f1: 0.3 mm.; f2: 0.2 mm. First flagellar segment with placoid sensillum at about a quarter of length from base and another at about a third from base of segment. Antennae with sparse but well developed setae. Eyes small, set well below level of vertex. IO/D: 2.5; PO: 0.8. No ocelli. Labrum with two trichoid sensilla and three pores arranged alternately along middle section of anterior margin. Labrum slightly lobed at anterior corners. Apex of lacinia (Fig. 12) with a large external tooth and a much smaller inner tooth divided into two minute lobes. Maxillary palp with





Figs. 10–16. Heterocaecilius rotundus sp.n. Female. (10) Fore wing; (11) Hind wing; (12) Lacinia; (13) Subgenital plate; (14) Paraproct; (15) Epiproct; (16) Gonapophyses.
Figs. 17–19. Pseudoscottiella papillosa. Male. (17) Fore wing; (18) Hypandrium; (19) Phallosome.

fourth segment long and tapering. Thoracic terga narrow, very strongly sclerotised. Measurements of hind leg: F: 0.51 mm.; T: 0.7 mm.; t1: 0.15 mm.; t2: 0.08 mm.; rt: 1.9:1. No ctenidiobothria and no coxal organ. Fore wing length: 0.18 mm.; width: 0.12 mm. Wings reduced to small, lateral, heavily sclerotised, flap-like extensions of tergum. Fore wings (Fig. 10) with row of setae near anterior margin distal to which is a trichoid sensillum. Basal half of wing with small, scattered, trichoid sensilla. Hind wing (Fig. 11) smaller than fore wing, being merely an extension of thoracic tergum, with two anterior setae near base, beyond and behind which is an area bearing small scattered trichoid sensilla. Abdomen heavily sclerotised dorsally with most of the terga fused. Sixth tergite demarcated from fused tergites anterior to it by a shallow suture, tergites 7–9 separate from each other. Heavy sclerotisation of the thoracic and abdominal terga and micropterous condition give the insects a beetle-like appearance. Abdominal terga each with irregular, transverse row of strong setae. Epiproct (Fig. 15) very heavily sclerotised with surface very finely sculptured with irregular, granular pattern (not indicated in figure) and single row of about nine strong setae. Hind margin curved, middle posterior section bearing group of fine setae. Paraproct (Fig. 14) heavily sclerotised with row of strong setae across middle adjacent to a fold in integument and with few, spaced, fine setae in area usually occupied by trichobothrial field, none with basal "rosettes". Surface of paraproct finely "granular" as in epiproct (not indicated in illustration). Hind margin of paraproct finely setose, as epiproct. No posterior cone on margin but a tiny seta is flanked ventrally by a very large and dorsally by a small seta. Epiproct and paraproct are so shaped that their margins are opposed to each in life, thus sealing off the apex of the abdomen. Subgenital plate (Fig. 13) posteriorly bilobed, each lobe with few marginal setae. Gonapophyses (Fig. 16) with ventral valve with broad membranous flap supported by narrow longitudinal sclerotised rod. Dorsal valve very broad, lightly sclerotised, with narrow, spiculate apophysis. External valve with few long fine setae (four in holotype).

Male

Unknown.

Material examined

1 female (holotype), in litter, alongside stream in rainforest, Tuglo Wildlife Refuge, 48 km. N. Singleton, New South Wales, 9.vii.1983. L.E. Watrous. 11 females, data as holotype. 2 females, in rainforest litter, alongside Turkey Creek, Tuglo Wildlife Refuge, 23.vii.1983. L.E. Watrous. Holotype and paratypes in Australian Museum.

Discussion

Lee and Thornton (1967) erected *Heterocaecilius* to hold species of Pseudocaeciliidae which could not be placed in other genera, several of which they established in the same publication. Microptery and brachyptery are common in adults of several families of Psocoptera but has seldom been reported in the Pseudocaeciliidae. *Diplocaecilius* Badonnel (a monotypic genus) and *Heterocaecilius nigricans* Badonnel, both from Madagascar, are, however, micropterous. *H. rotundus* is very similar to the latter species, sharing many of the features which are considered to be neotenic and associated with microptery in Psocoptera. These include loss of ocelli, loss of trichobothrial field and reduction or loss of coxal organ. Neither species, however, exhibits retention of a duplex seta or marginal cone on the hind margin of the paraproct, such retention also being a common neotenic feature. This does occur in *Diplocaecilius*. *H. rotundus* and *H. nigricans* stand apart from other species of *Heterocaecilius* by virtue of their microptery. It is not clear from the description of *H. nigricans* whether there is fusion of the abdominal tergites to the extent that this occurs in *H. rotundus* but the description of the colour of that species (dark dorsally, pale ventrally) suggests that this may be so. *H. rotundus* is distinguished from the also-micropterous *Diplocaecilius peyrierasi* Badonnel by the form of the genitalia which, in *Diplocaecilius* have a doubly lobed dorsal valve (single lobe in *H. rotundus*) and in lacking the marginal cone on the paraproct (present in *Diplocaecilius*). The only known species with which *H. rotundus* could be confused is *H.*

nigricans. It differs from that species in details of the form of the gonapophyses, in the shape of the area of sclerotisation of the subgenital plate, in having four setae on each subgenital plate lobe (two in *H. nigricans*) in lacking setae with "rosette" bases on the paraproct (two such in *H. nigricans*) and in having more setae on the reduced wings (two setae in *H. nigricans*). The fore wings in *H. nigricans* also bear a single trichoid sensillum. This is not present on the hind wing. A sensillum is present in the same position on the fore wing of *H. rotundus* but this species has a fairly extensive field of additional sensilla in the basal half of both fore and hind wings.

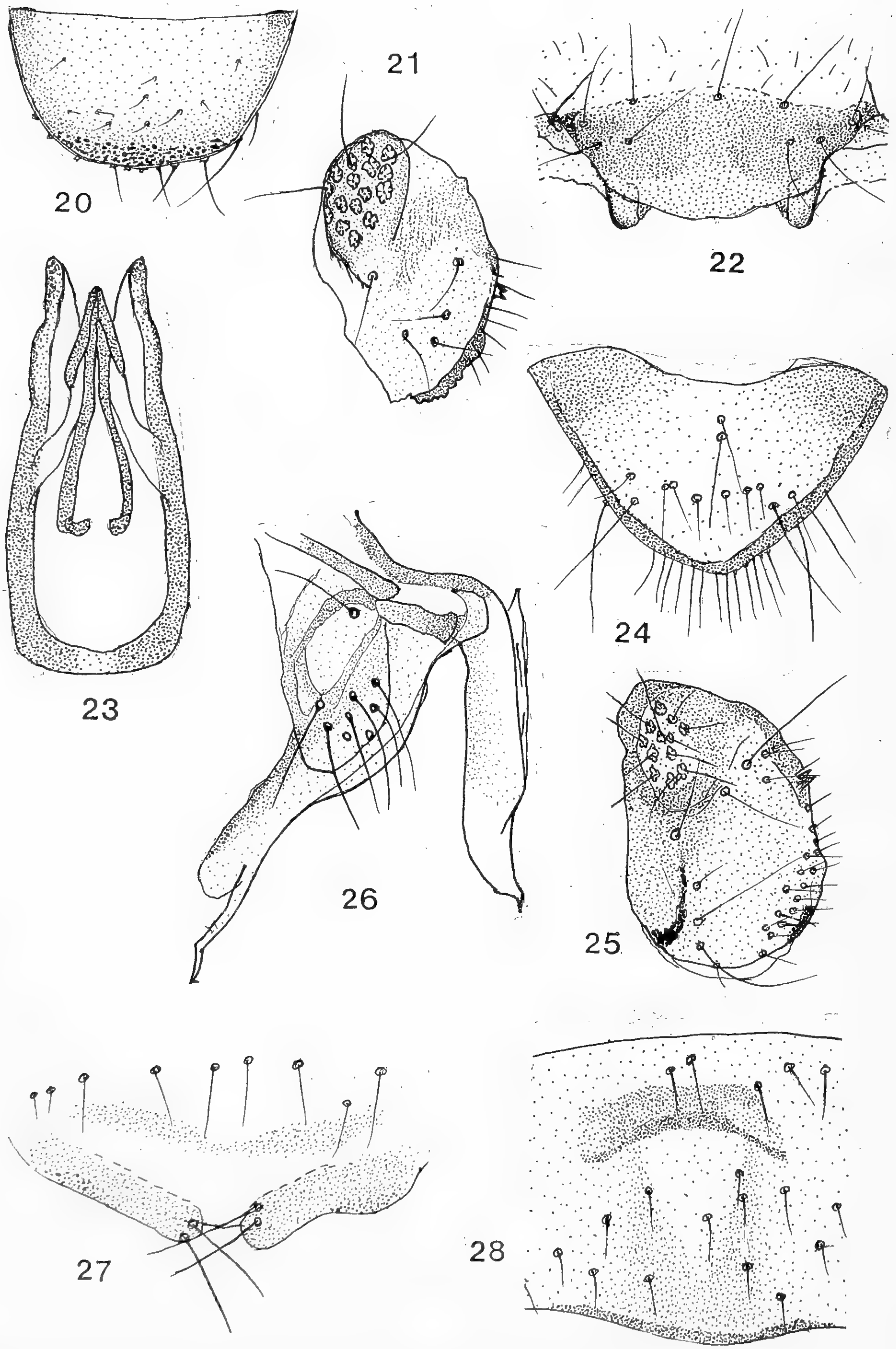
H. nigricans and *H. rotundus* appear to have undergone remarkable parallel evolution in Madagascar and Australia. Unfortunately, males are not known for either species so it would be preferable to retain them in *Heterocaecilius*, bearing in mind that they are anomalous in that genus and that with greater knowledge it may be necessary to place them in a separate genus.

