Palaeont. afr., **33**, 11-21 (1997)

TOWARDS NEW PARADIGMS IN PERMO-TRIASSIC KAROO PALAEOBOTANY (AND ASSOCIATED FAUNAS) THROUGH THE PAST 50 YEARS

by

Heidi Marguerite Anderson and John Malcolm Anderson

National Botanical Institute, Private Bag X101, 0001 PRETORIA

ABSTRACT

Advances through the past 50 years (1945 to 1995) have shown, indisputably, that the Permo-Triassic Karoo flora (with associated insect faunas) is as important globally as is the famous tetrapod fauna. We justify this in regard to the three most productive horizons: the Middle Ecca (Early to Middle Permian), Estcourt Formation (Late Permian) and the Molteno Formation (Late Triassic).

The Middle Ecca gained international prominence through the collections of Le Roux from 1946 to 1955 and the publications of Plumstead from 1952 to 1962, which demonstrated for the first time a wide suite of fructifications found attached to *Glossopteris* leaves. Similar finds have subsequently been made throughout the rest of the Gondwana Permian. The Glossopteridales remain unique among fossil gymnosperm orders in yielding such a diverse range of articulated (organically attached) foliage/fruit material.

The Estcourt Formation offers an unparalleled opportunity to study ecosystems of the Late Permian prior to the extinction event terminating the period. The formation is singular in that it yields an excellent, well known flora and insect fauna (sampled primarily by van Dijk from 1957 to 1984 and Benecke, Anderson and Anderson from 1969 to 1971) in conjunction with a diverse tetrapod fauna.

The Molteno Formation provides a window onto Late Triassic plant and insect communities, at around the time of origin of the mammals, dinosaurs and birds, perhaps unrivalled elsewhere in the world. The extensive/intensive collections of the Molteno (made by Anderson and Anderson over nearly 30 years from 1967 to the present) allow the application of a statistical projection hinting at the extraordinary possibility of biodiversities akin to those of today. The gymnosperms of the Late Triassic may well have been as rich in species and orders as are the extant angiosperms (flowering plants).

KEYWORDS: Karoo, Permo-Triassic, megaflora, insects, tetrapods, biodiversity.

INTRODUCTION

Three distinct phases in the 150-year history of fossil-plant collecting and research in South Africa can be discerned. Each lasted close on 50 years. The skeletal history here sketched is drawn from Anderson & Anderson (1985), as is most of the floral and faunal data outlined for the Middle Ecca and Estcourt Formations. The purpose of that earlier work, besides outlining the history of palaeobotanical collecting in South Africa, was to provide a full taxonomic revision and documentation of all pre mid-Cretaceous fossil floras in the country. Most traceable localities, aside from those of the Molteno, were revisited by us and many were further sampled. All available collections around the country were studied and incorporated. Our work on the Molteno has advanced considerably since, but relatively little has been added on the Ecca and Estcourt floras.

Reconnaissance phase (1845-1895)

This first period of activity may be traced to Charles Lyell's *Principles of Geology* (1830-33), generally regarded as the most influential text in the history of geology. With the denunciation of catastrophism and the popularisation of Hutton's uniformitarianism, it opened the way for a great flowering of geology and palaeontology not only in Britain but throughout the colonies and elsewhere. Andrew Geddes Bain, who was building frontier roads in the south-eastern Cape, chanced to read a copy of the book in 1837 and became (at age 40) the father of South African geology and palaeontology.

It is Richard Nathaniel Rubidge (ancestor of Bruce Rubidge, current director of the Bernard Price Institute), though, who takes credit for making the earliest collection (in 1845) of fossil plants in the country. These came from the Early Cretaceous Dunbrody locality in the Algoa Basin near Port Elizabeth. Further collectors of this period, including William Atherstone, George Stow, Alfred 'Gogga' Brown and Thomas Leslie, amongst others, were nearly all British, often they were medical doctors, all were self-taught amateurs in natural history. They were Renaissance men with remarkably diverse interests who flourished in and fostered the intellectual climate of the frontier towns. Collections remained small, and the part that was described was sent overseas for the purpose.

Transitional phase (1895-1945)

The Geological Commission of the Cape of Good Hope was instituted in 1895 to 'organise, control and direct the work of geological exploration and survey...'; and it ushered in a new era of palaeontology with a new character. The period is marked by the efforts of six men in particular: William Anderson, A.W. Rogers, E.H.L. Schwarz, A.L. Du Toit, S.H. Haughton and E.D. Mountain. All six were British or British trained and in marked contrast to the amateur enthusiasts of the earlier period, all were fully-trained professional geologists, though none were specialist palaeobotanists. They were the pioneers of systematic geological mapping in the country and their palaeobotanical collecting was mostly incidental.

Palaeobotanical research in the first half of the century was very largely taxonomic and still based on relatively small collections from few localities. Aside from Alexander Du Toit, who delved systematically into the fossil plants of the Karoo, most of this descriptive work was completed by overseas specialist palaeobotanists such as Sir Albert Charles Seward and Hugh Hamshaw Thomas, both of Cambridge, and Ove Arbo Hóeg of Oslo, Norway.

Post-war phase (1945-1995)

This third phase of palaeobotanical research coincides precisely with the fifty-year history of the Bernard Price Institute (BPI) and, in large measure, is directly linked to the Institute. Dr Edna Plumstead, of international renown, was the key figure and inspiration during the first half of this phase, whilst her post-graduate students, most enduringly Heidi and John Anderson, and a subsequent generation at BPI, Dick Rayner and Marion Bamford, took over in the later quarter century. The roles of researchers from other institutes, such as van Dijk (University of Natal, Pietermaritzburg) and Kovács-Endrödy (Geological Survey, Pretoria); from overseas, notably Kräusel (Senckenberg Museum, Germany), Townrow (Reading University, England and later Tasmania); and of independents, most importantly Le Roux of Vereeniging, are however significant.

A marked growth and widening of palaeobotanical activity is witnessed. Intensive collecting from many clearly-defined localities or taphocoenoses (TCs) plays an increasingly significant role. Whilst taxonomic studies still, by necessity, form the foundation of research, far more interest is given to palaeoecology, palaeogeography, palaeobiology, evolutionary theory and biodiversity trends. Interdisciplinary research and co-operative projects with an international flavour become more and more the pattern.

Though the emphasis in this paper is palaeobotanical, we summarise current knowledge on the major faunal groups, the insects and tetrapods, for the three formations discussed. This is in line with the rapidly increasing interest in evolutionary palaeoecology both in Karoo studies and globally. Evolution is a process based on the synergy between all plants and animals and their ever-changing physical environment. Our previously independent disciplines can no longer stand alone.

THE MIDDLE ECCA (E. – M. PERMIAN)

Significance

The Glossopteridales, by far the most prominent group of plants through the Gondwana Permian, invariably play a significant role in the cladistic analysis of the gymnosperms and the origin of the angiosperms (Crane 1985, 1988). They remain unique among fossil gymnosperm orders in yielding a morphologically diverse range of fruit borne directly on foliage. It was in the Middle Ecca beds of the northern Karoo Basin that this major discovery was first made and publicised: through the collections of Le Roux (1946-1955) and the papers of Plumstead (1952-1962). A wide suite of taxa within the order, showing similarly attached material, has since been unearthed through all the Gondwana continents.

