

Early Triassic therapsid footprints from the Sydney Basin, Australia

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A large rock slab collected in 1913 from the roof of the Bellambi Colliery in the southern Sydney Basin bears fossil tracks that are now known from recent radiometric and chemostratigraphic dating to be earliest Triassic, rather than latest Permian, in age. The tracks show two distinctive features of reptiles: scale impressions and claw marks. Both manus and pes are pentadactyl, ectaxonic, semidigitigrade and have an outer interdigital angle (digits IV-V) greater than inner interdigital angles. Digit proportions are consistent with a phalangeal formula of 23333. The fossil tracks are referred to the ichnospecies *Dicynodontipus bellambiensis* sp. nov. They are similar to the kinds of tracks thought to be produced by *Lystrosaurus* species. Given the abundance of these species in Early Triassic faunas of low diversity and the occurrence of members of the *Lystrosaurus* fauna in Queensland and Antarctica, chances are good that this is indeed a trackway of *Lystrosaurus*. If considered to be made by an animal of that type, the trackway was produced using the primitive alternate gait, rather than the mammalian amble, by an animal about 84 cm long and some 22 cm high. Preservation of bones of these creatures would not be expected given the non-calcareous nature of associated fossil soils in the Sydney Basin Triassic. Herbaceous lycopods, locally common in these and other Early Triassic strata worldwide, are among the most likely foods of these tusked, low-browsing herbivores.

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FOSSIL TRACKS are an important source of biological information (Thulborn 1990). The fossil trackway described in this paper was on display for many years at the old Mining Museum of the Geological Survey of New South Wales, and has been illustrated by Harper (1915, pl. 24), Herbert & Helby (1980, p.116) and White (1984, p.18). It is now understood to be Early Triassic in age and is interpreted here to have been made by a therapsid reptile, possibly a species of *Lystrosaurus*, the most common genus in the cosmopolitan but pauperate vertebrate fauna that survived the Permian extinctions (King 1990). Despite being common as fossils worldwide, these reptiles are poorly understood creatures, with debate continuing on how they lived, ate and moved (King 1991, King & Cluver 1991).

Unlike the bones found in calcareous red beds that record the death of animals, this trackway from fossil plant-bearing shales can give otherwise unobtainable information about life habits.

The fossil tracks described here are locally significant as a record of fossil reptiles, of which little is known in Permo-Triassic rocks of the Sydney Basin (Molnar 1991). The abundance of aquatic creatures such as labyrinthodonts in Triassic rocks of the Sydney Basin has been interpreted as a paleoecological peculiarity of the region's fauna (Thulborn 1986). However, this trackway and a variety of other fossil tracks and burrows (Fletcher 1948; Sherwin 1969a,b; Pepperill & Grigg 1973; Retallack 1976; Naing 1990, 1993) are evidence for both terrestrial and aquatic vertebrates in the Sydney Basin Triassic. Likely taphonomic reasons for the paucity of terrestrial vertebrate remains from the Sydney Ba-

sin, compared with other Gondwanan sequences, are examined in this paper.

Locality and age

The large slab of footprints described here was discovered following a 1913 fall of the roof of Bellambi Colliery (Fig. 1), near Wollongong, in the southern coalfield of New South Wales (Harper 1915). One large slab was collected by Mr W.S. Dun for the Geological Survey of New South Wales (Mining Museum specimen F13639). W.C. Downe, whose name is scratched into the surface of the slab in a florid cursive script, may have been involved in its collection.

The fossil tracks are preserved in an inter-laminated shale and ripple-marked siltstone oc-

curing 25-50 cm above the top of the uppermost coal, the Bulli Coal, of the Illawarra Coal Measures (Fig. 1), and hence from the lower Coal Cliff Sandstone of the Narrabeen Group (Hanlon 1956).

When found, the tracks were considered to be earliest Triassic in age because of the abrupt facies change from underlying coal measures known to be of Permian age to alluvial shales and sandstones with known Triassic fossil plants at much higher stratigraphic levels than the fossil trackways (Harper 1915). Subsequently, palynological evidence was used to argue for a latest Permian age for the Coal Cliff Sandstone (Balme 1969, 1989).

Two recent lines of evidence suggest that the facies change, and the transition from the *Dulhuntyispora* palynozone of the coal measures to the *Protohaploxylinus microcorpus* palyno-

