

LATE TRIASSIC ECOSYSTEMS OF THE MOLTENO/LOWER ELLIOT BIOME OF SOUTHERN AFRICA

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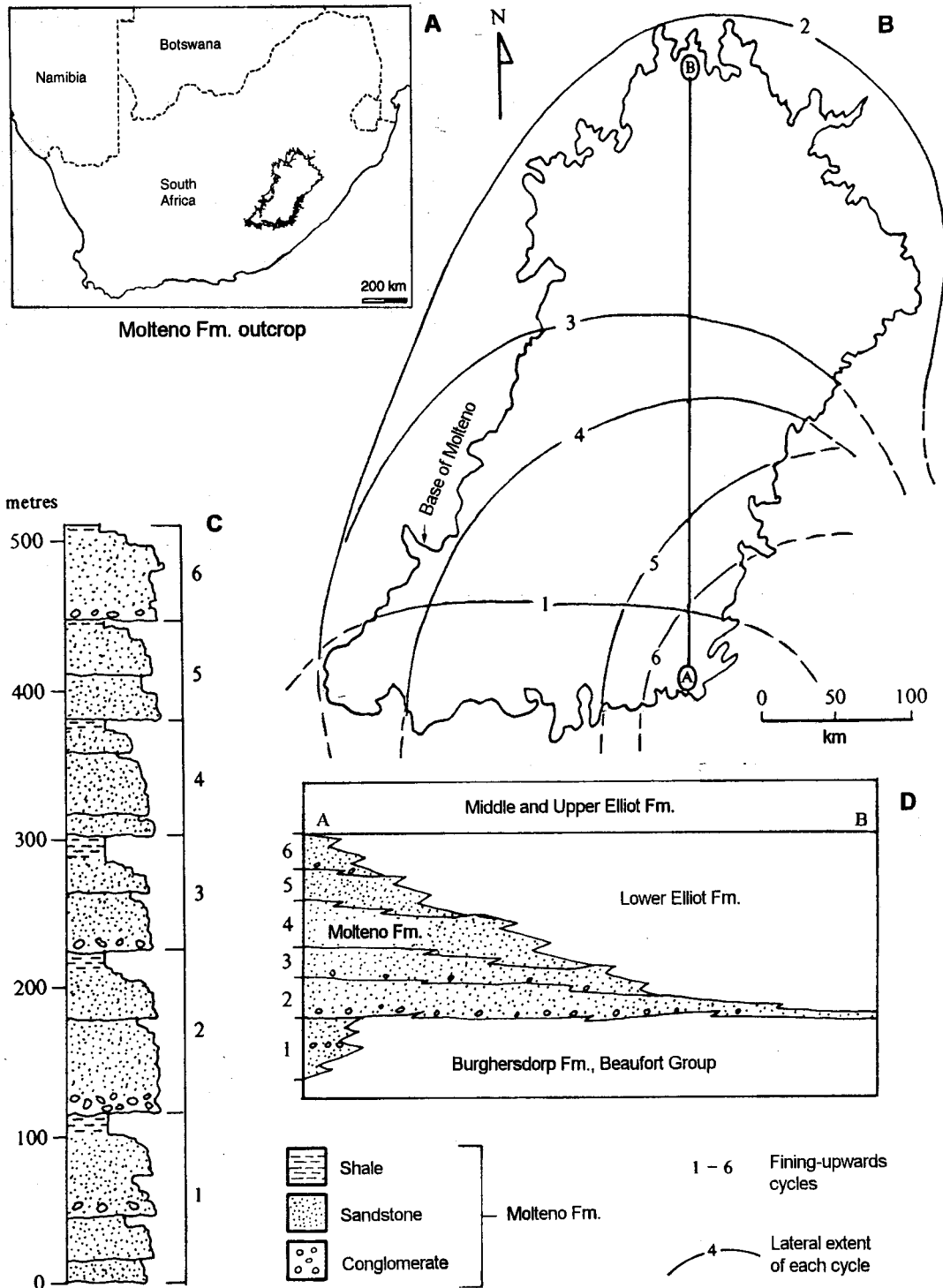
ABSTRACT. A first attempt is made to integrate the plant, insect and tetrapod elements of the Late Triassic (Carnian) intracontinental, braidplain ecosystems of the Karoo Basin, South Africa. These are probably the richest known for this pivotal early Mesozoic interval when the dinosaurs, mammals, some insect orders and possibly the birds and flowering plants made their earliest appearance. Intensive sampling of 100 Molteno Formation taphocoenoses has yielded 56 genera with 206 species of plant (vegetative taxa) and 117 genera with 335 species of insect. Seven major habitats are identified and described, ranging from two types of riparian forest through open woodland to coniferous thicket, horsetail marsh and fern meadow. Each shows a distinctive plant/insect co-association. The tetrapod-vertebrate component of these associations is based on the Lower Elliot Formation, the assumed distal facies and time equivalent of the upper four members of the Molteno Formation. This is a sparse (seven taxa) early dinosaur fauna including both body fossils and trackways. The Upper Elliot Formation has a richer tetrapod fauna and may, in future, be used to model possible missing elements of the Lower Elliot Formation. Comparison of the Molteno insect fauna with that of two other Carnian deposits, in Australia (Ipswich Basin) and North America (Newark Basin), reveals marked provinciality reflecting temperate and tropical latitudes.

It is becoming increasingly evident that the Late Triassic comprises an extraordinary interval in terrestrial evolutionary history (Anderson and Anderson 1993*a*, 1993*b*, 1995, in press; Benton 1993*b*; Rogers *et al.* 1993; Fraser *et al.* 1996). We appear to be witness to the heyday of the gymnosperms in a period of explosive diversification with biodiversities suggestive of those today (Anderson *et al.* 1996). In these rich ecosystems midwifing the extant world, appeared the earliest dinosaurs, mammals, several insect orders and possibly also the ancestral lineages of the birds and flowering plants.

The Molteno Formation offers a rare opportunity to examine rich co-associations of Upper Triassic (Carnian) plants and insects. Together with the tetrapod fauna of the largely coeval Lower Elliot Formation, we present for the first time a palaeoecological synthesis of these three major terrestrial components in the Late Triassic Karoo Basin of South Africa. The intracontinental Molteno/Lower Elliot floodplain biome is the canvas of our investigation.

The plants, insects and tetrapods differ widely in abundance and have been variously sampled and described, but the available sum of data is now sufficient to allow assembly of a preliminary composite picture. The plants are by far the most commonly preserved, comprehensively sampled and fully studied. The insects follow in abundance and level of sampling and, whilst only a small proportion have been formally described, the full collection is curated to species level following a provisional taxonomy. The coeval tetrapods are rarest, with considerable preparation and description of the material remaining.

As background we provide a brief review of Molteno/Elliot tectonics, depositional environment, lithostratigraphy, biostratigraphy, correlation, climate, preservation potential and biodiversity drawn from widely scattered sources. A summary account of the Molteno flora is given whilst the insects and tetrapods are discussed in more depth as the relevant information is mostly unavailable



TEXT-FIG. 1. For caption see opposite.

or is difficult to access in the literature. The text is accompanied by a series of tables presenting a succinct account of the flora and fauna of the Molteno and Elliot formations. Following from these basic data we delineate and systematically describe – in the form of annotated figures – seven primary habitats (ecozones) recognized within the floodplain biome. The flora and fauna of each are characterized and defined.

The Molteno plant and insect collection, on which this study is based, has been made by two of us (JMA and HMA) over the past 30 years and is all currently housed at the National Botanical Institute (NBI), Pretoria. The material collected before 1977 is on long-term loan from the Bernard Price Institute for Palaeontological Research (BPI), Johannesburg. Other collections are relatively minor, widely scattered and mostly from sites that have been resampled.

The Elliott tetrapod data are drawn very largely from two review articles: Kitching and Raath (1984) and Olsen and Galton (1984) on body fossils and trackways respectively. A good proportion of the skeletal material derives from four intensive collecting trips made from 1978 to 1982 by Kitching and colleagues. This material is housed at the Bernard Price Institute. Little to affect this study has been accumulated since.

The system adopted in naming Molteno collecting sites and assemblages was introduced and outlined in Anderson and Anderson (1983, pp. 3–4). The cryptic Umk 111 Dic 2spp, for instance, provides both geographical and assemblage data: Umk 111 refers to the first recorded collecting site (of an area of less than 100 m diameter) in the Umkomaas Valley; Dic 2spp indicates that two species of the foliage genus *Dicroidium* are dominant in the assemblage. For the full site names and map locations, see Anderson and Anderson (1983, 1989) and Cairncross *et al.* (1995). The term taphocoenosis or phytotaphocoenosis (for plant assemblage) is abbreviated to TC. The plant and insect specimens illustrated on Plates 1–2 and Text-figure 3 are catalogued with the prefixes: BP/2/ – Bernard Price Institute/fossil plants; or PRE/F/ – Pretoria (National Botanical Institute)/fossils.

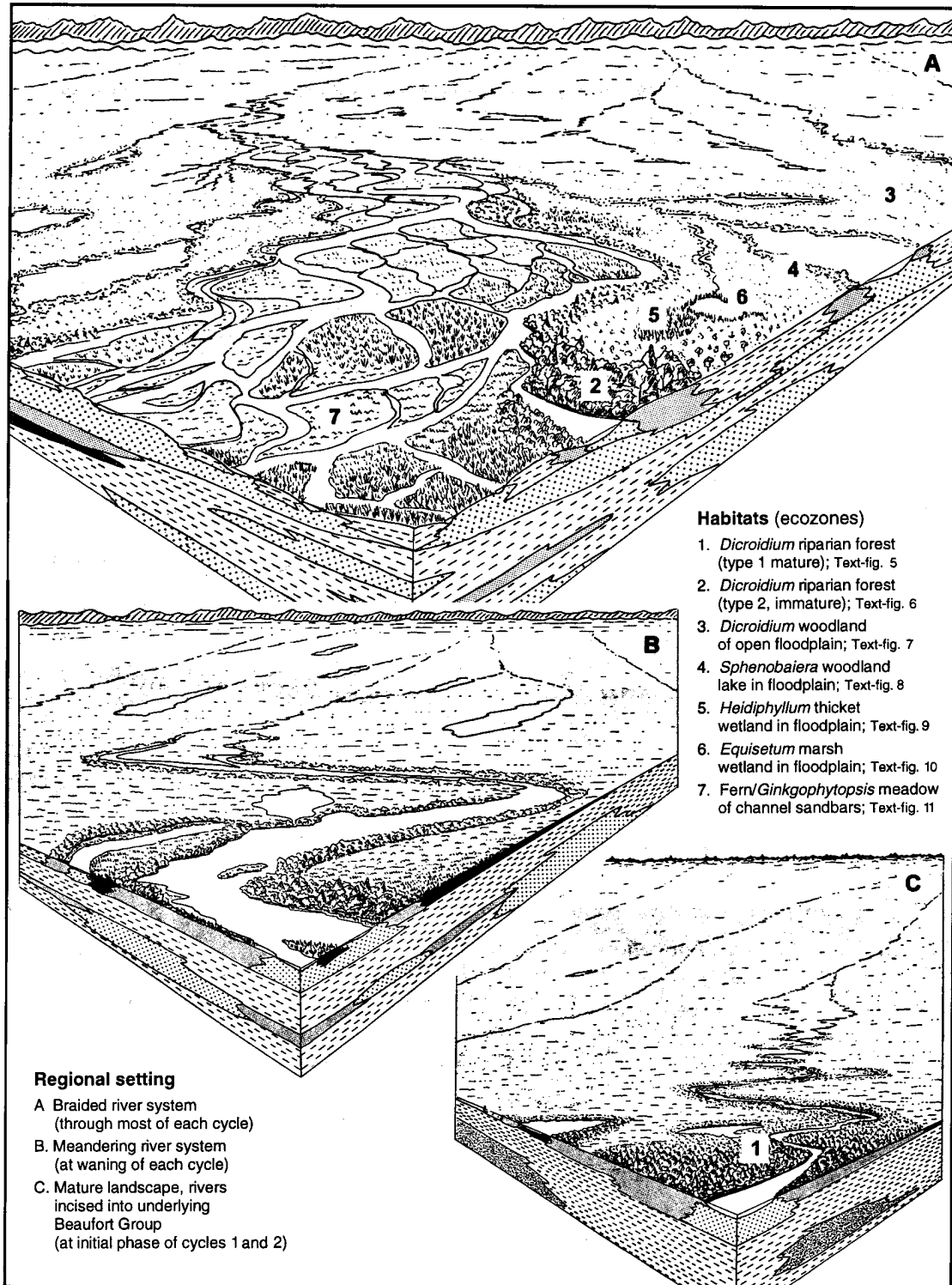
The plant and insect sections in this paper are essentially the work of Anderson and Anderson, the tetrapod compilations and their rôle in the ecosystems that of Cruickshank.

GEOLOGICAL AND PALAEOONTOLOGICAL BACKGROUND

Tectonics

The Molteno Formation and its supposed distal, fine-grained, red-bed facies equivalent, the Lower Elliot Formation, were laid down on a northerly prograding floodplain in an extensive land-locked foreland basin (Text-fig. 1). This was positioned towards the southern periphery of the Pangaeian supercontinent and now forms a part of the Karoo Basin (Turner 1975, 1980, 1983, 1986; Visser 1984; Smith *et al.* 1993). To the south, the basin was bounded by a range of substantial mountains, the result of earlier destructive plate-margin activity, rising to at least 4000 m above sea level. These are thought to have supported permanent ice-fields. Tensional stresses, brought on by the commencement of the break-up of Pangaea, resulted in pulses of sedimentation accompanied by scarp retreat (Turner 1975). The major episodes of fault-controlled uplift of the largely quartzitic sediment source are reflected in the six cycles of upward-fining, sandstone–shale–coal sequences of the Molteno Formation (Text-fig. 1c). Early in the period of deposition of the Molteno Formation (Bamboesberg Member, cycle 1) the source area lay to the south of the basin; subsequently (from the Indwe Sandstone Member, cycle 2 upwards) the source area shifted to the south-east (Turner

TEXT-FIG. 1. Outcrop, lithostratigraphy and tectonics of the Molteno Formation. A, outcrop area of the Molteno Formation in Southern Africa. B, plan view of the Molteno basin showing areal extent of the six individual depositional cycles; only cycle 2 (the Indwe Sandstone) persists from south to north, thinning considerably. C, generalized stratigraphical column of the Molteno Formation, showing six major cycles of sedimentation. D, section through the Stormberg Basin, along line A–B marked on map (B), showing relationship of the Molteno Formation to the distal-facies-equivalent Elliot Formation; note that the Lower Elliot Formation is regarded as the time equivalent of at least the upper four cycles of the Molteno, and that the Middle and Upper Elliot Formation overlies them. B–D modified from Turner (1983), Kitching and Raath (1984) and Cairncross *et al.* (1995).