Stratigraphy

With the melting of the Dwyka ice and for the duration of deposition of the Ecca Group, there developed an extensive, essentially non-marine epicontinental sea across the greater part of South Africa. Deltas and coal swamps characterised the northern margin of the sea, in the former northern Orange Free State (OFS), southern Transvaal and northern Natal, during the regressive Middle Ecca phase of deposition. The Middle Ecca (Vryheid Formation) attains its fullest development of 425m in the Vryheid area where it comprises a clear regressive cycle: delta front to delta with coal swamps to delta front. This arenaceous formation wedges out southwards into the typical carbonaceous siltstones of the Lower and Upper Ecca.

History of collecting

The earliest plant collections from the Middle Ecca – some 200 slabs in total – were made by George William Stow in 1878, David Draper from c.1890 to 1895 and Thomas Nicolas Leslie from c.1892 to 1904. It was Stow who first discovered the coalfields (Vereeniging included) in the northern Orange Free State and adjoining Transvaal and correctly interpreted their regional setting. A long interval followed before Le Roux initiated his extensive collecting from various sites in the Vereeniging district in 1941.

The Vereeniging Brick & Tile Company carried out large-scale quarrying of refractory shales (2 quarries) on the farm Leeukuil, 4 km south west of Vereeniging, between 1946 and 1952. Le Roux frequently visited these two quarries, and a third earlier one in the near vicinity, during this interval and made comprehensive systematic collections (Le Roux & Anderson 1977). He made the seminal discovery at these quarries in 1949/50 of the now famous fructifications found attached to the midrib of *Glossopteris* leaves. The recognition of their significance persuaded Plumstead to shift her research interests from coal petrology to palaeobotany.

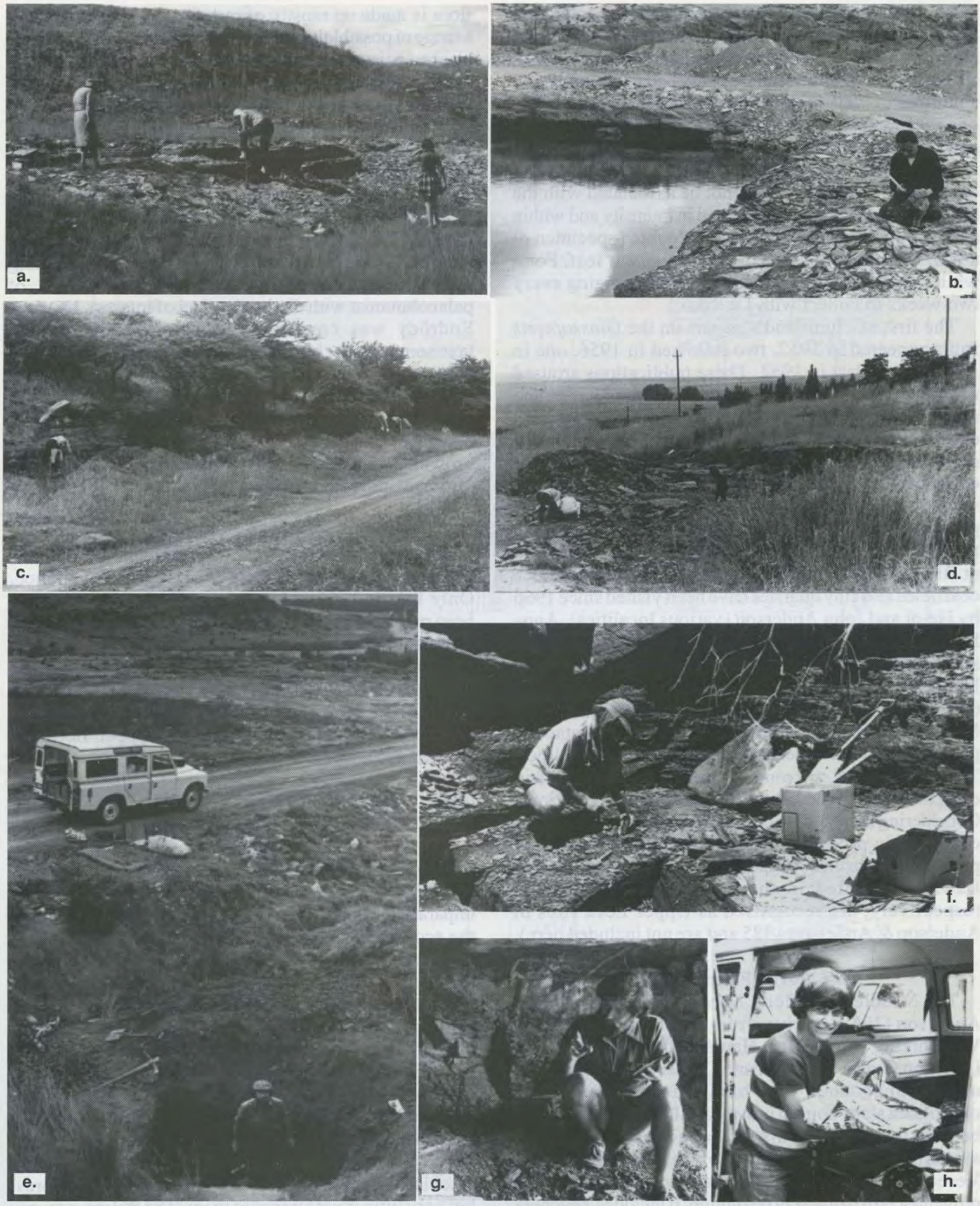


Figure 1 a-h. Collecting Karoo plants. **a.** Middle Ecca, E/M. Permian; Vereeniging (Ver 111), at Leeukuil Quarry. Left to right: Edna Plumstead, Anna Benecke, Shirley Dickinson. Photo by HMA, 30/4/1969. **b.** Middle Ecca, E/M. Permian; Hammanskraal (Ham 111), N. of Pretoria. Eva Kovács-Endrödy cleaving slabs. Photo by HMA, July 1973. **c.** Estcourt Formation, L. Permian; Rondedraai, near Estcourt (Est 211). Left to right: Ann Anderson, Anna Benecke, John Anderson, Mr Green. Photo by HMA, 15/12/1969. **d.** Estcourt Formation, L. Permian; Bergville (Ber 111). Left to right: Judy Roets, Brian Maguire, Brian Turner. Photo by HMA, 19/4/1969. **e.** Molteno Formation, L. Triassic; Matatiele (Mat 111). John Anderson excavating. Photo by HMA, 31/7/1982. **f.** Molteno Formation, L. Triassic, "Waterfall locality", Upper Umkomaas (Umk 111). John Anderson cleaving slabs. Photo by HMA, 24/1/1979. **g.** Molteno Formation, L. Triassic; Little Switzerland (Lit 111). John Anderson examining specimens. Photo by HMA, 13/10/1980. **h.** Kombi and 6 metal trunks; our standard procedure for transporting plant fossils. Heidi Anderson unpacking. Photo by JMA, 30/1/1979.

