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PALAEOZOIC INSECTS OF SOUTHERN AFRICA: A REVIEW

by

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ABSTRACT

Although a substantial number of Triassic insect fossils have been discovered in southern Africa, relatively few insect fossils are known from the Permian deposits of this region. Fossil insects from the Permian period elsewhere, including the extensive entomological fauna from Eastern Europe (including Russia), Brazil and Australia is well-documented. The Irati Formation in the Parana Basin of Brazil, the temporal and lithological correlate of the Permian Whitehill Formation of South Africa, has yielded fossil insects belonging to Homoptera, Neuroptera, Coleoptera and Mecoptera. Fossil insects from the Whitehill Formation are usually poorly preserved and only seven specimens are mentioned in the literature. An overview is given of the more recent discoveries of Permian fossil insects in South Africa. This includes the discovery of the oldest beetle in Africa, the oldest longhorned grasshopper in the Southern Hemisphere and a survey of the Permian insects from the Beaufort Group of Natal. Reasons for the paucity of Permian insects are briefly discussed.

KEYWORDS: Permian, KwaZulu-Natal, Western Cape, fossil insects

INTRODUCTION

Winged insects were already in existence by the Lower Permian. This, from the point of view of the palaeo-entomologist, is rather fortunate as the classification of insects is largely based on features of the wing. Most adult insects possess two pairs of wings, each pair often differing in size, shape and texture. Membranous wings are traversed by veins which strengthen the wings, provide resistance against excessive bending, and impart particular patterns of wing flexibility, which are associated with particular manners of flight and folding of the wings when at rest. The pattern of veins, or venation, was early on established in insect evolution. Venation is best developed in the fore wings. A universal system of naming each vein enables comparison and description of the different venational patterns and allows the classification of insects. The classification of adult insects is based largely on differences in wing shape, texture and venation, differing to a greater or lesser degree between orders, families, genera and species.

Figure 1. Wing fragment peeled off surface of fossil insect.

The preservation potential of insects is very high because chitin, the main constituent of the exoskeleton, is extremely resistant. For example, in a sample from Lidgetton, KwaZulu-Natal, a partial insect was found in a HF digest of carbonaceous shale and a wing fragment of about 1 mm width was peeled off the surface of another specimen (Figure 1). The parts of an insect preserved as recognizable fossils are almost invariably the wings or fragments of the wings. Sometimes the wings, being fairly pliable, fold over or under, complicating their study. Normally insect fossils are uncommon among plant fossil material, but it does happen that wings may be selectively concentrated. A specimen from Balgowan shows five such wings and a conchostracan shell close together and with some overlap (Figure 2). Only rarely are insects completely preserved, often with the wings intact. Fossils of immature insects are even more scarce than adult insects as the majority of such potential fossils consist of skin casts which usually disintegrate before being deposited under conditions favourable for fossilization.

When insects fall on the surface of water, the soft parts macerate quickly, unless the insect is washed rapidly to the water margin and deposited above water along a fluctuating shore-line where it can dry rapidly before further deterioration.

The present discussion is limited to the period from the Late Permian to the Permian/Triassic boundary, a period characterized by a gradually warming climate, and to two geographical regions in southern Africa, the western part of KwaZulu-Natal, east of Lesotho, and part of the Western Cape Province, this area corresponding to the Karoo Basin consisting of the Beaufort Group and underlying Ecca Group (Figure 3).