TEXT-FIG. 2. Regional palaeoenvironmental reconstruction of the Molteno Biome, showing the seven habitat types or ecozones (1–7) described in Text-figures 5–11.

1975; Smith *et al.* 1993). Later sedimentary cycles (3–6) seem to have had their northern limits controlled by incipient crustal upwarping about half way out into the basin, but this may also have been due to the degree and rate of scarp retreat. The formation reaches a maximum thickness of *c.* 600 m and the erosional remnant, largely overlain by younger Karoo strata, extends over an area roughly 400 km north to south and 200 km west to east.

Depositional environment

Bedload (braided) fluvial systems deposited the bulk of the Molteno sediments (Text-fig. 2A). A wide range of lithologies, from boulder conglomerates through a variety of sandstones to siltstones, mudstones and coals, occurs. Three primary facies are encountered: upward-fining, coarse-grained, channel-fill deposits; upward-coarsening crevasse-splay and sheet-flood sequences, and rhythmically laminated lacustrine and marsh shales deposited in the floodplain (Cairncross *et al.* 1995). The high source-area relief, low winter temperatures at high palaeolatitude, strong orographic precipitation, and sparsely vegetated interfluvies in the proximal, upper reaches of the mountain valleys contributed to rapid erosion and heavily loaded stream beds (Turner 1980; Smith *et al.* 1993). The upper levels of the Molteno Formation appear to grade distally into the Lower Elliot Formation, a fine-grained, red-bed facies laid down by meandering river systems. There may also have been intervals of low-sinuosity, meandering-river activity during deposition of the Molteno Formation at the waning of each cycle (Text-fig. 2B) when the source area was inactive and the basin was of low relief. One such case may have been towards the close of Bamboesberg Member sedimentation and before the deposition of the Indwe Sandstone Member (Turner 1975, Cairncross *et al.* 1995).

Lithostratigraphy

The lower contact of the Molteno Formation with the Burghersdorp Formation is diachronous across the basin and has proved difficult to define. It is generally taken that this contact is marked by the first occurrence of typical Molteno pebble beds or coarse-grained sandstones of characteristic bedload geometry (P. J. Hancox, pers. comm.). This is largely allied with the change in sediment colour from red/purple to grey/buff. The break marks a shift from a floodplain with ephemeral streams to a braided-river complex, and is defined by an unconformity which may be more than regional in nature (Charig 1963; Drysdall and Kitching 1963; Keyser 1973; Cruickshank 1986; Cox 1991; Hancox and Rubidge 1996). The upper boundary of the Molteno Formation apparently has an interdigitating relationship with the lower part of the Elliot Formation (Turner 1983; Visser 1984; Cairncross *et al.* 1995, fig. 2a) as indicated earlier. This, in turn, is separated from the Middle Elliot Formation by a distinct palaeosol horizon (Kitching and Raath 1984). The middle and upper components of the Elliot Formation are bracketed together and constitute a flood-basin facies of still finer-grained sediments than the Lower Elliot Formation. These retrograde southwards towards the eroded remnants of the 'Molteno' mountains.

Biostratigraphy

The 100 Molteno phytotaphocoenoses (TCs) or plant assemblages can be ordered, with reasonable confidence, in stratigraphical sequence. All but the last of the six cycles of the formation are fairly well represented, yet no marked biozonation is evident. A few well-defined gymnosperm taxa, *Dicroidium zuberi*, *Gontriglossa verticillata*, *Pseudoctenis fissa*, *P. harringtoniana* and *Moltenia* spp. are, however, confined to the Indwe Member (cycle 2). These occur fairly frequently and commonly within the member, but this may well be of more palaeoecological than biostratigraphical significance: the Indwe Member is the most prominent, arenaceous, and widespread of the Molteno members and is the only one to extend the full south–north extent of the formation (Text-fig. 1B, D).

The Moltano insect faunas have not, as yet, been tabulated in such a way as to assess how far they show biostratigraphical significance. Plant fossils are apparently extremely rare and fragmentary in the Elliot Formation (C. E. Gow, pers. comm.); but, based on Ellenberger (1972), there seems to be a broad correlation of a characteristically Triassic *Dicroidium* flora with the Lower Elliot Formation (= Lower 'Red Beds') and of a Jurassic-like flora with the Middle and Upper Elliot Formation (= Upper 'Red Beds') (Ellenberger 1972, pp. 346–348; Kitching and Raath 1984).

The Elliot Formation is divided into two biostratigraphical units, each with a distinctive tetrapod fauna. The lower division coincides with the Lower Elliot Formation and has been ascribed to the *Euskelosaurus* Range Zone (Kitching and Raath 1984). This fauna has a distinctly Triassic imprint, comprising temnospondyl amphibians, a possible chelonian, a gomphodont cynodont, a dicynodont, a thecodont and a large, primitive, sauropodomorph dinosaur. The presence of a primitive sauropod in the Lower Elliot Formation helps confirm its Carnian age (Benton 1993a; Padian and May 1993). The lower fauna contrasts with that of the Middle to Upper Elliot Formation, which is ascribed to the *Massospondylus* Range Zone. This younger zone contains a more diverse fauna, of Jurassic aspect, including advanced cynodonts, crocodiles, ornithischian dinosaurs and primitive mammals (Kitching and Raath 1984). We have incorporated a faunal summary of the *Massospondylus* Range Zone to provide some indication of what forms of animal life might possibly be missing from the seemingly incomplete Lower Elliot fauna.

Global correlation

The correlation of exclusively terrestrial Gondwana deposits against the international standard-reference sections based on northern marine sequences is always difficult. The quoted age of any particular tetrapod or plant-bearing formation is often based more on tradition than any secure framework of correlation. The ages of the Moltano and Elliot formations are by no means fixed. On the basis of earlier comprehensive systematic efforts to correlate the Karoo strata globally (e.g. Anderson and Anderson 1970, 1983; Anderson and Cruickshank 1978; Anderson 1981), we settled on a Early Carnian age for the Moltano Formation and a Late Norian/Rhaetian age for the Elliot Formation. The putative interfingering, coeval nature of the upper members of the Moltano and the Lower Elliot Formations, as accepted in this paper, was not accounted for in the earlier papers.

The Burghersdorp Formation, which is separated from the Moltano Formation by an unconformity (Turner 1972; Cruickshank 1986; Hancox and Rubidge 1996), is taken to extend from the upper Lower Triassic (Spathian) to within the Anisian, whereas the Moltano Formation (and its distal equivalent, the Lower Elliot Formation) is considered to be Carnian (e.g. Gauffre 1993). A post-Anisian sedimentary break is widespread throughout southern Africa at least. It indicates a halt to basin formation, followed by uplift and erosion, and is thus likely to coincide with tensional stresses presaging the break-up of Pangaea.

Although there are recently published alternative 'dates' (Aigner and Bachmann 1993; Retallack *et al.* 1993; Rogers *et al.* 1993; Lucas 1994b) for the various stages within the Triassic, we take the period to have had a duration of *c.* 40 million years (within limits of a few million years) from 247 to 204 Ma (Menning 1991). The lower boundaries of the intervening stages are placed at 240 Ma for the Anisian, 234 Ma for the Ladinian, 229 Ma for the Carnian and 222 Ma for the base of the Norian. A time gap of at least 5 million years representing the post-Anisian unconformity can be recognized. If the Moltano/Lower Elliot Formations occupy the whole of the Carnian, then this depositional event would represent a slice of history of some 7 million years duration, but we have generally considered the Moltano Formation to have been laid down over a shorter period of time (e.g. Anderson 1981).

If the Upper Elliot Formation is placed in the lowest Jurassic, as is traditional, then the unconformity recognized between the Lower and Upper Elliot Formations (Kitching and Raath 1984) would represent the whole of the Norian and Rhaetian (18 My). This gap might be very much reduced if the Upper Elliot Formation were to extend down into the Upper Triassic and Lower Elliot Formation up into the Norian.

TABLE 1. The Molteno flora; plant form and preferred habitat are of necessity first approximations.

CLASS SUBCLASS Genera	app.	fre- quency	abund- ance	plant form	preferred habitat	
BRYOPHYTA						
<i>Muscites</i>	1	16	rare	} mosses & liverworts	damp/shady undergrowth	
HEPATOPHYTA						
<i>Marchantites</i>	9	18	rare			
INCERTAE SEDIS						
<i>Thalites</i> (+2 gen.)	9	6	v. rare			
LYCOPHYTA						
<i>Cylomeia</i> (+1 gen.)	6	7	v. rare	herbaceous	floodplain wetlands	
SPHENOPHYTA (horsetails)						
<i>Phyllothea</i>	5	} 21	6	} horsetails; reed-like, low to high	riverine and floodplain wetlands	
<i>Schizoneura</i>	4		9			
2 genera	3		16			
<i>Equisetum</i>	9		50			dominant
FILICOPHYTA (ferns)						
<i>Drepanozamites</i>	1	} 46	2	} ferns	riverine forest (varied) wide spectrum riverine forest (varied)	
11 genera	32		44			
<i>Dictyophyllum</i>	3		8			v. rare
<i>Asplenites</i>	2		4			occasional
miscell. (4 gen.)	8		13			v. rare
PINOPHYTA						
PINOPSIDA (conifers)						
<i>Heidiphyllum</i>	2	} 5	62	dominant	woody, reed-like	
<i>Rissikia</i>	2		21	common	large tree	
<i>Pagiophyllum</i>	1		1	v. rare	tree	
CYCADOPSIDA						
<i>Pseudoctenis</i>	9	} 21	21	occasional	} cycad-like, generally small	
<i>Jeanjacquesia</i>	3		3	v. rare		
<i>Ctenis</i>	2		2	"		
<i>Moltenia</i>	4		5	"		
PELTASPERMALES (seed ferns)						
<i>Kurtziana</i> (+2 gen.)	18	} 40	13	rare	small tree	
<i>Lepidopteris</i>	2		30	common	med. shrub	
<i>Dicroidium</i>	19		75	dominant	shrub to large tree	
<i>Dejerseya</i>	1		5	common	shrub or small tree	
GINGKGOALES						
<i>Sphenobaiera</i>	9	} 16	43	dominant	shrub to med. tree	
<i>Ginkgo</i>	7		19	occasional	shrub to tall tree	
NEW ORDER						
<i>Ginkgophytopsis</i> -like	8	25	occasional	herbaceous pioneer	wide spectrum	
INCERTAE SEDIS						
<i>Linguifolium</i>	1	} 6	9	rare	herbaceous pioneer	
<i>Saportaea</i>	1		1	v. rare	herbaceous undergrowth	
<i>Chiropteris</i>	4		10	"	creeper	
PENTOXILOPSIDA						
<i>Taeniopteris</i>	8	38	common	shrub to small tree	forest to woodland	
BENNETTOPSIDA						
<i>Halleyoctenis</i>	3	11	common	cycad-like	open woodland	
GNETOPSIDA						
<i>Gontriglossa</i>	3	} 8	8	occasional	herbaceous pioneer	
<i>Yabeiella</i>	3		30	occasional	large tree	
<i>Jungites</i>	2		1	rare	shrub or tree	

Total diversity – 59 genera, 206 species.
Species – based on full taxonomic review of Molteno flora.
Sampling – based on the 100 sampled taphocoenoses (TCs).
Frequency – the number of TCs in which the genus occurs.

Abundance (the norm in the TCs in which it occurs)
 v. rare – 1–5 individuals
 rare – 5–10 individuals
 occasional – 10 individuals to 1 per cent.
 common – 1 per cent – 5 per cent.
 dominant – dominates the communities.

Climate

As proposed by Anderson and Anderson (1983, 1993b), the climate during deposition of the Molteno Formation was governed by Pangaea forming a landmass stretching from pole to pole. This landmass formed a barrier to the westward-flowing warm equatorial currents, which would have been deflected north and south along the eastern shoreline of Pangaea, resulting in evaporation and copious precipitation along this belt. The cold West-Wind Drift would likewise have found a barrier in the opposite margin of Pangaea, resulting in a belt of temperate rainfall between palaeolatitudes 33° S and 66° S. The Molteno depositional basin, lying as it did towards the Gondwana interior at around 60° S, may have been fairly arid with warm to hot, dry summers and cold, wetter winters. Sufficient winter precipitation fell on the mountains of the Proto-Cape Fold Belt to ensure perennial flow in the major Molteno river systems, with enhanced flow and flooding in spring through melting snow and ice in the highlands.

The preservation enigma

The coarser-grained, grey/buff sediments of the Molteno Formation yield abundant, well-preserved plants and insects to the virtual exclusion of tetrapods (body fossils or trackways); the finer-grained, red beds of the Elliot yield abundant and often well-preserved tetrapods and their trackways to the virtual exclusion of plants and insects. This pattern of exclusivity, plant or tetrapod, appears to be general throughout the terrestrial fossil record: certainly it is seen all through the richly fossiliferous Early Permian to Early Jurassic Karoo strata of South Africa. There remains no fully convincing explanation for this enigmatic balance of preservation.

It is well known that the macroscopic remains of plants (foliage, fruit) and tetrapod vertebrate (bone) are equally likely to be preserved in the various depositional settings (channel, crevasse splay, floodplain, lake) of the braidplain environment (Behrensmeyer *et al.* 1992, p. 17). It is additional factors, such as pH, drainage and oxygenation, that control the preservation of either plant or bone. Plants are best preserved where there are high levels of humic acids (i.e. low pH) coupled with poor drainage and low oxygenation (such as in the Molteno Formation), whilst bone is best preserved under alkaline conditions (i.e. neutral to high pH) coupled with high oxygenation (such as in the Elliot Formation). It remains difficult, however, to explain why the Molteno Formation should be nearly devoid of coprolites and trackways.