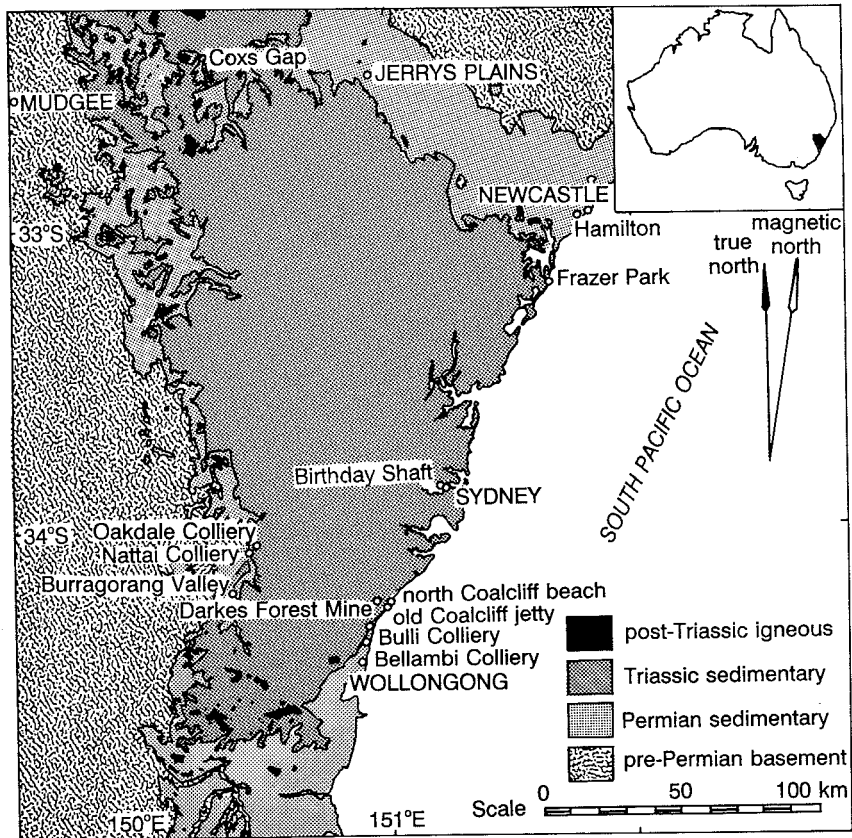


Fig. 1. Location of Bellambi Colliery and other localities for earliest Triassic fossil floras characterised by *Dicroidium callipteroides*.

zone of the overlying Coal Cliff Sandstone, does indeed correspond to the Permian-Triassic boundary (Retallack 1995). First, a marked lightening of the ^{13}C isotopic ratio of kerogen in sediments of the Sydney Basin at the base of the *P. microcorpus* palynozone and Coal Cliff Sandstone can be correlated with similar isotopic excursions in non-marine Bowen and marine Canning Basins of Australia and in numerous marine sequences worldwide where this isotopic excursion falls at the Permian-Triassic boundary (Morante 1993, Morante *et al.* 1994). Second, new radiometric dating of tuffs in the upper coal measures of the Gunnedah Basin (Veevers *et al.* 1994) and of Triassic volcanics in Australia and New Zealand (Retallack *et al.* 1993) indicates an age for the boundary between coal measures and clastics of about 250 Ma, in agreement with recent high precision dating of the Permo-Triassic boundary in China and Siberia (Claoué-Long *et al.* 1991, Renne & Basu 1991, Campbell *et al.* 1992, Renne *et al.* 1995).

Thus, it now seems likely that the tracks are of earliest Triassic age.

Nature of the tracks and sedimentary environment

The Bellambi fossil trackway is preserved in such a way that it looks as though the animal passed by only recently. The tracks are depressions in a thin (2 mm) layer of shale, that in places has preserved scale and claw impressions (Figs 2-4) but elsewhere has been removed to reveal an underlying layer of ripple-marked siltstone. The shale was presumably a thin layer of sticky clay which adhered to the feet of the maker of the main trackway of six consecutive preserved prints, leaving exposed the underlying silt. At a separate time when the thin clay layer was less sticky and not disrupted, a second, larger animal passed in the opposite direction, but there are only two complete prints of this trackway on the slab

