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Leaf preservation in *Eucalyptus* woodland as a model for sclerophyll fossil floras

GREGORY J. RETALLACK

A comparison of 29 identifiable vascular plant species in litter beneath *Eucalyptus* woodland with at least 74 species living nearby showed that the litter is a poor representation of standing vegetation. The leaf litter is dominated by sclerophyll leaves, which are a factor of 6.2 over-represented in litter for *Angophora costata*, factor of 5.7 for *Melaleuca linariifolia*, of 3.6 for *Eucalyptus* spp., of 3.5 for *Pteridium esculentum* and of 2.1 for *Acacia linifolia*. *Angophora* leaves are favored by lignification, with denser venation than *Eucalyptus* leaves. Sparse emergent oil glands of *Angophora* also provide fewer entry points for bacteria than rotted internal oil glands of *Eucalyptus*. The myrtaceous taxa *Angophora*, *Eucalyptus*, *Melaleuca* and *Kunzea* all have oils dominantly of preservative terpene. *Melaleuca linariifolia* and *Acacia linifolia* also have leaves and phyllodes (respectively) that are narrow with a thick lignin midrib. Thickly cuticled, succulent, hirsute, pubescent, and pinnate leaves, and green stems are not favored for preservation, because they rot from the inside out. Conspicuously absent in the leaf litter are nonsclerophyll leaves, most grasses and low herbs. This modern sclerophyll leaf litter matches Sydney Basin Permian and Triassic fossil plant localities above nutrient-poor siliceous paleosols, which may have had much more diversity than the preserved fossil flora. Clayey calcareous paleosol leaf litters and lake deposits may record a truer record of local floristic diversity in deep time than sclerophyll leaf litters.

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PLANT TAPHONOMY has emphasized physical sedimentary comminution and distribution of fossil leaves (Ferguson 1985, Spicer 1991, Gastaldo *et al.* 2005), but another filter for what remains to join the rock record is decay within leaf litters of soils (Burnham 1989, Greenwood 1992). Many fossil leaf deposits and plant taphonomic studies have been based on lacustrine (Drake & Burrows 1980, Ferguson 1985, Hill & Gibson 1986, Gastaldo *et al.* 1989, Spicer 1991, Sniderman *et al.* 2013, Astorga *et al.* 2016), deltaic (Gastaldo 1989, Gastaldo *et al.* 2005), or fluvial depositional models (Howarth & Fisher 1976, Blackburn & Petr 1979, Steart *et al.* 2002), but there also are fossil leaf litters, marked by root traces, small plants in growth position, and matted, skeletonized, and dry-curled leaves (Retallack 1977a, Retallack *et al.* 2000, Retallack & Dilcher 1988, 2012). Fossil leaf litters are much more common than typically appreciated, like associated paleosols, which have only been generally recognized in the past few decades (Retallack 2013a). Table 1 enumerates 102 leaf litter localities represented by plant fossils in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon (online portal: paleo.uoregon.edu). Leaf litter localities are 14.6% of the total of 697 plant localities in the Condon Collec-

tion, which has 35.0% lacustrine plant localities, 16.0% permineralized stumps rooted in paleosols, 16.0% localities in coal-roof clays, 10.9% plant localities in marine rocks, 4.9% localities within coal underclays, and 2.4% coal ball localities. These other kinds of deposits were described by (Scott 1977a, 1977b, Retallack 1981, 1997a, Retallack & Dilcher 1988, Gastaldo *et al.* 1995, Scott *et al.* 1996). Fossil leaf litter assemblages are widely recognized as 'foliar roofs' (Krassilov 1975, Holmes 1982), and as 'obrution deposits' (Libertín *et al.* 2009, Stevens & Hilton 2009, Dunn *et al.* 2012). Fossil leaf litters have also been called 'silcrete plant fossils' (Rozefelds 1990, Carpenter *et al.* 2011), 'ganisters' (Retallack 1977a, Percival 1983), and 'nut beds' (Manchester 1994, Retallack *et al.* 2000). Like permineralized fossil forests, coal balls, underclays, and coal-roof floras, fossil leaf litters are a record of vegetation in its place of growth within a sedimentary depositional basin (Retallack 1977a, Steart *et al.* 2006), unlike leaves in lake or marine deposits mixed from several surrounding communities (Retallack 1985, Retallack *et al.* 2000).

Fossil leaf litters have their own biases as records of past vegetation because of decay: extremes of preservational quality are mull and mor humus. Finely comminuted mull humus of grassland soils (Mollisols) retains little identifiable plant material (Barratt 1968, Sanborn & Pawluk 1989). Plant debris is also actively commin-

Ma	Age	Formation	Location	Locality no.
4	Pliocene	Deschutes Formation	Madras, Oregon	12157
5	Pliocene	Yonna Formation	Klamath Falls, Oregon	15786
5	Pliocene	Troutdale Formation	Troutdale, Oregon	12274
12	Miocene	Mehrten Formation	Gold Lake, California	12560
14	Miocene	Fort Ternan Beds	Fort Ternan, Kenya	11675
16	Miocene	Cucaracha Formation	Gaillard Cut, Panama	12423
16	Miocene	Imnaha Basalt	Juliaetta, Idaho	13490
17	Miocene	Little Bay Shale	Maroubra, New South Wales	13489
17	Miocene	Teanaway Basalt	Teanaway, Washington	13119
18	Miocene	Kaswanga Tuff	Rusinga Island, Kenya	11406
18	Miocene	Deschutes Formation	Gateway, Oregon	11720
21	Miocene	Eagle Creek Formation	Stevenson, Washington	13223
21	Miocene	Eagle Creek Formation	Eagle Creek, Oregon	13487
23	Miocene	Sardine Formation	Collawash, Oregon	10688
23	Miocene	Little Butte Volcanics	Disston, Oregon	11502
25	Oligocene	Little Butte Volcanics	Sweet Home, Oregon	11283
30	Oligocene	Little Butte Volcanics	Springfield, Oregon	12235
30	Oligocene	Yaquina Formation	Seal Rock, Oregon	12547
32	Oligocene	John Day Formation	Painted Hills, Oregon	11871
35	Eocene	Ione Formation	La Porte, California	12561
35	Eocene	Fisher Formation	Goshen, Oregon	11429
37	Eocene	Fisher Formation	Comstock, Oregon	11226
38	Eocene	Swauk Formation	Liberty, Washington	10968
43	Eocene	Clarno Formation	Sheep Smother Spring, Oregon	12154
44	Eocene	Clarno Formation	Clarno, Oregon	11733
45	Eocene	Tukwila Formation	Seattle, Washington	10842
50	Eocene	silcrete	Bevendale, New South Wales	12697
51	Eocene	Bridger Formation	Blue Rim, Wyoming	12514
54	Paleocene	Hanna Formation	Hanna, Wyoming	15777
55	Paleocene	Herren Formation	Arbuckle Mountain, Oregon	11648
56	Paleocene	Herren Formation	Denning Spring, Oregon	12149
56	Paleocene	Eyre Formation	Stuart Creek, South Australia	12499
57	Paleocene	Chuckanut Formation	Bellingham, Washington	12215
59	Paleocene	Dawson Arkose	Castle Rock, Colorado	13262
66	Cretaceous	Hell Creek Formation	Buffalo, North Dakota	11905
75	Cretaceous	Laramie Formation	Colorado Springs, Colorado	13260
95	Cretaceous	Windrow Formation	Springfield, Minnesota	10687
96	Cretaceous	Dakota Formation	Hoisington, Kansas	11664
99	Cretaceous	Dakota Formation	Kanapolis, Kansas	11372
130	Cretaceous	Days Creek Formation	O'Brien, Oregon	13488
150	Jurassic	Riddle Formation	Thompson Creek, Oregon	13365
168	Jurassic	Curio Bay Beds	Curio Bay, New Zealand	12395
168	Jurassic	Coon Hollow Formation	Pittsburgh Landing, Idaho	12487
170	Jurassic	Cloughton Formation	Cayton Bay, Yorkshire	10832
175	Jurassic	Marburg Subgroup	Durikai, Queensland	11172
210	Triassic	Pekin Formation	Gulf, North Carolina	13160
229	Triassic	Stockton Formation	Phoenixville, Pennsylvania	10913
230	Triassic	Cacheuta Formation	Potrerillos, Argentina	13462
230	Triassic	Molteno Formation	Sterkstroom, South Africa	10779
236	Triassic	Falla Formation	Schroeder Hill, Antarctica	12013
240	Triassic	Tank Gully Coal Measures	Tank Gully, New Zealand	11984
241	Triassic	Fremouw Formation	Fremouw Peak, Antarctica	13269
242	Triassic	Nymboida Coal Measures	Nymboida, Australia	10611
245	Triassic	Bringelly Shale	Camden, New South Wales	12941
247	Triassic	Lashly Formation	Allan Hills, Antarctica	11935
248	Triassic	Camden Head Claystone	Camden Head, New South Wales	11168
248	Triassic	Newport Formation	Avalon, Australia	10364
248	Triassic	Fremouw Formation	Graphite Peak, Antarctica	12033
252	Triassic	Weller Coal Measures	Allan Hills, Antarctica	11943
253	Permian	Coal Cliff Sandstone	Oakdale Colliery, N.S.W	12133
253	Permian	Buckley Formation	Graphite Peak, Antarctica	12031
256	Permian	Newcastle Coal Measures	Swansea, Australia	11174
262	Permian	Weller Coal Measures	Portal Mountain, Antarctica	12405
263	Permian	Longtan Formation	Meishan, China	12087