Biodiversity

The application of recently derived statistical techniques (Generalized Inverse Gaussian-Poisson Distribution – GIGP) to the observed (sampled) Molteno floral and insect diversity has yielded estimates of the corresponding preserved (potentially available) diversity (Anderson *et al.* 1996). Three extrapolations were made on the basis of these rich megafloral/insect co-assemblages from 100 taphocoenoses (TCs): insect species – 335 observed, 7740 preserved; vegetative species – 206 observed, 667 preserved; gymnosperm ovulate orders – 16 observed, 84 preserved. Further extrapolations of these results hint at global Late Triassic floral and faunal richness akin to that of the present day, which conflicts with the traditionally held model of a cone of increasing biodiversity

EXPLANATION OF PLATE 1

The dominant plant genera defining habitats 1–4 of the Molteno Formation.

- 1–2. *Dicroidium* (seed fern). 1, BP/2/057; Umk 111; × 1. 2, PRE/F/1790; Mat 111; bedding plane showing forked fronds; × 0.75.
3. *Sphenobaiera*; BP/2/4849; Bir 111; bedding plane of overlapping leaves of two species; × 1.
4. *Rissikia* (conifer); PRE/F/1326; Hla 213; × 1.5.



ANDERSON *et al.*, *Dicroidium*, *Sphenobaiera*, *Rissikia*

through time (Anderson and Anderson 1995). This suggests a hitherto unsuspected phase of explosive plant and insect evolution in the Triassic – following the Late Permian extinction – crucial in understanding the evolution of the Mesozoic terrestrial biota (Anderson and Anderson 1993a, 1993b, 1995; Anderson *et al.* 1996). The low frequency, abundance and *observed* diversity of the tetrapods in the Lower Elliot Formation preclude them from similar statistical treatment.

MOLTENO FLORA

The Molteno flora (Table 1) is apparently the most comprehensively sampled and richest known for the Triassic world. It has been extensively and intensively sampled from 100 taphocoenoses (from 69 localities, i.e. areas of up to 1 km in diameter) and is represented by some 30000 catalogued slabs with 300000 identifiable vegetative specimens. A comprehensive taxonomic study of this material, partly published, has revealed 56 genera with 206 vegetative species of plant (Anderson and Anderson 1983, 1985, 1989). The flora is characterized by a fairly equal range of gymnosperm and pteridophyte taxa. The former are dominated by a number of species of the 'seed fern' *Dicroidium* and by various ginkgophytes, conifers and cycads, although a wide spectrum of ovulate fruiting structures indicates a host of new gymnosperm orders making their appearance. The pteridophytes are strongly dominated by horsetails and ferns, with lycopods very rare. Mosses and liverworts are scattered.

In spite of the overall diversity, it is the species of only a few genera – *Dicroidium* (seed fern, Peltaspermales), *Sphenobaiera* (Ginkgoales), *Heidiphyllum* (conifer, Voltziales), *Equisetum* (horsetail, Equisetales) and, to a lesser extent, *Rissikia* (Coniferales) – that dominate the discernible plant associations (Table 1; Pls 1–2). It has been possible to define six plant habitats based largely on the occurrence of these genera (Cairncross *et al.* 1995), whilst a seventh is characterized by the rarer ferns and *Ginkgophytopsis* (Pl. 2, figs 5–6). These seven habitats are further characterized by distinctive lithologies and insect assemblages.

MOLTENO INSECTS

In the continuing shift of interest from descriptive systematics to evolutionary palaeoecology, palaeobiology and related fields (Behrensmeyer *et al.* 1992; Tiffney 1992; Anderson and Anderson 1993a, 1993b) it has become evident that the dearth of knowledge concerning fossil insects is a particularly pressing defect. This is all the more significant when it is acknowledged that the impact of insects in present-day ecosystems is no less than that of vertebrates. The discovery over the last few years, therefore, that the insects are far more plentiful in the Molteno Formation than was previously suspected is very encouraging. A systematic study of fossiliferous slabs under the stereomicroscope has revealed that virtually all Molteno phytotaphocoenoses yield a steady, if rare, return of insects (Table 2).

This ubiquitous occurrence of insects has opened an entirely new perspective on the palaeoecology of the formation. Analysis of the full collection of 2056 individuals now available from 43 taphocoenoses (TCs) has led to the recognition of a clear pattern of plant/insect co-associations (Tables 3–4).

EXPLANATION OF PLATE 2

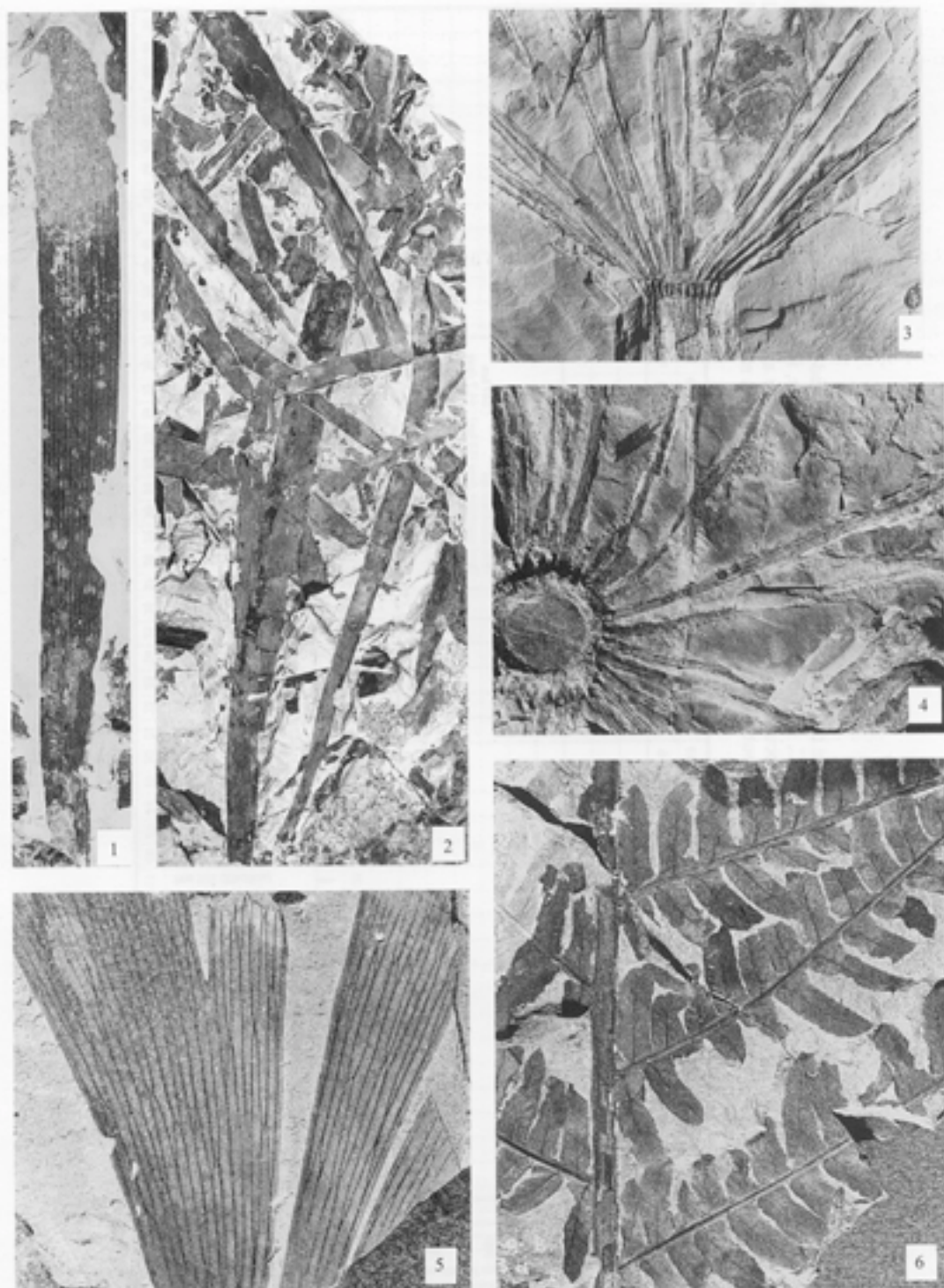
The dominant plant genera defining habitats 5–7 of the Molteno Formation.

1–2. *Heidiphyllum* (conifer); Tel 111. 1, PRE/F/7705b; $\times 1$. 2, BP/2/5617; bedding plane of overlapping leaves; $\times 0.5$.

3–4. *Equisetum* (horsetail); Gre 111. 3, PRE/F/7572a. 4, PRE/F/7577a. Both $\times 1$.

5. *Ginkgophytopsis*; PRE/F/10157b; Mat 111; showing characteristic anastomosing venation; $\times 2$.

6. fern frond; BP/2/3344b; Kan 111; $\times 1$.



ANDERSON *et al.*, Moltano Formation flora

Preservation and yield

All Molteno insect faunas have been found together with plant macrofossil assemblages. The insect specimens, mostly isolated wings, less often abdomens, nymphs or larvae, and rarely complete or partially complete adult individuals, occur as very rare elements scattered amongst the plant remains. Nowhere have we encountered a bedding plane, lens or horizon within the main body of a site to show an abnormally high concentration of insects. The yield varies quite widely between TCs (Table 2), from one insect per ten man-microscope hours scanning plant-bearing slabs, through to 64 per ten hours, but with a marked norm at around 10–20 per 10 hours. These data are internally consistent in so far as they are based throughout on just one of us (JMA) working at the binocular microscope. They are significant taphonomically and palaeoenvironmentally as they relate broadly to the conditions of deposition: the highest yield generally being encountered in quiet-water deposits (e.g. lakes of the floodplain) and the lowest in turbid-water deposits (e.g. certain channels in the braided river). It should be noted that the total insect counts (as recorded in Table 2 for each TC) include individuals found in the field in addition to those found under the microscope in the lab.

Collection size and faunal patterns

Although a total of 2056 individuals from 43 TCs is now available, the number from each TC varies greatly (Table 2). Around half the TCs have yielded ten or more insects, whilst as many as seven are represented by over 100 individuals. A sufficient tally of specimens from a significant number of sites is thus available for clear repetitive faunal patterns to emerge. These different faunas are seen to occur with distinctive plant associations and under definite depositional regimes (Tables 3–4).

Provisional taxonomy

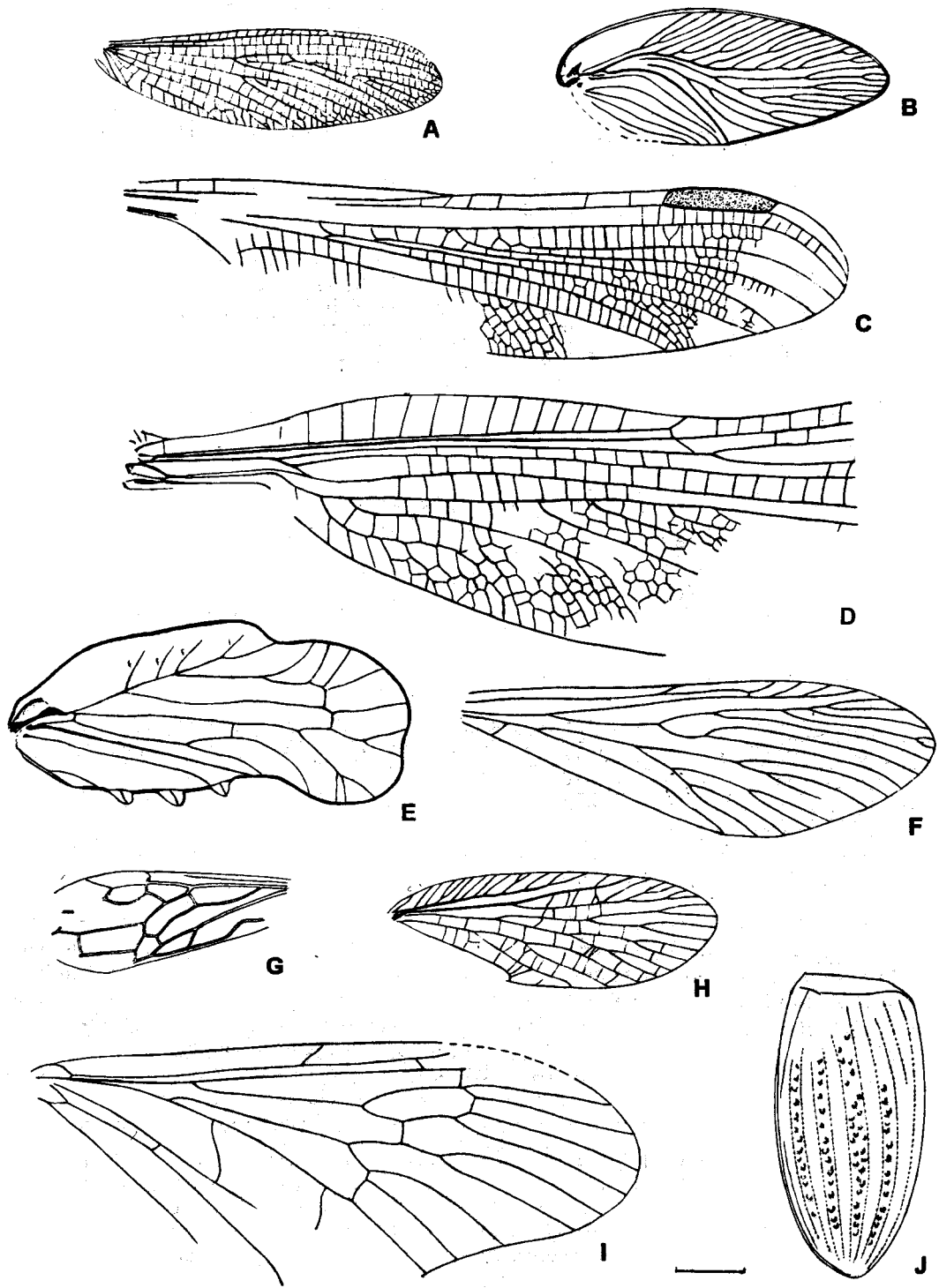
Only five formal taxonomic papers covering a small part of the insect fauna have been published (Zeuner 1961; Riek 1974, 1976a, 1976b; Hubbard and Riek 1977). The full insect collection, considerably enhanced since the late 1970s, has, however, been comprehensively curated following a provisional taxonomy to order, genus and species. The recorded diversity now reads 18 orders, 117 genera, 335 species. The continuing systematic work owes much to Riek (Canberra, Australia) who has to date undertaken four study trips to South Africa: 1973 (twice), 1985 and 1991. A selection of Molteno insect wings is illustrated in Text-figure 3.