Pseudoscottiella alettae sp.n.

Male

Colouration (in alcohol). Head brown with slightly paler, broad transverse bands between compound eyes. Antennae brown, distally paler. Eyes black. Ocellar tubercle not darker than surrounding cuticle. Maxillary palps pale, fourth segment pale brown. Mesonotum brown with paler central area and pale, fine median stripe on antedorsum. Legs uniformly pale. Fore wings hyaline, with brown pattern as in *Pseudoscottiella tanei* Smithers (Smithers 1977, fig. 66).

Morphology. Length of body: 2.3 mm. Median epicranial suture distinct, anterior arms present but less obvious. Vertex somewhat flattened with long, erect setae, some of which are curved; a row of very long setae across vertex, the longest in the row reaching back almost to base of fore wing. Length of flagellar segments: f1: 0.49 mm.; f2: 0.24 mm. Antennae with long, erect setae, much longer than diameter of flagellum. Eyes large but not reaching level of vertex. IO/D: 2.0; PO: 0.83. A few small hairs between ocelli and two long setae arising from posterior edge of ocellar tubercle between lateral ocelli. Measurements of hind leg: F: 0.40 mm.; T: 0.81 mm.; t1: 0.22 mm.; t2: 0.11 mm.; rt: 2:1; ct: 14,0. Claws without preapical tooth. Fore wing length: 2.75 mm; width: 0.85 mm. Fore wing long and narrow, widening gradually to widest part. Costa very broad in pterostigma, about a third as wide as pterostigma opposite widest part. Costa broad to wing apex but not as broad as in pterostigma. Rs and M fusion long. Rs distal to separation from M almost straight. R_{2+3} slightly sinuous. R_{4+5} straight, ending at wing apex. Fork of M beyond radial fork but before end of areola postica. Areola postica long and narrow. Setae well developed on all veins except Cu_2 and at base of hind margin, where margin is slightly thicker at anal angle. Hind wing length; 2.0 mm.; width: 0.54 mm. Hind wing without setae on veins except distal part of R_1. Main marginal setae from R_1 to anal angle of two lengths, longer setae alternating with shorter, some of the latter lying at an angle to the large setae. Hind margin of ninth tergite thickened and slightly rugose on each side of epiproct. Epiproct (Fig. 20) with strongly sclerotised margin, body of epiproct more heavily sclerotised towards edges than elsewhere; coarsely rugose near posterior margin. Paraproct (Fig. 21) with ovoid trichobothrial field of about sixteen trichobothria with finely ridged "rosettes" and a small seta at one end of field. Paraproct with a few long, scattered setae, a row of setae and a double cone on hind margin. Hypandrium (Fig. 22) with posterior rounded lobe at each side and sinuous hind margin between them. Phallosome (Fig. 23) with somewhat transverse anterior end, weakly sclerotised in middle of anterior end. Sclerification of penial bulb in form of a pair of posteriorly tapering rods, separate at the base and each bent at a small, partially separated, basal sclerite.



Figs. 20–28. Pseudoscottiella alettae sp.n. (20) Male epiproct; (21) Male paraproct; (22) Hypandrium; (23) Phallosome; (24) Female epiproct; (25) Female paraproct; (26) Gonapophyses; (27) Posterior lobes of subgenital plate; (28) Ninth tergite of female.

Female

Colouration (in alcohol). As in male but vertex, frons and postclypeus ivory instead of various shades of brown. Fore wing pattern similar to that of male but with middle part of cell R_3 to Cu_{1a}. Hind wing with broad, transverse, irregular pale brown band.

Morphology. Length of body: 2.3 mm. Median epicranial suture distinct, anterior arms not evident. Vertex, frons and postclypeus wider than in male and all in same plane, that is, head appearing flat and broad with a sloping upper surface. Length of flagellar segments: f1: 0.27 mm.; f2: 0.19 mm. Eyes smaller than in male, well below level of vertex when seen from the side. IO/D: 3.2; PO: 0.8. No ocelli. Measurements of hind leg: F: 0.43 mm.; T: 0.7 mm.; t1: 0.19 mm.; t2: 0.094 mm.; rt: 2:1; ct: 11,0. Fore wing length: 2.3 mm.; width: 0.73 mm. Fore wing form and venation as in male, also with slight thickening of hind margin at anal angle. In one specimen M not branched, reaching margin as single vein in both wings. Hind wing as in male. Epiproct (Fig. 24) with rounded margin, well sclerotised with narrow, heavily sclerotised edge; few setae. Paraproct (Fig. 25) with strongly developed posterior double cone, trichobothrial field of about twelve trichobothria. Ninth tergite (Fig. 28) with strongly sclerotised, slightly curved margin opposite epiproct. Subgenital plate (Fig. 27). Gonapophyses (Fig. 26).

Material examined

5 males (including holotype), 2 females (including allotype), Tuglo Wildlife Refuge, 49 km N. Singleton, New South Wales, 17.xii.1978, A.S.Smithers. 1 female, same locality, 18.v.1974. 1 female, same locality, 1.x.1978. 1 female, same locality, 21.x.1978. 1 female, same locality, 24.vi.1980. A.S.Smithers. Holotype and paratypes in the Australian Museum. This species is named for my wife, who collected most of the specimens in the Tuglo Wildlife Refuge survey.

Discussion

The only Australian species of *Pseudoscottiella* with which *Ps. alettae* might be confused on general appearance are *Ps. tanei* Smithers and *Ps. yenoides*. The eyes of *Ps. alettae* are larger than those of *Ps. tanei*. The male phallosome of *Ps. tanei* has broad outer parameres and the fused apices of the inner parameres are spiculate whereas in *Ps. alettae* the outer parameres are narrow and the inner not apically spiculate. Anteriorly the phallosome is broad and transverse in *Ps. alettae* but is narrowed in *Ps tanei*. In the females the most obvious differences are to be seen in the posterior lobes of the subgenital plate. Beyond Australia only *Ps. ornatus* (Banks), from Guam, has a similar wing pattern but in that species the phallosome has apically spiculate inner parameres and the outer parameres are narrow, with spatulate ends. The sclerites of the penial bulb are clearly different from those of *Ps. alettae* in proportions, being long, thin and inwardly curved, crossing distally. The female of *Ps. ornatus* has not been described. The genitalia of *Ps. alettae* are very similar to those of *Ps. yenoides* but differ in some details. The wing pattern, on the other hand, differs considerably. In male *Ps. yenoides* there is no pattern. In the female the coloured areas are less extensive than in *Ps. alettae* and confined to the basal two thirds of the wing. The male epiproct differs in the two species, being rounded behind in *Ps. alettae* but more transverse in *Ps. yenoides*. The paraproct of male *Ps. yenoides* has about ten trichobothria, whereas there are about sixteen in *Ps. alettae*. The hypandrium of *Ps. alettae* has lateral lobes which are not present in *Ps. yenoides*.

First description of the male of Pseudoscottiella papillosa

Pseudoscottiella papillosa Schmidt and Thornton, 1992.

Schmidt and Thornton (1992) did not have male material of this species. Material collected in the survey includes 3 females and 2 males, the latter providing the material on which the following description is based.

Male

Colouration (in alcohol). Head, body and appendages pale creamy white. Fore wing (Fig. 17) hyaline, pterostigma greyish, opaque, suggestion of pale brown in areola postica. Veins pale. Hind wings hyaline, veins pale.

Morphology. Length of body: 1.9 mm. Median epicranial suture distinct, anterior arms evanescent. Head setose, with a pair of exceptionally long, fine setae arising from each epicranial plate and curving back above prothorax. Hind margin of head slightly sinuous between compound eyes. Length of flagellar segments: f1: 0.54 mm.; f2: 0.27 mm. First flagellar segment slightly curved. Eyes very large, on sides of head but upper margin only just level with vertex. IO/D: 0.8; PO: 0.8. Apex of lacinia divided, outer tine much larger than inner. Fourth segment of maxillary palp long and narrow, length 3.7 times width. Measurements of hind leg: F: 0.45 mm.; T: 0.78 mm.; t1: 0.24 mm.; t2: 0.08 mm.; rt: 3:1, ct: 16,0. Claws without preapical tooth. Pulvilli broad, apically very broad. Fore wing length: 2.5 mm.; width: 0.81 mm. Stigmapophysis shallow. Costa a little more heavily sclerotised in basal third of pterostigma than elsewhere. Rs-M fusion long, stem of Rs somewhat sinuous as is R_{2+3}. Rs and M branch opposite widest part of pterostigma. Veins, except Cu_2, setose. Wing margin slightly thickened at anal angle. Hind wing Rs-M fusion long, R_{4+5} reaches wing margin behind apex. Veins without setae, except for R_1 near wing margin. Ninth tergite with hind margin with a group of papillae on each side of midline, the middle part of the margin smooth, gently curved. Epiproct simple, more or less triangular, with a few scattered setae. Paraproct similar to that of *H. alettae* sp. n. (described below). Hypandrium (Fig. 18). Phallosome (Fig. 19) with external parameres slightly expanded towards tip and somewhat spatulate. Internal parameres likewise, without apical spicules. Penial bulb with sclerotised rods which are flattened and broadened towards tip.

Material examined

2 males, 1 female, 17.xii.1978, 1 female, 24.vi.1980. 1 female, 3.i.1988. A.S. Smithers.

Discussion

The male of *P. papillosa* is easily recognised by the parameres which are broadened, somewhat flattened and spatulate, of a shape not previously recorded in the genus.