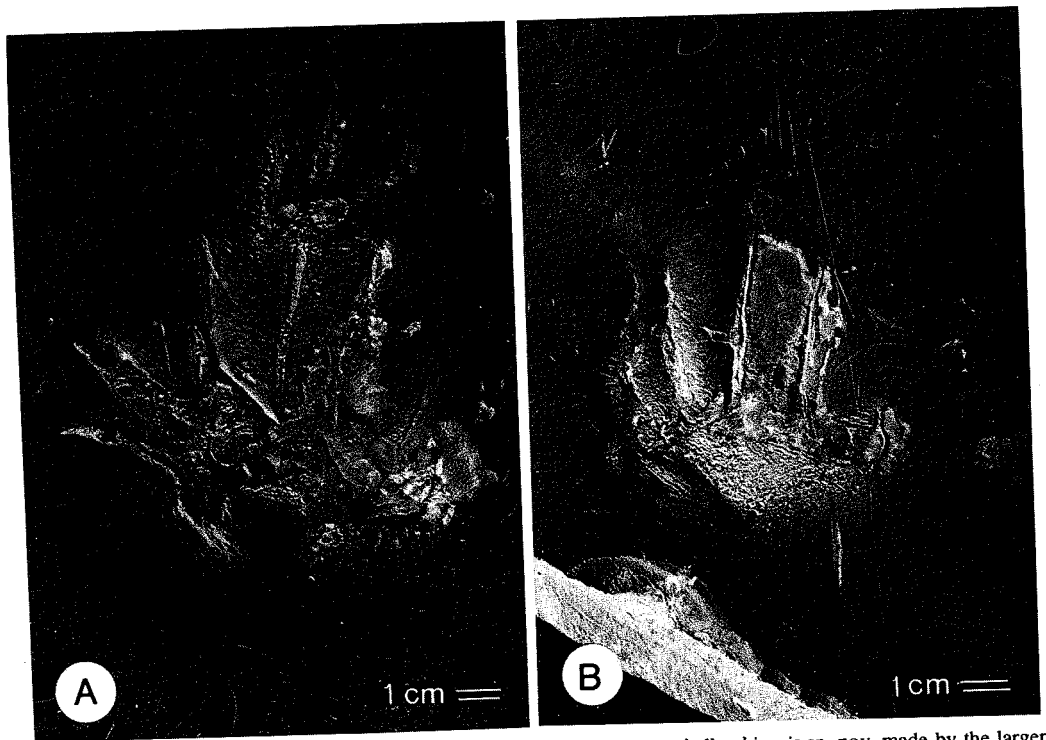


Fig. 2. Detail of scale and claw impressions on a track of *Dicynodontipus bellambiensis* sp. nov. made by the larger animal to one side of the main trackway (MMF13639): A, right manus; B, right pes. Scale bar is 1 cm.



saved. The larger animal presumably came along later, when the clay was drier, because there are no rill marks or rain prints as evidence of subsequent rewetting. All the prints are impressed by as much as 4 mm, even after burial flattening. This indicates a soft substrate that had settled or dried little after deposition and exposure.

Also on the slab are several invertebrate trackways, consisting of two parallel rows of obliquely transverse markings, similar to the ichnogenus *Tasmanadia* Chapman (Häntzschel 1975). The invertebrate trackways were made by an animal of a size that could have, but did not, break through the thin clayey surface layer, as did the vertebrate track-maker. It left relatively faint tracks with shallow sharp incisions, probably because the clay was drying, sometime after passage of the vertebrate. The invertebrate tracks lack the paired markings of millipede tracks, the internal sinusoidal wave of centipede tracks, the claw marks of velvet worms (Onychophora) or the serried ranks of trails expected from spiders (see also Johnson *et al.* 1994). Probably it was made by an insect. Judging from known Permo-Triassic insect faunas of the Sydney Basin (McKeown 1937; Riek 1950, 1954, 1968; Evans 1963), this may have been a beetle, bug or cockroach. A single fossil grasshopper wing (*Elcanopsis sydneyensis*, Order Orthoptera, Suborder Ensifera) has been recorded from this particular stratigraphic level in the Sydney Basin (Tillyard 1918). This seems an unlikely identity for the trace fossil with its evenly sized tracks.

Identity of the track-maker

Two features especially mark the vertebrate tracks as reptilian: claw impressions at the ends of the digits and scale impressions on the soles of the feet (Fig. 2). Each of the toe impressions is sharp, as if clawed. Curved claws show especially well on digits V and IV on the right manus of the larger trackway (two right hand digits of

Fig. 2A, which has two overlapping impressions). This trackway also shows wrinkling on its fleshy pads similar to scale impressions (Fig. 2A,B). The scale-like impressions are ellipsoidal, 1 x 2 mm in size, and oriented in a broad arc transverse to the long axis of the manus and pes.

The Bellambi tracks are surrounded by local halos of fine radial striations (Fig. 2) that look like hair impressions. These are not as obvious as they are in modern rabbit footprints (Ellenberger 1976). Therapsids have been thought by some to have been hairy (Bakker 1986), and such impressions could represent an important diagnostic feature. However, the striations could also be interpreted as wrinkling of a cyanobacterial scum. There are also many oriented scratches (Fig. 3) resulting from overenthusiastic cleaning of the slab with a wire brush. Neither explanation for the markings can be ruled out, and the presence of hair impressions remains unproven.

The identity of the track-maker can be narrowed further by considering digit numbers, relative length and divarication. The organism was pentadactyl, with digit proportions (Table 1) and joints (Figs 2,3) compatible with a phalangeal formula of 23333, both in manus and pes. The outer digit (V) of the manus was angled outwards and the whole manus more divaricate than the pes (Table 2). These proportions are found in the therapsid suborders Therocephalia, Cynodontia and Anomodontia, with other proportions found in likely Late Permian to Early Triassic groups such as Procolophonomorpha (manus 23453, pes 33454) and the therapsid suborders Dinocephalia (manus 23343, pes 23333) and Eotheriodontia (23453; Haubold 1971, Kemp 1982, Leonardi 1987). Footprints of creatures related to lizards and crocodiles generally have more slender digits that are strongly curved, more highly divaricate and unequal in length. Thecodont footprints such as those of *Chirotherium*, common in Triassic rocks (Haubold 1971), have a much more divaricate

Fig. 3. Consecutive manus (divaricate) and pes (less divaricate) impressions of the holotype trackway of *Dicynodontipus bellambiensis* sp. nov. (MMF13639). Scale bar is 1 cm.