(Continued)

Table 1.   (Continued).

Ma	Age	Formation	Location	Locality no.
265	Permian	Vyrheid Formation	Vereeniging, South Africa	15749
270	Permian	Kazankov-Martin Formation	Novokutznesk, Siberia	10808
289	Permian	Vale Formation	Lake Abilene, Texas	11671
300	Pennsylvanian	Pituil Formation	Barreal Hill, Argentina	13455
303	Pennsylvanian	Alykaev Formation	Novokutznesk, Siberia	10800
305	Pennsylvanian	Organ Rock Shale	Moab, Utah	10857
306	Pennsylvanian	Mazurov Formation	Novokutznesk, Siberia	10794
310	Pennsylvanian	Seaham Formation	Lochinvar, New South Wales	10275
319	Pennsylvanian	Sheffield Blue Ganister	Langsett, England	11409
320	Pennsylvanian	Glen Eyrie Formation	Manitou Springs, Colorado	10896
321	Pennsylvanian	Spotted Ridge Formation	Paulina, Oregon	11357
322	Pennsylvanian	Pocahontas Formation	Ghent, West Virginia	11764
345	Mississippian	Mauch Chunk Formation	Scranton, Pennsylvania	12537
347	Mississippian	Calciferous Sandstone	Oxroad Bay, Scotland	10949
348	Mississippian	Calciferous Sandstone	Foulden, Berwickshire	10834
361	Devonian	Wutong Formation	Kongshang, China	12076
361	Devonian	Hampshire Formation	Valley Head, West Virginia	11147
362	Devonian	Duncannon Member	Burtville, Pennsylvania	11330
363	Devonian	Duncannon Member	Hyner, Pennsylvania	12333
370	Devonian	Witpoort Formation	Grahamstown, South Africa	15750
374	Devonian	Oneonta Formation	Prattsville, New York	11610
374	Devonian	Oneonta Formation	Pond Eddy, New York	11605
375	Devonian	Mandagery Formation	Bindogandri Creek, N.S.W.	12699
380	Devonian	Walton Formation	Hancock, New York	10866
383	Devonian	Oneonta Formation	East Windham, New York	12003
384	Devonian	Oneonta Formation	West Durham, New York	12507
395	Devonian	Wojciechowice Formation	Zachełmie, Poland	13096
400	Devonian	Nellenköpfschichten	Alken-an-der-Mösel, Germany	13070
403	Devonian	Stadfeldschichten	Müsch, Germany	12124
404	Devonian	Hünsruckschiefer	Waxweiler, Germany	12120
405	Devonian	Beacon Heights Orthoquartzite	West Beacon, Antarctica	11956
425	Silurian	Bloomsburg Formation	Palmerton, Pennsylvania	12822
438	Silurian	Shawangunk Formation	Delaware Water Gap, New Jersey	12828
443	Ordovician	Juniata Formation	William Bean Gap, Tennessee	13203
444	Ordovician	Juniata Formation	Potters Mills, Pennsylvania	12332
464	Ordovician	Douglas Dam Member	Douglas Dam. Tennessee	15725
484	Ordovician	Grindstones Range Sandstone	Grindtone Range, South Australia	12378

Table 1. Fossil leaf litter localities in the Condon Collection (online portal: paleo.uoregon.edu).

uted in tropical soils (oxisols) by armies of termites and leaf-cutter ants (Lavelle *et al.* 1993). At the other extreme is mor humus of conifer soils (Spodosols), consisting of thick accumulations of well-preserved, pine needles (Tian *et al.* 1997). Between these extremes is the mix of well-preserved and partially decayed remains of the leaf litter type known as moder (Ponge 2003), as studied here. Leaf litters provide easily accessible examples of decay of leaves from the inside out, with nutritious mesophyll attacked by bacteria and fungi before refractory cuticle, and finally lignin of veins remaining as a leaf skeleton (Spicer 1991, Tian *et al.* 1997). Thus, particular kinds of leaves last longer in litter, and leaf quality measures, such as carbon/nitrogen, and lignin/nitrogen ratios, may be predictors of rates of leaf decomposition (Hannon 1956, 1958, Berg *et al.* 1996, Berg & Matzner 1997, Aerts 1997, Berg 2000). Past studies of leaf litter representation of vegetation (Burnham 1989, Greenwood 1992, Ellis & Johnson 2013) have been undertaken in young, often disturbed, fertile landscapes (YODFEL of Hopper 2009), but this study examines an old climatically buffered infertile landscape (OCBIL of Hopper 2009). This study of a modern leaf litter aims to document the features of leaves that are resistant to decay in an oligotrophic sclerophyll woodland as a modern analog for fossil leaf litters of oligotrophic paleosols in deep time.