Plumstead first met Le Roux and saw the collection at his Vereeniging home in c.1949. The meeting had been arranged by Mr Leach, a mining engineering student at Witwatersrand University. Le Roux had in his collection a number of well-preserved detached fruits, as well as one specimen of the foliage *Glossopteris retifera* which appeared to have a narrow fruit-like body attached to its midrib. It was mooted whether *Glossopteris*, being dominant in the beds, might not be associated with the fruits. Le Roux's collecting gained in intensity and within a month he discovered the first undoubted specimen of a fruit *(Scutum)* attached to a *Glossopteris* leaf. For a while after that, Plumstead visited Vereeniging every two weeks to collect with Le Roux.

The first of Plumstead's papers on the *Glossopteris* fruits appeared in 1952, two followed in 1956, one in 1958 and the last in 1962. These publications aroused much controversy over morphological interpretation and suggestions on the origin of angiosperms, and established Plumstead's international reputation. It seems a pity that Le Roux did not publish jointly on some of the material, thereby sharing in the world acclaim.

Le Roux, together with Plumstead and her post-graduate students, continued collecting from Vereeniging till 1974: by which date some 2500 slabs, mostly housed at BPI, were available for study. Other Middle Ecca coalfields and clay quarries have been visited since 1966 by Heidi and John Anderson (various localities), Anna Benecke (Vereeniging), Shirley Smithies (Hammanskraal), Eva Kovács-Endrödy (Hammanskraal and other localities), Colin MacRae (Ermelo) and Dick Rayner (various sites). These have yielded a further 2000 slabs. Many additional specimens of attached and detached glossopterid fruits were unearthed at these new localities. The Middle Ecca still remains clearly undersampled in comparison with the Estcourt and Molteno formations. Considering the extent of coal mining and other quarrying currently in progress, there exists almost unlimited potential for further systematic collecting. (Cedara and Lawley, sampled in the early 1970s and 1980s respectively, are recognised as Upper Ecca sites in Anderson & Anderson 1985 and are not included here).

The flora (Figures 2-7)

The Middle Ecca flora, as revised in Anderson & Anderson (1985), derives from five broad localities – Vereeniging (Figure 1a), Hammanskraal (Figure 1b), Libernon Gold Mine, Hlobane Colliery, and Ermelo, in order of importance – and has yielded a total of 4,500 catalogued slabs housed mostly at BPI. The flora cannot be discussed in terms of taphocoenoses (TCs, assemblages) as the bulk of the material from Vereeniging and Hammanskraal was not originally provenanced to sufficient resolution. It includes 23 genera with 42 species, about twice as rich as the later Permian Estcourt Formation, but far less so than the Triassic Molteno Formation. The glossopterids (Figures 2-6) heavily dominate the flora in abundance and diversity, though lycopods (Figure 7) and conifers are also common. Horsetails are rare and lacking in diversity. The remaining flora is made up mostly of rare ferns (in 3 genera) and a range of possible ginkgophytes (4 genera). Two primary plant associations can be defined: glossopterid-dominated, medium-diversity forest and woodland along river banks (levees) and other elevated ground; and dense monospecific lycopod stands fringing interdistributary pans and swamps – the niche later filled by the sphenophytes.

Further papers since our 1985 review include Rayner (1985, 1986, 1988) on lycopods and Kovács-Endrödy (1987, 1990, 1991) on glossopterid foliage. In a very tangible sense these two reseachers, though publishing concurrently, represent successive generations of palaeobotanist with distinctive foci of interest. Kovács-Endrödy was concerned almost exclusively with taxonomy and the historical intricacies of nomenclature, whilst Rayner's attention was drawn to the overall plant and its palaeobiology. Through a study of leaf characteristics most sensitive to climate, Rayner (1995) concluded that extremely favourable conditions for plant growth, comparable to tropical regions today, prevailed during Middle Ecca times.