PHILOTARSIDAE RECORDED FROM TUGLO WILDLIFE REFUGE

Haplophallus sinus Thornton and New (January, June, November)

Latrobiella guttata (Tillyard) (January, May, June)

Latrobiella medialis (Thornton and New) (April)

Latrobiella ornata (Thornton and New) (January, May)

Latrobiella paraguttata Thornton and New (November)

ELIPSOCIDAE RECORDED FROM TUGLO WILDLIFE REFUGE

Paedomorpha gayi Smithers (May, June)

Pentacladus eucalypti Enderlein (January, February, June, August, October, November, December)

Propsocus pulchripennis (Perkins) (January, February, March, April, May, August, October, November, December)

Spilopsocus ruidis Smithers (June, August)

ACKNOWLEDGEMENTS

I would like to thank my wife for collecting nearly all the specimens mentioned in this paper, Max Moulds and Larry Watrous for contributing material taken during visits to the Refuge and Graeme Smithers and Heidi Marks for taking care of a Malaise trap in my absence.

REFERENCES

Lee, S.S. and Thornton, I.W.B. (1967). The family Pseudocaeciliidae (Psocoptera) — a reappraisal based on the discovery of new Oriental and Pacific species. *Pacific Insects Monographs* **16**:1–116.

Schmidt, E.R. and Thornton, I.W.B. (1992). The Psocoptera of Wilsons Promontory National Park, Victoria, Australia. *Memoirs of the Museum of Victoria* **53**:137–220.

Shields, J.M., York, A. and Binns, D. (1992). Fauna and Flora Survey of Mt. Royal Management Area, Newcastle Region. *Forest Resources Series* No. 16, i-v, 111 pp. Forestry Commission of New South Wales, West Pennant Hills.

Smithers, C.N. (1977). The Psocoptera of Muogamarra Nature Reserve. *Records of the Australian Museum* **31**:251–306.

Smithers, C.N. (1989). Two new species of Amphientomidae (Insecta: Psocoptera), the first record of the family for Australia. *Proceedings of the Linnean Society of New South Wales* **111**:31–35.

Smithers, C.N.. (1993a). A note on the Megaloptera, Neuroptera and Mecoptera of Tuglo Wildlife Refuge, New South Wales. *Australian Entomologist* **20**:67–71.

Smithers, C.N. (1993b). New species and new records of Caeciliinae (Psocoptera: Caeciliidae) from the Mount Royal area, Hunter Valley, New South Wales, with a key to the Australian species of *Caecilius* Curtis. *General and applied Entomology* **25**:16–21..

Smithers, C.N. (1994). A note on the Peripsocidae (Psocoptera) of Tuglo Wildlife Refuge, Hunter Valley, New South Wales. *Australian Entomologist* **21**:7–10.

Tardigrades of the Australian Antarctic Territories: the Northern Prince Charles Mountains, East Antarctica

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(Communicated by D.S. Horning, Jr.)

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MILLER, W.R. AND HEATWOLE, H. (1996). Tardigrades of the Australian Antarctic Territories: the Northern Prince Charles Mountains, East Antarctica. Proc. Linn. Soc. N.S.W. 116: 245–260

During the austral summer of 1990–91, a survey of Tardigrada inhabiting terrestrial mosses and lichens was conducted in the northern Prince Charles Mountains, East Antarctica. Five genera and six species were recovered including *Echiniscus jenningsi, Diphascon sanae, Hypsibius antarcticus, Macrobiotus blocki, Macrobiotus stuckenbergi, and Milnesium tardigradum.* A model is proposed for the dispersal of tardigrades to and within East Antarctica. Cryptobiotic tardigrade tuns are carried aloft and over Antarctica via upper air currents, then descend over the centre of the continent and radiate outward to peripheral areas on katabatic winds. The deflection of surface winds by Coriolis forces allows for east to west dispersal from established populations along the East Antarctic Coast. Males have seldom been reported in the genus *Echiniscus*, but 30% of the *E. jenningsi* found were male. The strategy of sexual reproduction is discussed relative to distributional and survival challenges of tardigrades in East Antarctica.

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INTRODUCTION

The presence of tardigrades in Antarctica has been known for most of the twentieth century. Richters (1904) reported the first tardigrades from East Antarctica on the Wilhelm II Coast (see review by Miller et al. 1988), but the makeup of the fauna and the distribution of the member species is only beginning to emerge. There are no previous records of tardigrades from the northern Prince Charles Mountains although the animals have been reported from other East Antarctic locations. West of the Prince Charles Mountains, tardigrades have been recorded from Robertskollen (Ryan et al. 1989, Dastych et al. 1990, Dastych and Harris 1994), the Prince Olav Coast near the Japanese station at Syowa (Morikawa 1962; Sudzuki 1964, 1979; Sudzuki and Shimoizumi 1967; Utsugi and Ohyama 1989), Enderby Land around the Russian base at Molodezhnaya (Opalinski 1972, Dastych 1984, Utsugi and Ohyama 1991), and along the Mawson Coast (Miller and Heatwole 1995). To the east, tardigrades have been collected in the Larsemann Hills (Miller et al., 1994a), the Vestfold Hills near the Australian research base of Davis (Everitt 1981, Miller et al. 1988), the Wilhelm II Coast (Richters 1904, 1907), the Bungar Hills (Korotkevich 1964), and the Windmill Islands around the Australian research station at Casey (Thomas 1965; Dastych 1989; Miller et al. 1994b, 1996).

Continental Antarctica has a few truly terrestrial ecosystems. Mosses, lichens and a few algae persist in the harsh conditions (Filson 1966). These plants are widely scattered

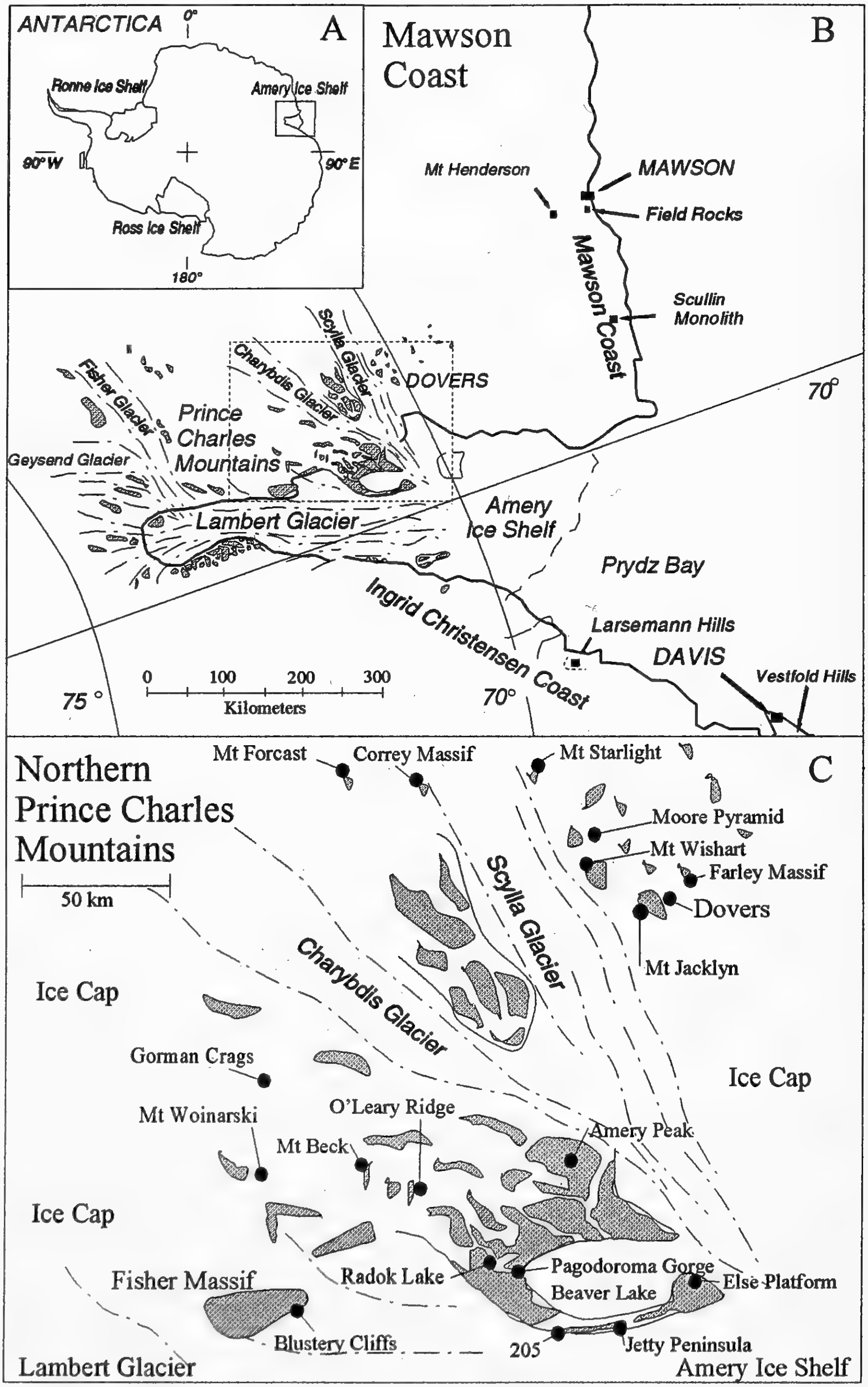

Fig. 1. Location maps of: A, Antarctica; B, Mawson Coast, Amery Ice Shelf, Lambert Glacier, and the Prince Charles Mountains; C, Northern Prince Charles Mountains showing study areas.

over the small areas of unfrozen land that ring the edge of the continent or protrude through the ice as nunataks. Heatwole (1983) and Heatwole et al. (1989) characterised the bacteria, yeasts, fungi, unicellular algae, rotifers, nematodes, tardigrades, and mites that inhabit the mosses, lichens, and rudimentary polar soils. The present paper treats the phylum Tardigrada from the Prince Charles Mountains, East Antarctica.