Location of study

The study area is a grid laid out on a track 200 m from an origin at S33.764347° E151.109374°, west of Culloden Road and 50 m north of Motorway M2, north of Macquarie University in the northern suburbs of the Sydney metropolitan area, NSW (Fig. 1). The track is on a plateau and the sampled grid slopes from there down 20 m in elevation toward Mars Creek, some 100 m south of its junction with the Lane Cove River at Brown's Waterhole (Fig. 2).
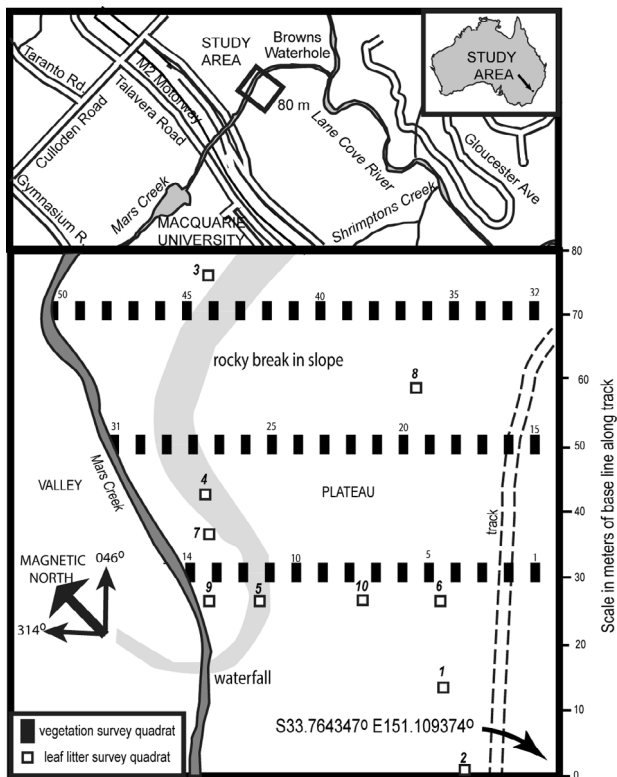
Fig. 1. Map of study area and experimental design east of Mars Creek north of Macquarie, University, North Ryde, N.S.W.

Bedrock is Middle Triassic (Anisian) Hawkesbury Sandstone, which crops out as low benches in the sampled slope (Mayne *et al.* 1974). The uppermost sample locations along the track have 1 m of weathered sandstone and shale of the Middle Triassic (Ladinian) Mittagong Formation (Retallack *et al.* 2011). Soils are immature, sandy, quartz-rich Tenosols with low base saturation and acid reaction, and limited supply of phosphorus, nitrogen and potassium (Hannon 1956, Beadle 1962, 1968, Chapman & Murphy 1989, Chittleborough 1991, McKenzie *et al.* 2004). The climate from 1970 to 2016 has been warm temperate, humid (Australian Bureau of Meteorology 2016), with mean annual precipitation of 1156 mm and mean annual temperature of 17.0 °C at Macquarie Park, 2 km south (Fig. 3). A distinctive feature of this and nearby weather stations is a June peak in winter precipitation.

Vegetation is woodland of scribbly gum, *Eucalyptus haemastoma* (Beadle, 1981), but there are variations between this plateau sclerophyll woodland with 6 m canopy and woodland of Mars Creek with 8 m canopy (Lake & Leishman 2004). On the rocky break in slope, *Eucalyptus haemastoma* is less common than *E. piperita* (Sydney peppermint) and *Angophora costata* (rose gum). The flora of the Hawkesbury Sandstone plateaus around Sydney is famous for its shrub diversity in Proteaceae, Fabaceae and Ericaceae (Beadle 1981). It is an

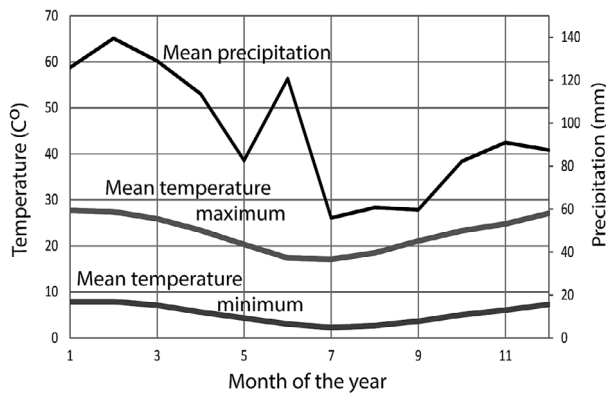*Fig. 2. Eucalyptus* woodland near Browns Waterhole, on Lane Cove River, near junction with Mars Creek.

Fig. 3. Climate of Macquarie Park (Australian Bureau of Meteorology 2016).

OCBIL with high diversity but low fertility similar to the kwongan of Western Australia, fynbos of South Africa, and campo rupestre of Brazil (Hopper 2009, Silveira *et al.* 2016). Valley-bottom trees include nonsclerophyll native plants, such as black wattle (*Callicoma serratifolia*) and coachwood (*Ceratopetalum apetalum*). Introduced trees (*Ligustrum sinense*), climbers (*Lonicera japonica*), grasses (*Cenchrus clandestinus*) and gotu kola (*Centella asiatica*) were very common at Browns Waterhole in the Lane Cove River, a disturbed access point for plant invasion just beyond the study area.

Materials and Methods

Site sampling was done on compass traverse from a baseline anchored at S33.764347° E151.109374° northeast of Macquarie University and oriented northeast (46° magnetic azimuth) along a track, with orthogonal traverses down to Mars Creek to the west. Litter was sampled at 10 sites on June 16, 1972 and located using a random number table from the grid (Fig. 1). This was done to approximate a typical collecting area and random outcrop of fossil plant localities. Litter was taken from a square 20 × 20 cm all the way down (15–20 cm) into leafless soil: for a volume of 0.8 m^3 and weight of 1–2 kg, including soil discarded when leaves and other plant debris were cleaned. The total volume of litter analyzed in all ten quadrats was 8 m^3 and 15.7 kg. Each litter sample was designed to mimic a small fossil pit though a paleosol A horizon, and yielded more leaves than the 0.5 m^2 quadrat used in plant paleoecology (Scott 1977a, 1977b, Scott & Collinson 1983). The mean and standard deviation for the identifiable items per quadrat were 16.3 ± 1.7 and of the species per quadrat were 9.0 ± 2.5. The samples were air-dried for a week, then sorted into species and weighed. Weight was used because it was easier to measure than leaf area commonly used in plant paleoecology (slab cover of Scott 1977a, 1977b, Scott & Collinson 1983) and quadrat cover of plant ecology (Curtis and MacIntosh 1951, Méndez-Toribio *et al.* 2014). All

16 species found in the leaf litter show a good correlation between leaf area and weight (Fig. 4). Leaves of *Angophora costata* 13 cm long by 3 cm wide have mean areas of about 1950 mm^2 and mean weights of 2.4 g, whereas less lignified 2.2 g leaves of *Eucalytpus haemastoma* 15 cm long by 3 cm wide have areas of about 2250 mm^2. These dominant plants of the area are thus mesophyll in the scoring system of Wolfe (1993). Numbers of countable parts were also recorded, together with the number of quadrats with a record of that species (frequency). Frequency, number of parts and dry weight were combined into a litter relative importance value (LRIV) combined from each of three relative importance values for each species, defined as follows.

LRIV = frequency (% quadrats with species/total quadrats) + items (% pieces of species/total pieces) + dry weight (% grams of species/total grams).

This adapts an approach used widely in plant ecology (Curtis & MacIntosh 1951, Méndez-Toribio *et al.* 2014), known as importance value (IV, Rodrigues *et al.* 2004) or species importance value (Kanade *et al.* 2008). Paleoecology of fossil plants commonly uses only one measure such as 'slab cover' (Scott 1977a, 1977b, Scott & Collinson 1983), which can be gained from correlation with weight (Fig. 4), but importance values add other dimensions for evaluating species representation.