Other invertebrates

The insects are by far the most important component of the Molteno fauna. The Conchostraca (small, mainly freshwater crustaceans) are the next most significant faunal element with a provisional taxonomy indicating three genera and eight species from 20 plant assemblages. They occur in relative abundance on certain bedding planes in several of the assemblages. The remaining fauna is very sparse, including just two genera with two species of bivalve from one assemblage, and two specimens of spider from two assemblages (Selden *et al.* in press). These additional invertebrates are not discussed further in this paper.

THE DOMINANT INSECT ORDERS

In terms of abundance and diversity (Tables 3–4), three orders (and to a lesser extent a fourth) strongly dominate the Molteno faunas. The cockroaches are by far the most abundant with 956 individuals, the beetles are second with 453 individuals, and the bugs third with 229 individuals. The



TEXT-FIG. 3. For caption see opposite.

beetles, though, are clearly the most diverse order with close on half of all taxa (161 species), the bugs fall second with 69 species, and the dragonflies third with 22 species. It is the abundance ratios between these four orders that largely characterize the faunal components of the plant/insect co-associations recognized in the Molteno Formation. The variable role of taphonomic bias remains to be assessed fully. In view of their palaeoecological importance, these four orders are discussed in regard to their known habitat and diet in the extant world and their patterns of occurrence in the Molteno Formation.

Blattodea (cockroaches)

Habitat and feeding of extant representatives. Cockroach nymphs and adults exhibit the same patterns of habitat and feeding, both being essentially terrestrial omnivores. They are primarily nocturnal, unspecialized scavengers in leaf litter, feeding largely on decomposing plant material.

Molteno Formation. The cockroaches easily outnumber other insect groups in the Molteno (Table 3). With 956 individuals, mostly isolated forewings, less common nymphs, abdomina, hindwings or fully articulated adults, from 34 TCs they amount to nearly half the total faunal count of 2056 individuals. In diversity (Table 4), however, with a mere three genera and ten species recognized, they come only sixth after the beetles, bugs, dragonflies, scorpionflies and Paraplecoptera. Their relative abundance is markedly highest in the closed-canopy terrestrial habitats – *Heidiphyllum* thicket, *Sphenobaiera* closed woodland and the *Dicroidium* riparian forest (types 1 and 2) – where ample leaf litter, ideal for their scavenging, would have accumulated.

Coleoptera (beetles)

Habitat and feeding of extant representatives. The beetles are hugely diverse in the extant world, with an estimated 350 000 species having been described (Scholtz and Holm 1985). They vary greatly in size, shape, habit and biology and are found in virtually all terrestrial and freshwater habitats. Both larvae and adults utilize virtually all plant parts, dead or alive. Plant debris provides a particularly rich food source. Carnivores (predators) are also common, some being specialists, others opportunists.

Molteno Formation. The beetles are the second most abundant insect order in the Molteno Formation (Table 3), but are by a wide margin the most diverse (Table 4). A total of 453 individuals (from 36 TCs), including 30 genera and 161 species, occurs in the collection. They are found more or less equally prominently, in abundance and diversity, in all the Molteno habitats (apart from the fern/*Ginkgophytopsis* meadows for which insects are as yet unknown). In virtually all Molteno TCs yielding insects, the beetles make up half or more of the diversity, a characteristic that heralds patterns in the world today. Whilst beetles first appear in the Lower Permian, their dramatic

TEXT-FIG. 3. Selected genera from the more significant Molteno insect orders. A, *Litophebia* (Ephemeroptera, mayflies); BP/2/21549; Bir 111. B, *Samaroblatta* (Blattodea, cockroaches); PRE/F/10118; Bir 111. C, *Triassoneura* (Odonata, dragonflies); BP/2/20983; Bir 111. D, new genus of Meganisoptera (protodragonflies); PRE/F/5118; Bir 111. E, *Tenmentsia* (Homoptera, bugs); BP/2/21034; Bir 111. F, new genus of Mecoptera (scorpionflies); PRE/F/10124; Bir 111. G, new genus of Hymenoptera (wasps, bees, ants); PRE/F/10438; Bir 111. H, new genus of Paraplecoptera (extinct); PRE/F/10436; Bir 111. I, *Mesoses* (Lepidoptera, butterflies); PRE/F/10617; Aas 411. J, new genus of Coleoptera (beetles); PRE/F/10822; Bir 111. Scale bar represents 4 mm (A, C–F, H–I), 2 mm (B, G) or 1 mm (J).

radiation appears to have been a feature of the Late Triassic (Crowson 1975; Anderson and Anderson 1993a, 1993b). A significant proportion of the Molteno beetles, as suggested by their morphology, was evidently aquatic or semi-aquatic. A similarly high proportion was particularly small in size. It is uncertain as to what extent the tough exoskeleton and especially the elytrification might contribute to an apparent prominence of beetle remains.

Homoptera (bugs)

Habitat and feeding of extant representatives. Homopterans are herbivores with mouth parts adapted for sucking sap from plant groups ranging from ferns to angiosperms. In all but one (Cicadoidea) of the major superfamilies (Cercopoidea, Fulgoroidea, Psylloidea and Aleurodoidea) represented in the Molteno Formation, the nymphs and adults live in essentially the same arboreal habitat and follow similar feeding preferences. The taxa are often host-specific and well camouflaged. In Cicadoidea the nymphs are terrestrial soil burrowers feeding on roots of grasses or trees, whilst the adults are arboreal feeding on the sap of trees and shrubs.

Molteno Formation. With 229 individuals from 25 TCs, the bugs come a clear third in abundance in the Molteno fauna (Table 3), whilst in diversity, with 34 genera and 69 species, they come an equally clear second after the beetles (Table 4). Their most favoured habitat, on comparing relative abundance of individuals with that of the other prominent orders, was evidently the open *Dicroidium* woodland, followed by the *Sphenobaiera* woodland and the *Heidiphyllum* thicket. They occur relatively rarely in the riparian-forest habitats. Bug diversity comes closest to that of the beetles in the *Sphenobaiera* woodland peripheral to the floodplain lakes.

Odonata (dragonflies and damselflies)

Habitat and feeding of extant representatives. The nymphs are aquatic carnivores, living in standing or flowing water. They are predatory, with mouth parts adapted for a wide diet ranging from insects, conchostracans and other small crustaceans to immature fish. The adults are predatory aerial carnivores, taking other insects whilst on the wing.

Molteno Formation. With a total of 91 individuals from 16 TCs, Odonata is the fourth most abundant order in the Molteno Formation (Table 3). In diversity, with eight genera and 22 species, it comes third after the beetles and bugs (Table 4). As with the other more primitive orders with aquatic nymphs and aerial adults, odonatans are clearly found most abundantly in the floodplain-lake deposits (e.g. Bir 111, Aas 411) associated with *Sphenobaiera* closed woodland; and next most commonly in deposits laid down in abandoned channels of the braided river (e.g. Kap 111, Mat 111), associated with *Dicroidium* riparian forest (type 2). They are markedly rare elsewhere.

PLANT-INSECT CO-ASSOCIATIONS

The abundance and diversity data for the 18 Molteno insect orders are plotted against the 43 TCs in a pair of matrix tables: Table 3 records specimen counts and Table 4 species counts. On arranging the TCs according to vegetation type, and sedimentary facies where feasible, a distinctive pattern of six plant/insect co-associations is seen. Insects are not yet known from the seventh vegetation type: the fern/*Ginkgophytopsis* meadows.

Even though some proportion of the insect fauna in each TC presumably constitutes noise from associations further afield (i.e. is allochthonous), the initial patterns that emerge are striking and

obviously meaningful. The faunas of the *Sphenobaiera* woodland peripheral to floodplain lakes are, for instance, markedly different from those of the *Dicroidium* woodland of the open floodplain (Table 3). Particularly evident in this comparison is the common occurrence of the more primitive orders – mayflies, protodragonflies, dragonflies, and Paraplecoptera, all closely associated with open water – in the former habitat and their rarity in the latter.

These co-associations and their habitats are described in some detail in Text-figures 5–11 along with the tetrapod components of the Lower Elliot Formation that are considered most likely to have been allied with each.

ELLIOT FORMATION TETRAPODS (WITH MINOR MOLTENO FORMATION COMPONENTS)

Abundance and localities

The material on which the Elliot faunal lists (Tables 5–6) are based has been accumulated over more than a century. Details concerning localities, number of specimens, and mode of preservation are largely lacking. Localities may vary considerably in extent from a district, to a farm, to a system of erosion gullies or a single site in one such gully. It follows that the abundance data for the different taxa as reflected in the Tables are more relative than real. The tally of 55 cited for *Euskelosaurus*, for instance, is the number of localities at which the taxon has been collected and records the minimum number of individuals represented. Fish are excluded from consideration.

We include the full section on the vertebrates under the heading ‘Elliot tetrapods’, as virtually all the material derives from this formation. The Molteno contribution is minimal and speculative.

Molteno Formation vertebrates

Vertebrate body fossils in the Molteno Formation are restricted to 32 specimens of fish (impressions) from three plant localities, primarily Birds River (Bir 111). These are ascribed to four genera: *Semionotus* and three new forms (Jubb 1973; E. K. Sytchevskaya, pers. comm.).

Published reports of tetrapod trackways in the Molteno Formation are confined to a single locality (two sites 200 m apart) near the town of Maclear in the north-eastern Cape (Raath *et al.* 1990; Raath 1996). Further sites are now known from the same vicinity as well as from the Qwa Qwa National Park (either uppermost Molteno or Lower Elliot Formation) in the northern Molteno outcrop (P. J. Hancox, pers. comm.). The Maclear site was originally assigned to cycle 1 in the Molteno (Raath *et al.* 1990), but is now considered high (cycle 5; Transitional Member of Turner 1975) in the formation (P. J. Hancox, pers. comm.) and therefore of the same age as the Lower Elliot Formation (Text-fig. 1D). The original Maclear trackways include those of a *Grallator*-like theropod, a possible chelonian (proganochelyid) and tail drags suggesting a large quadrupedal prosauropod dinosaur (Table 5).

Euskelosaurus Range Zone fauna (Lower Elliot Formation)

The faunal list for the Lower Elliot Formation (Table 5) reflects the minimum possible diversity at generic level and is based largely on the latest general reviews at hand: Kitching and Raath (1984) on the body fossils; Olsen and Galton (1984) primarily on the trackways. In these references a considerable number of generic and specific names from earlier literature were already reduced to synonyms or dropped as *nomina dubia*. The ‘cleaned’ list of taxa that remains, reduced further by linking body fossils and trackways as attempted here, reflects a rather meagre diversity of just seven genera (including the Molteno material). Descriptive and taxonomic work remains insufficient to consider specific taxa. The fauna consists of three carnivores comprising a large riverine capitosaur, the top carnivore *Basutodon*, and a small bipedal theropod, along with four herbivores comprising the high-level dinosaurian browser *Euskelosaurus*, a lumbering kannemeyeriid low-level browser/grazer, a smaller low-level omnivore *Scalenodontoides*, and an omnivorous proganochelyid tortoise.

TABLE 5. Tetrapods of the Lower Elliot Formation, including minor Molteno components (e.g. the chelonian), with an interpretation of lifestyles.

CLASS SUBCLASS SUPERORDER ORDER SUBORDER FAMILY Genus	Body fossils no. of localities (=min no. of indivs)	Niche diet	Size overall (unless stated)	Associated trackway (ichno taxa)	habitat, diet etc.
AMPHIBIA LABYRINTHODONTIA TEMNOSPONDYLI CAPITOSAURIDAE <i>Capitosaurid</i> indet.	9	P/C	to 4 m	-	habitat: riverine (not lake) analogue: crocodile (skulls to c. 1 m long) diet: piscivore, carnivore association: with <i>Euskelosaurus</i> preservation: cranial and postcranial fragments trackway: (unknown)
REPTILIA ANAPSIDA CHELONIA PROGANOCHELYIDAE <i>Proganochelyid</i> indet.	-	H/O	to 1 m	FAM. indet. <i>?Episcopus</i>	habitat: full spectrum (forest to open woodland) analogue: med.-large tortoise diet: herbivore/omnivore (scavenger, plants to inverts) association: theropod and <i>Euskelosaurus</i> preservation: body fossils unknown trackway: single indistinct trackway (Molteno)
ARCHOSAURIA THECODONTIA PSEUDOSUCHIA RAUISUCHIDAE <i>Basutodon</i>	10	C	3 m	CHEIROTHERIDAE <i>Brachycheirotherium</i>	habitat: full spectrum (forest to open woodland) analogue: large Komodo dragon diet: top carnivore association: not documented preservation: cranial and postcranial fragments trackway: most common
SAURISCHIA THEROPODA Theropod indet.	-	V/C	1 m	GRALLATORIDAE <i>Grallator</i>	habitat: primarily open woodland analogue: small bipedal dinosaur diet: insectivore (juveniles); carnivore association: unknown preservation: (known only from trackways) trackway: 2nd most common
SAUROPODOMORPHA ANCHISAURIDAE <i>Euskelosaurus</i>	55	H	10 m	NAVAHOPODIDAE <i>Tetrasauropus</i>	habitat: principally riparian forest analogue: med-sized quadruped dinosaur diet: high level browser association: with capitosaur preservation: fully articulated to fragmentary trackway: apparently infrequent
SYNAPSIDA THERAPSIDA DICYNODONTIA KANNEMEYERIIDAE <i>Kannemeyeriid</i> indet.	-	H	2-3 m	PENTASAUROPODIDAE <i>Pentasauropus</i>	habitat: forest and closed woodland analogue: cow/ox diet: herbivore, browser/grazer, low level association: unknown preservation: (known only from trackways) trackway: moderate frequency
CYNODONTIA DIADEMODONTIDAE <i>Scalenodontoides</i>	6	H/O	300 mm (skull)	-	habitat: full spectrum (aside from <i>Equisetum</i> marsh) analogue: small bear diet: herbivore/omnivore, fruit and foliage, low level association: unknown preservation: rare fragments, 1 good skull trackway: (unknown)

How comprehensively does this observed fauna represent the full preserved or existing fauna of the time and place? It does seem remarkably scanty considering the very high diversity of the plants and insects in the Molteno Formation.