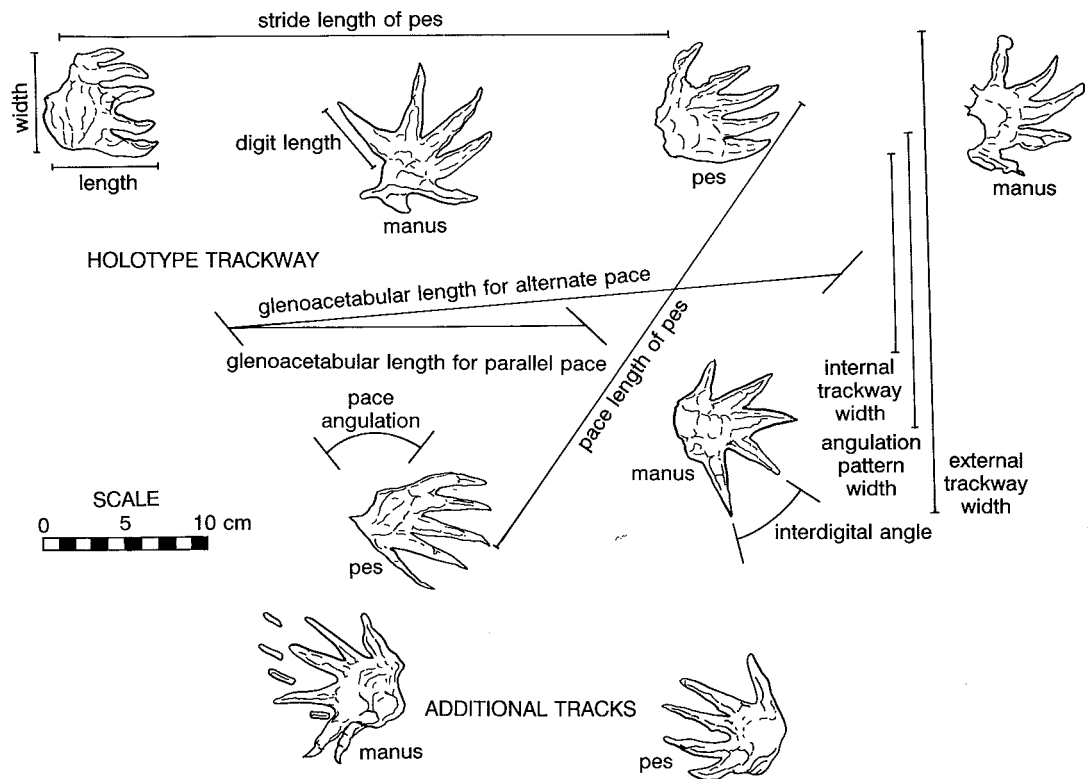


Fig. 4. Diagrammatic sketch of trackway slab of *Dicynodontipus bellambiensis* sp. nov., showing orientation and limits of measurements.

and outwardly curved digit V in both manus and pes than the Bellambi animal.

The earliest Triassic age of the fossil trackway, now apparent from chemostratigraphy (Morante *et al.* 1994) and radiometry (Veevers *et al.* 1994), can be used to narrow the field further. This was a time of very low reptilian diversity worldwide (King 1990). Apart from amphibians, thecodonts, procolophonids and lizard-like forms, plausible track-makers include the carnivorous therocephalian *Scaloposaurus* and cynodont *Thrinaxodon*, and the herbivorous anomodont dicynodonts *Myosaurus* and *Lystrosaurus*. All but *Lystrosaurus* species are too small to have made the Bellambi tracks. Additionally, the carnivores have rather more gracile digits. Indeed the Bellambi tracks are very similar to those attributed to species of *Lystrosaurus* from South Africa (Watson 1960) and Antarctica

(MacDonald *et al.* 1991, for their type 2 tracks). Both the Antarctic and South African tracks include a manus more divaricate than the smaller pes, and are comparable in size and track spacing to the Bellambi tracks.

The feet of *Lystrosaurus* species are not well known, with restoration (Watson 1911) based largely on an incomplete articulated forearm of *L. maccaigi* (Watson 1913). Although *Lystrosaurus* is represented by common articulated skeletons at some horizons, for example near Bergville and Harrismith, Natal (pers. obs. 1984), ankle and wrist bones have not been found, and were presumably weakly ossified. Nevertheless, digit proportions of the manus of Watson's (1913) *L. maccaigi* (1.135, 1.47, 1.71, 1.71) are similar to those of the fossil tracks from Bellambi (Table 1). The size of the Bellambi tracks, estimated in the following section, is also

similar to those of adult specimens of several species of *Lystrosaurus*.

The occurrence of *Lystrosaurus* in Australia is by no means unexpected, considering that the genus has been found in Antarctica, South Africa, India, Russia and China (Cosgriff *et al.* 1982). The genus was provisionally thought to have been represented by a quadruped from the Arcadia Formation of Queensland, but that fossil is now regarded to be referable to *Kannemeyeria*, geologically younger Early Triassic therapsids (Thulborn 1983, Molnar 1991). The Bellambi trackway appears to provide indirect evidence that *Lystrosaurus* was represented in Australia at the very beginning of the Triassic.