STUDY AREA

The northern Prince Charles Mountains, East Antarctica, consist of hundreds of nunataks and several large massifs located on the continental ice cap at the western edge of the Lambert Glacier and south of the Amery Ice Shelf (Figs. 1A, 1B). They extend 500 km to the south of Dovers, a temporary Australian Antarctic research camp on the north edge of the range. Dovers is on the ice cap (Fig. 1 C), 1500 m above sea level on the edge of the Scylla Glacier about 500 km west of the Australian station of Davis and 300 km south of Mawson station, at 70° 36' South and 66° 50' East (Fig. 1B). The Dovers camp was inhabited only during the austral summers of 1989–90 and 1990–91.

These mountains consist mainly of Precambrian basement rocks of the extensive East Antarctic Shield (Trail and McLeod 1965, Tingey 1982, James and Tingey 1983, Fitzsimons and Thost 1992), protruding above the ice cap at elevations mostly of 1000–2000 m above sea level (actual collecting sites 830–2160 m). However, three areas of importance to the present study, Jetty Peninsula, Else Platform, and Pagodroma Gorge, differed by being located at lower elevations (sea level-215 m) in the Beaver Lake garden, an area of downfaulted Permian to Early Triassic strata of sandstones and subordinate conglomerates, siltstones, shales, and coal (Mond 1972, McKelvey and Stephenson 1990).

The study area included 17 localities encompassed by the coordinates: 70° to 72°S; 65° to 70°E (Table 1; Figs. lB, lC). Of those, 13 did not yield tardigrades and are not described here, except to note that all but one (Else Platform) were nunataks at higher elevations where lower temperatures, higher winds, and more desiccation prevailed than at lowland sites. The upland sites either lacked lichens and/or mosses, or had them represented only as small widely scattered clumps or encrustations in sheltered rock-crevices. In some cases, several days of intensive search yielded only 1–3 thalli or cushions, all less than 1 cm in diameter.

Blustery Cliffs is located on the northern end of the Fisher Massif. The site consists of a flat, granite plateau bordered by steep rock slopes (Fig. 2A) that level off at the base into a scree slope and then another rocky plain. The plateau is partly covered by shallow drift snow up to 50 cm deep, from which boulders protrude. There are occasional patches of bare soil (up to 1 m in diameter) exposed between rocks, as well as more extensive areas swept bare of snow. The gray-brown soil is up to 3 cm deep and consists of small gravels with some pebbles and cobbles on top. On warm days snow melts and conditions are moist until re-freezing occurs. In places the surface 1–2 cm of soil dries out. The lower plain is similar except that the soil is deeper (15 cm) and boulder beds are interspersed with snow banks. Basal slopes are of jumbled boulders with only occasional, small pockets of soil about 20 cm in maximum diameter.

A few mosses occur only as small, widely scattered cushions 1 cm or less in diameter, located on moist soil either in sheltered rock-crevices on the cliff face, or between boulders on the plains. There are at least three species of lichens, all occurring as crustose thalli up to 5 cm in diameter (Fig. 3A). They grow on rock in crevices on the cliff face or on sheltered surfaces of boulders on the plain or scree slope.

Jetty Peninsula is a thin strip of exposed land (Fig. 2B) extending 60 km south of Else Platform and separating the frozen Beaver Lake from the Lambert Glacier. It consists of highly weathered sandstone, broken into frost polygons usually 20 cm or less in diameter. The substrate is of sand strewn with pebbles, cobbles, and occasional large boulders. There are local areas of flat rock. Scattered patches of snow supply meltwater. The soil is usually 3–13 cm deep and is moist, or if dry, only in the top centimetre.

This was the most highly vegetated area visited. Cushions of mosses grow where boulders shelter the ground. Lichens encrust on small stones in the furrows between polygons, on the northern faces of large boulders (Fig. 3B), and occasionally on flat rock in the open. There were at least four species of lichens and one of mosses.

Amery Peak rises west of the Loewe and Manning Massifs between Dovers base camp and the Jetting Peninsula. This area was visited by Dr Chris Fielding, who donated a moss specimen described as moss collected growing on the ground on the northeastern side of the Peak.

Radok Lake is fed by the Bathye Glacier and drains via Pagodroma Gorge into Beaver Lake. A single moss-covered soil sample collected by Dr Don Adamson in early 1989, and donated by Ms Penelope Greenslade, contained tardigrades.

TABLE 1.

Collection localities in the Prince Charles Mountains.

Locality	Altitude	Mosses	Lichens	Dates
		Tardigrades found		
Blustery Cliffs	830–1135	Yes	Yes	20-21 Jan, 1990
Jetty Peninsula		Yes	Yes	25-26 Jan, 1990
Amery Peak		Yes**	—	Early 1990
Radok Lake		Yes**	—	Early 1990
		Tardigrades not found		
Mt Woinarski	1100–1560	No	No	13-18 Jan, 1990
Pagodroma Gorge	215	No	Yes	22-24 Jan, 1990
Else Platform		Yes	Yes	28Jan, 1990
Mt Wishart	1300–1670	Yes*	Yes*	Jan-l Feb, 1990
Moore Pyramid	1900–2160	No	Yes*	3-4Jan, 1990
Mt Starlight	2150	No	No	6 Feb, 1990
Mt Forcast		Yes	Yes	9Feb, 1990
Correy Massif	2060	No	Yes	10-11 Feb, 1990
Mt Jacklyn		No	Yes	13 Feb,1990
Farley Massif		No	Yes	16 Feb, 1990
O'Leary Ridge		—	Yes**	—
Mt Beck		—	Yes**	—
Gorman Crags		—	Yes	—

* Only 1–3 small samples, each less than 1 cm found in area

** Not visited by authors, samples donated by other expeditioners

— Data not avaliable

METHODS

Field work was carried out by the junior author in January and February 1990 with logistical support from Dovers base camp. It served as a helicopter base from which expeditioners were distributed in pairs to distant localities where they set up a tent and carried out their research. Field work at each locality was conducted on foot; all available habitats were searched for mosses and lichens. At each sampling site, lichens were scraped from rocks with a knife and either entire moss cushions or 25 mm diameter cores

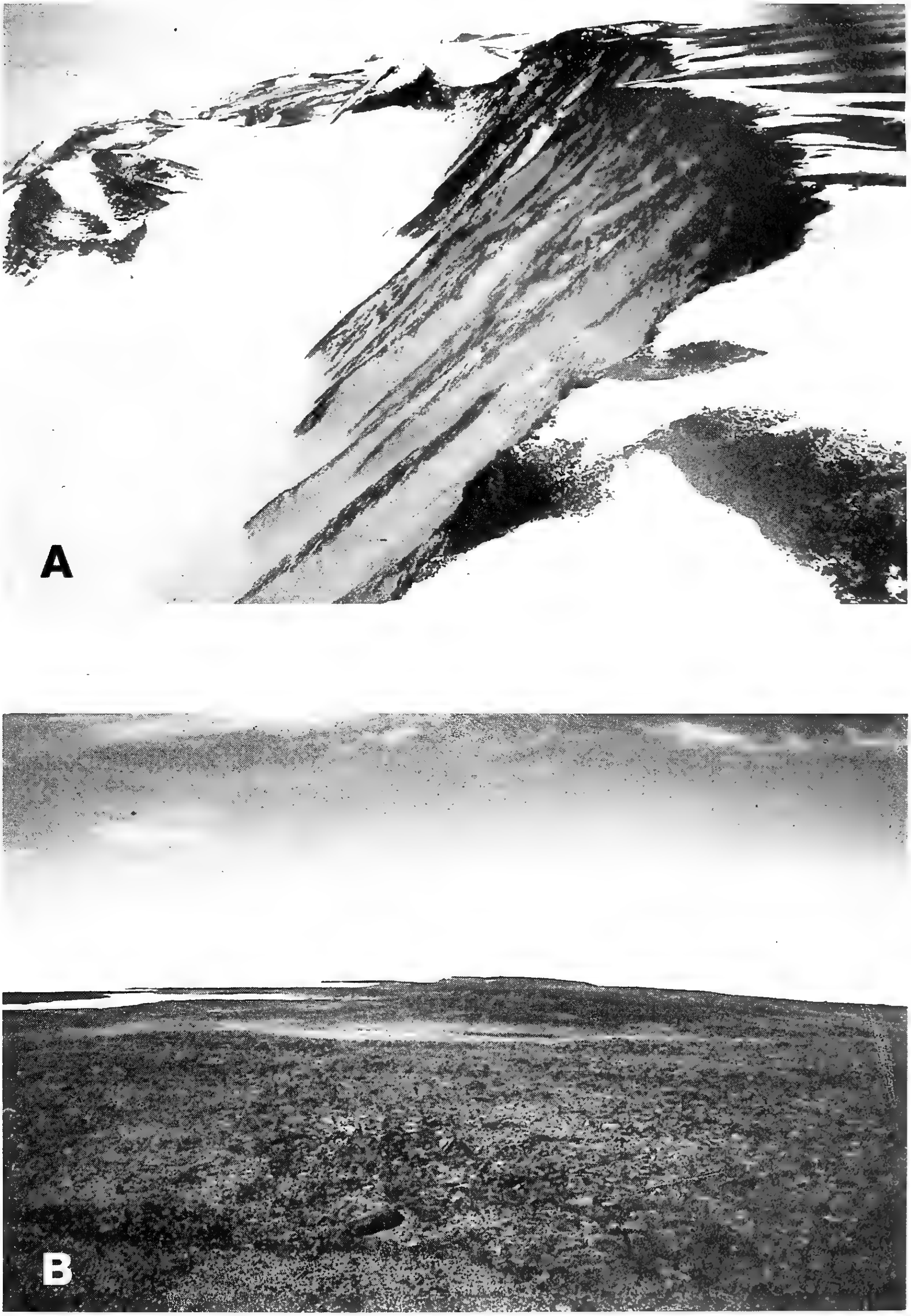

Fig. 2. Photograph of A, Blustery Cliffs; B, Jetty Peninsula.