The vegetation survey aimed to capture changes in vegetation down the slope, in June 1972. Quadrats 25 × 100 cm (0.25 m^2) in size were placed every 4 m down the slope for a total of 50 quadrats in three transects 20 m apart on the west-facing slope only, because the litter samples fell on that slope. This quadrat size was selected because the scale of interest was leaves 0.5–16 cm long. Cover was estimated on a 6-point scale: 1 = 1–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 95–100%. Frequency (number of quadrats with that species) and density (number of individuals of a species overhanging each quadrat) were based on main trunks including those rooted outside the quadrat, but on tufts in the case of bunch grasses. The mean number of species and standard deviation per quadrat was 7.2 ± 0.39, which is 6% of the mean. Fre-
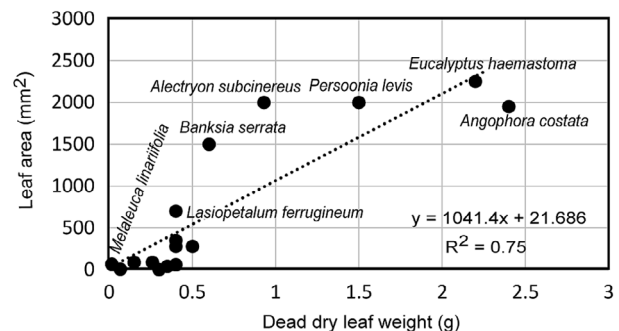

Fig. 4. Relationship between leaf area and weight in species found in leaf litter of Mars Creek, N.S.W. Many leaves in this vegetation are small and light weight.

quency, density and cover were added to make a vege-
tation relative importance value (VRIV), as follows:

they are rarely encountered in fossil plant assemblages,
and were mostly crustose forms on rocks. Only one

$$VRIV = \text{frequency (\% quadrats with species/total quadrats)}$$
$$+ \text{density (\% numbers of species per quadrat/total number for species)} + \text{cover (average \% light interception of species /quadrat)}$$

Representation of particular species in litter com-
pared with standing vegetation was calculated as a
preservability index (PI), based on the ratio of LRIV
and VRIV as follows:

$$PI = \frac{LRIV + 1}{VRIV + 1}$$

The constant of 1 was added to both denominator
and numerator to correct for anomalous values of infin-
ity when the numerator was zero. When the propor-
tional representation of species in both litter and
vegetation is equal, the PI is 1. Leaves that are particu-
larly decay-resistant have a PI greater than 1.

The approach used here is novel compared with
other studies of leaf litter taphonomy, which have used
a census approach to modern vegetation and a leaf area
approach to litter (Burnham 1989, Greenwood 1992,
Ellis & Johnson 2013). Census data do not take into
account the number of leaves produced by each individ-
ual plant, which is difficult to assess independently
(Ellis & Johnson 2013). The approach used here
includes leaf production by comparing both dead and
living leaves on comparable scales (quadrat), and on
multiple measures (weight-area, frequency, number),
because this is the scale of fossil leaf litter assemblages
atop paleosols (Retallack 1977a, Retallack & Dilcher
1988, 2012, Retallack et al. 2000). The additional mea-
sures of frequency and number are also useful for Per-
mian leaf litters of the Coalcliff Sandstone and Triassic
leaf litters of the Newport Formation of New South
Wales (Retallack 1997a, 1999, Retallack et al. 2011),
chosen for comparison with this study.

Results

LRIVs and their component metrics are shown in Fig. 5
for all the species and various parts of plants recog-
nized. These values and the PI for particular species are
compared in Fig. 6. Only seven out of 74 species are
more important in litter than they are in vegetation (PI
> 1). This dominance of only a few species is reflected
in a broad plateau on a rarefaction curve of number of
species with continued sampling (Fig. 7).

Vegetation survey

The vegetation survey revealed 74 species in this small
area (2340 m^2 or 0.23 ha) of woodland (Fig. 6). Some
grasses were common identifiable species, but winter
sampling did not allow identification of six distinctive
grass leaf forms. Lichens were not identified because

stand was dominated by bracken (*Pteridium esculen-
tum*), and it was close to a litter sample. This survey
was especially useful in identifying a diversity of native
sedges (*Chordifex fastigiatus* and *Carex polyantha* in
order of importance) and sclerophyllous shrubs (*Acacia
longifolia*, *Lasiopetalum ferrugineum*, *Banskia serrata*,
Grevillea buxifolia and *Hakea sericea*, in order of
importance). The relative order of importance of trees
was *Eucalyptus piperita* (13.4 VRIV), *Melaleuca linari-
ifolia* (13.1), *Eucalyptus haemastoma* (4.1), *Angophora
hispida* (3.3) and *Angophora costata* (3.1).

Leaf litter survey

Only 29 species were recognized in the 10 leaf litter sam-
ples, and many of them were represented by both repro-
ductive material and leaves (Fig. 5). Reproductive
structures were much rarer than leaves, as is typical of
fossil leaf litters (Retallack 1977a, Retallack et al. 2000).
Some of the herbaceous taxa, such as *Dianella* (Aspho-
delaceae) and grasses were represented by both live
(green and pliable) and dead (dry and brown) material in
the litter samples. Two species of sedge (*Chordifex fasti-
giatus* and *Baloskion tetraphyllum*) and of *Eucalyptus* (*E.
haemastoma* and *E. piperita*) could be distinguished
when complete, but not from fragments; and fragments
were combined in the litter metrics (Fig. 6).

Individual litter sample sites are very uneven in spe-
cies representation, with many species recorded in only
one quadrat. Most species recorded in only one sample
are rare in that sample, but bracken fern (*Pteridium
esculentum*) was an exception, locally dominating one
litter sample.

Twigs and other unidentifiable debris were most com-
mon in the litter samples, followed by leaves; and repro-
ductive structures were less common (Fig. 5). The most
important leaves in the litter were *Melaleuca linariifolia*
(74.9 LRIV), *Eucalyptus* spp. (24.5), *Angophora costata*
(12.7) and, to a lesser extent, *Acacia linifolia* (10.5). By
dry weight alone, the most important leaves in the 10 lit-
ter samples were *Eucalyptus* spp. (12.4%), *Angophora
costata* (4.5%) and *Pteridium esculentum* (8.6%). The
high relative importance of *M. linariifolia* and *A. linifolia*
is due to the large numbers and frequency of these small
linear leaves in the litter samples.

PI (Preservability Index)

PIs show that leaves of *Angophora costata* were
favored for preservation over other leaves by a factor of

LITTER RELATIVE IMPORTANCE VALUE (LRIV)

		number	
	frequency	of parts	dry weight (g.)