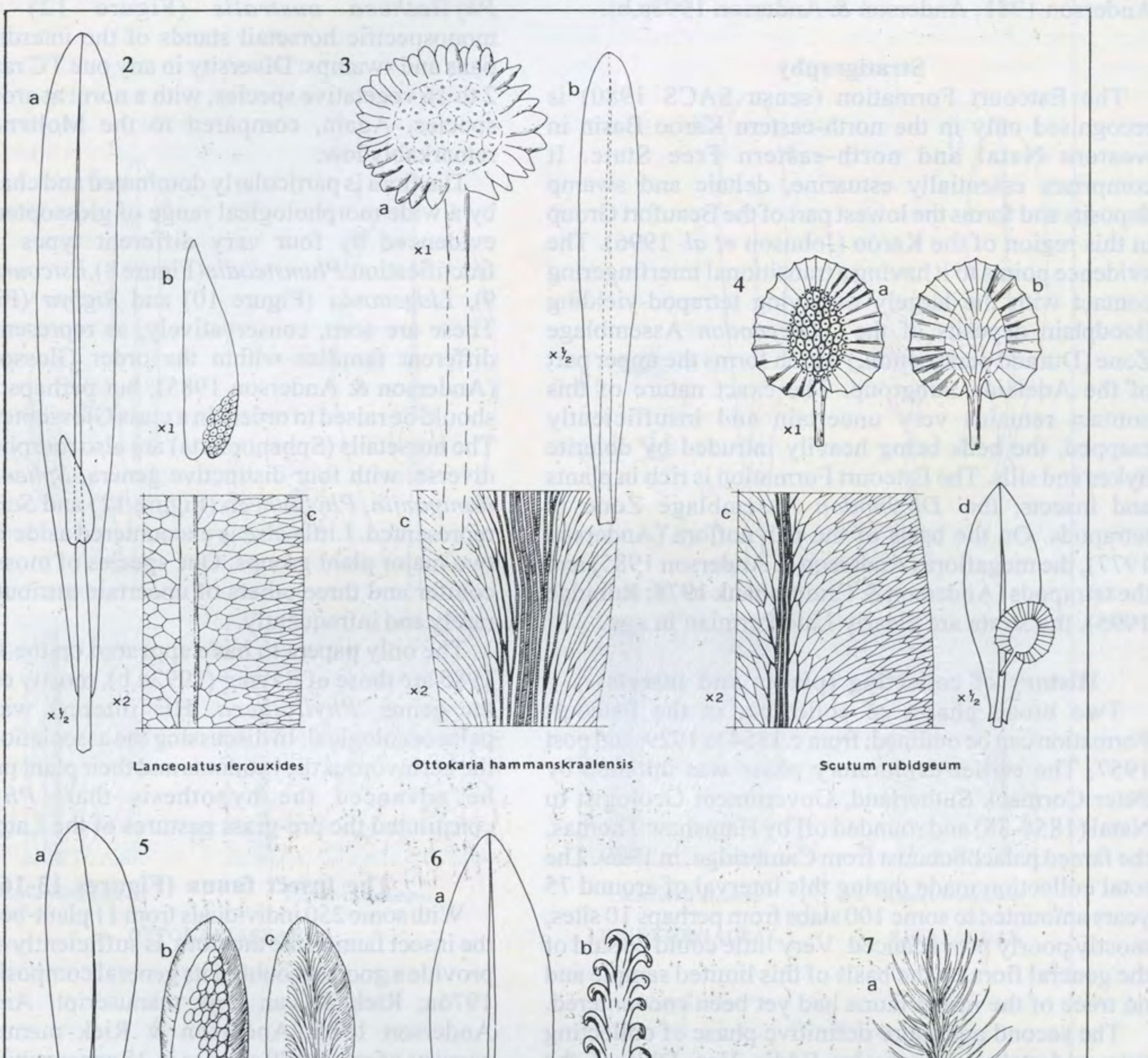
The insect fauna

Unlike in the later Estcourt and Molteno formations, the insect fauna of the Middle Ecca is extremely limited. Only four individual specimens (Riek 1976c,d) have been recovered from the Hammanskraal locality (Figure 1b) – by Kovács-Endrödy in the years 1973-75. It is difficult to explain why the other Middle Ecca localities are apparently barren of insect remains and yet show evidence of insect activity on the leaves (Plumstead 1963). (The Lawley locality of the Upper Ecca has yielded a few specimens.)

THE ESTCOURT FORMATION (L. PERMIAN)

Significance

The combined Estcourt Formation/*Dicynodon* Assemblage Zone of the Natal midlands provides an unparalleled opportunity, at least for Gondwana, to study the ecosystems of the Late Permian prior to the global extinction terminating the Palaeozoic. This uniqueness stems from the co-occurrence of abundant plants, insects and tetrapods. Whilst Late Permian floras are well-developed in all the Gondwana continents, they are largely inadequately documented in regard to frequency and abundance of taxa, the composition of taphocoenoses (TCs), the delineation of associations and palaeoecology. Taxonomic revision and palaeoecological analysis on a supracontinental basis would prove invaluable. Good insect faunas are probably associated with many of these Gondwana-wide floras, but very little is yet known of them. The Belmont fauna, from the Sydney Basin of Australia, is the only other well-sampled and described fauna to compare with that of the Estcourt Formation. It includes some 450 individuals with around 140 described species in 100 genera, but much of the taxonomic work goes back to the 1920s and 30s and needs updating. Late Permian



Figures 2–7. Middle Ecca Flora

2–6 Portrayal of five of the six genera of glossopterids characterising the Middle Ecca; the plant group heavily dominated the flora in abundance and diversity. 7. *Cyclodendron leslii*, one of two lycopod taxa interpreted as forming monospecific stands fringing interdistributary pans and swamps.

tetrapod faunas from elsewhere in Gondwana remain very poorly known (Anderson & Cruickshank 1978; Anderson 1981; Anderson & Anderson 1993a,b).

Stratigraphy

The Estcourt Formation (sensu SACS 1980) is recognised only in the north-eastern Karoo Basin in western Natal and north-eastern Free State. It comprises essentially estuarine, deltaic and swamp deposits and forms the lowest part of the Beaufort Group in this region of the Karoo (Johnson *et al.* 1996). The evidence points to it having a transitional interfingering contact with the largely overlying tetrapod-yielding floodplain deposits of the *Dicynodon* Assemblage Zone (Durand pers. comm.) which forms the upper part of the Adelaide Subgroup. The exact nature of this contact remains very uncertain and insufficiently mapped, the beds being heavily intruded by dolerite dykes and sills. The Estcourt Formation is rich in plants and insects, the *Dicynodon* Assemblage Zone in tetrapods. On the basis of the palynoflora (Anderson 1977), the megaflora (Anderson & Anderson 1985) and the tetrapods (Anderson & Cruickshank 1978; Rubidge 1995), the strata are clearly Late Permian in age.

History of collecting (plants and insects)

Two broad phases of collecting in the Estcourt Formation can be outlined; from c.1854 to 1929, and post 1957. The earlier exploratory phase was initiated by Peter Cormack Sutherland, Government Geologist to Natal (1854-56) and rounded off by Hamshaw Thomas, the famed palaeobotanist from Cambridge, in 1929. The total collection made during this interval of around 75 years amounted to some 100 slabs from perhaps 10 sites, mostly poorly provenanced. Very little could be said of the general flora on the basis of this limited sample and no trace of the insect fauna had yet been encountered.

The second and more definitive phase of collecting was undertaken largely by Eddie Van Dijk of the University of Natal (Pietermaritzburg) with his colleagues, friends and family from 1957 to 1984; and by Anna Benecke and ourselves (and to lesser extent Anne Anderson and Judy Maguire) of the Bernard Price Institute especially in the years 1969 to 1971. Particular emphasis was placed on making intensive collections from as many localities as possible: c.9 000 slabs from 21 localities (25 TCs), housed at the Natal Museum, Pietermaritzburg (NMP) and the Bernard Price Institute (BPI), are at hand. Two of these localities, Rondedraai near Estcourt (Figure 1c) and Bergville (Figure 1d), are illustrated. Close on half the TCs have yielded insects (c. 250 individuals in total) in association with the plants.

The flora (Figures 8-12)

Though thoroughly sampled, the flora, especially compared to that of the Molteno Formation, is not diverse. As revised in Anderson & Anderson (1985) it includes just 24 vegetative species (in 14 genera). Only two basic floral associations can be recognised: *Lidgettonia* (Figure 10) (and other glossopterid genera) – medium diversity forest and woodland along river banks (levees) and other elevated ground; and *Phyllotheca australis* (Figure 12) – dense monospecific horsetail stands of the interdistributary pans and swamps. Diversity in any one TC ranges from 2 to 16 vegetative species, with a norm at around 5 or 6 species. Again, compared to the Molteno, this is remarkably low.

The flora is particularly dominated and characterised by a wide morphological range of glossopterid taxa as evidenced by four very different types of female fructification: *Plumsteadia* (Figure 8), *Estcourtia* (Figure 9), *Lidgettonia* (Figure 10) and *Rigbya* (Figure 11). These are seen, conservatively, as representing three different families within the order Glossopteridales (Anderson & Anderson 1985); but perhaps their rank should be raised to orders in a class Glossopteridopsida. The horsetails (Sphenophyta) are also morphologically diverse, with four distinctive genera, *Sphenophyllum*, *Raniganjia*, *Phyllotheca* (Figure 12) and *Schizoneura*, represented. Little else is encountered aside from these two major plant groups. One species of moss, one of a conifer and three others of uncertain attribution occur rarely and infrequently.