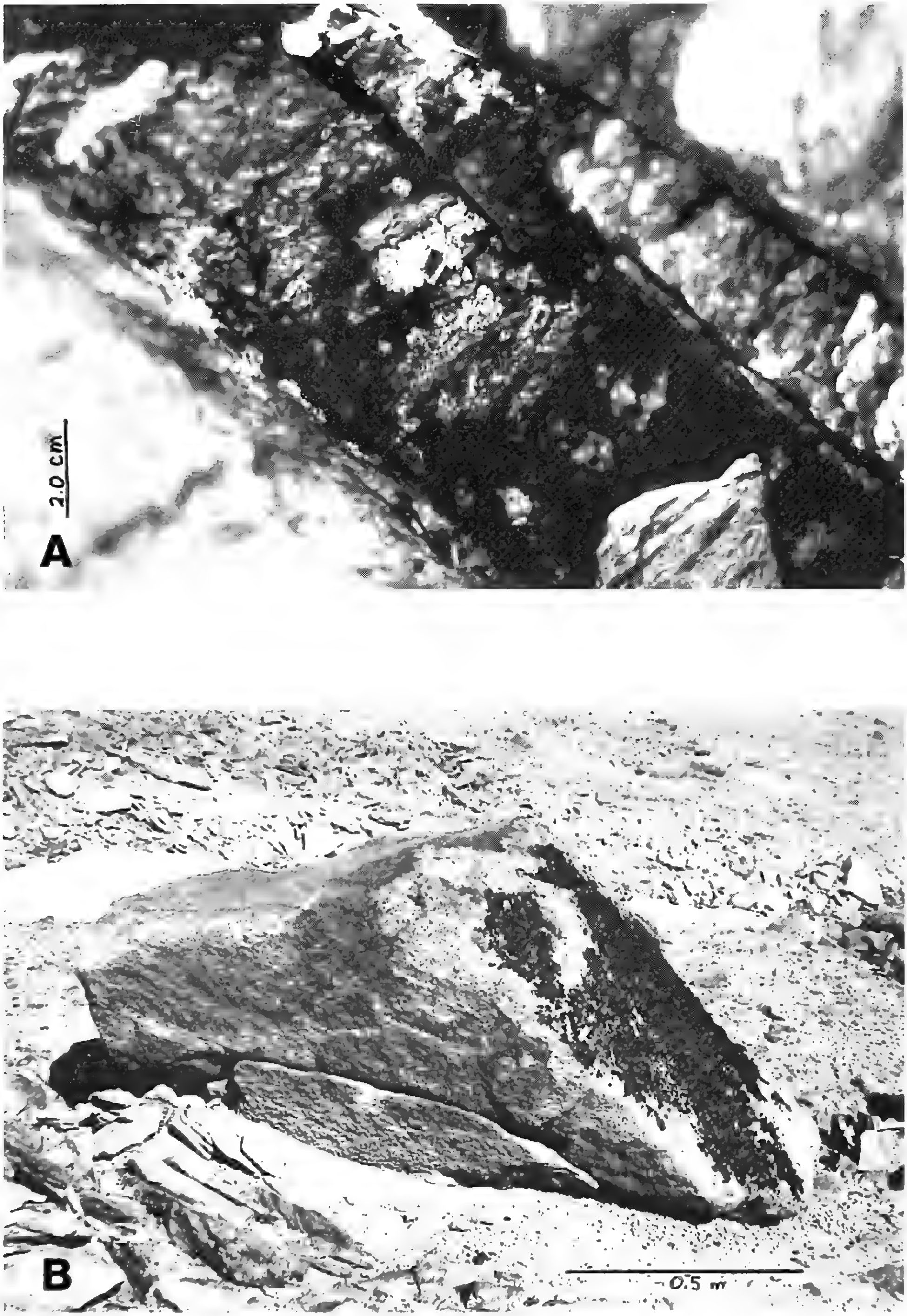

Fig. 3. Photograph of lichens at A, Blustery Cliffs; B, Jetty Peninsula

were taken. All samples were frozen and returned to Australia for extraction of animals. Fourteen moss and 46 lichen samples were obtained.

Extraction of animals was carried out by soaking the moss or lichen for 48 hours in a 4% sucrose solution with a drop of sodium pentobarbitone additive. Several washings, during which the plant was squeezed, were filtered through a 63-micrometer nylon mesh to strain out finer material. The debris was preserved in 5% buffered formalin. Later the tardigrades were separated under a dissecting microscope. Individual animals were transferred to slides with an Irwin Loop, mounted in iodine enhanced Hoyer's medium, capped with a glass coverslip and sealed by epoxy paint.

Identification of tardigrades was established using a phase-contrast microscope. The microscopic image was captured with a CCD video camera and a personal computer to produce video-micrographs. The image was printed by laser printer and used for measurements and drawings.

The works of Homing et al. (1978), Schuster et al. (1980), Ramazzotti and Maucci (1983) and Dastych (1984) were used for primary identification. Taxonomic criteria and terminology follows Ramazzotti and Maucci (1983), except as noted. Representative specimens were deposited at the Australian National Insect Collection, CSIRO Division of Entomology, Canberra, ACT, Australia and in the Zoological Museum, Hamburg.

RESULTS

From the 725 tardigrades collected, five genera and six species were identified. There were 369 (50.9%) specimens identified as *Hypsibius antarcticus* (Richters 1904), 276 (38.1%) as *Macrobiotus blocki* Dastych 1984, 46 (6.3%) as *Echiniscus jenningsi* Dastych 1984, 20 (2.8%) as *Macrobiotus stuckenbergi* Dastych, Ryan, and Watkins 1990, 13 (1.8%) as *Milnesium tardigradum* Doyere 1840, and one (0.1%) as *Diphascon sanae* Dastych, Ryan, and Watkins 1990 (Table 2). Each species conforms to the descriptions reported by the same authors from the Mawson Coast (Miller and Heatwole 1995).

Of the 60 samples (1 soil, 14 mosses, and 45 lichens) collected, only 14 (23%) contained tardigrades. Representation by species within the positive samples was not uniform. *Macrobiotus blocki* was found in 10 (71%) of the 14 positive samples and *Macrobiotus stuckenbergi* in five (35.7%). Less frequent were *Echiniscus jenningsi* which occurred in four of 14 (28.6%) and *Milnesium tardigradum* which was found in three (21.4%). The least frequent were *Hypsibius antarcticus,* present in only two of 14 (14.3%) and *Diphascon sanae,* present in only one (7.1%).

Species occurrence at any positive site was low. Only one of 14 sites (7.1%) yielded four of the six species and two sites (14.3%) had three. Eleven of the positive samples (78.6%) had two species or less. Different mixtures of genera and species were found at different collection sites. Table 2 details the number of animals found at each site and shows the co-occurrences of the species. The collections at Blustery Cliffs contained five of the six species of the collective tardigrade fauna. The collections along Jetty Peninsula yielded four of the six species. Only one species was recovered from Amery Peak and Radok Lake.

DISCUSSION

The nunataks and massifs of the northern Prince Charles Mountains are free of ice in summer and are not unlike islands in a sea (Miller et al. 1988). The water around them may be frozen but the problems of dispersal and survival for plants and animals are as real as for any island. Mosses and lichens were first collected from the Prince Charles Mountains of MacRobertson Land in 1962 (Filson 1966). Even under the harsh environ-

TABLE 2.

Species and numbers of tardigrades collected from various habitats in the Prince Charles Mountains.

Site	Localities	Habitat	*Echiniscus jenningsi*	*Diphascon sanae*	*Hypsibius antarcticus*	*Macrobiotus blocki*	*Macrobiotus stuckenbergi*	*Milnesium tardigradum*
1	Blustery Cliffs	Moss				28		
2	Blustery Cliffs	Moss	1			5		
3	Blustery Cliffs	Lichen				1		
4	Blustery Cliffs	Lichen			368		1	
5	Blustery Cliffs	Soil		1	1		6	
6	Jetty 205	Lichen				1	1	
7	Jetty 205	Lichen	1					1
8	Jetty Peninsula	Moss	43			3	1	7
9	Jetty Peninsula	Moss				3		
10	Jetty Peninsula	Moss	1			58	11	
11	Jetty Peninsula	Lichen				28		5
12	Jetty Peninsula	Lichen				2		
13	Amery Peak	Moss				107		
14	Radok Lake	Moss				40		
Total:		**725**	**46**	**1**	**369**	**276**	**20**	**13**

mental conditions found along the Lambert Glacier and the Amery Ice Shelf, tardigrades were expected to be found because the phylum is known to survive greater extremes than exist naturally (Crowe 1972).