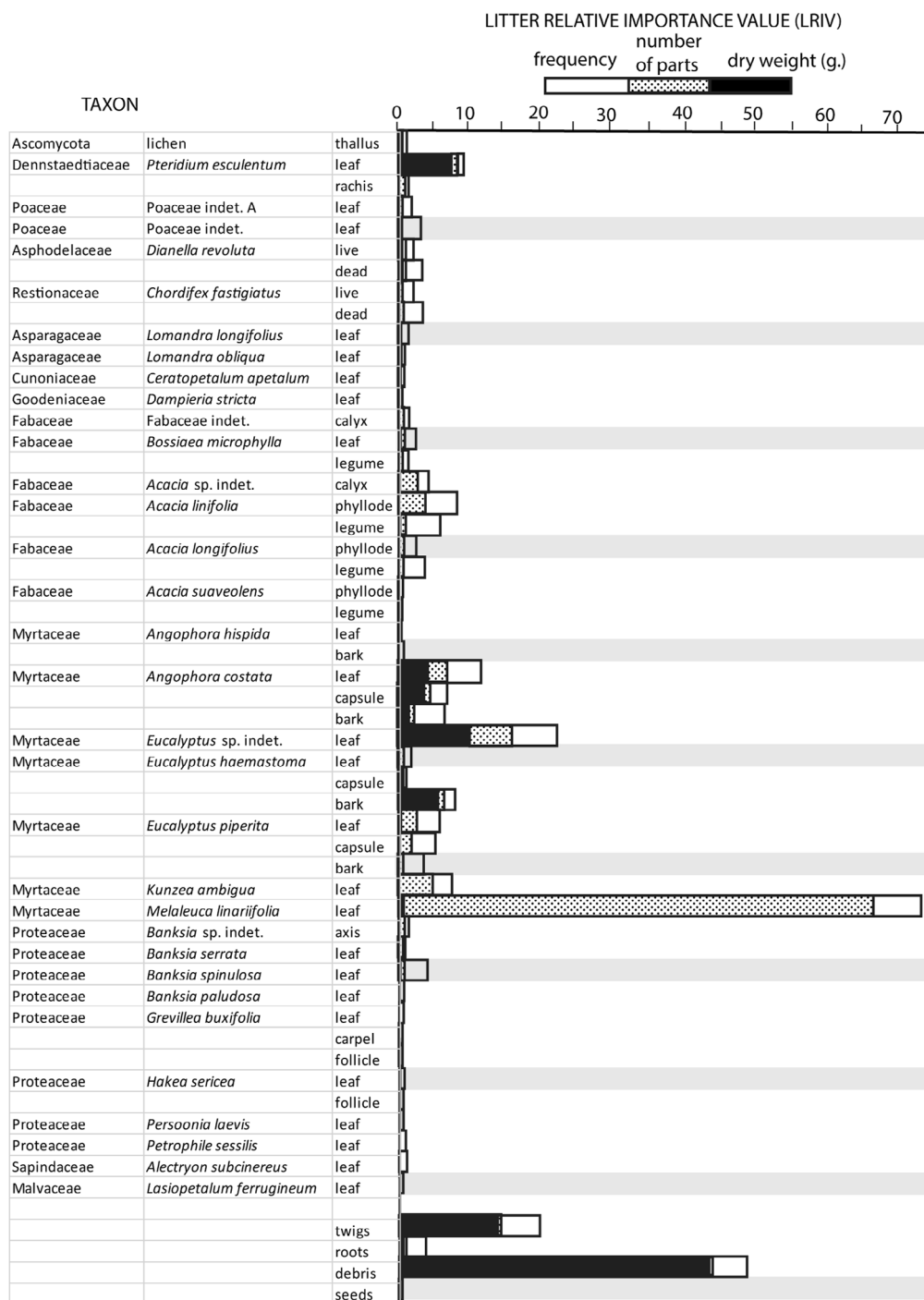| TAXON			0 10 20 30 40 50 60 70
Ascomycota	lichen	thallus	
Dennstaedtiaceae	*Pteridium esculentum*	leaf	
		rachis	
Poaceae	Poaceae indet. A	leaf	
Poaceae	Poaceae indet.	leaf	
Asphodelaceae	*Dianella revoluta*	live	
		dead	
Restionaceae	*Chordifex fastigiatus*	live	
		dead	
Asparagaceae	*Lomandra longifolius*	leaf	
Asparagaceae	*Lomandra obliqua*	leaf	
Cunoniaceae	*Ceratopetalum apetalum*	leaf	
Goodeniaceae	*Dampieria stricta*	leaf	
Fabaceae	Fabaceae indet.	calyx	
Fabaceae	*Bossiaea microphylla*	leaf	
		legume	
Fabaceae	*Acacia* sp. indet.	calyx	
Fabaceae	*Acacia linifolia*	phyllode	
		legume	
Fabaceae	*Acacia longifolius*	phyllode	
		legume	
Fabaceae	*Acacia suaveolens*	phyllode	
		legume	
Myrtaceae	*Angophora hispida*	leaf	
		bark	
Myrtaceae	*Angophora costata*	leaf	
		capsule	
		bark	
Myrtaceae	*Eucalyptus* sp. indet.	leaf	
Myrtaceae	*Eucalyptus haemastoma*	leaf	
		capsule	
		bark	
Myrtaceae	*Eucalyptus piperita*	leaf	
		capsule	
		bark	
Myrtaceae	*Kunzea ambigua*	leaf	
Myrtaceae	*Melaleuca linariifolia*	leaf	
Proteaceae	*Banksia* sp. indet.	axis	
Proteaceae	*Banksia serrata*	leaf	
Proteaceae	*Banksia spinulosa*	leaf	
Proteaceae	*Banksia paludosa*	leaf	
Proteaceae	*Grevillea buxifolia*	leaf	
		carpel	
		follicle	
Proteaceae	*Hakea sericea*	leaf	
		follicle	
Proteaceae	*Persoonia laevis*	leaf	
Proteaceae	*Petrophile sessilis*	leaf	
Sapindaceae	*Alectryon subcinereus*	leaf	
Malvaceae	*Lasiopetalum ferrugineum*	leaf	
		twigs	
		roots	
		debris	
		seeds	

Fig. 5. Relative importance index of identifiable objects in the leaf litter east of Mars Creek, N.S.W.

6.2. Other leaves in the litter in order of PI were *Melaleuca linariifolia* (PI 5.7), *Eucalyptus* spp. (3.6), *Pteridium esculentum* (3.5), *Acacia linifolia* (2.1), *Alectryon subcinereus* (2.7) and *Kunzea ambigua* (2.3). The linear leaves of *Melaleuca, Acacia* and *Kunzea* attain high representation by number of parts rather than by dry weight. The fern *Pteridium* is an exceptional case, which dominated only one sample. Native quince (*Alectryon subcinereus*, Sapindaceae) is the only other soft and pliable, nonsclerophyll leaf well preserved in the litter. The other 66 species known in the local vegeta-

tion have a PI of 1 or less, and so less than even odds of preservation.