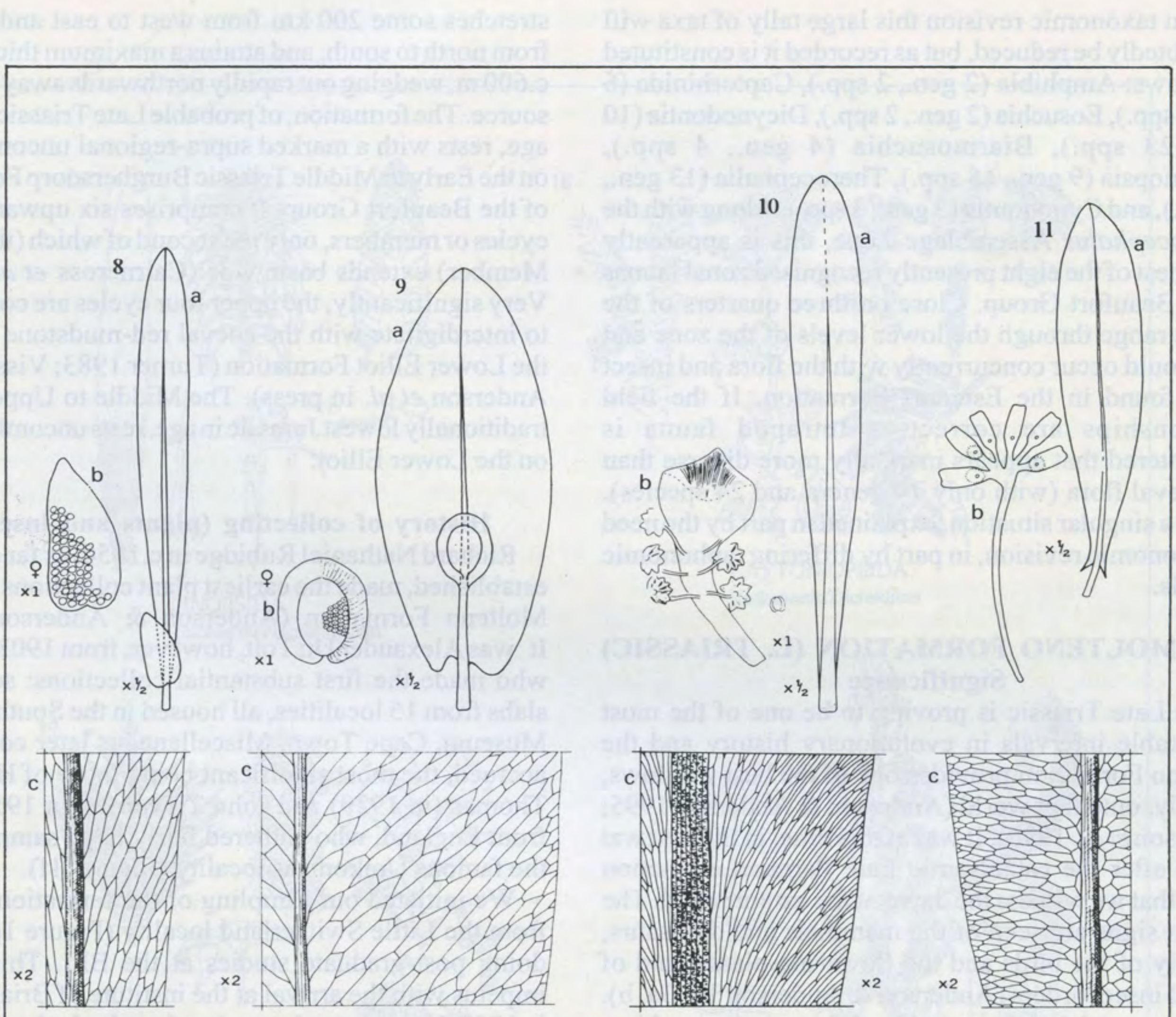
The only papers to have appeared on the flora since 1985 are those of Rayner (1992a,b), mostly concerning the genus *Phyllotheca*. His interest was largely palaeoecological. In discussing the association between the herbivorous dicynodonts and their plant preferences he advanced the hypothesis that *Phyllotheca* constituted the pre-grass pastures of the Late Permian.

The insect fauna (Figures 13-16)

With some 250 individuals from 11 plant-bearing TCs, the insect fauna, like the flora, is sufficiently sampled to provide a good account of its general composition (Riek 1976a; Riek & van Dijk manuscript; Anderson & Anderson 1985; Anderson & Riek manuscript). It consists of around 70 species in 25 genera and 14 orders. The Homoptera (bugs) (Figures 15, 16), with some 80 individuals in at least 20 species and almost as many genera, clearly dominate the fauna. The Paraplecoptera (extinct) (Figure 14) and Plecoptera (stoneflies) (Figure 13), together, are also represented by about 80 individuals, but by fewer taxa (some 10 species in 8 genera). Next in prominence come the Mecoptera (scorpionflies) with around 20 individuals, 13 species and 7 genera. The remaining orders are distinctly less well represented. Particularly notable, when compared with the Late Triassic Molteno fauna, is the complete absence of Blattodea (cockroaches) and the distinct rarity of the Coleoptera (beetles).

The tetrapod fauna of the *Dicynodon* Assemblage Zone

Considering its full stratigraphic and geographic extent through the main Karoo Basin and into the north-eastern outcrop area in Natal, the tetrapod fauna of the *Dicynodon* Assemblage Zone, as currently known, includes 49 genera with 73 species (Rubidge 1995). With



Figures 8–16. Estcourt Formation Flora and Insects

8–11. Foliage and fruit of the four genera of glossopterids identified in the Estcourt flora; as earlier in the Permian, this plant group still dominates in abundance and diversity. 12. *Phyllotheca australis*, the dominant horsetail taxon found widely through the formation that may have formed the pastures of the Late Permian. 13–16. Representative wings of the three most prominent insect orders found directly associated with the Estcourt plants.

modern taxonomic revision this large tally of taxa will undoubtedly be reduced, but as recorded it is constituted as follows: Amphibia (2 gen., 2 spp.), Captorhinida (6 gen., 6 spp.), Eosuchia (2 gen., 2 spp.), Dicynodontia (10 gen., 23 spp.), Biarmosuchia (4 gen., 4 spp.), Gorgonopsia (9 gen., 18 spp.), Therocephalia (13 gen., 14 spp.), and Cynodontia (3 gen., 3 spp.). Along with the *Tapinocephalus* Assemblage Zone, this is apparently the richest of the eight presently recognised zonal faunas of the Beaufort Group. Close on three quarters of the genera range through the lower levels of the zone and thus would occur concurrently with the flora and insect fauna found in the Estcourt Formation. If the field relationships are correct, a tetrapod fauna is encountered that appears markedly more diverse than the coeval flora (with only 14 genera and 24 species). This is a singular situation, explained in part by the need for taxonomic revision, in part by differing taphonomic controls.