Size of the track-maker

Many Late Permian and Early Triassic therapsid reptiles have a similar build to species of *Lystrosaurus*, and this is used here as a model to estimate the size of the animal that made the Bellambi trackway. Only digit V is complete in the described manus of *L. maccaigi* (Watson 1913), and measurements of this digit in the fossil trackway are here assumed to be in the proportions of the reconstructed skeleton of *L. declivis* (Watson 1911; following taxonomic revision of Colbert 1974). Estimates vary depend-

Table 1. Digit lengths and proportions (mm).

	I	II	III	IV	V
manus	19.3	36.8	48.4	49.3	46.2
	29.3	41.9	38.8	42.7	38.3
	<u>26.1</u>	<u>39.6</u>	<u>42.8</u>	<u>39.4</u>	<u>63.5</u>
average	<u>24.9</u>	<u>39.4</u>	<u>43.3</u>	<u>43.8</u>	<u>40.3</u>
proportion	1	1.58	1.74	1.75	1.61
pes	35.5	44.8	37.9	42.6	38.4
	53.9	53.8	50.6	44.5	40.5
	<u>48.4</u>	<u>48.9</u>	<u>50.1</u>	<u>49.3</u>	<u>39.1</u>
average	<u>45.9</u>	<u>49.2</u>	<u>46.2</u>	<u>45.5</u>	<u>39.3</u>
proportion	1	1.07	1.01	0.99	0.85

Table 2. Interdigital angles and total divarication (degrees).

	I-II	II-III	III-IV	IV-V	total
manus	43	22	33	53	152
	32	23	25	38	124
	<u>36</u>	<u>25</u>	<u>23</u>	<u>32</u>	<u>122</u>
average	37	23	27	41	133
pes	17	19	14	11	58
	12	13	16	22	69
	<u>12</u>	<u>14</u>	<u>17</u>	<u>27</u>	<u>68</u>
average	14	15	16	20	65

ing on the track used (Table 1) and this is expressed by error at the 95% confidence level (2σ); this does not take into account uncertainties in Watson's (1913) restoration. By this reckoning, the track-maker had an estimated body length from forehead to tailtip of 84 ± 20 cm, a forelimb length of 18 ± 4 cm and a hindlimb length of 28 ± 8 cm.

Basal skull length, which is used in taxonomic studies (Cosgriff *et al.* 1982), can also be estimated for the track-maker (130 ± 32 mm) by making similar assumptions. This is intermediate in size for species of *Lystrosaurus*, and typical for adult *L. murrayi*, *L. declivis* and *L. curvatus*. Although *L. maccaigi* has commonly been regarded as a larger species, specimens similar in size to the Bellambi track-maker also are known, and the species is especially common in the lowest parts of the *Lystrosaurus* zone of Colbert (1974).

Gait of the track-maker

The regular progression of manus and pes prints, with the manus more deeply impressed than the pes, is typical for a walking quadrupedal animal in which the forelimbs were habitually load-bearing. The manus impressions do not lie outside the lane formed by the pes impressions, yet *Lystrosaurus* species were barrel-chested and slim-hipped (width between glenoids being greater than between acetabula; Watson 1911).

If the Belambi trackway is that of a species of *Lystrosaurus*, it suggests that the elbows were not directed outwards as in some reconstructions of *Lystrosaurus* (e.g. P. Trusler in Rich & Rich 1991, G. Paul in King 1990), but rather held alongside the animal so that the toes splayed outwards. The sole and palm prints indicate a plantigrade stance that was not in any way cursorial. The impressions are neither so large nor deeply impressed that the animal would be characterised as graviportal.

The glenoacetabular length of the animal measured from the trackway, from opposed diagonals connecting two manus and two pes prints and assuming the reptilian alternate pace, is 345 mm. Assuming a mammalian amble, where limbs move in parallel, it is 207 mm (following Leonardi 1987). The latter is too short for an animal with so wide a carriage, and well out of proportion to therapsid skeletons such as that of *Lystrosaurus declivis* (Watson 1913), which was an animal of apparently comparable size to the track-maker but with a glenoacetabular length of about 439 mm. The mammalian gait presumably appeared at some time during the therapsid-mammal evolutionary transition, but is not yet evident in either this Early Triassic therapsid track or a Late Triassic therapsid track described by Hunt *et al.* (1993).

The speed of the Bellambi track-maker can be estimated by using Alexander's (1976) formula

$$V = 0.25g^{0.5}S^{1.67}h^{-1.17}$$

where V is velocity of the animal, g is the acceleration due to gravity, S is stride-length measured from the trackway (Table 3), and h is the height of the animal at the hip, estimated above (Thulborn 1990). The resulting speed is very slow (0.2 m.s⁻¹), and is compatible with the even spacing of prints and change of direction in the trackway compared with the first pes in the series. This, together with the opposing direction of the two trackways, the orientation of tracks parallel to the crests of current ripples on the slabs and the depositional setting of the trackways, suggests that the track-makers could have been slowly approaching and returning from water

Table 3. Footprint size and other measures (mm).