Discussion

Humification processes

Changes to plant material on the ground begin with physical destruction by wind, rain, hail and sand abrasion (Ferguson 1985). Waves of bacteria turn the leaves black to brown with oxidizing enzymes, and some
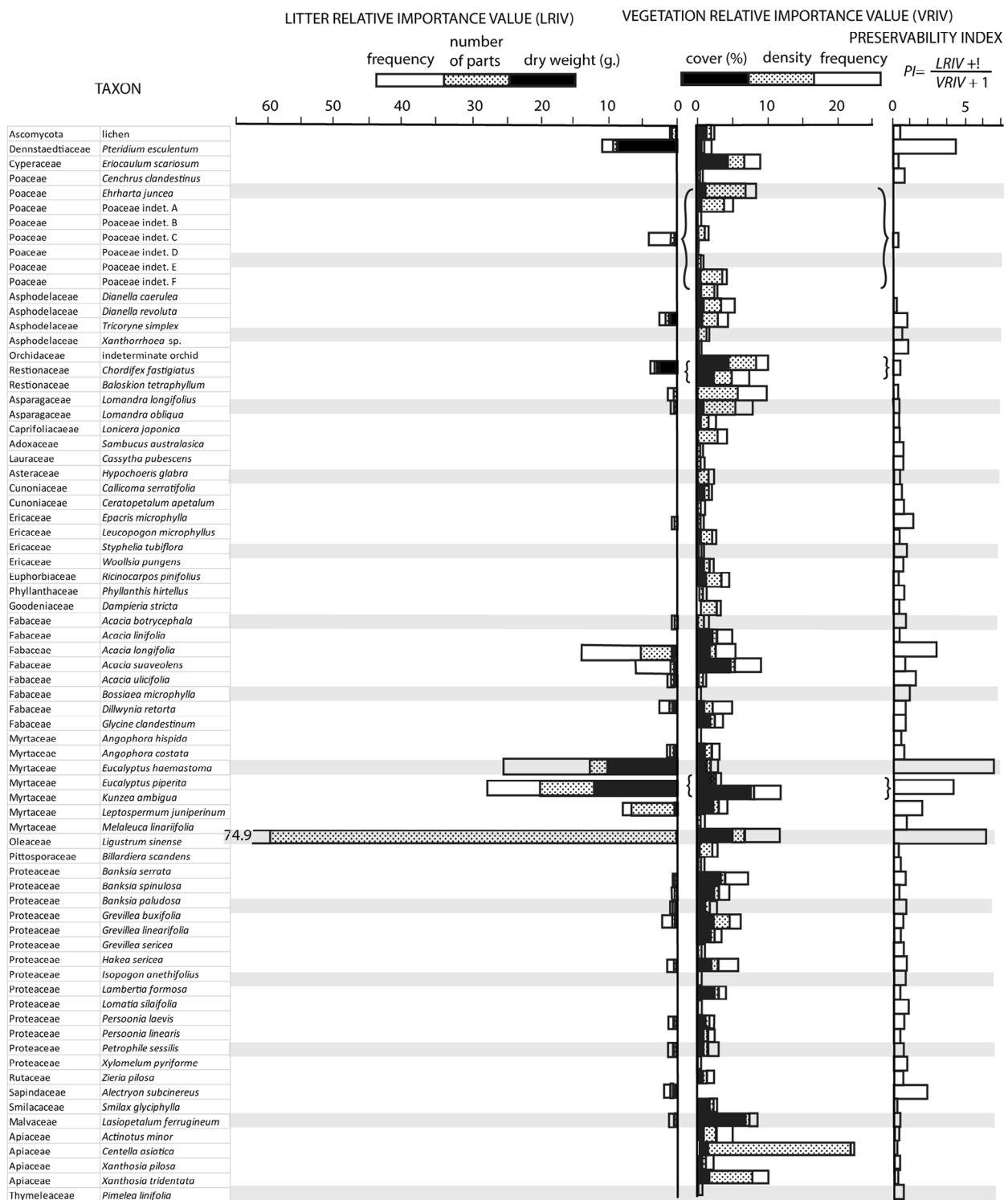
Fig. 6. Preservability index for species in leaf litter compared with standing vegetation east of Mars Creek, N.S.W.

leaves then can bleach with age (Spicer 1991). Litter with mainly bleached and intact leaves is called mor humus (Tian *et al.* 1997). Fungi and cyanobacteria cause leaves to skeletonize and aggregate, stuck together with slime, in a humus type called moder (Ponge 2003). Mites and springtails, insect larvae and earthworms eat the leaves and excrete a finely comminuted mull humus (Barratt 1968, Sanborn & Pawluk

1989). The litter and humus of Mars Creek is mor to moder from top to bottom, with many intact and some skeletonized leaves, but little mull. This is because most of the species are scleromorph, with thick cuticle, hypodermis, lignified and tannin-bearing cells and sunken stomata. The scleromorphy in this case is not interpreted as xeromorphy owing to inadequate moisture, but rather peinomorphy owing to low soil nutrients
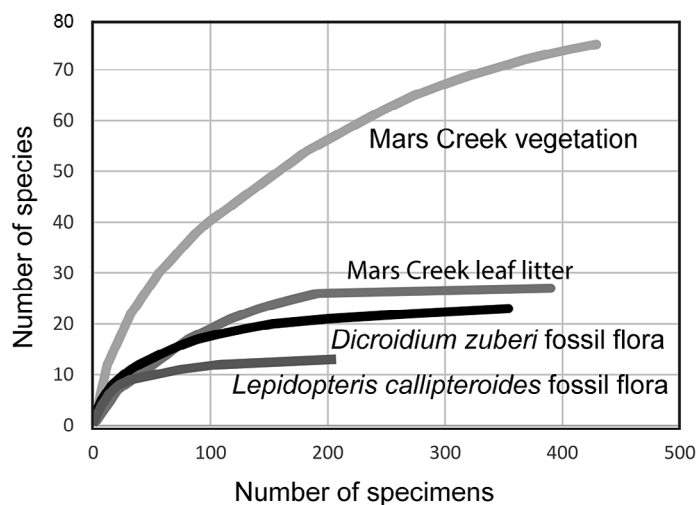
Fig. 7. Rarefaction analysis of specimens of species in the modern litter and living vegetation at Mars Creek, compared with late Permian (*Lepidopteris callipteroides*) and late Early Triassic (*Dicroidium zuberi*) fossil plant assemblages from the Sydney Basin.

(Retallack 2009). Hannon (1956) showed that there is adequate precipitation and soil moisture, but little nitrogen in the soil or parent rock. Beadle (1962, 1968) extended this work to show that phosphate and potassium is also limiting for Hawkesbury Sandstone plateau floras.

Because of this slow decomposition in the leaf litter of Mars Creek, dry leaves accumulate until they become a fire hazard, as in other eastern Australian forests (Fox *et al.* 1979). The last ground fire through the study area was in 1967, before sampling in 1972. Charcoal fragments in the litter samples were included in the category of twigs (Fig. 5). Thus, the litter samples represent accumulation over five years.

Summer rain near Sydney is often in the form of violent, late afternoon thunderstorms, which wash away leaves and pile them into litter dams (Mitchell & Humphreys 1987). These thick piles decay while moist until the litter dries, so that there is small-scale lateral heterogeneity in quality of humus.

Leaf features preferentially preserved

The dominance of *Angophora costata* over *Eucalyptus* in leaf litter was also noted by Hannon (1956), and is especially striking considering that rose gum is not a large proportion of the standing vegetation (Fig. 6). *Angophora costata* leaves have 'extremely dense venation' (0.21 mm tertiary vein spacing) comparable with *A. hispida* (0.22 mm), unlike 'sparse reticulation' of *Eucalyptus haemastoma* (1.7 mm) and *E. piperita* (0.45 mm: Brooker & Nicolle 2013). Dead *Angophora* leaves are light yellow like hay, whereas dead *Eucalyptus* leaves are dark brown with internal decay. *Angophora* has sparse small emergent oil glands with four papillate cap cells and bristle glands, unlike *Eucalyptus* with internal oil glands (Baker & Smith 1920, Ladiges 1984, Brooker & Nicolle 2013). Emergent oil glands in

Angophora costata have densities of 950/cm^2 and *A. hispida* lacks glands, whereas the large internal island glands of *Eucalyptus haemastoma* are 1650/cm^2, and those of *E. piperita* are 350/cm^2 (Brooker & Nicolle 2013). *Angophora* and *Eucalyptus* have cuticles of about the same thickness (2–4 µm: Baker & Smith 1920, Ladiges 1984). A reasonable hypothesis accounting for greater decay of *Eucalyptus* than *Angophora* is less abundant decay-resistant lignin and leakage of abundant oil glands, allowing internal pathways for bacteria additional to substomatal chambers.