THE MOLTENO FORMATION (L. TRIASSIC)

Significance

The Late Triassic is proving to be one of the most remarkable intervals in evolutionary history and the Molteno Formation provides one of the best windows, globally, onto that world (Anderson & Anderson 1995; Anderson *et al.* 1996). It was at this time, in the renewal of life after the cataclysmic Late Permian extinction event, that we witness the dawn of the extant world. The earliest signs are seen of the mammals and dinosaurs, possibly of the birds and the flowering plants, and of several insect orders (Anderson & Anderson 1993a, b). These terrestrial plant and animal groups emerged in a biota conceivably as rich in diversity as today; and in this diversity we appear to witness the heyday of the gymnosperms with seemingly as many taxa at all levels (species to orders) as in the extant angiosperms.

The Molteno is, by a wide margin, the richest plant-bearing formation in South Africa (Anderson & Anderson 1985). It is also, so far as we can ascertain, the richest known anywhere in the Triassic world and possibly throughout the geological column prior to the radiation of the flowering plants in the mid-Cretaceous. The outcrop is particularly extensive and the scope for sampling almost limitless. The uniqueness is considerably enhanced in that the formation also yields a rich insect fauna and, in the partly coeval, partly overlying Elliot Formation, a good tetrapod fauna (Anderson *et al.* in press). Certainly there is no other Gondwana Triassic formation or formation-pair (Molteno/Elliot) that is remotely comparable in terms of plant, insect and tetrapod yield.

Stratigraphy

The arenaceous Molteno Formation was deposited in an extensive land-locked floodplain inland of the east-west fold-belt zone which formed the southern periphery of Pangaea. The erosional remnant of the Molteno stretches some 200 km from west to east and 400 km from north to south, and attains a maximum thickness of c.600 m, wedging out rapidly northwards away from the source. The formation, of probable Late Triassic Carnian age, rests with a marked supra-regional uncomformity on the Early to Middle Triassic Burghersdorp Formation of the Beaufort Group. It comprises six upward-fining cycles or members, only the second of which (the Indwe Member) extends basinwide (Cairncross *et al.* 1995). Very significantly, the upper four cycles are considered to interdigitate with the coeval red-mudstone strata of the Lower Elliot Formation (Turner 1983; Visser 1984; Anderson *et al.* in press). The Middle to Upper Elliot, traditionally lowest Jurassic in age, rests uncomformably on the Lower Elliot.

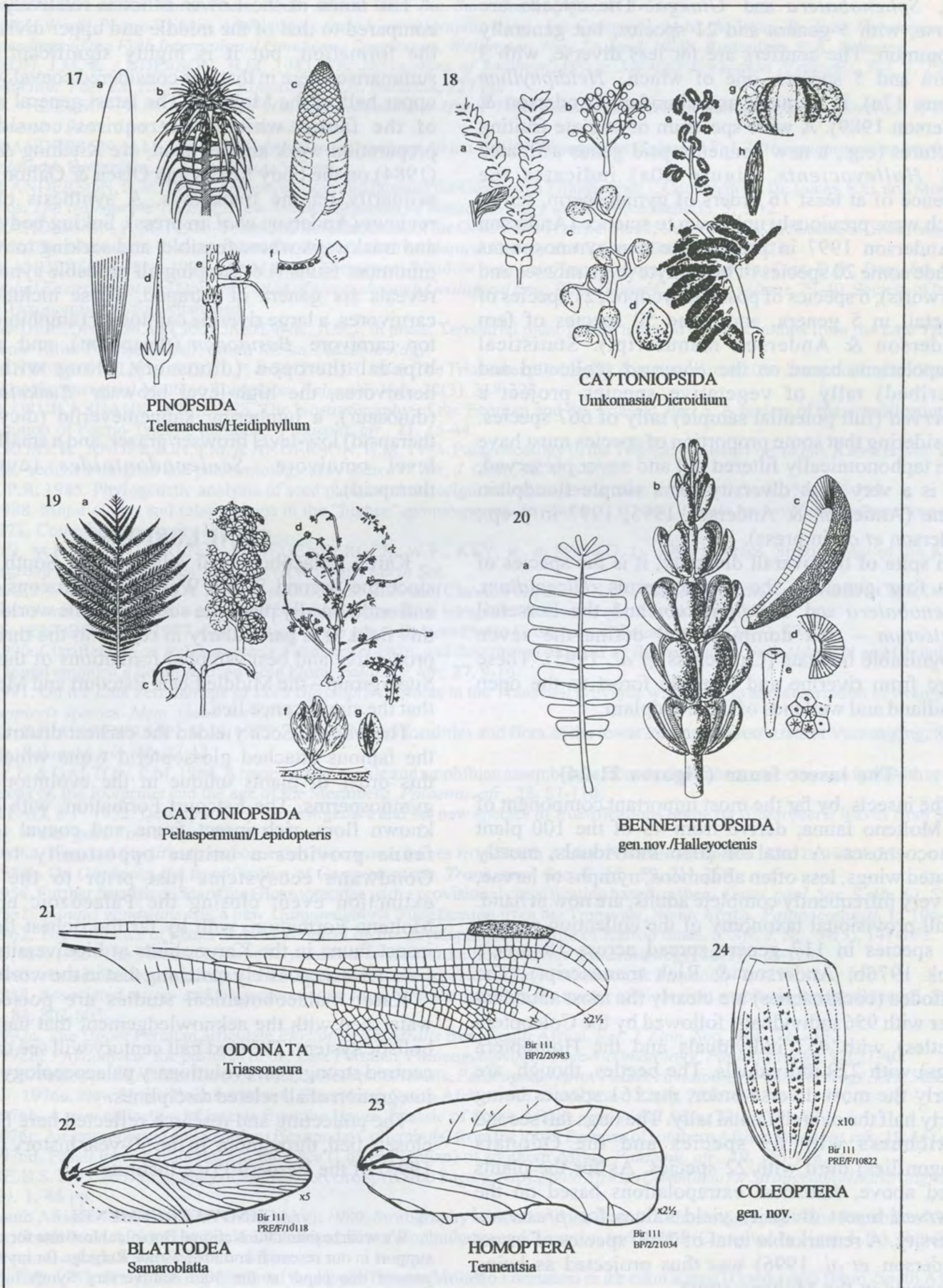
History of collecting (plants and insects)

Richard Nathaniel Rubidge in c.1850, as far as can be established, made the earliest plant collections from the Molteno Formation (Anderson & Anderson 1985). It was Alexander Du Toit, however, from 1903 to 1913, who made the first substantial collections: some 500 slabs from 15 localities, all housed in the South African Museum, Cape Town. Miscellaneous later collections accrued, the most significant being those of Hamshaw Thomas (in 1929) and John Townrow (in 1956), both from England, who gathered fairly large samples from the famous Umkomaas locality (Figure 1f).

We initiated our sampling of the formation in 1967 from the Little Switzerland locality (Figure 1g) whilst doing post-graduate studies at the BPI. This gained impetus with the arrival at the institute of Brian Turner in 1969. He undertook a regional geological study of the Molteno outcrop for his PhD thesis and in the course of his fieldwork discovered many new plant localities, eg. Matatiele (Figure 1e). Over the past nearly 30 years we have collected (Figure 1h) c.30,000 curated slabs from 100 taphocoenoses (69 localities). These reasonably represent, within the constraints of outcrop and exposure, the geographic and stratigraphic extent of the formation, as well as the major palaeo-habitats encountered. The material is currently all housed at the National Botanical Institute (NBI), Pretoria (that gathered prior to 1978 being on loan from BPI). Though this is possibly the most comprehensive sample available for any pre-Tertiary formation, the potential for finding and sampling further localities with TCs yielding new taxa or improved material remains considerable.