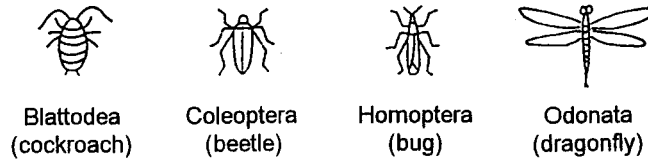
Massospondylus Range Zone fauna (Middle to Upper Elliot Formation)

The tetrapod fauna of the Middle to Upper Elliot Formation – compiled from the same sources and following the same procedure as for the Lower Elliot Formation – is presented (Table 6) to give an idea of the structure of a distinctly richer assemblage of a slightly later time interval. This may, in future work, enable a model to be constructed of possible missing elements of the Lower Elliot Formation. The *Massospondylus* Zone fauna includes, amongst others, a wider spread of dinosaurs and two genera of early mammals. It is not discussed further in this paper.

TABLE 6. Tetrapods of the Middle and Upper Elliot Formation, with an interpretation of lifestyles.

CLASS SUBCLASS SUPERORDER ORDER SUBORDER FAMILY Genus	Body fossils no. of localities (=min indiv)	Niche diet	Size overall (unless stated)	Associated trackway (ichno taxa)	habitat, diet etc.
AMPHIBIA LABYRINTHODONTIA TEMNOSPONDYLII BRACHYOPIIDAE Brachyopid indet.	2	NP	>250 mm (skull)	-	habitat: river &/or lake analogue: 'salamander', c1½ m in length diet: piscivore (ambush predator) association: with <i>Massospondylus</i> & lungfish preservation: 1 partial skull trackway: unknown
REPTILIA ANAPSIDA CHELONIA AUSTROCHELYIDAE <i>Austrochelys</i>	1	OH	>0,6 m	FAM. indet. <i>Episcopus</i>	habitat: full spectrum (terrestrial) analogue: tortoise diet: omnivore/herbivore (scavenger, plants to inverts) association: with <i>Massospondylus</i> preservation: 1 good skull trackway: frequency/abundance uncertain
LEPIDOSAURIA SPHENODONTIA SPHENODONTIDAE <i>Clevoosaurus</i>	1	I	50 mm (skull)	-	habitat: probably burrowing, dry river banks etc. analogue: tuatara diet: wide spectrum invertebrates association: unknown preservation: 1 fair skull trackway: unknown
ARCHOSAURIA CROCODYLIA PROTOSUCHIA PROTOSUCHIDAE <i>Orthosuchus</i> <i>Notochampsia</i> <i>Baroquesuchus</i> SPHENOSUCHIDAE <i>Sphenosuchus</i> <i>Pedeticosaurus</i> <i>Clarencea</i>	1 2 2 1 1 1	↑ ↑ ↓ ↓	↑ ↑ ↓ ↓	BATRACHOPODIDAE <i>Batrachopus</i> spp.	habitat: primarily open woodland (interfluvium) analogue: gracile, fast (greyhound) diet: insectivore/carnivore (skull c100 mm) association: <i>Pachygenelus</i> (3x), <i>Massospondylus</i> (1x) preservation: v. well preserved articulated skull/skeleton trackway: most abundant small non-dinosaur
THECODONTIA ?AETOSAURIA ?Aetosaurid indet.	2	H	3 m	-	diet: ?root & tuber eater
SAURISCHIA THEROPODA PODOKESAURIDAE <i>Syntarsus</i>	4	C	1 m	GRALLATORIDAE <i>Grallator</i>	habitat: primarily open woodland analogue: small bipedal dinosaur diet: insectivore (juveniles), carnivore association: <i>Tritylodon</i> (2x), <i>Fabrosaurus</i> (2x), etc. preservation: partial skeletons trackway: most common
SAUROPODOMORPHA ANCHISAURIDAE <i>Massospondylus</i>	116	H	4 m	-	habitat: principally riparian forest analogue: small-med. facultative bipedal dinosaur diet: medium-level browser association: <i>Trityl.</i> (20x), <i>Pachygen.</i> (6x), crocs (6x), etc. preservation: good, fully articulated skull/skeleton trackway: unknown
ORNITHISCHIA ORNITHOPODA FABROSAURIDAE <i>Fabrosaurus</i>	7	H	1,5 m	ANOMOEPODIDAE <i>Anomoepus</i>	habitat: forest margin to open woodland analogue: small dinosaur diet: herbivore, low-level browser (to 1 m) association: <i>Massospondylus</i> (3x), <i>Syntarsus</i> (2x), etc. preservation: good, fully articulated skull/skeleton trackway: 2nd most common
HETERODONTOSAURIDAE <i>Heterodontosaurus</i> <i>Lycorhinus</i> <i>Abrictosaurus</i> <i>Lanasaurus</i> <i>Lesothosaurus</i>	5 1 2 1 1	↑ H ↓	↑ 1,5 m ↓	↑ ↓	habitat: forest margin to open woodland analogue: small dinosaur diet: herbivore, low-level browser (to 1 m) association: mostly, isolated occurrences preservation: good, fully articulated skull/skeleton trackway: unknown
SUBORDER indet. Ornithischian indet.	9	H	1,5 m	-	diet: low-level browser
SYNAPSIDA THERAPSIDA CYNODONTIA TRITHELEDONTIDAE <i>Tritheledon</i> <i>Pachygenelus</i>	1 17	I I	(skulls) 45 mm 35 mm	- -	habitat: forest to open woodland analogue: elephant shrew diet: insectivore (arboreal or in leaf litter) association: <i>Massospondylus</i> (5x), <i>Crocodylia</i> (2x), etc. preservation: fragmentary jaws & teeth trackway: unknown
TRITYLODONTIDAE <i>Tritylodon</i>	35	H	1,5 m	AMEGHINICHIDAE <i>Ameghinichnus</i>	habitat: primarily riparian forest analogue: giant rodent (to 1,5 m) diet: herbivore (?bark eater) association: <i>Massospondylus</i> (20x) & various others preservation: good, fully articulated skull/skeleton trackway: relatively abundant (?)
MAMMALIA PROTOTHERIA TRICONDONTA MORGANUCODONTIDAE <i>Megazostrodon</i> <i>Erythrotherium</i>	1 5	I I	100 mm	-	habitat: forest to open woodland analogue: nocturnal, arboreal tree shrew diet: insectivore association: <i>Massosp.</i> (1x), <i>Tritylodon</i> (1x), <i>Fabros.</i> (1x) preservation: fair to good, fully articulated skull/skeleton trackway: unknown

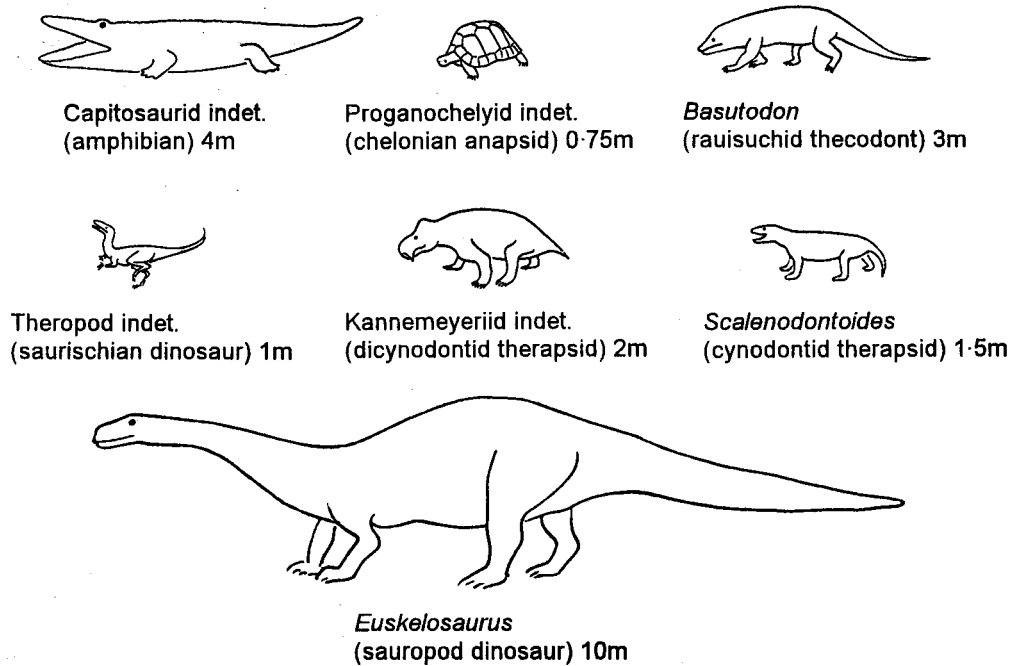
INSECTS



cockroaches : beetles : bugs : dragonflies 3 : 1 : 1 : 1

Proportional abundance (number of individuals),
based on reference taphocoenosis, e.g. Bir 111

TETRAPODS



TEXT-FIG. 4 Key to the insects and tetrapods of the Molteno/Lower Elliot Biome (as used on Text-figs 5–11).

The tetrapod genera of the Euskelosaurus Range Zone fauna (Lower Elliot Formation)

The seven body-fossil/trackway 'genera' recognized here (including the single dubious trackway taxon from the Molteno Formation) are each discussed in regard to their rôle in the fauna and their likely habitat preferences. Relevant details are summarized systematically in the right-hand column of Table 5 (see Text-fig. 4 for thumbnail sketches).

Capitosaurid indet. (amphibian). These crocodile-like aquatic animals are represented by cranial and postcranial fragments from nine sites. Trackways remain unknown. The fragmentary nature of the material indicates break-up in a high-energy flow system and, therefore, that these capitosaurids

were riverine and not lake dwellers. It is assumed that they were piscivores with a skull up to 1 m long and an overall body length of up to 4 m. They may possibly also have scavenged on the carcasses of *Euskelosaurus* whose remains have been found in association with them.

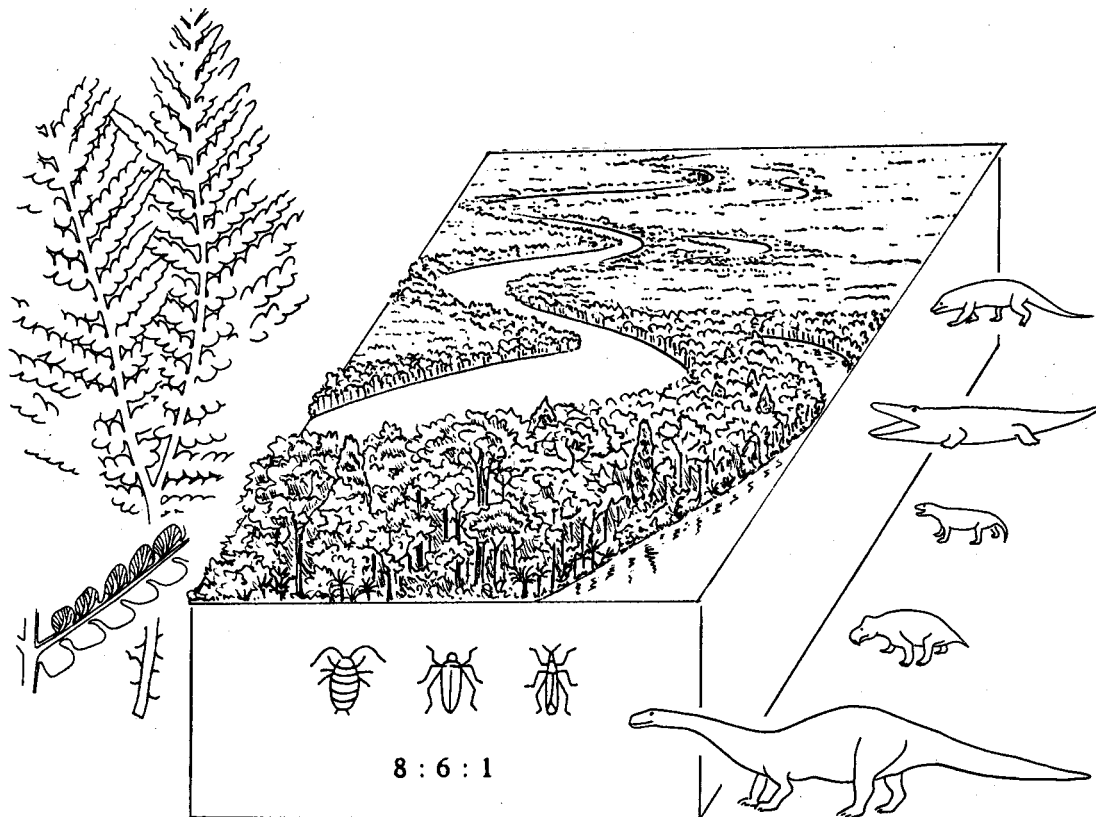
Proganochelyid indet (chelonian anapsid). This taxon (*Episcopus?*) is known from just one unclear trackway at the Maclear site (Molteno Formation) described by Raath *et al.* (1990) and its maker is assigned with some doubt to the Chelonia. A primitive chelonian, *Austrochelys* Gaffney and Kitching, 1994, is known from the Upper Elliot Formation, and the present form may have been an earlier relative. The Maclear animal would have been a medium to large tortoise-like herbivore/omnivore scavenging on plants and invertebrates that probably ranged the full spectrum of habitats from forest to open woodland, although with possible preferences as indicated on Text-figures 8 and 10–11.