Angophora and *Eucalyptus* have similar loadings of antibiotic terpenes, including bicyclogermacrene (Dunlop *et al.* 1999). The myrtaceous taxa *Angophora*, *Eucalyptus*, *Melaleuca* and *Kunzea* all have such terpenes with antibiotic effects on bacteria (Keszei *et al.* 2010). Furthermore, these taxa are also more densely veined with lignin than other taxa. An inverse assay of leaf lignin is nitrogen content, because nitrogen is not found in refractory lignin, but is abundant in other easily decomposed tissues (Berg *et al.* 1996, Berg & Matzner 1997, Berg 2000). The nitrogen content of leaves of *Angophora costata* is 3600–5700 ppm, and that of *Eucalyptus haemastoma* is *ca* 5700 ppm, but associated legume leaves have a nitrogen content of 8800–20 500 ppm (Hannon 1956). *Melaleuca linariifolia* and *Acacia linifolia* also share leaves and phyllodes (respectively) that are narrow with a thick lignin midrib that remains recognizable when the soft tissues are decayed. These oils and lignin may explain the preferred preservation of these taxa compared with other species (Fig. 5).

Preservation of bracken (*Pteridium esculentum*) was exceptional and due to recent death of a clone in one quadrat remaining from a ground fire of five years previously. This thicket of bracken was so dense that few other leaves shed by surrounding plants found their way into that litter sample.

Alectryon subcinereus (Sapindaceae) was the only nonsclerophyll leaf showing preferential preservation in the leaf litter, albeit with a low preservation index like *Kunzea ambigua*. This species has flanged papillae partly occluding abaxial stomata, and also persistent trichomes (Pole 2010), which would not be especially effective in blocking bacterial entry on death. Antibiotic chemicals are yet not reported from *Alectryon subcinereus*, but are known from other species of that genus. Polysaccharide extracts of *Alectryon tomentosus* are antimicrobial against *Bacillus subtilis* and cytotoxic (Aboutabi *et al.* 2016), and *Alectryon excelsus* has high levels of hydrocyanic acid (Greshoff 1909). A chemical defense in the form of terpenes (Hutchinson & Blackman 2002, Llorens *et al.* 2009), may also explain the similarly puzzling preferential preservation of *Nothofagus* over associated *Eucalyptus* leaves in some Victorian leaf litters (Steart *et al.* 2005, 2009).

This study also shows that thickly cuticled, succulent, hirsute, pubescent and pinnate leaves, and green stems are not favored for preservation in leaf litters. *Banksia serrata* has one of the thickest cuticles (5–6 μm), with abaxial stomata encrypted in grooves (Jordan *et al.* 2008), but low PI. Also under-represented in the leaf litter were hirsute leaves (*Grevillea linearifolia*), pubescent leaves (*Xanthosia pilosa*, *X. tridentata*, *Phyllanthus hirtellus*), pinnate leaves (*Isopogon anethifolius*, *Lomatia silaifolia*), broad phyllodes (*Acacia longifolia*), terete leaves (*Hakea sericea*), semisucculent leaves (*Dampieria stricta*) and photosynthetic stems (*Cassytha pubescens*). Ericaceae and Proteaceae are locally diverse, but poorly represented in the leaf litter. Conspicuously absent in the leaf litter compared with standing vegetation immediately above are nonsclerophyll species (*Callicoma serratifolia*, *Ceratopetalum apetalum*, *Ligustrum sinense*, *Lonicera japonica*), most grasses and low herbs (*Centella asiatica*). These observations support the hypothesis of Spicer (1991) that parenchyma, trichomes and stomatal openings provide pathways for bacterial invasion (Spicer 1991).

Relevance to paleobotany

These modern litter samples are analogs for certain kinds of fossil plant collections found atop paleosols (Retallack 1977a, 1977b, 1999), or what also have been called 'foliar roofs' (Krassilov 1975, Holmes 1982), 'obrution deposits' (Libertín *et al.* 2009, Stevens & Hilton 2009, Dunn *et al.* 2012), 'silcrete plant fossils' (Rozefelds 1990, Carpenter *et al.* 2011), 'ganisters' (Retallack 1977a, Percival 1983) and 'nut beds' (Manchester 1994, Retallack *et al.* 2000). Mars Creek leaf litter has dominance of only a few species of thick, heavily lignified leaves, and thus a broad plateau in the rarefaction curve of litter, not seen in the rising rarefaction curve of its standing vegetation (Fig. 7). The rarefaction curves of the Late Permian *Lepidopteris*

callipteroides and Early Triassic *Dicroidium zuberi* assemblages of the Sydney Basin are similar to Mars Creek litter, but other fossil floras have a continually rising rarefaction curve (Barclay *et al.* 2003, Wilf *et al.* 2003) more like standing vegetation of Mars Creek (Fig. 7).

For some fossil floras, this kind of dominance is not just at one locality as expected from local derivation of leaf litter samples (Burnham 1989, Greenwood 1992), but regional. The late Permian (Changhsinghian) fossil seed fern *Lepidopteris callipteroides*, for example, is found throughout the 36 000 km^2 Sydney Basin (Mayne *et al.* 1974) in a low diversity (13 species) assemblage of megafossil plants associated with nutrient-poor paleosols (Retallack 1999, Retallack *et al.* 2011). The early Triassic (Spathian) fossil seed fern *Dicroidium zuberi* is comparably widespread in a megafossil flora of 23 species associated with infertile quartzose paleosols (Retallack 1977a, 1977b, 1997b). An indication of greater source floral diversity comes from 77 species of dispersed pollen and spores in the Changhsinghian assemblage, and 43 species in the Spathian assemblage (Retallack 1995). Collection bias may also explain these differences, because these Permian and Triassic assemblages have not been collected as extensively as Middle and Late Triassic fossil floras (Anderson *et al.* 1996, Holmes & Anderson 2013). Both *Lepidopteris* and *Dicroidium* leaves are remarkable for the thickness of their cuticles and durability during maceration of internal organic matter in nitric acid: a week or more of digestion is needed to clear the leaves to the extent taking only 20 min for the same genera in Middle Triassic fossil floras (Retallack 1999, Holmes & Anderson 2013). This maceration resistance is found throughout the Sydney Basin for both floral assemblages (Retallack *et al.* 2011), so is not due to changing coal rank, which increases from the southern to northern Sydney Basin (Diessel 1992). Both *Lepidopteris* and *Dicroidium* are also much larger (up to 40 cm long) and more dissected than eucalypt leaves, and migrated southward into the Sydney Basin with paleotemperature rise (Retallack 2013b). These are both common fossils in their assemblages and so taken as zonal indicators, but like modern *Angophora* in this study, they may not have been so dominant in their original vegetation. What appear to have been low diversity fossil floras, may originally have been more diverse like the associated palynoflora (Retallack 1995) and the remarkable extant flora growing on the Hawkesbury Sandstone (Beadle 1968, Hopper 2009).