The flora (Figures 17-20)

A comprehensive taxonomic study, partly published and partly in manuscript, of the vegetative component of the flora has revealed 56 genera including 204 species of plant (Anderson & Anderson 1983, 1989, 1997 in prep.). The diversity amongst the gymnosperms and non-gymnosperms is approximately equal. The seed-fern *Dicroidium* (Figure 18a), which strongly characterises the Gondwana Triassic, is



Figures 17–24. Molteno Formation Flora and Insects

17–20. Selected foliage and fruit of four of the 16 orders of gymnosperm recognised in the Molteno suggesting the great diversity in the formation; the bennettitopsid is one of 10 of these orders that are new to science. 21–24. Representative wings of the four most prominent insect orders found in intimate association with the Molteno flora.

represented in the Molteno by 19 species. Other prominent seed ferns include *Lepidopteris* (Figure 19a), *Sphenobaiera* and *Ginkgo*. The cycads are diverse, with 5 genera and 21 species, but generally uncommon. The conifers are far less diverse, with 3 genera and 5 species, one of which, *Heidiphyllum* (Figure 17a), is frequent and abundant (Anderson & Anderson 1989). A wide spectrum of ovulate fruiting structures (e.g., a new bennettitopsid genus affiliated with *Halleyoctenis,* Figure 20a) indicates the presence of at least 16 orders of gymnosperm, ten of which were previously unknown to science (Anderson & Anderson 1997 in prep.). The non-gymnosperms include some 20 species of bryophyte (e.g., mosses and liverworts), 6 species of possible lycopod, 21 species of horsetail in 5 genera, and some 50 species of fern (Anderson & Anderson manuscript). Statistical extrapolations based on the *observed* (collected and described) tally of vegetative species project a *preserved* (full potential sample) tally of 667 species. Considering that some proportion of species must have been taphonomically filtered out and never preserved, this is a very high diversity for a simple floodplain biome (Anderson & Anderson 1995, 1997 in prep.; Anderson *et al.* in press).

In spite of the overall diversity, it is the species of only four genera – the gymnosperms *Dicroidium*, *Sphenobaiera* and *Heidiphyllum* and the horsetail *Equisetum* – that dominate and define the seven recognisable habitats (Cairncross *et al.* 1995). These range from riverine and lakeside forest to the open woodland and wetlands of the floodplain.

The insect fauna (Figures 21-24)

The insects, by far the most important component of the Molteno fauna, derive from 43 of the 100 plant taphocoenoses. A total of 2056 individuals, mostly isolated wings, less often abdomens, nymphs or larvae, and very infrequently complete adults, are now at hand. A full provisional taxonomy of the collection reveals 333 species in 117 genera spread across 18 orders (Riek 1976b; Anderson & Riek manuscript). The Blattodea (cockroaches) are clearly the most abundant order with 956 individuals, followed by the Coleoptera (beetles) with 453 individuals and the Homoptera (bugs) with 229 individuals. The beetles, though, are clearly the most diverse order, the 161 species being nearly half the overall faunal tally. The bugs fall second in richness with 69 species and the Odonata (dragonflies) third with 22 species. As for the plants noted above, statistical extrapolations based on the *observed* insect diversity yield values for *preserved* diversity. A remarkable total of 7740 species of insect (Anderson *et al.* 1996) was thus projected as being *preserved* in the Molteno strata.

The tetrapod fauna of the Lower Elliot Formation (coeval with the Upper Molteno)

The fauna of the Lower Elliot is relatively sparse compared to that of the middle and upper divisions of the formation, but it is highly significant and is summarised here in that it is considered coeval with the upper half of the Molteno. The latest general reviews of the fauna, which still requires considerable preparation work and revision, are Kitching & Raath (1984) on the body fossils and Olsen & Galton (1984) primarily on the trackways. A synthesis of these reviews (Anderson *et al.* in press), linking body fossils and trackways where feasible, and seeking to record a minimum fauna (i.e. lumping all probable synonyms), reveals six genera of tetrapod. These include three carnivores, a large riverine capitosaur (amphibian), the top carnivore *Basutodon* (thecodont), and a small bipedal theropod (dinosaur); along with three herbivores, the high-level browser *Euskelosaurus* (dinosaur), a lumbering kannemeyeriid (dicynodont therapsid) low-level browser/grazer, and a smaller low-level omnivore *Scalenodontoides* (cynodont therapsid).

CONCLUSIONS

Karoo palaeobotanical advances in South Africa since the Second World War have been considerable and undoubtedly place the country on the world map in this field. It is particularly in regard to the three most productive and best sampled formations of the Karoo Supergroup – the Middle Ecca, Estcourt and Molteno – that the significance lies.

The Middle Ecca yielded the earliest discoveries of the famous attached glossopterid fruits which make this order of plants unique in the evolution of the gymnosperms. The Estcourt Formation, with its well known flora, rich insect fauna and coeval tetrapod fauna provides a unique opportunity to study Gondwana ecosystems just prior to the global extinction event closing the Palaeozoic era. The Molteno Formation, with by far the richest flora and insect fauna in the Karoo, hints at biodiversity in the Late Triassic possibly matching that in the world today.

Karoo palaeobotanical studies are poised on a watershed with the acknowledgement that nature is a holistic system. The next half century will see the focus centred strongly on evolutionary palaeoecology and the integration of all related disciplines.

The collecting and research reflected here has been closely tied, throughout, to the 50-year history (1945 to 1995) of the Bernard Price Institute.

ACKNOWLEDGEMENTS

We wish to thank the National Botanical Institute for continued support in our research and Prof. Bruce Rubidge for inviting us to present this paper at the 50th Anniversary Symposium at the Bernard Price Institute for Palaeontological Research.

REFERENCES

ANDERSON, J.M. 1977. The biostratigraphy of the Permian and Triassic – Part 3. A review of Gondwana Permian palynology with particular reference to the northern Karoo Basin, South Africa. *Mem. Bot. Surv. South Africa*, **41**,1-65.

-------- 1981. World Permo-Triassic correlations: their biostratigraphic basis. **In:** Cresswell, M.M. & Vella, P., Eds, *Gondwana Five (Proceedings of the Fifth International Gondwana Symposium, Wellington, New Zealand, 1980)*. Rotterdam, A.A. Balkema.

ANDERSON, J.M. & ANDERSON, H.M. 1983. *The palaeoflora of Southern Africa: Molteno Formation (Triassic), Vol. 1, Part 1, Introduction, Part 2A, Dicroidium.* Rotterdam, A.A. Balkema, 227 pp.

-------- & ANDERSON, H.M. 1985. *The Palaeoflora of southern Africa: Prodromus of southern African megafloras, Devonian to Lower Cretaceous* . Rotterdam, A.A. Balkema, 423 pp.