Measure	Manus	Pes
width	45.3	48.6
	42.3	48.2
	<u>38.3</u>	<u>41.2</u>
average width	42.0	46.0
length	79.9	72.9
	64.4	71.8
	<u>63.7</u>	<u>n.d.</u>
average length	69.3	72.
stride length	331	342
	<u>367</u>	<u>n.d.</u>
av. stride length	349	n.d.
pace length	214	268
	<u>232</u>	<u>257</u>
av. pace length	223	263
pace angulation	92°	77°
angulation pattern width	153.9	213.9

across an open floodway between the receding river and a forested bank (Fig. 5).

Preservational biases

The Coal Cliff Sandstone of the basal Narrabeen Group has preserved a locally abundant fossil flora (Retallack 1977b, 1980) and occasional freshwater bivalves (Bowman 1980), conchostacans (Etheridge 1988) and an insect (Tillyard 1918), in addition to the fossil tracks described here. This is a very small sample of the likely biota of these ancient ecosystems. All the fossils were preserved as shells or organic impressions in shales that accumulated in ponds within swales of a loosely sinuous river system (Retallack 1977b, 1980). There are also palaeosols associated with the fossils (Retallack 1980, 1977b), and like other Early Triassic palaeosols from the Sydney area (Retallack 1976, 1977a), these are non-calcareous, clayey and gray, and represent low-land poorly drained wet forests. In this kind of soil, bones and shells of land animals are destroyed by soil acids (Retallack 1984), and it is not surprising that so little is known of land faunas of Early Triassic age in southeastern Aus-

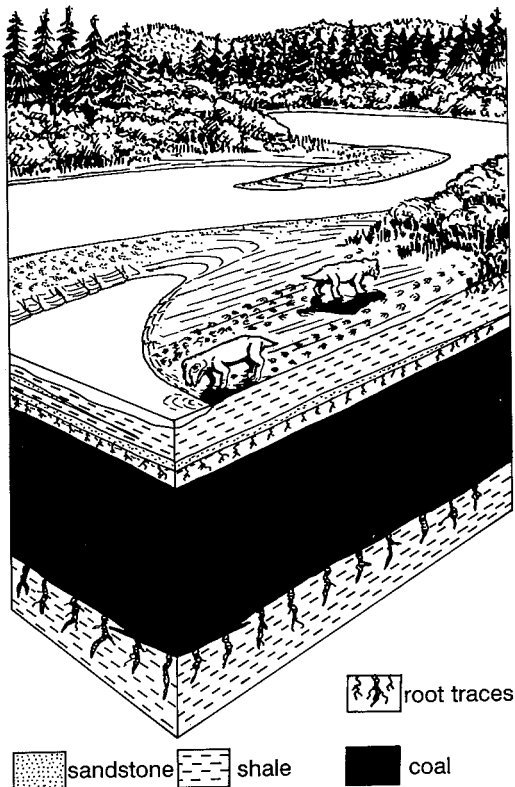


Fig. 5. A reconstruction of the palaeoenvironment of *Dicynodontipus bellambiensis* sp. nov. during earliest Triassic time in the southern coalfield of New South Wales. The Permo-Triassic boundary is now recognised to be at the top of the Bulli Coal.

tralia. Almost all Early Triassic vertebrates from southeastern Australia are known from either compressions in lacustrine shales or broken fragments among conglomerates of fluvial palaeochannels. In South Africa, by contrast, calcareous red clayey palaeosols, similar to Alfisols of subhumid to semiarid climates, are littered with bones of *Lystrosaurus*, and include calcified burrows enclosing articulated specimens of *Procolophon* and *Thrinaxodon* near Bergville and Harrismsith, Natal (pers. obs. 1984). The fossil trackway from Bellambi, together with a variety of other tracks and burrows of vertebrates (Naing 1993), indicates that land animals were diverse in southeastern Australia during the Early Triassic, despite the meagre

record of actual bony remains (Molnar 1991).

This profound taphonomic bias has broad implications for the interpretation of Triassic life on land. Much of the apparent palaeobiogeographic distinctiveness of the southeastern Australian Early Triassic fauna results from the abundance of aquatic creatures such as labyrinthodonts (Thulborn 1986). This may be a product of taphonomic bias related to humid climate and acidic soils of southeastern Australia during the Early Triassic, compared with drier climates elsewhere in Gondwana. Similarly, in South Africa terminal Permian dicynodont diversity appears to decline (King 1990) at a time of apparent labyrinthodont diversification (Kitching 1978) as green-purple palaeosols are overlain by gray and coal-bearing strata (Anderson & Anderson 1985). In addition, Benton (1983, 1986) has argued that dinosaur-dominated faunas abruptly replaced labyrinthodont-dominated faunas during a Late Triassic facies shift from gray, locally-coaly facies to overlying red beds. These examples could also represent the taphonomic bias towards fully terrestrial forms in calcareous red beds and aquatic forms in non-calcareous and coaly facies (Retallack 1984). It could be that Australian Early Triassic faunas were as cosmopolitan as those elsewhere in the world, that dicynodont decline did not predate the Permian extinctions and that the rise to dominance of dinosaurs was gradual, contrary to the prior claims cited above. These questions of biogeography and of evolutionary history could profitably be re-examined from the perspective of an increasingly rich record of palaeosols and vertebrate trackways.