Basutodontid (rauisuchid thecodont). Disarticulated cranial and postcranial fragments – not found associated with the remains of other taxa – have been collected from ten sites. At 3 m in length this is seen as the top carnivore of the Lower Elliot fauna. Although body fossils are far less common than those of the dinosaur *Euskelosaurus*, trackways, identified as *Brachycheirotherium* (Olsen and Galton 1984; Martin 1987), are the most frequently encountered form in the Lower Elliot. The prints have a five-toed pes with V reduced, and a forward-pointing five-toed manus. *Basutodon* approximates very closely the size range of the extant *Varanus komodoensis* (Komodo dragon) and may have had similar habits. It is the largest terrestrial predator known from the Lower Elliot Formation and would have been a formidable opponent, capable of dealing with anything in the fauna with the exception of an adult *Euskelosaurus*, unless aged or ill. If it hunted in a similar manner to the Komodo dragon, then it would have been an ‘olfactory’ animal and could have ranged over a wide spectrum of habitats, from riverine forest to open woodland.

Theropod indet (saurischian dinosaur). Records consist of trackways (*Grallator*) only, made by a bipedal dinosaur perhaps twice the size of the small coelurosaur *Syntarsus* (Raath 1969), i.e. c. 1 m tall. The prey of the juveniles could have been any of the larger insects, whilst the adults would have taken the young of *Euskelosaurus*, *Scalenodontoides*, or the dicynodont. It is also tempting to believe that, in addition to the known insects and juvenile tetrapods, this animal could have preyed on such unknowns as lizards, small cynodonts and early mammals. It is portrayed in the reconstructed plant/animal assemblages as an insectivore. These speedy, gracile little dinosaurs, whose footprints are the second most common in the fauna, are seen as hunting primarily in the open *Dicroidium* woodland.

Euskelosaurid (sauropod dinosaur). Found at 55 sites, *Euskelosaurus* is by far the most common of the body-fossil tetrapods of the Lower Elliot Formation. Preservation varies from fragmentary to fully articulated animals including skull and skeleton. The latter may represent animals entombed in the mud or quicksand of the braided rivers (the necessary site details to confirm this are lacking). The number of carcasses found at each site has not been recorded systematically. This was a medium-sized (10 m long), browsing quadruped dinosaur. If it were an obligate quadruped, depending only on neck mobility (Martin 1987), then it may not have been able to browse above the 5 m level; but if it were a facultative biped (being able to rear up on its hindlegs) then it may have been able to browse to as high as 7 m above ground level.

The trackways assigned to *Euskelosaurus* are placed in the ichnogenus *Tetrasauropus*. These, in spite of the abundance of the body fossils, are relatively uncommon. The prints have a *Brachycheirotherium*-like pes with small V and manus with a falciform medially directed claw on I. Bones of *Euskelosaurus* are sometimes found alongside those of the riverine capitosaurid amphibians (Kitching and Raath 1984), suggesting that they were primarily browsing along the riparian forest. They would possibly have spread out as well into the open *Dicroidium* woodland, the more closed *Sphenobaiera* woodland of the lake margin and the *Heidiphyllum* thicket.



TEXT-FIG. 5. Reconstruction of *Dicroidium* riparian forest (type 1, mature), bordering channels in the mature basement landscape (Habitat 1).

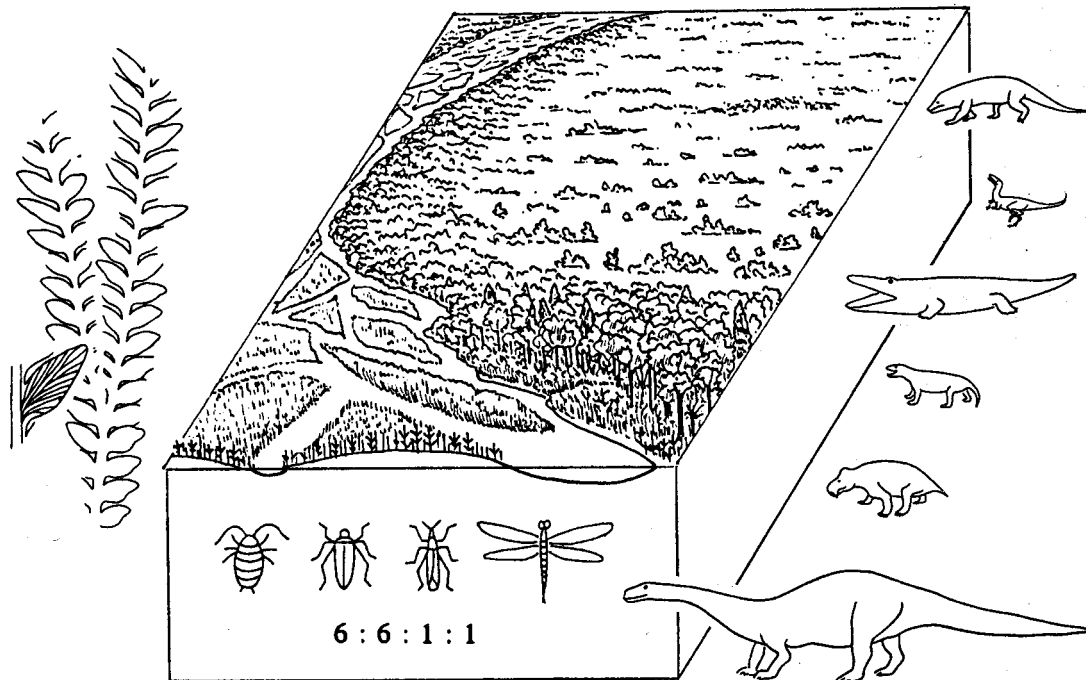
Reference taphocoenosis (TC): Upper Umkomaas (Umk 111 Dic 2 spp); Text-fig. 2c.

Fossiliferous bed. The deposit consists of a 2.3 m thick, dark grey, rhythmically bedded, carbonaceous shale, exposed in the bed of a small mountain stream. It crops out along strike for at least 10 m, but its full extent remains unclear. The bed is interpreted as the infill of an abandoned channel (e.g. oxbow lake) incised into the underlying Beaufort Group.

Floral associations (Pls 1–2; Tables 1, 3–4). The Umk 111 flora, with 73 vegetative species (44 gymnosperm, 29 non-gymnosperm) is by far the most diverse of the 100 Molteno TCs. It is strongly dominated by a range of species of the seed fern *Dicroidium* (69 per cent.), *Heidiphyllum* (7 per cent.), *Rissikia* (5 per cent.), *Sphenobaiera* (5 per cent.) and *Gontriglossa* (5 per cent.) follow next in abundance. Though remarkably diverse, with eight species of horsetail and 19 species of fern, the non-gymnosperms amount to less than 5 per cent. of the flora in abundance.

Insect fauna (Text-fig. 3; Tables 2–4). 166 individuals, 42 species, 11 insects/10 man-microscope-hours. With 42 species, the Umk 111 fauna is of medium to high diversity, although at order level it is markedly low in diversity. These features are matched closely in the only other fauna in the collection, Lit 111, representing the mature type of *Dicroidium* riparian forest. The fauna shows strong domination by the three orders, cockroaches (80 individuals), beetles (63 individuals) and bugs (12 individuals), in the proportion 8:6:1. The four additional orders encountered, dragonflies, stoneflies, crickets and alderflies, occur very sparsely. The beetles are by far the most diverse group with 28 species, whilst there are only six species of bug and four of cockroach.

Tetrapod fauna (Text-fig. 4; Table 5). Capitosaur amphibians most probably inhabited the river channels, whilst the forested levée supported *Euskelosaurus* (high-level browser), *Scalenodontoides* (low-level omnivore) and the kannemeyeriid dicynodont *Pentasauropus* (low-level browser/grazer). The last is seen as skulking in the cover of the denser bush, possibly more on the dry side of the gallery forest than close to the water. *Basutodon* was the predator in this habitat, its trackways (*Brachycheirotherium*) occurring alongside those of *Pentasauropus*.



TEXT-FIG. 6. Reconstruction of *Dicroidium* riparian forest (type 2, immature), bordering channels in immature landscapes (Habitat 2).

Reference taphocoenosis (TC): Kapokkraal (Kap 111 Dic/Ris); Text-fig. 2A.

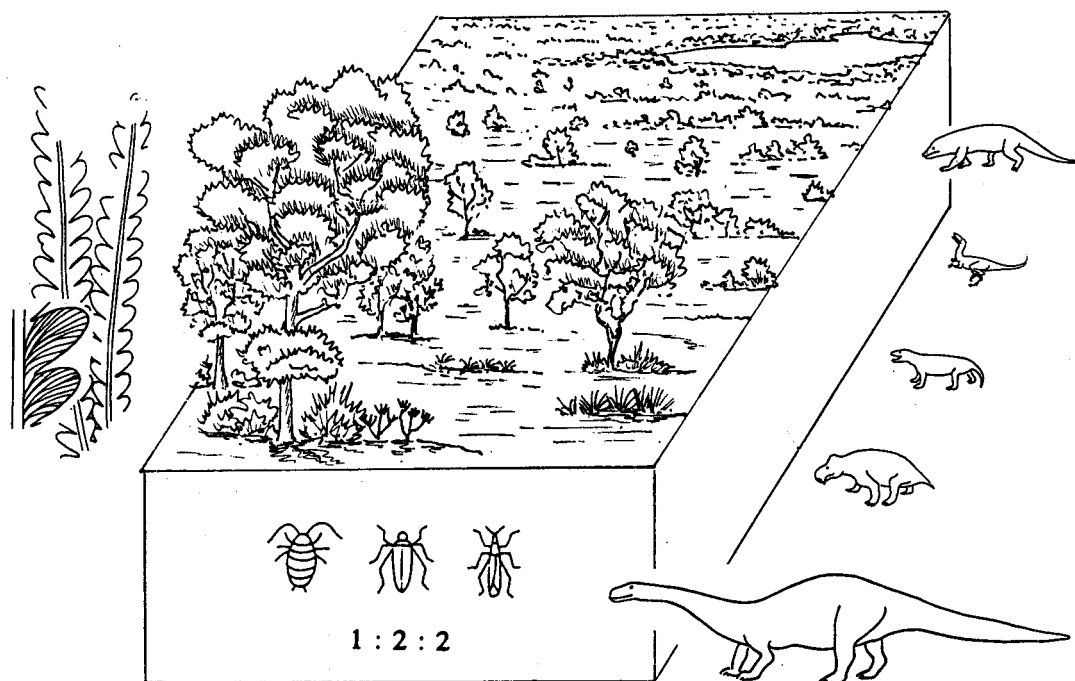
Fossiliferous bed. The bed, up to 1.3 m thick, is a black, highly fissile, metamorphosed shale cleaving at 1 mm intervals. It is exposed for 30 m along a stream bank and appears to lense out towards either end. It caps a thick channel-fill sequence of bedload sandstones. Considering the lithofacies, Kap 111 may be interpreted as having been deposited under very quiet conditions in an abandoned channel within the braided river.

Floral associations (Pls 1–2; Tables 1, 3–4). The phytotaphocoenosis, of medium diversity with 14 genera and 20 species (vegetative taxa), includes the seed fern *Dicroidium* (50 per cent.) and the conifer *Rissikia* (38 per cent.) as dominants and *Equisetum* (horsetail) (10 per cent.) as a common element. This combination of plants presumably represents both riparian forest and *Equisetum* stands of the river margin and adjacent sandbanks.

Insect fauna (Text-fig. 3; Tables 2–4). 178 individuals, 43 species, 18 insects/10 man-microscope-hours. The Kap 111 faunotaphocoenosis, a medium/high diversity cockroach/beetle fauna, includes 28 genera and 43 species. The presence of dragonflies (eight individuals), protodragonflies (three individuals), Paraplecoptera (four individuals) and stoneflies (one individual), provides ample supporting evidence of deposition in a river channel. The abundance ratio between the four dominant orders, cockroaches, beetles, bugs and dragonflies, (6:6:1:1), is intermediate between that seen in the mature riparian forest (e.g. Umk 111 and Lit 111) and the floodplain-lake (e.g. Bir 111 and Aas 411) faunas – reflecting well the environment portrayed for Kap 111. The beetles are, again, by far the most diverse group with 23 species, whilst there are six species of bug and three of cockroach.

Tetrapod fauna (Text-fig. 4; Table 5). The fauna of this more immature forest habitat would have been very much like that of the previous ecozone. It is possible that in the more open aspects of the forest, the fauna would have included the maker of the *Grallator* (theropod) trackways.

Kannemeyeriid indet (dicynodontid therapsid). Based on the preserved trackways *Pentasauropus*, this form is seen as a large ox-like animal c. 3 m in overall length and with a short stride. The moderately common trails show sub-equal manus and pes, with five toes on each foot. By the Late Triassic the majority of dicynodonts were tuskless (Keyser and Cruickshank 1979) and it has been proposed (Cruickshank 1978) that these forms occupied ‘close-cover’ niches or were nocturnal. The overall height of this Elliot Formation animal would have limited it to feeding at about 1 m above ground



TEXT-FIG. 7. Reconstruction of *Dicroidium* woodland of the open floodplain (Habitat 3).

Reference taphocoenosis (TC): Peninsula (Pen 321 Dic/Ris); Text-fig. 2A.

Fossiliferous bed. The bed (0.1–0.2 m) consists of a light blue-grey, moderately laminated, chertified shale and is exposed for over 100 m along a grassy hillslope. Intermittent exposures of the same stratum can be traced over at least 2.5 km, clearly suggesting deposition during flooding of the distal floodplain.