When subjected to adverse conditions, many tardigrade species enter a deeply dormant state, known as cryptobiosis, a reversible suspension of metabolism (Clegg 1973, Crowe 1975, Kinchin 1994, Wright et al. 1992). When cryptobiotic, tardigrades shrivel into a tun and can tolerate experimental extremes such as lack of moisture, strong vacuums, ionising radiation, noxious chemicals, high heat, and cold approaching absolute zero (Ramazzotti and Maucci 1983). Tardigrades have remained viable in the cryptobiotic state for over a century (Franceschi 1948, Kinchin 1994). Clearly, tardigrades have the capacity to sustain life for long periods of time, through the rigours of long distance dispersal, and within a hostile environment upon reaching a destination.

Logs of distant origin have been reported as washing up on Subantarctic Heard and Macquarie Islands (Smith et al. 1989). However, none were reported to contain lichens or mosses and it is likely that tardigrades, along with their habitat, usually would be washed off such flotsam well before arriving in polar regions. No wood has been reported on continental Antarctic shores. Thus, sea dispersal of tardigrades to Antarctica via flotsam seems unlikely, or at best rare, and in any event could not account for range extensions from the coast to interior locations like the Prince Charles Mountains.

Birds regularly fly between the Antarctic and distant regions and could transport tardigrades either in mud on their feet, or perhaps in their feathers. Most are sea birds and periodically settle on the water and would have their legs rinsed of any mud. Furthermore, even after arrival few stray very far into the interior. Three species of birds have been recorded from the northern Prince Charles Mountains, the Snow Petrel *(Pagodroma nivea),* the South Polar Skua *(Catharacta maccormicki),* and Wilson's Storm Petrel *(Oceanites oceanicus)* (Heatwole et al. 1991). The last has only been noted as an accidental visitor, but the former two nest there, although in only a few localities. The Snow Petrel nests in crevices in cliffs and along boulders, habitats that are occupied by mosses and lichens (see Study Area above). Even if dislodged in a bare crevice, a tardigrade tun might survive until the arrival and growth of a lichen or moss. The skua nests in the open, but on ground where it could contact moss or lichens. Thus, dispersal via birds, even to areas as remote as the Prince Charles Mountains, is a possibility that cannot be discounted. However, it would appear to be an unlikely event.

Wind seems to be a more probable mode. There are three known wind patterns of relevance. The first consists of easterly, high-altitude winds that circulate from lower latitudes to over the South Pole (Gabler et al. 1990) (Fig. 4A) where it descends in the low pressure trough that exists over the highest, coldest part of the continent as described in the United Kingdom Meteorological Office's Unified Model for the climate of Antarctica (Connolley and Cattle 1994) (Fig. 4B). The second prevailing wind pattern is the katabatic drainage of cold air from the Polar Plateau toward the periphery (Connolley and Cattle 1994, Rubin 1965) (Figs. 4B, C). These winds are often of high velocity and would blow straight north except for the easterly rotation of the earth that bends them in a counterclockwise direction around the South Pole, the Coriolis effect (Fig. 4C). Finally, there are eddies and local winds of a temporary character that can shift direction but generally flow counterclockwise and parallel to the coast (Fig. 4C).

A model of tardigrade dispersal to, and within, East Antarctica is now proposed that is consistent with these wind patterns. It is suggested that on other continents, tardigrade tuns are blown airborne with dust and other debris where they are carried aloft, picked up on the upper air easterlies (Figs. 4A, B), and flow toward the south. Over central Antarctica, they descend over the eastern Polar Plateau, drawn into the polar trough of low pressure, and from there are dispersed peripherally by the surface level, katabatic wind drainage (Figs. 4B, C). Coriolis deflection and the shape of the Antarctic land mass, cause these winds and the debris carried with them to be directed laterally along the coast (Fig. 4C).

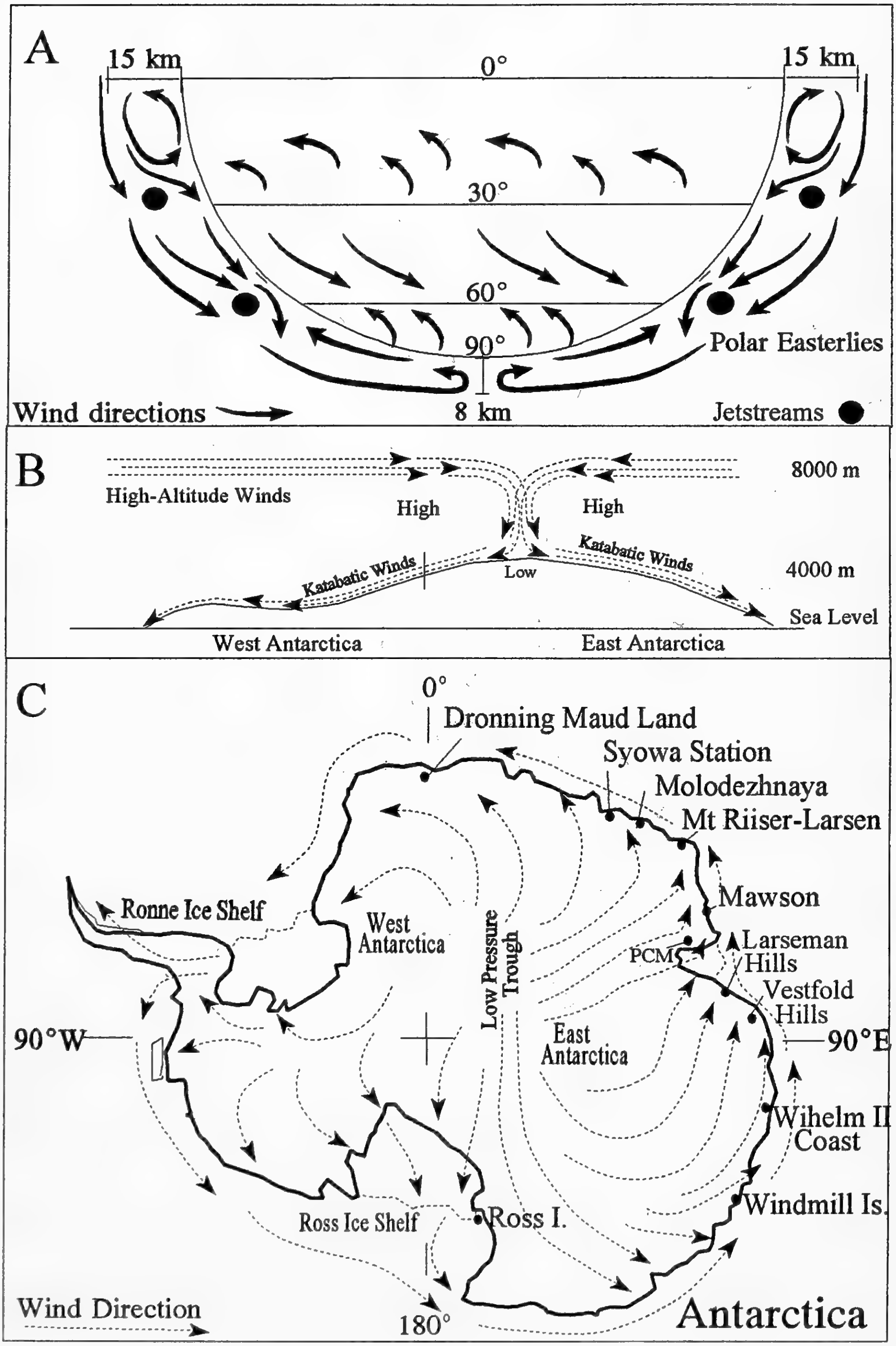

Fig. 4. Model of East Antarctic wind patterns.

The Prince Charles Mountains may have two external sources of tardigrades. Upper level winds are known to carry small plant propagules and animals much larger and heavier than tardigrade tuns for long distances and even over Antarctica (Gresitt et al. 1960, Clegg 1966). Many tardigrades have very broad, even cosmopolitan ranges, and two of these species, *Milnesium tardigradum* and *Hypsibius antarcticus* (McInnes 1994), were found in this study. The katabatic winds draining off the central ice cap down through the channel of the Lambert Glacier could carry propagules originating beyond the continent and it is likely that cryptobiotic tuns are dispersed to the Prince Charles Mountains in this way. In addition, the counterclockwise movement of the winds could bring propagules from upwind populations on the coast of eastern Antarctica. Once established in the mountains, local populations could serve as foci for further distribution via eddies of episodic winds, or further movement on katabatic winds.

On the basis of dispersal from the coast internally, one would expect that inland locations would be barren in comparison to coastal ones because of the filtering effect of distance on dispersal. In fact, the Prince Charles Mountains and the Mawson Coast have identical species of tardigrades (Miller and Heatwole 1995) and the same number of species as found in the Larsemann Hills (Miller et al. 1994a). There are two probable reasons for this. (1) The present model suggests that dispersal is a combination of centrifugal movement and transit from east to west along the East Antarctic Coast. Under this scenario, the Prince Charles Mountains have the same sources of tardigrade propagules as the Mawson Coast and in terms of distances travelled are marginally closer, rather than farther, from extra continental sources. (2) The long-term tolerance of tardigrades to harsh conditions reduces the effect of distance or time on their capacity to disperse. Indeed, their physiological capabilities might enable them to sustain even the conditions of outer space for a considerable period.

Available habitat “targets” might be a more significant determinant of tardigrade distribution in the Antarctic, these decrease from coast toward the interior. Mosses and lichens are larger and more abundant on ice free areas of the coast as compared to the inland nunataks and massifs, probably because of the harsher climate in the interior. Furthermore, on the coast they sometimes are exposed on open, flat surfaces where the wind can sweep over them, whereas further toward the centre these plants grow mainly in crevices and among rocks where they are sheltered from the wind and, consequently, from access to tardigrade propagules. Despite the Prince Charles Mountains being further inland and with a moss and lichen density much lower and less accessible than on the coast, they have the same species of tardigrades as does the Mawson area (Miller and Heatwole 1995). The determinative role of mosses and lichens in tardigrade distribution would be lessened to the extent that these animals can prosper in other habitats, e.g., Antarctic soils. It should be noted that three species of the present study were extracted from a soil sample.