Both fossil zones also have some localities with locally abundant ferns, like the clump of *Pteridium esculentum* seen in Mars Creek: local dominance of the fern *Cladophlebis carnei* was seen in both the *Lepidopteris callipteroides* Zone (Retallack 1999) and *Dicroidium zuberi* Zone (Retallack 1977a, 1977b). These fossil ferns may have been preserved despite thin cuticles and lack of lignification by local abundance

and rapid burial of leaf litters. Such rarities, conflation of leaf litter and lacustrine assemblages, and evolutionary diversification account for high diversity of Middle Triassic fossil plants (Anderson *et al.* 1996, Holmes and Anderson 2013).

Paleosols associated with *Dicroidium zuberi* in the Newport Formation and *Lepidopteris callipteroides* in the Coal Cliff Sandstone (Table 1) are noncalcareous and low in nutrient cations and phosphorus (Retallack 1977a, 1977b, 1997a, 1999, Retallack *et al.* 2011), like modern soils on the Hawkesbury Sandstone (Hannon 1956, Beadle 1962, 1968, Chapman & Murphy 1989, McKenzie *et al.* 2004). The Avalon and Warriewood paleosols associated with *Dicroidium zuberi* (Retallack, 1997a) and the Wybung paleosol associated with *Lepidopteris callipteroides* (Retallack, 1999) are clay poor with chemical index of alteration [$Al_2O_3/(Al_2O_3+CaO+Na_2O+K_2O) \times 100$] of 80–95%, and 200–700 ppm P_2O_5. This compares well with 230–720 ppm P_2O_5 for local soils on the Narrabeen Group and 23–263 ppm for soils on the Hawkesbury Sandstone (Beadle 1962). The paleosols also compare well with the chemical index of alteration of modern soils on the Hawkesbury Sandstone of 70–94% (Chittleborough 1991).

This deep weathering during the Early Triassic was due to quartz-rich parent material but also may be related to CO_2 greenhouse crises revealed by the stomatal index of *Lepidopteris* and carbon isotopic composition of organic matter (Retallack *et al.* 2011, Retallack 2013b). Paleosols reveal that CO_2 greenhouse spikes coincide with spikes of mean annual precipitation and mean annual temperature, which increased chemical weathering at these particular fossiliferous levels (Retallack *et al.* 2011, Retallack 2013b). These were times (latest Changhsinghian and late Spathian) of the most severe life crises in the history of life (Retallack 1999), and the marked peinomorphic sclerophylly of *Dicroidium zuberi* and *Lepidopteris callipteroides* may in part be related to these exceptional atmospheric crises. *Dicroidium zuberi* and other species of *Lepidopteris* at higher stratigraphic levels have had much less sclerophyllous leaves (Holmes & Anderson 2013, Retallack 2013b).

The rarefaction curve for the Mars Creek leaf litter has a broad plateau (Fig. 7) unlike many fossil plant assemblages from lakes (Barclay *et al.* 2003, Wilf *et al.* 2003, Ellis & Johnson 2013), which continue to rise like the rarefaction curve of extant species found near Mars Creek (Fig. 7). Lakes are better preservational environments for plants than leaf litters of acidic soils (Drake & Burrows 1980, Ferguson 1985, Gastaldo *et al.* 1989, Spicer 1991), or fertile volcaniclastic paleosols (Retallack *et al.* 2000, Retallack & Dilcher 2012). Little trace of fossil plants is left by many other paleosols, such as former grassland soils (Mollisols: Retallack 2013c) and tropical forest soils (Oxisols: Retallack & German-Heins 1994). The 29 species recovered from

litter compared with 74 species in Mars Creek, or 34% of the flora represented in litter is comparable with the high end of 5–35% of species in other studies of leaf litters (Burnham 1989, Greenwood 1992, Ellis & Johnson 2013). This agreement of total species representation is surprising considering the very different technique of tree survey used in those other studies, and the eutrophic soils of those forests. What stands out in the Mars Creek litter and comparable fossil floras (Retallack 1977a, 1977b, 1999) is the overwhelming dominance of only a few kinds of leaves.

The various features of leaves found to promote preferential preservation in this study are also apparent in the fossil record. High vein densities can be measured in both cleared and impression leaves (Retallack *et al.* 2011). Thickness of cuticle, and features, such as trichomes, oil glands, and stomatal occlusion can be observed in suitably preserved fossil plants (Mösle *et al.* 1998, Retallack *et al.* 2011). There is also the prospect of biochemical characterization of fossil leaves (Niklas *et al.* 1978). Although cutan content of cuticle has been linked to preferential preservation (Tegelaar *et al.* 1991), subsequent studies have challenged that view (Gupta *et al.* 2006). More promising from the findings of this study are analyses of polysaccharide and phenolic antibiotic compounds in fossils (Mösle *et al.* 1998, Yang *et al.* 2005).

Conclusions

The *Eucalyptus* woodland litter samples for this study are an under-representation of the actual floral diversity (only 29 out of 74 species), comparable with other sampled leaf litters (Burnham 1989, Greenwood 1992, Ellis & Johnson 2013). However, unlike those other studies of nonsclerophyll and eutrophic leaf litters, the Mars Creek oligotrophic eucalypt litters show a very strong bias toward sclerophyll leaves of *Angophora costata*, *Melaleuca linearifolia* and *Eucalyptus haemastoma*, in that order. These sclerophyll genera are also prominent trees in the living vegetation, but in the reverse order of importance. These strong biases in the leaf litter can be attributed to extreme sclerophylly in the most commonly preserved leaves (Retallack 2009), and these features are considered peinomorphic adaptations to very low soil fertility in phosphorus, nitrogen and potassium (Hannon 1956, Beadle 1968). Key adaptations of *Angophora costata* and *Melaleuca linearifolia* are high lignin content with dense venation. The sparse emergent oil glands of *Angophora costata* also provide fewer entry points for bacteria than internal oil glands of *Eucalyptus haemastoma* and *Melaleuca linearifolia* (Ladiges, 1984). All these myrtaceous taxa *Angophora*, *Eucalyptus*, *Melaleuca* and *Kunzea* also have oils with preservative terpenes (Dunlop *et al.* 1999, Keszei *et al.* 2010). Thick cuticles and sunken stomata are ineffective defenses against decay, because leaves rot from the

inside out by bacteria entering stomatal and trichome bases (Spicer 1991, Tian *et al.* 1997).

The modern sclerophyll leaf litter of Mars Creek is not similar to other leaf litters studied for comparison with fossil assemblages (Burnham 1989, Greenwood 1992, Ellis & Johnson 2013), and is a better analog for fossil floras of low-nutrient terrains (Retallack 1977a, 1977b, 1999). Fossil floras with overwhelming dominance of only a few sclerophyll leaf types may have been derived from a much more diverse original flora, and represent an extremely biased record of past vegetation. Examples of such fossil floras associated with nutrient-poor paleosols in the Sydney Basin include the latest Permian (Changhsinghian) flora dominated by *Lepidopteris callipteroides* (Retallack 1999, Retallack *et al.* 2011), and late Early Triassic (Spathian) *Dicroidium zuberi* flora (Retallack 1977a, 1977b, 1997b).

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Disclosure statement

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