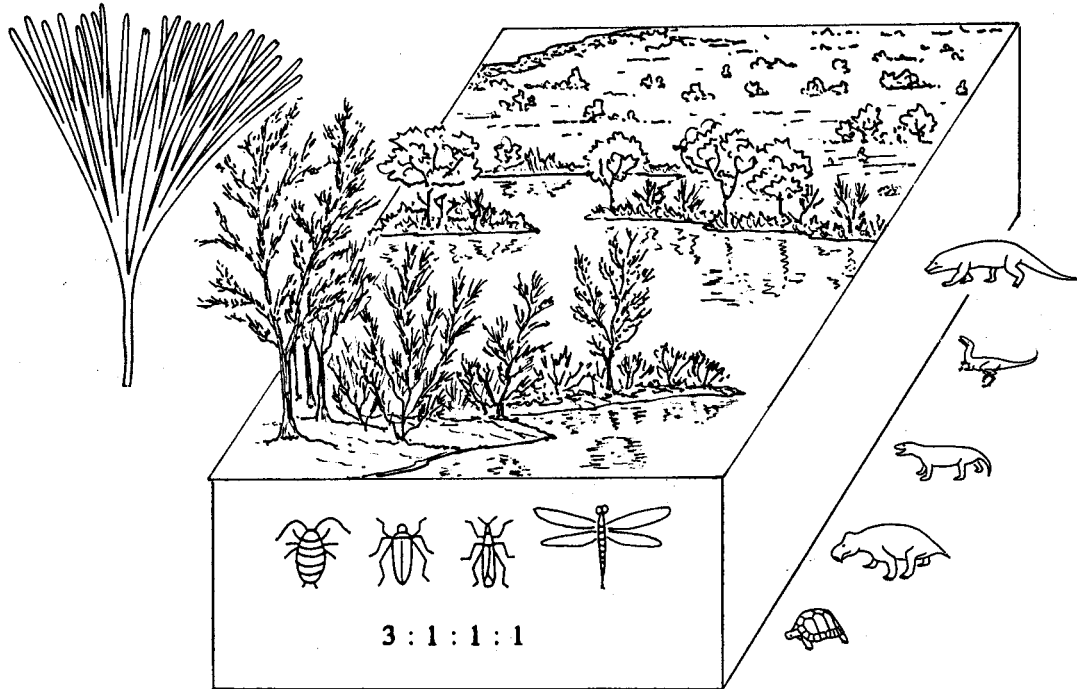
Floral associations (Pls 1–2; Tables 1, 3–4). The flora, with 13 genera and 18 species, is dominated by the seed fern *Dicroidium odontopteroides* (50 per cent.) and the conifer *Rissikia media* (35 per cent.) representing a medium-diversity *Dicroidium* woodland in the vicinity. The presence of *Schizoneura* (horsetail), *Equisetum* (horsetail) and *Heidiphyllum* (conifer) in unusually low proportions indicates derivation from communities further afield.

Insect fauna (Text-fig. 3; Tables 2–4). 25 individuals, 12 species, 9 insects/10 man-microscope-hours. The faunotaphocoenosis (medium-diversity beetle/bug fauna), including 11 genera and 12 species of insect, is typical for the *Dicroidium* woodland co-associations. It is dominated equally by bugs (seven individuals) and beetles (seven individuals), whilst the cockroaches (three individuals) are only half as commonly encountered. A few insect remains may have been washed in via flood waters, but the bulk of the fauna appears to constitute a true reflection of this habitat. The total absence of dragonflies and the other more primitive insect orders (e.g. stoneflies) corroborates a model of deposition from flood waters, with occasional ephemeral pools.

Tetrapod fauna (Text-fig. 4; Table 5). *Euskelosaurus* (high-level browser), *Scalenodontoides* (low-level omnivore) and the kannemeyeriid dicyodont (low-level browser/grazer) are seen as the herbivore community in these woodlands, with *Basutodon* as the principal predator. The *Grallator*-trackway maker could have found a niche here, especially if it operated in packs in the open. There is no firm evidence (mass trackways on bedding planes) for this, however.

level. It may alternatively have been a low-level 'grazer' (Cruickshank 1978). We visualize it as ranging through the shrubby growth of the drier, outer margins of the riparian forest, the closed *Sphenobaiera* woodland fringing floodplain lakes and the *Heidiphyllum* thicket. *Cheirobrachytherium* (*Basutodon*) and *Pentasauropus* trackways have been found in association (Olsen and Galton 1984), suggesting a likely predator-prey relationship.

Scalenodontoides (*cynodontid therapsid*). These cynodontids were, apparently, relatively scarce.



TEXT-FIG. 8. Reconstruction of *Sphenobaiera* woodland, in floodplain lake (Habitat 4).

Reference taphocoenosis (TC): Birds River (Bir 111 Sph 2 spp); Text-fig. 2A.

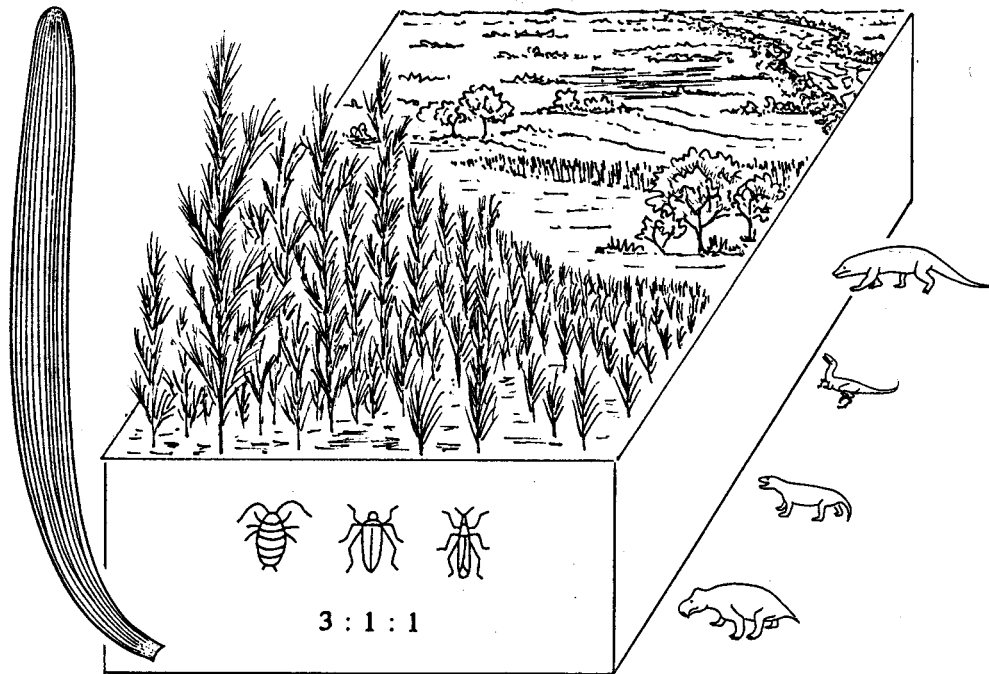
Fossiliferous bed. The buff-coloured, rhythmically bedded, richly fossiliferous shales, reaching c. 2.5 m thick, are exposed along the gently sloping bank of a farm dam. They crop out over a good 150 m of strike, but the full extent of the bed is hidden beneath a grass-covered soil overburden. Similar strata appear intermittently to some 500 m distance, in a stream bed and other exposures, suggesting a fairly extensive lake.

Floral associations (Pls 1–2; Tables 1, 3–4). The phytotaphocoenosis (with 21 genera and 33 species of vegetative taxa) is interpreted as deriving from three distinctive communities: (1) the first heavily dominated by two species of *Sphenobaiera*, *S. pontifolia* (50 per cent.) and *S. schenkii* complex (35 per cent.), which characterize a medium-diversity closed-woodland community bordering a lake in the floodplain; (2) *Heidiphyllum* (conifer), at 10 per cent. of the assemblage, represents a more or less monospecific community of rush-like conifers colonizing sandy areas of the lake shore; (3) certain other gymnospermous elements such as *Dicroidium* (seed fern), with no fruit present, and *Halleyoctenis* (bennettitalean), with only two detached gynoecia, may well represent the more open woodland some distance from the lake.

Insect fauna (Text-fig. 3; Tables 2–4). 474 individuals, 99 species, 30 insects/10 man-microscope-hours. This is clearly the best sampled and most diverse of the 43 Moltano insect faunas. In the wide spread of orders represented and the proportions (3:1:1:1) between the dominant orders, cockroaches, beetles, bugs and dragonflies, it is most like the fauna from Aas 411, the only other well-sampled Moltano insect fauna of the floodplain lake-margin. Particularly notable, also, is the relatively common occurrence of the more primitive insect orders, the mayflies (five individuals), protodragonflies (five individuals), dragonflies (47 individuals), protostoneflies (27 individuals) and stoneflies (seven individuals), that are associated with open water bodies.

Tetrapod fauna (Text-fig. 4; Table 5). This is not thought to be the preferred habitat for the large herbivore, *Euskelosaurus*, but would provide browsing for both the dicynodont and *Scalenodontoides*, the former possibly more so in the denser vegetation near the water's edge. *Basutodon* was once again the dominant predator, whilst the *Grallator* trackway maker hunted for insects amongst the vegetation. The chelonian could have been grazing on pond weeds, waterside vegetation or acting as an aquatic predator on insect larvae and small fish.

Their disarticulated remains (only one good skull is known) have been recovered from only six sites and trackways remain unknown. With a skull c. 300 mm long, and therefore a body length of up



TEXT-FIG. 9. Reconstruction of *Heidiphyllum* thicket in areas of high water table in the floodplain or on channel sandbars (Habitat 5).

Reference taphocoenosis (TC): Aasvoëlberg (Aas 311 Hei elo); Text-fig. 2A–B.

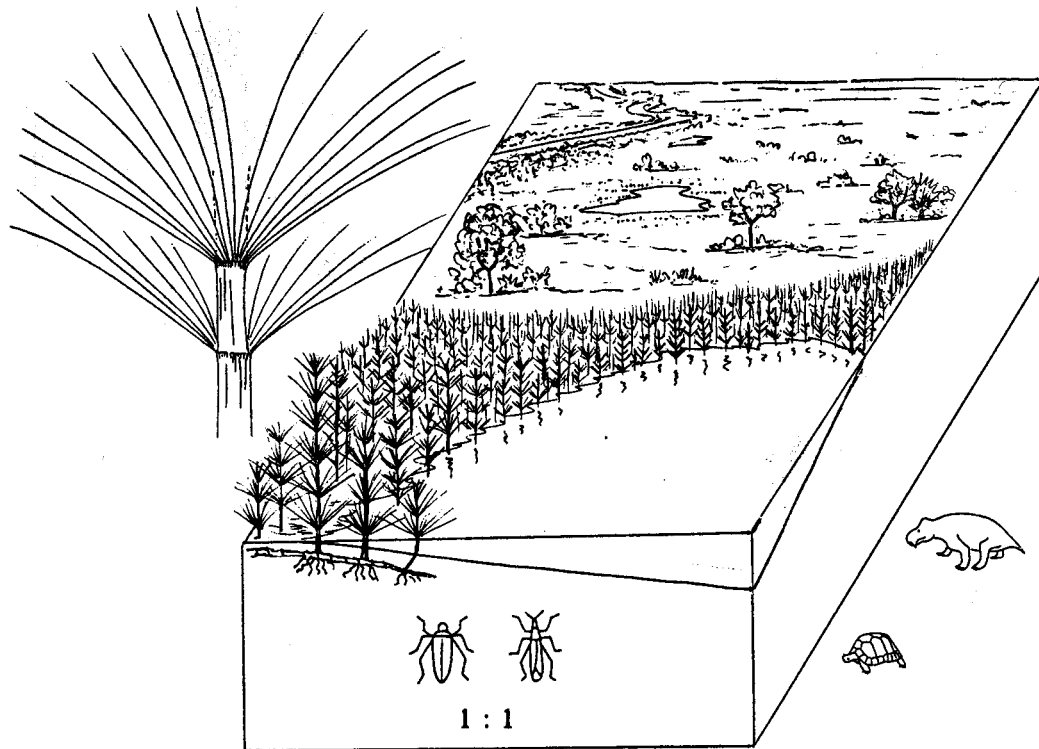
Fossiliferous bed. The bed, a 0.7 m thick, poorly laminated, light khaki/beige mudstone, is exposed uniformly for 75 m along strike. Two very similar horizons (Aas 111, Aas 211) appear at the same level at 2 km and 6 km distance. The unit grades, above and below, into palaeosols rich in roots and slender woody fragments (to 30 mm diameter), and lies above a 3–4 m thick sequence of monotonous, barren, floodplain mudstones. Aas 311 yields an autochthonous to parautochthonous assemblage associated with low-energy sheetflood deposition in the distal floodplain.

Floral associations (Pls 1–2; Tables 1, 3–4). The phytotaphocoenosis is heavily dominated by the conifer *Heidiphyllum elongatum* (99 per cent.), with the other vegetative taxa (eight genera and nine species) being very rare. A virtually monospecific coniferous thicket in close proximity is clearly indicated. The remaining elements of the assemblage probably represent *Dicroidium* (seed fern) and *Sphenobaiera* woodland communities growing some distance away.

Insect fauna (Text-fig. 3; Tables 2–4). 146 individuals, 31 species, 15 insects/10 man-microscope-hours. The faunotaphocoenosis (medium-diversity cockroach/beetle/bug fauna) includes 23 genera and 31 species. The insects, although typically fragmentary, are particularly clearly preserved. Aas 311 is the best sampled of the nine *Heidiphyllum* thicket co-associations thus far examined and includes a fauna typical for this type of assemblage. The cockroaches are clearly dominant, being three to four times as numerous as the beetles and bugs. The five further orders present are represented by rather few specimens. The TC is possibly a nearly clean sample of the fauna inhabiting the *Heidiphyllum* thicket, with little contamination from more distant habitats. The leaf litter of the coniferous thicket provides the ideal niche for the abundant cockroaches. The medium-to-high insect yield suggests a relatively low-energy flow regime, whilst the rare occurrence of dragonflies and Paraplecoptera points to the absence of permanent water.

Tetrapod fauna (Text-fig. 4; Table 5). These monospecific coniferous stands might have provided good grazing and browsing for the dicynodont and *Scalenodontoides*, whilst harbouring a varied insect diet for the *Grallator* trackway maker. *Basutodon* could have hunted in the drier areas of this habitat.

to 1.5 m, this therapsid is visualized as a small, bear-like omnivore. Its dentition, of 'gomphodont' pattern with a diastema (Gow and Hancox 1993), was apparently adapted to pulping vegetable matter. It would not have been able to crop vegetation much higher than 0.5 m above ground level



TEXT-FIG. 10. Reconstruction of *Equisetum* marsh in the floodplain (Habitat 6).

Reference taphocoenosis (TC): Greenvale (Gre 111 Equ sp.); Text-fig. 2A.