Although dispersal events are difficult to observe and the proposed model cannot be tested easily, it is a consistent with observed distribution and with wind patterns. It accounts for the presence of cosmopolitan species like *Hypsibius antarcticus* and *Milnesium tardigradum* as well as local endemics. The latter, once established by a rare, chance dispersal and cut off from further significant gene flow, could speciate. Katabatic winds could disperse them to downwind localities on the coast. Local winds would distribute them to adjacent localities. Because of this pattern, East Antarctica may not be an exporter of species.

Table 3 presents the distribution along the East Antarctic coast of the tardigrade species found in the Prince Charles Mountains. All six species are found further downwind but only the two cosmopolitan species have been found upwind. *Hypsibius antarcticus* has a near continuous distribution around the Antarctic continent (Dastych 1991), including all collected upwind locations. This would indicate either a continuous influx from off continent or good lateral distribution or both and wide environmental

TABLE 3.

East Antarctic wind distribution model for tardigrade species collected in the Prince Charles Mountains.

Location	Dronning Maud Land 72S;02W	Syowa Station 69S;39E	Molodez-hnaya 68S;45E	MtRiiser-Larsen & Thala Hills 67S;SIE	Mawson Coast 62S;67E	Prince Charles Mountains 66S;72E	Larsemann Hills 66S;76E	Vestfold Hills 68S;78E	Wilhelm II Coast 66S;9OE	Windmill Islands 66S;110E	Ross Isl & Victoria Land 78S;168E
Reference Code	1	2,3	4	4,5	6	7	8	9,10	11	12,13,14,15	16
Echiniscus jenningsi					←X	X					
Diphascon sanae	←X				X	X					
Hypsibius antarcticus		←X	X	X	X	X	X	X	X	X	X
Macrobiotus blocki				←X	X	X					
Macrobiotus stuckenbergi	←X				X	X					
Milnesium tardigradum		←X	X	X	X	X	X				

Species collected **X** Wind Direction

References

1. Ryan et al. 1989
2. Utsugi & Ohyama 1989
3. Sudzuki 1964
4. Utsugi & Ohyama 1991
5. Dastych 1984
6. Miller & Heatwole 1995
7. This paper
8. Miller et al.1994a
9. Everitt 1981
10. Miller et al. 1988
11. Richters 1904
12. Thomas 1965
13. User & Dastych 1989
14. Miller et al. 1994b
15. Miller et al. 1996
16. Dougherty & Harris 1963

tolerance. *Milnesium tardigradum* is known from a few locations on the Antarctic Peninsula and some of the maritime islands on the other side of the continent (Dastych 1984, Dastych 1989, McInnes and Ellis-Evans 1987, Usher and Dastych 1987), but from only one location directly upwind, the Larsemann Hills (Miller et al. 1994a). This pattern would indicate colonisation from off continent and downwind distribution around part of East Antarctica. We would caution that these patterns may be an artefact of collection and may change as more data becomes available for distributional and ecological analysis.

Three species seem restricted to East Antarctica. *D. sanae* and *M. stuckenbergi* have dispersed around one-quarter of the continent from the Prince Charles Mountains and Mawson Coast to Dronning Maud Land while *M. blocki* has a more limited distribution, being known only from the Prince Charles Mountains, Mawson, and down wind to Enderby Land. These species may have originated in the Prince Charles Mountains and are in the process of being dispersed.

Echiniscus jenningsi is known only from Antarctica. There appears to be two separate concentrations, on opposite sides of the continent. The western concentration is on the Antarctic Peninsula (Dastych 1989, Usher and Dastych 1987) and the maritime islands of the South Shetland Islands (Dastych 1984; Jennings 1976a, 1976b), Signey Island, South Orkney Islands (McInnes and Ellis-Evans 1987). The eastern concentration is along the Mawson Coast (Miller and Heatwole 1995) and the Prince Charles Mountains (this study). We conjecture that *E. jenningsi* developed as a species in the Prince Charles Mountains, has been dispersed counterclockwise downwind around the periphery of the continent to the Antarctic Peninsula, and out along the maritime islands. This distribution follows the wind pattern defined in the model where wind flows around the periphery and outward along the peninsula, not vice versa.

The presence of large, plentiful males is believed by Kristensen (1987) to be a plesiomorphic condition, and as such would indicate that the populations of *E. jenningsi* found on the Mawson Coast and in the Prince Charles Mountains have not evolved far from their ancestral characteristics. Bertolani et al. (1990) suggested that species abundance after dispersal is a function of either a large environmental tolerance or a lower environmental tolerance and parthenogenesis. The finding of amphimictic populations of *E. jenningsi* at widely separated Antarctic locations (Dastych 1987, 1989; Miller and Heatwole 1995) would suggest that for successful long range dispersal, both sexes of *E. jenningsi* must find suitable habitat together. Once established, local dispersion of the species would be realistic because of the increased opportunity for opposite sexes to meet. Between the Mawson Coast collections (Miller and Heatwole 1995) and this report, *E. jenningsi* is reported from moss, lichen, and soil implying tolerance of diverse environments.

The active season in Antarctica is very short, and while a tardigrade could survive a winter or several winters, eventually it must encounter suitable habitat, food, and water and then reproduce. *E. jenningsi* may not have been found at intervening sites because it did not encounter acceptable habitat upon arrival or it may have encountered livable environments but not endured for lack of the opposite sex (Bertolani 1987). By chance, a pair or a gravid female, was carried by the peripheral winds, arrived on the Antarctic Peninsula, survived, reproduced, and further dispersed from there.

This evidence of localised dispersal by an amphimictic species does not conflict with Pilato's (1979) general view that parthenogenesis is an adaptation for successful colonisation by passive dispersal. He and Bertolani (1987) argued that a single parthenogenetic animal reaching an uninhabited but suitable location could establish a population. This probably explains the cosmopolitan distribution of *H. antarcticus* and maybe *M. tardigradum,* although the latter species has discernible sexes and may also reproduce sexually. Two of the six species identified from the Prince Charles Mountains, *M. blocki* and *M. stuckenbergi* are known to have populations with viable eggs at several locations (personal communication, Dr Dastych; and unpublished data, Miller and Heatwole). This is evidence of successful colonisation, but does not demonstrate either sexual or asexual reproduction. Karyological work, such as Bertolani (1982), will be necessary on the Antarctic tardigrades to define whether any of these species reproduce sexually or parthenogenetically.

It would appear that several separate strategies for survival and dispersion are simultaneously in evidence in East Antarctica. Parthenogenetic, cosmopolitan species with wide distributions; bisexual species with limited distribution; and some that are undetermined, can be identified. Dispersal, available habitat, and sexual strategies are, each singly and in combination, limiting factors in East Antarctic tardigrade distribution. Thus, existing tardigrade faunas at any given locality are those that have arrived, reproduced, and survived over time and this process may still be occurring.

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REFERENCES

Bertolani, R. (1982). Cytology and reproductive mechanisms in tardigrades. In 'Proceedings of Third International Symposium on Tardigrada' (Ed. D.R. Nelson) pp. 93–114 (East Tennessee State University Press: Johnson City, Tennessee).

Bertolani, R. (1987). Sexuality, reproduction and propagation in tardigrades. In 'Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.' (Ed. R. Bertolani) pp. 93–101 (Mucchi: Modena).

Bertolani, R., Rebecci, L., and Beccaccioli, G. (1990). Dispersal of *Ramazzottius* and other tardigrades in relation to type of reproduction. *Invertebrate Reproduction and Development* **18**, 153–157.

Clegg, H.B. (1966). Trapping of Air-Borne Insects in the Atlantic-Antarctic Area. *Pacific Insects* **8**, 455–466.

Clegg, H.B. (1973). Do dried cryptobiotes have a metabolism? In 'Anhydrobiosis' (Eds. J.H. Crowe and J.S. Clegg) pp. 141–146 (Dowden, Hutchinson and Ross: Stroudsburg, Pennsylvania).

Connolley, W.H. and Cattle, H. (1994). The Antarctic climate of the UKMO Unified Model. *Antarctic Science* **6**, 115–122.

Crowe, J.H. (1972). Evaporative water loss by tardigrades under controlled relative humidities. *Biological Bulletin of the marine biological laboratory, Woods Hole* **142**, 407–416.

Crowe, J.H. (1975). The physiology of cryptobiosis in tardigrades. In 'Proceedings of the first international symposium on tardigrades' (Ed. R.P. Higgins) *Memorie dell 'Istituto Italiano di Idrobiologia* **32** (Supplemento), 37–59.

Dastych, H. (1984). The Tardigrada from Antarctic with descriptions of several new species. *Acta Zoologica Cracoviensia* **27**, 377–436.

Dastych, H. (1987). Two new species of Tardigrada from the Canadian Subarctic with some notes on sexual dimorphism in the family Echiniscidae. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* **8**, 319–334.

Dastych, H. (1989). An annotated list of Tardigrada from the Antarctic. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* **9**, 249–257.

Dastych, H. (1991). Redescription of *Hypsibius antarcticus* (Richters, 1904), with some notes on *Hypsibius arcticus* (Murray, 1907) (Tardigrada). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut* **88**, 141–159.