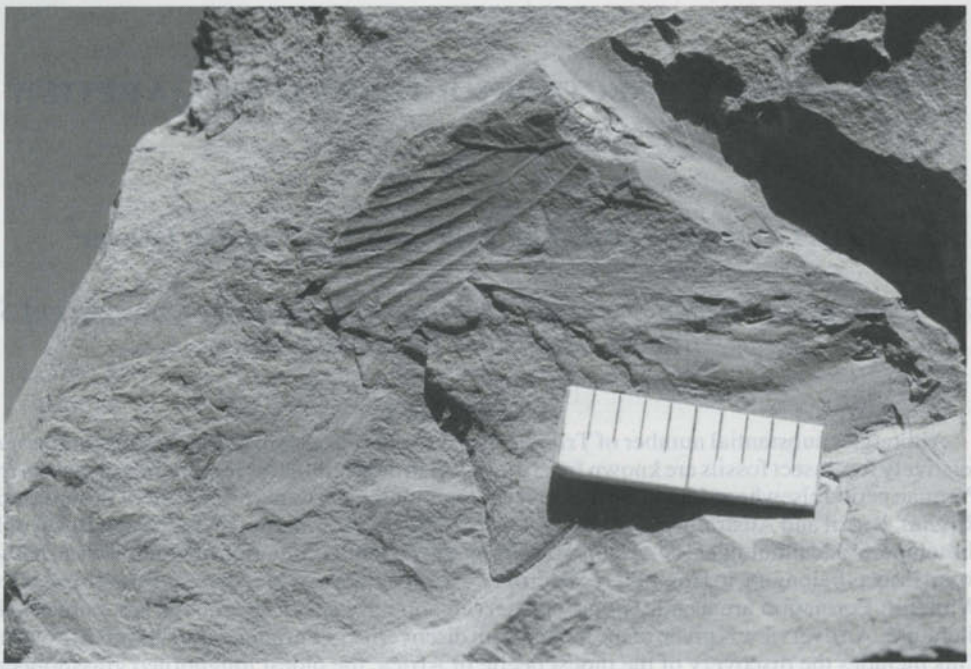

Figure 2. At least five fossil insect wings with some overlapping. Balgowan, KwaZulu-Natal.

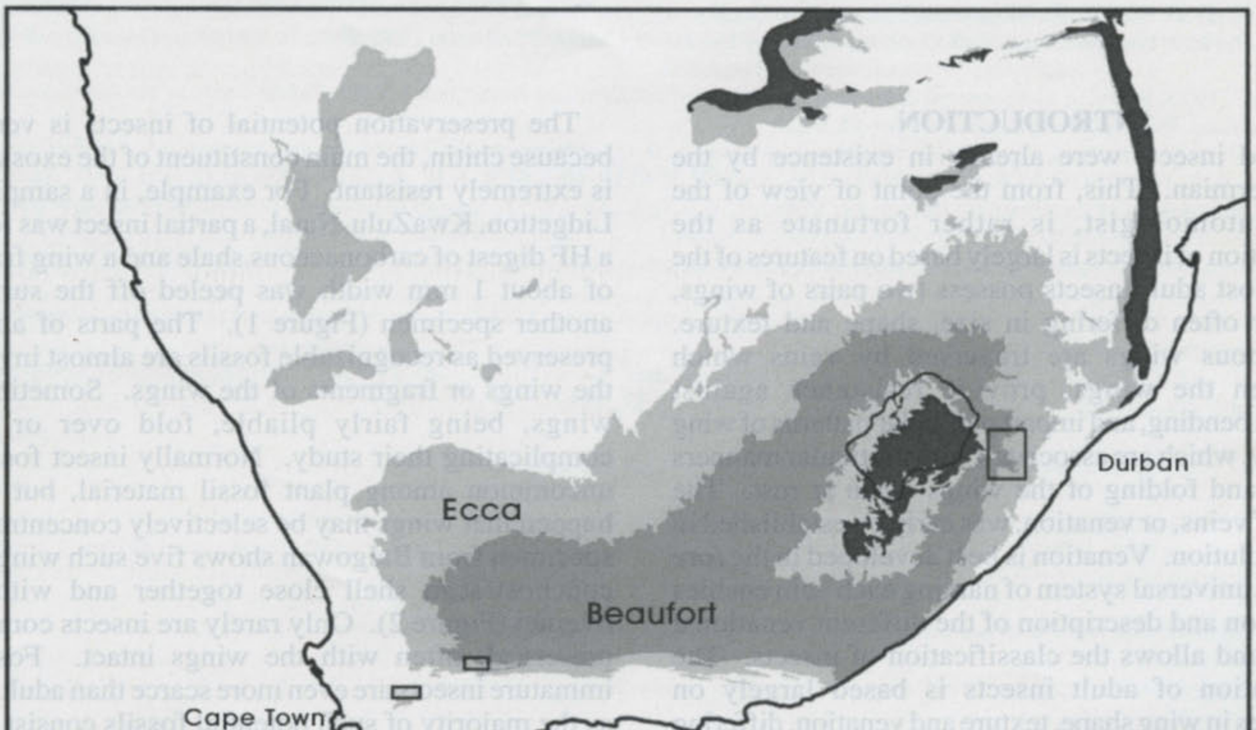

Figure 3. Map of South Africa showing the location of the Karoo Basin, consisting of the Beaufort Group and underlying Ecca Group, and fossil sites in KwaZulu-Natal and in the Western Cape.