Palaeoecology of *Lystrosaurus*

The fossil tracks from Bellambi, along with other trace fossils also attributed to *Lystrosaurus* species (Watson 1960, Macdonald *et al.* 1991), may help resolve two long-standing puzzles concerning these enigmatic beasts. Were they amphibious? What did they eat?

The idea that species of *Lystrosaurus* were aquatic or amphibious dates back to the turn of

the century and has been remarkably persistent (Kemp 1982). The interpretation has recently been challenged by King (1991) and King & Cluver (1991), who argue that these reptiles were fully terrestrial and capable of burrowing. This view is supported by the absence of webbing between the toes on all plausible footprints (Watson 1960, MacDonald *et al.* 1991), of which the Bellambi examples are most convincing due to their preservation in fine-grained matrix.

A fully terrestrial habitat for *Lystrosaurus* species is also indicated by their common occurrence in palaeosols, a point not noted in discussion of their geological occurrence by King & Cluver (1991). At localities near Harrismith and Bergville in Natal, South Africa, palaeosols are littered with bones of *Lystrosaurus murrayi* (pers. obs. 1984). Furthermore, these palaeosols were well drained, as seen from the deeply-penetrating drab-haloed root traces and vertebrate burrows, from aggregation of thick clay skins into a subsurface clay-rich horizon that is highly oxidized and red in color, and from subsurface enrichment in carbonate nodules, that also indicate a subhumid-semiarid climate (comparable palaeosol features are described by Retallack 1990). Many Antarctic specimens of *Lystrosaurus* come from sandstone palaeochannels (Cosgriff *et al.* 1982), but I recently discovered a partial skeleton, probably of *L. murrayi*, on the surface horizon of a gray-green palaeosol with deeply-penetrating root traces in the saddle between sandstone ribs northwest of Graphite Peak, central Transantarctic Mountains (85° 2.99'S 172° 21.65'E). Hard green nodules of berthierine in this palaeosol indicate a moderately stable soil with shallow water table and a humid climate. I have not been able to examine in the field *Lystrosaurus* localities along the Vetluga River, Russia, in the Tunguska region of Siberia, and near Dalongkou, China, but colour slides of these fossil localities (presentations of Losovsky 1993, Cheng 1993) reveal the presence of red calcareous palaeosols comparable to those of Natal. It is possible that *Lystrosaurus* specimens came from palaeochannel or flood deposits interbedded with these sequences of formerly well-

drained palaeosols, but in the Siberian case at least gymnosperm roots within a palaeosol encased the skull (V. R. Losovsky pers. comm. 1993). The theory that *Lystrosaurus* species lived on dry land will be on a firmer footing when their relationship to associated palaeosols is documented more widely.

Species of *Lystrosaurus* were presumably herbivorous but were toothless except for a pair of tusks in the upper jaw only (Crompton & Hotton 1967, Hotton 1986). The Bellambi tracks occur in a stratigraphic level rich in fossil plants (Retallack 1980), unlike the tracks and bones of *Lystrosaurus* in palaeosol sequences of Antarctica, South Africa, Russia and China. The fossil flora of the basal Coal Cliff Sandstone is dominated by the seed fern *Dicroidium callipteroides* (Carpentier) White, 1984 and the conifer *Voltziopsis africana* Seward (Townrow, 1967), with less common ferns, horsetails and an *Isoetes*-like lycopod ('*Cylomeia undulata*' of White 1981, based on AMF58791). Although there have been some records of *Glossopteris* persisting at this stratigraphic level, I have not been able to find any evidence of it (Retallack 1980; a mislabelled example of Diessel 1992 is actually from the roof of the Borehole Seam: C. Diessel pers. comm. 1994), and Middle Triassic fossil leaves similar to *Glossopteris* appear to have non-glossopterid (perhaps gnetalean) affinities (Anderson & Anderson 1989, Holmes 1992). Although a case has been made that glossopterid foliage fed Permian therapsids of South Africa (Zavada & Mentis 1992), these plants were extinct by the time of the *Lystrosaurus* zone (Retallack 1990, 1994). *Dicroidium callipteroides* has been reconstructed as a early successional shrub and *Voltziopsis* and other conifers as forest trees (Retallack 1977b, 1980); these had very coriaceous leaves that would have been largely out of browse range of *Lystrosaurus* species. Although both horsetails and ferns are rare in the Coal Cliff Sandstone of the Sydney Basin, a case for horsetails as a staple of Permian therapsids has been made by Rayner (1992), and abundant ferns are a striking feature of earliest Triassic 'Korvunchanian' floras of Siberia