Dastych, H. and Harris, J.M. (1994). A new species of the genus *Hebesuncus* from the Antarctic nunataks, Dronning Maud Land, (Tardigrada). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* **11**, 139–145.

Dastych, H., Ryan, P.G., and Watkins, B.P. (1990). Notes on Tardigrada from western Dronning Maud Land (Antarctica) with a description of two new species. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* **10**, 57–66

Dougherty, E.C, and Harris, L.G. (1963). Antarctic Micrometazoa: Fresh-water species in the McMurdo Sound Area. *Science* **140**, 497–498.

Doyere, M.P.L.N. (1840). Memoire sur les Tardigrades. *Annales des Sciences naturelles, 2. Serie. T. Zool.***14,** 269–361.

Everitt, D.A. (1981). An ecological study of an antarctic freshwater pool with particular reference to Tardigrada and Rotifera. *Hydrobiologia* **83**, 225–237.

Filson, R.B. (1966). The lichens and mosses of MacRobertson Land. *ANARE Science Reports., Series. B (II) Botany,* Publication. No. 82, 1–169.

Fitzsimons, I.C.W. and Thost, D.E. (1992). Geological relationships in high-grade basement gneiss of the northern Prince Charles Mountains, East Antarctica. *Australian Journal of Earth Sciences* **39,** 173–193.

Franceschi, T. (1948). Anabiosis nei Tardigradi. *Bolletino dei Musei e degli Instutit Biologici dell Universta de Genoa* **22**, 47–49

Gabler, R.E., Sager, R.J., and Wise, D.L. (1990). 'Essentials of Physical Geography'. (Holt, Rinehart and Winston: Orlando).

Gresitt, J.L., Leech, R.E., and O'Brien, C.W. (1960). Trapping of Air-Borne Insects in the Antarctic Area. *Pacific Insects* **2**, 245–250.

Heatwole, H. (1983). Community structure of organisms in Antarctic and sub-Antarctic soils. *ANARE News Supplement* **1**, 81.

Heatwole, H., Betts, M., and Crosthwaite, P. (1991). Birds of the northern Prince Charles Mountains, Antarctica. *Corella* **15**, 120–122.

Heatwole, H., Saenger, P., Spain, A., Kerry, E. and Donelan, J. (1989). Biotic and chemical characteristics of some soils from Wilkes Land, Antarctica. *Antarctic Science* **1**, 225–234.

Horning, D.S., Schuster, R.O. and Grigarick, A. A. (1978). Tardigrada of New Zealand. *New Zealand Journal of Zoology* **5**, 185–280.

James, P.R. And Tingey, R.J. (1983). The Precambrian geological evolution of the East Antarctic metamorphic shield — a review. In 'Antarctic Earth Science' (Eds. R.L. Oliver, P.R. James and J.B. Jago) pp. 5–10 (Australian Academy of Sciences: Canberra).

Jennings, P.G. (1976a). The Tardigrada of Signy Island, South Orkney Islands, with a note on the Rotifera. *British Antarctic Survey Bulletin* **44**, 1–25.

Jennings, P.G. (1976b). Tardigrada from the Antarctic Peninsula and Scotia Ridge region. *British Antarctic Survey Bulletin* 44, 77–95.

Kinchin, I.M. (1994). 'The Biology of Tardigrades'. (Portland Press: London).

Korotkevich, V.A. (1964). Concerning the population of water bodies in the oasis of east Antarctica. *Soviet Antarctic Expedition Information Bulletin* **1**, 154–161.

Kristensen, R.M. (1987). Generic revision of the Echiniscidae (Heterotardigrada), with a discussion of the origin of the family. In 'Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.' (Ed. R. Bertolani) pp. 261–335 (Mucchi: Modena).

McInnes, S.J. (1994). Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. *Journal of Natural History* **28**, 257–352.

McInnes, S.J. and Ellis-Evans, J.C. (1987). Tardigrades from maritime Antarctic freshwater lakes. In 'Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.' (Ed. R. Bertolani) pp. 111–123 (Mucchi: Modena).

McKelvey, B.C. and Stephenson, N.C.N. (1990). A geological reconnaissance of the Radok Lake area, Amery Oasis, Prince Charles Mountains. *Antarctic Science* **2**, 53–66.

Miller, J.D., Horn, P., Heatwole, H., Miller, W.R. and Bridges, L. (1988). A survey of the terrestrial micrometazoa of the Vestfold Hills, Antarctica. I. Tardigrada. *Hydrobiologica* **165**, 197–208.

Miller, W.R., Heatwole, H.F. (1995). Tardigrades of the Australian Antarctic Territories: the Mawson Coast, East Antarctica. *Invertebrate Biology* **114**, 27–38.

Miller, W.R., and Heatwole, H., Pidgeon, R.W.J., and Gardiner, G.R. (1994a). Tardigrades of the Australian Antarctic Territories: the Larsemann Hills, East Antarctica. *Transactions of the American Microscopical Society* **113**, 142–160.

Miller, W.R., Miller, J.D., and Heatwole, H.F. (1994b). Tardigrades of the Australian Antarctic Territories: assessing diversity within a sample. *Memoirs of the Queensland Museum* **36**, 139–147.

Miller, W.R., Miller, J.D., and Heatwole, H.F. (1996). Tardigrades of the Australian Antarctic Territories: The Windmill Islands, East Antarctica. *Zoological Journal of the Linnean Society* **116**, 175–184

Mond, A. (1972). Permian sediments of the Beaver Lake, Prince Charles Mountains. In 'Antarctic Geology and Geophysics' (Ed. R.J. Adie) pp. 585–598 (Universitetsforlaget: Oslo).

Morikawa, K. (1962). Notes on some Tardigrada from the Antarctic region. *Biological Results of the Japanese Antarctic Research Expedition* **17**, 1–7.

Opalinski, K.W. (1972). Flora and fauna in freshwater bodies of the Thala Hills oasis (Enderby Land, Eastern Antarctica). *Polskie Archiwum Hydrobiologh* **19**, 383–398.

Pilato, G. (1979). Correlations between cryptobiosis and other biological characteristics in some soil animals. *Bollettino di Zoologia* **46**, 319–332.

Ramazzotti, G. and Maucci, W. (1983). Il Philum Tardigrada. 3rd edition. *Memorie dell Istituto Italiano de Idrobiologica Dott. Marco de Marchi* **41**, 1–1012.

Richters, F. (1904). Volaufiger Bericht uber die antarktische Moosfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft* **24**, 236–239.

Richters, F. (1907). Die Fauna der Moosrasen des Gaussbergs und einiger Sudlicher Inseln. Deutsche Sudpolar-Expedition 1901–1903. *Zoologie* **9**, 259–302.

Rubin, M. J. (1965). Antarctic climatology. *Biologicae Monographiae* **15**, 72–96.

Ryan, P.G., Watkins, B.P., Lewis-Smith, R.I., Dastych, H., Eicker, A., Foissner, W., Heatwole, H., Miller, W.R., and Thompson, G. (1989). Biological survey of Robertskollen, western Dronning Maud Land: area description and preliminary species list. *South African Journal of Antarctic Research* **19**, 1989.

Schuster, R. O., Nelson, D.R., Grigarick, A. A. and Christenberry, D. (1980). Systematic criteria of the Eutardigrada. *Transactions of the American Microscopical Society* **99**, 284–303.

Smith, J.M.B., Rudall, P., and Keage, P.L. (1989). Driftwood on Heard Island. *Polar Record* **25**, 223–228.

Sudzuki, M. (1964). On the microfauna of the Antarctic region. I. Moss-Water Community at Langhovde. *Japanese Antarctic Research Expedition Scientific Report, Series E, Publication* **19** (Dept. Polar Research, National Science Museum: Tokyo), 1–41.

Sudzuki, M. (1979. On the microfauna of the Antarctic region. III. Microbiota of the terrestrial interstices. In 'Proceedings of the Symposium on Terrestrial Ecosystems in Syowa Station Area' (Eds. R.J. Adie, T. Matsuda and T. Hoshia) pp. 104–126.

Sudzuki, M. and Shimoizumi, J. (1967). On the Fresh-Water Microfauna of the Antarctic Region II. Stability of Faunistic Composition of Antarctic Microorganisms. *Japanese Antarctic Research Expedition Scientific Reports, Special Issue* **1**, 216-235.

Thomas, C.W. (1965). On populations in antarctic meltwater pools. *Pacific Scientist* **19**, 515–521.

Tingey, R.J. (1982). The geologic evolution of the Prince Charles Mountains — an Antarctic Archean cratonic block. In 'Antarctic Geoscience' (Ed. C. Craddock,) pp. 455–464 (University of Wisconson Press: Madison).

Trail, D.S. and McLeod, I.R. (1965). 'Geological map of the sector of Antarctica between the longitudes 45 E and 80 E (Scale 1:1,000,000), with commentaries'. (Department of National Development. Bureau of Mineral Resources, Geology and Geophysics: Canberra).

Utsugi, K. and Ohyama, Y. (1989). Antarctic Tardigrada. *Proceedings of the National Institute of Polar Research Symposium on Polar Biology* **2**, 190–197.

Utsugi, K. and Ohyama, Y. (1991). Antarctic Tardigrada II. Molodezhnaya and Mt. Riiser-Larsen areas. *Proceedings of the National Institute of Polar Research Symposium on Polar Biology* **4**, 161–170.

Usher, M.B. and Dastych, H. (1987). Tardigrada from the maritime Antarctic. *British Antarctic Survey Bulletin* **77**, 163–166.

Wright, J.C., Westh, P., and Ramlov, H. (1992). Cryptobiosis in Tardigrada. *Biological Reviews of the Cambridge Philosophical Society* **67**, 1–29.

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