-------- & ANDERSON, H.M. 1989. *The Palaeoflora of southern Africa: Molteno Formation (Triassic) Vol. 2: The gymnosperms (excluding Dicroidium).* Rotterdam, A.A. Balkema, 567 pp.

-------- & ANDERSON, H.M. 1993a. Terrestrial flora and fauna of the Gondwana Triassic. Part 1, Occurrences. **In:** Lucas, S.G. and Morales, M., Eds, *The Nonmarine Triassic.* New Mexico Museum of Natural History and Science Bulletin, **3**, 3-12.

-------- & ANDERSON, H.M. 1993b. Terrestrial flora and fauna of the Gondwana Triassic. Part 2, Co-evolution. **In:** Lucas, S.G. and Morales, M., Eds, *The Nonmarine Triassic.* New Mexico Museum of Natural History and Science Bulletin, **3**, 13-25.

-------- & ANDERSON, H.M. 1995. The Molteno Formation: Window onto Late Triassic floral diversity. **In:** Pant, D.D., *Proc. Int. Conf. on Global Environment and Diversification of plants through Geological time. Birbal Sahni Centenary volume*, 27-40, Society of Indian Plant Taxonomists, India, Allahabad.

-------- ANDERSON, H.M. & CRUICKSHANK, A.R.I. in press. Terrestrial plant/insect/ tetrapod co-associations from the Late Triassic Molteno/ Elliot Formation pair, South Africa. *Palaeontology.*

--------, ANDERSON, H.M., FATTI, L.P. & SICHEL, H. 1996. The Triassic explosion (?): A statistical model for extrapolating biodiversity based on the terrestrial Molteno Formation. *Palaeobiology,* **22**(3), 318-328.

-------- & CRUICKSHANK, A.R.I. 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeont. afr.,* **21**, 15-44.

CAIRNCROSS, B., ANDERSON, J.M. & ANDERSON, H.M. 1995. Palaeoecology of the Triassic Molteno Formation, Karoo Basin, South Africa – sedimentological and palaeontological evidence. *S. Afr. J. Geol.,* **98**, 452-478.

CRANE, P.R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Miss. Bot. Gard.*, **72**, 716-793.

-------- 1988. Major clades and relationships in the "higher" gymnosperms. **In:** Beck, C.B., Ed., *Origin and evolution of gymnosperms*, 218-272, Columbia University Press.

JOHNSON, M.R., Van VUUREN, C.J., HEGENBERGER, W.F., KEY, R. & SHOKO, U. 1996 in press. Stratigraphy of the Karoo Supergroup in southern Africa – an overview. *J. Afr. Earth Sci.*

KITCHING, J.W. & RAATH, M.A. 1984. Fossils from the Elliot and Clarens Formation (Karoo Sequence) of the North-eastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeont. afr.,* **25**, 111-125.

KOVÁCS – ENDRÖDY, E. 1987. Clarification of the genus *Palaeovittaria* Feistimantel. *Palaeont. afr.,* **26**(6), 59-68.

-------- 1990. Clarification of *Belemnopteris* Feistmantel 1876, and description of a leaf of *Belemnopteris pellucida* Pant and Choudhury 1977 found amongst a South African Ecca Flora. *Palaeont. afr.,* **27**, 9-16.

-------- 1991. On the Late Permian age of Ecca *Glossopteris* Floras in the Transvaal province with a key to and description of twenty five *Glossopteris* species. *Mem. Geol. Surv*., **77**, 1-111.

LE ROUX, S.F. & ANDERSON, H.M. 1977. A review of the localities and flora of the lower Permian Karoo strata at Vereeniging, South Africa. *Palaeont. afr.,* **20**, 27-42.

OLSEN, P.E. & GALTON, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa with special emphasis on the footprints and the age of the Stormberg. *Palaeont. afr.,* **25**, 87-110.

PLUMSTEAD, E.P. 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves from South Africa. *Trans. geol. Soc. S. Afr.,* **55**, 281-328.

-------- 1956a. Bisexual fructifications borne on *Glossopteris* leaves from South Africa. *Palaeontographica*, Abt. B, **100**, 1-25.

-------- 1956b. On *Ottokaria*, the fructification of *Gangamopteris. Trans. geol. Soc. S. Afr.,* **59**, 211-236.

-------- 1958. Further fructifications of the Glossopteridae with a provisional classification based on them. *Trans. geol. Soc. S. Afr.,* **61**, 51-76.

-------- 1962. *Vannus gondwanensis,* a new *Gangamopteris* fructification from the Transvaal, South Africa. *Palaeobotanist,* **11** 106-114.

-------- 1963. The influence of plants and environment on the developing animal life of Karroo times. *S. Afr. J. Sc.,* **59**(5), 147-152.

RAYNER, R.J. 1985. The Permian Lycopod *Cyclodendron leslii* from South Africa. *Palaeontology,* **28**(1), 111-120.

-------- 1986. *Azaniadendron*, a new genus of Lycopod from South Africa. *Rev. Palaoebot. & Palynol.*, **47**, 129-143.

-------- 1988. Associated micro- and megaspores form the Lower Permian. On the matter of biological species in the fossil record. *S. Afr. J. Sc.,* **84**, 802-805.

-------- 1992a. The Upper Permian articulate *Phyllotheca australis* from South Africa. *Bot. J. Linn. Soc.*, **108**, 321–332.

-------- 1992b. *Phyllotheca:* the pastures of the Late Permian. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **92**, 31-40.

-------- 1995. Palaeoclimate of the Karoo: evidence from plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **119**, 385-394.

RIEK, E.F. 1976a. New Upper Permian insects from Natal, South Africa. *Ann. Natal Mus*., **22**(3), 755-789.

-------- 1976b. A new collection of insects from the Upper Triassic of South Africa. *Ann. Natal Mus*., **22**(3), 791-820.

-------- 1976c. An entomobryid collembolan (Hexapoda: Collembola) from the lower Permian of southern Africa. *Palaeont. afr.,* **19**, 141-143.

-------- 1976d. Fossil insects from the Middle Ecca (Lower Permian) of southern Africa. *Palaeont. afr.,* **19**, 145-148.

RUBIDGE, B.S. 1995. Biostratigraphy of the Beaufort Group (Karoo Supergroup). *South African Committee for Stratigraphy (Biostratigraphic Series).* **1**, 46 pp.

SACS (South African Committee for Stratigraphy), 1980. Stratigraphy of South Africa. Part 1: Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia and the Republics of Bophuthatswana, Transkei and Venda (Compiled by Kent, L.E.). Handbook **8**, 690 pp., Geological Survey South Africa.

TURNER, B.R. 1983. Braidplain deposition of the Upper Triassic Molteno Formation in the main Karoo (Gondwana) Basin, South Africa. *Sedimentology*, **30**, 77–89.

VISSER, J.N.J. 1984. A review of the Stormberg Group and the Drakensberg volcanics in southern Africa. *Palaeont. afr.*, **25**, 5–27.