Fossiliferous bed. The bed, up to 1 m thick, consists of rhythmically laminated grey mudstones. It is exposed for 30 m along strike in a road cutting, and occurs within a rather monotonous mudstone sequence with occasional thin siltstones. A lake or marsh in the distal floodplain is indicated.

Floral associations (Pls 1–2; Tables 1, 3–4). The phytotaphocoenosis, with eight genera and ten species (vegetative taxa), is strongly dominated by *Equisetum* (horsetail) (97 per cent.), clearly indicating a horsetail marsh. Rare elements such as *Dicroidium* (seed fern) (2 per cent.) and fern (1 per cent.) presumably represent more distant communities. The absence of upright, rooted *Equisetum* stems indicates parautochthony rather than autochthony.

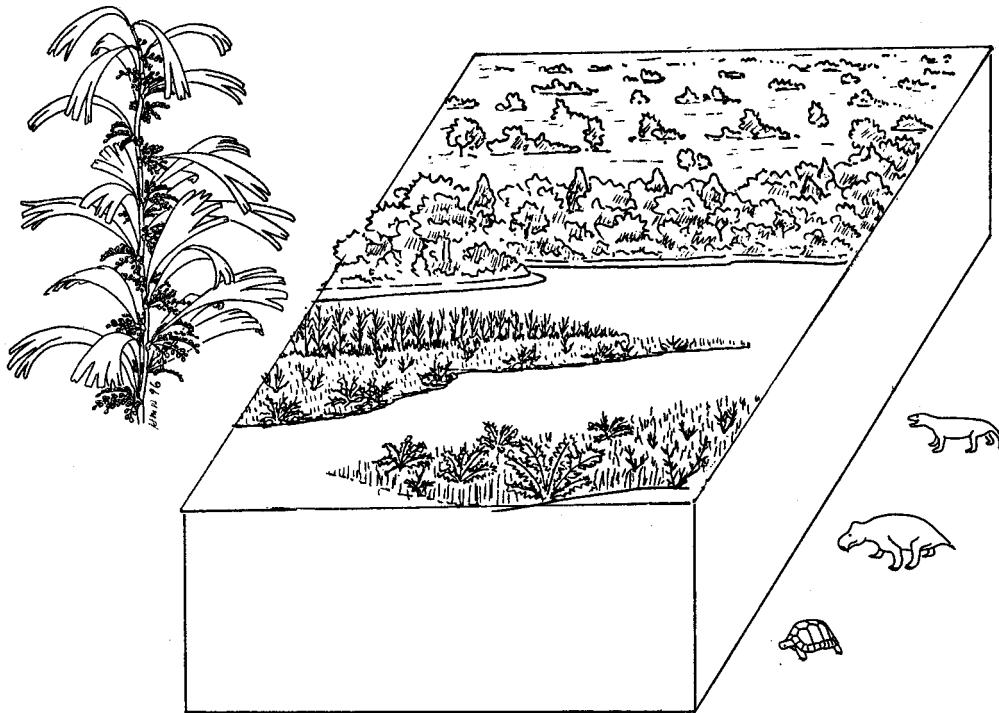
Insect fauna (Text-fig. 3; Tables 2–4). Five individuals, four species, 10 insects/10 man-microscope-hours. The faunotaphocoenosis, a low-diversity beetle/bug assemblage, remains sparse, with only five individuals including four genera and four species (two species of bug, one of beetle and one scorpionfly). Although the sample is small, it appears typical of horsetail marshes in the Molteno. Cockroaches are conspicuously absent, the standing water and absence of leaf litter being an unfavourable habitat for these usually abundant insects. The relatively common occurrence of Conchostraca (three species, 15 individuals), and the appearance of pelecypods (one genus, three species, three individuals), unique for the Molteno, are further indicators of marsh conditions.

Tetrapod fauna (Text-fig. 4; Table 5). The dicynodont might have been found here, but *Equisetum* would not have been attractive to the other herbivores, nor would there have been much to draw an insectivore. The chelonian might have ventured into this marshy setting.

and was thus restricted to the foliage and fructifications of smaller shrubs and undergrowth – probably in all the described habitats except *Equisetum* marsh.

PLANT-ANIMAL CO-ASSOCIATIONS IN THE MOLTENO/LOWER ELLIOT BIOME

The seven primary habitats (ecozones) of the Molteno Formation, characterized by distinctive plant/insect co-associations, were first outlined in Cairncross *et al.* (1995) together with lithofacies



TEXT-FIG. 11. Reconstruction of fern/*Ginkgophytopsis* meadow colonizing sandbars in the braided river (Habitat 7).

Reference taphocoenosis (TC): Kannaskop (Kan 111 Ast spA); Text-fig. 2A.

Fossiliferous bed. This bed, a 0.25 m thick, massive, conchoidally fracturing, khaki mudstone, is exposed for 2–3 m along a road cutting. It lies at the base of a series of stacked channel-fill sequences, all erosively based. Kan 111 was evidently deposited under turbid conditions in a restricted channel within a sand-dominated braided river.

Floral associations (Pls 1–2; Tables 1, 3–4). The low-diversity phytotaphocoenosis (five genera and seven species) is dominated by a single species of fern (63 per cent.) preserved *in situ* or nearly so. These are found as virtually whole plants, with fronds, rhachis and rhizomes preserved together. *Equisetum* (horsetail) (20 per cent.), *Heidiphyllum* (conifer) (10 per cent.) and *Ginkgophytopsis* (5 per cent.) are relatively common. The last is found with both leaves and fruit attached to fragments of herbaceous shoot. The association evidently colonized sandbanks of the braided river, the plants being preserved in place or close to their place of growth and being rapidly engulfed by sediment. *Heidiphyllum* thickets appear, likewise, to have flourished on the sandbanks.

Insect fauna (Text-fig. 3; Tables 2–4). The Kan 111 TC is unique among the 7 habitat assemblages discussed here in that it has yielded no fauna, insect or Conchostraca. Four hours of scanning plant-bearing slabs under the microscope yielded no specimens of either category. This might be anticipated considering the high flow velocity indicated by both the sediment and the plant assemblage. Insect faunas representing this habitat remain unknown.

Tetrapod fauna (Text-fig. 4; Table 5). Whereas the vegetated sandbars of the braided-river system could have supported periodic forays by the smaller tetrapod herbivores (*Scalenodontoides*), it is unlikely that the insectivore (theropod) or the larger carnivore (*Basutodon*) would be found in this habitat. The proganochelyd might well have found it rewarding foraging territory, as might the lumbering kannemeyeriid in the safety of the night hours.

descriptions of vertical profiles including the reference and other significant TCs. In the present study we provide the basic insect data on which the ecozonal patterns are based (Tables 3–4) and integrate the associated coeval Lower Elliot Formation tetrapods for the first time.

Here we aim to synthesize the three components of the study: the flora, insects and tetrapods. The seven habitats are portrayed in a series of annotated reconstructions (Text-figs 5–11) along with succinct, comparative text on the associated flora and fauna. Each is based, in particular, on a selected reference taphocoenosis (TC): e.g. Upper Umkomaas (Umk 111 Dic 2spp) for the mature type of *Dicroidium* riparian forest (Text-fig. 5). The incorporation of the tetrapods is based on our assessment of their likely habitat preferences as previously discussed. Thumbnail sketches (key on Text-fig. 4) of the insects, with proportions of the dominant orders, and of the tetrapods are appended, as is a line drawing of each dominant plant genus.

A COMPARISON OF THREE CARNIAN BASINS

The three most productive Carnian-age 'basins', known to us globally, that yield both good plants and insect faunas are the Karoo Basin, South Africa (Molteno Formation); the Ipswich Basin, Queensland (Ipswich Group), and the Newark Supergroup, eastern USA (Solite Quarry, Cow Branch Formation) (Fraser *et al.* 1996; N. C. Fraser, pers. comm.). It is interesting in the context of this paper to compare the insect faunas (Table 7) of these three areas as it throws light on the widely differing biota and ecology of the tropical and temperate latitudes of the Late Triassic. The comprehensiveness and currency of the data available are highly variable yet sufficient to highlight the magnitude of the faunal differences. Whilst it is beyond the scope of this study to attempt a synthesis of the three floras, it is clear that those of the Molteno Formation and Ipswich Group are alike and belong to the Gondwana Kingdom, whereas that of the Newark Supergroup is quite different, belonging to the Laurasian Kingdom. In particular, the two southern floras are strongly characterized by the seed fern *Dicroidium*, whilst the northern flora is dominated by conifers (*Pagiophyllum*, *Brachyphyllum*) and cycadeoids.

In Table 7 we plot the diversity and abundance of insects per order for the 21 orders identified in the Molteno Formation (*c.* 60° S palaeolatitude), Ipswich Group (*c.* 50° S) and Newark Supergroup (*c.* 10° N). To attain a closer balance for the two temperate Gondwana occurrences, we include only the single richest fauna (Birds River, Bir 111, a lake deposit) from the Molteno Formation, but the full published fauna (Mt Crosby and Denmark Hill localities) from the Ipswich Group. There are differences between the two southern faunas, especially the strong presence of Neuroptera, Mecoptera and Trichoptera in Australia, but the similarities are more striking. The beetles, cockroaches and bugs are particularly prominent in each and the general spread of orders is similar. The Newark Supergroup fauna is very different (Fraser *et al.* 1996; N. C. Fraser pers. comm.). Most notably, the beetles and cockroaches are rare in the Newark Supergroup, whilst the flies, absent in Gondwana, are prominent and diverse, with five families already recognized.

The three deposits discussed are all variations on the fluvio-lacustrine theme: the Molteno Formation having been laid down in an intracontinental basin, the Ipswich Group in a small intramontane depression and the Newark Supergroup in a series of grabens. The faunal differences in some degree reflect these environments, but the overriding factor was presumably palaeolatitude: *c.* 50–60° S for the two Gondwana occurrences and *c.* 10° N for the Laurasian occurrence.

CONCLUSIONS

The Molteno Formation appears uniquely rich, at least for the Triassic world, possibly the pre-Cretaceous world, in the quantity and diversity of its fossil flora. This flora is relatively well documented now and is based on the extensive collections made from 100 taphocoenoses over the past 30 years. The diversity is expressed not only in the observed taxa, but in statistical projections hinting at Late Triassic floras being as rich as those in the extant world.

Only recently, though, in systematically scanning plant-bearing slabs under the microscope, have we become aware of the real richness of the associated insect fauna. Like the flora, the fauna hints at diversity akin to that of today. The insect fauna combined with the flora greatly enhances our understanding of the ecology of the Molteno Biome and its varied habitats. In that most of the 18

TABLE 7. A comparison between two temperate and one tropical insect fauna of the Upper Triassic (Carnian), from fluvio-lacustrine basins.

Insect order	Common name	Basin					
		Molteno (60°S)		Ipswich (50°S)		Newark (10°N)	
		spp	nos	spp	nos	fam.	nos
Thysanoptera	thrips	-	-	-	-	1	✓
Microcoryphia	bristletails	1	7	-	-	-	-
Ephemeroptera	mayflies	1	5	-	-	-	-
Meganisoptera	protodragonflies	3	5	-	-	-	-
Odonata	dragonflies	12	47	6	8	-	-
Paraplecoptera	extinct	5	27	-	-	-	-
Plecoptera	stoneflies	2	7	2	3	-	-
Blattodea	cockroaches	5	185	18	24	1	?
Mantodea	mantids	2	3	1	9	-	-
Orthoptera	grasshoppers	5	13	9	43	1	?
Homoptera	bugs	24	68	66	168	4	✓✓
Phasmatodea	stick insects	-	-	1	1	-	-
Megaloptera	alderflies	1	1	-	-	-	-
Glosselytrodea	extinct	1	2	1	2	-	-
Neuroptera	lacewings	2	2	12	31	-	-
Mecoptera	scorpionflies	4	6	13	64	-	-
Trichoptera	caddisflies	-	-	3	41	1	?
Lepidoptera	butterflies	2	6	1	8	-	-
Hymenoptera	wasps, bees	1	1	1	2	-	-
Coleoptera	beetles	28	56	58	70	2	?
Diptera	flies	-	-	-	-	5	✓✓
Incertae sedis		-	33	-	-	-	-
Totals		99	474	192	474	15	?

Faunas

Molteno (S. Africa) – based only on Birds River (Bir 111).
 Ipswich (Australia) – based on Mt. Crosby and Denmark Hill.
 Newark (USA) – based on the Cow Branch fauna.
 The Homoptera include the Heteroptera.

References to faunas

Molteno – this paper.
 Ipswich – unpublished data
 Newark – Fraser *et al.* (1996), Fraser pers. comm.

Abundance

185 – individuals
 ✓ – rare
 ✓✓ – uncommon
 ✓✓✓ – abundant
 ? – not given in reference

Palaeolatitudes

Follow the Late Triassic reconstruction of Pangaea used in Lucas 1994a.

orders of insect represented in the Molteno Formation are extant today, they lend much insight into the palaeoenvironment. Clear patterns of plant/insect co-associations emerge for seven primary habitats (ecozones) identified in the formation.

Adding yet another dimension to the Molteno Formation is the existence of a coeval tetrapod fauna in the Lower Elliot Formation. Although relatively well sampled, the Elliot Formation material remains poorly described taxonomically and not at all faunistically. We have, with some necessary simplification, attempted to reduce the published data to a meaningful fauna and to integrate this into the known Molteno biota. As sister strata, the Molteno/Elliot formation pair, yielding plants, insects and tetrapods, offers an unparalleled window onto the Late Triassic temperate world. We paint here the first strokes of the synergistic picture played out in the Karoo Basin between these three major terrestrial groups. The potential for filling out the picture, both in the Karoo and elsewhere (e.g. the Ipswich Group, Australia and Newark Supergroup, USA), is manifold.

A global inventory of Late Triassic biomes, with their habitats, flora and fauna, coupled with finely resolved global correlations will enable more explicit understanding of the evolutionary biology of this critical period. What was the real magnitude of diversity and how comprehensive was the postulated extinction event(s) pre-empting the Jurassic? Did the very scale of alternating richness and decimation invest the interval with unique potential for biological invention?

The moment in Earth history was pregnant with significance. In those exceptionally diverse ecosystems of the Late Triassic emerged many major new lineages, not least the dinosaurs, mammals and possibly the flowering plants.

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