(Meyen 1987). Highly nutritious tubers and rhizomes known in horsetails and ferns (Berry 1924, Watson & Berry 1990) have not yet been found with earliest Triassic examples, but stems and foliage could well have been part of the diet of *Lystrosaurus* species. A more abundant source of food would have been the cormose lycopods because these and similar plants are locally abundant and geographically widespread in Early Triassic rocks. Similar *Isoetes*-like herbaceous lycopods, including species of *Annalepis* and *Tomiostrabus*, are abundant in Early Triassic rocks of Europe and Russia (Meyen 1987, Pigg 1992), matching the cosmopolitan distribution of *Lystrosaurus* (Retallack 1995). Their Late Triassic decline in abundance and diversity (Pigg 1992) is also paralleled by declining abundance and diversity of dicynodonts (King 1990). The contagious distribution of these lycopods in large populations in growth position and all at a similar degree of development on a single bedding plane of gray shale (White 1981) is evidence that they were pioneering aquatic plants of oligotrophic lakes. Living *Isoetes* and related forms are similar ecologically, but also spread into salt marshes, meadows and rocky hillsides (Britton & Brown 1970). The fossil *Isoetes*-like plants offered abundant weakly cutinized and fleshy leaves as well as a very shallowly buried corm. The wide muzzle, prominent tusks and broad forefeet of species of *Lystrosaurus* would have been well suited to such low browse with nutritious underground storage organs (King & Cluver 1991).

Systematic ichnology

Dicynodontipus Rühle von Lilienstern, 1944

Dicynodontipus bellambiensis sp. nov.

Holotype. Specimen MMF13639 (Figs 2,3) shows two trackways, here regarded as conspecific, but the main track represented by six prints is designated the holotype for the species.

Locality. Bellambi Colliery, southern coast New

South Wales, in Early Triassic Coal Cliff Sandstone.

Diagnosis. *Dicynodontipus* trackway with scale impressions, claws and relatively elongate digits (19-54 mm). Manus somewhat divaricate (133°), 64-80 mm long and 38-45 mm wide. Pes with digits more nearly parallel (divarication 65°), 72-73 mm long and 41-49 mm wide.

Description. All footprints known of this species are on a single slab, which includes a trackway of six prints plus two prints of a second trackway going in the opposite direction (Figs 2-4). The tracks are those of a medium-sized animal, and are some 3-6 cm in size (Table 3). The animal was wide-bodied, as indicated by the spacing of the tracks (Table 4). The larger, more deeply impressed and more divaricate prints are from the forefeet (manus), and the smaller, narrower prints from the hindfeet (pes; Table 3). In both manus and pes, the outer four digits (II-V) are about the same length, but the inner one (I) is markedly shorter. The inner digit is also somewhat separated from the others, but is curved into the line of the rest of the track, rather than outwards (Table 2).

Comparison. The best known species of this genus, *Dicynodontipus geinitzi* from the Triassic of Germany and Britain (Haubold 1971), is a smaller trackway, with less elongate digits than *D. bellambiensis*. The maker of *D. geinitzi* may also have been a more agile creature than proposed for the Bellambi track-maker. Haubold (1984) estimates speeds of 8.2-10 km h⁻¹ for some trackways made by *D. geinitzi*. *Deuterotetrapous* (Haubold, 1971), *Cynodontipus* Ellenberger (1976) and *Therapsipus* (Hunt *et al.*, 1993) have all been attributed to therapsids (Haubold 1984), but are based on larger tracks

Table 4. Overall trackway measures (mm).

internal trackway width	95
external trackway width	299
glenoacetabular length for alternate pace	345
glenoacetabular length for parallel pace	207

with shorter and wider digits than *Dicynodontopus bellambiensis*.

Of the trackways of non-therapsid affinities, the Bellambi trackway is most like the Permian ichnogenera *Chelichnus* and *Laoporus*, attributed to caseid synapsids by Haubold (1971). These ichnogenera have short toes, and very similar manus and pes, both usually directed inwards, unlike *Dicynodontopus bellambiensis*. Dun (for Harper 1915) informally compared the Bellambi trackway to '*Ichnium gampsodactyloides*' from the Permian of Britain. This ichnospecies is regarded as a junior synonym of *Dromopus lacertoides*, and as a track of an araeoscelid stem reptile by Haubold (1971). These kinds of tracks are very distinct from *Dicynodontopus bellambiensis* in having digits of unequal length and strong distal curvature.

The un-named trackway illustrated and discussed by Watson (1960) from the *Lystrosaurus* zone of South Africa is similar in all details visible to *D. bellambiensis*. Unfortunately, the South African track is deeply impressed in a fine-grained sandstone that appears to have dried and slumped into the impressions, and so has few of the details visible on the Australian trackway described here. An interesting feature of the South African trackway is a short impression of the tail, not seen in the Australian material. A very similar track from the *Lystrosaurus* zone of Antarctica (MacDonald *et al.* 1991) is unfortunately also poorly preserved.

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