Compared to the approximately 2 500 Triassic insect fossils found in the region around Lesotho, mainly through the activities of John and Heidi Anderson, only a limited number of Permian insects have so far been found in South Africa, of which most are from the western part of KwaZulu-Natal. The only recorded Permian insects from southern Africa by 1973 are *Rhodesiomylacris bondi* (Blattaria: Mylacridae) from the "Lower Beaufort Series" in Zimbabwe (Zeuner 1955), *Boutakovia saleei* (Protorthoptera: Homalophlebiidae) from the base of the Ecca in Zaire (Pruvost 1934), and two undescribed South African specimens. *Hadentomoides dwykensis* (Protorthoptera: Hadentomoidae) was described by Riek (1974a) from the "Dwyka Series", lying below the Ecca at the base of the Permian, of Zimbabwe. This species is the oldest recorded insect in the southern hemisphere. Three insects, *Thaumatophora pronotalis* (Paraplecoptera), *Sysciophlebia kovacsae* (Blattaria) and a protopsyllidiid nymph, were described by Riek (1976a) from carbonaceous shales of the middle Ecca from Hammanskraal, near Pretoria, South Africa. A collembolan was described from the same sediments and site (Riek 1976b). Subsequently, mainly through the work of Van Dijk and associates, substantial numbers of Permian fossil insects have been found and described (Riek 1973 1974a,c, 1976c; Van Dijk 1997; Van Dijk & Geertsema 1999).

The larger part of South Africa is covered by the Karoo Basin extending eastwards far beyond the present coastline. Into this basin Ecca shales and sandstone, followed by the Beaufort Group, were deposited. The Beaufort Group also consists largely of shales, but with beds of mudstone and sandstone in a complex sequence indicating much flooding and drying up. Shallow lakes and swamps covered most of the basin and in these and on the dry land lived a variety of amphibians, some fish, reptiles, therapsids and molluscs. The Beaufort rocks were laid down from the Upper Permian to the Lower Triassic Periods.

PERMIAN INSECTS FROM KWAZULU-NATAL

Most Palaeozoic insects from southern Africa have been collected from Beaufort deposits in KwaZulu-Natal in an area of about 90 km by 50 km (Figure 3). This area includes all Palaeozoic sites which have yielded more than one specimen.

Riek (1973) described 12 new insect species from the *Dicynodon* Assemblage Zone of the Middle Beaufort Group. Most species were from near Mooi River, with three other specimens from near Estcourt. The insect fauna consists mainly of Homoptera (five species) and Protorthoptera (= Paraplecoptera) (three species), Plecoptera (two species) (Figure 4) and one each of Miomoptera and Mecoptera. In 1974 an immature homopteran was described from Mooi River (Riek 1974c) (Figure 5). A somewhat similar form is known from Permian strata in Australia, but a greater diversity of forms occurs in the Upper Permian of the Kuznetsk Basin, Russia. Subsequently, an additional 19 species of insects were described by Riek (1976c). Most of the specimens were again from Mooi River, but some specimens from Bulwer, Lidgetton and from near Empangeni were also included. Two taxa, *Mioloptera stuckenbergi* (Protorthoptera) and *Euxenoperla* (Plecoptera), were common and the orders Megasecoptera, Protoblattodea, Protelytroptera, Orthoptera and Neuroptera were recorded from the fauna for the first time. Odonata and Trichoptera were reported for the first time from these deposits by Van Dijk & Geertsema (1999). They also placed three new species in genera not previously recorded in South Africa and described two new genera and eight new species. The number of fossil insects from this area now consists of 13 orders, 34 genera and 39 species (Table 1). An inventory of Upper Permian Beaufort Group fossil insects is given in Van Dijk & Geertsema (1999). Most of the later material came from two new sites, Mount West, near Mooi River, and Balgowan, near Lidgetton, or from Bulwer and Lidgetton, previously known localities. A plecopteran (Figure 4) from Bulwer is presently being described (Van Dijk and Geertsema, in prep.). All these sites lie in the Beaufort Group of the Karoo Sequence of Late Permian age with the uppermost site, Bulwer, at the Permian/Triassic boundary. The sediments of the Beaufort Group, deposited in fluvial and lacustrine environments, consist of shales, with subordinate cross-bedded sandstones and occasional thin coal seams. The insects, and associated plant fossils, occur in minor upward-coarsening sequences, interpreted as bays between the distributaries of deltas. The layers containing the fossils have probably been produced by over-bank spill, while the overlying upward-coarsening sediments represent overriding distributaries which bury the bay deposits.

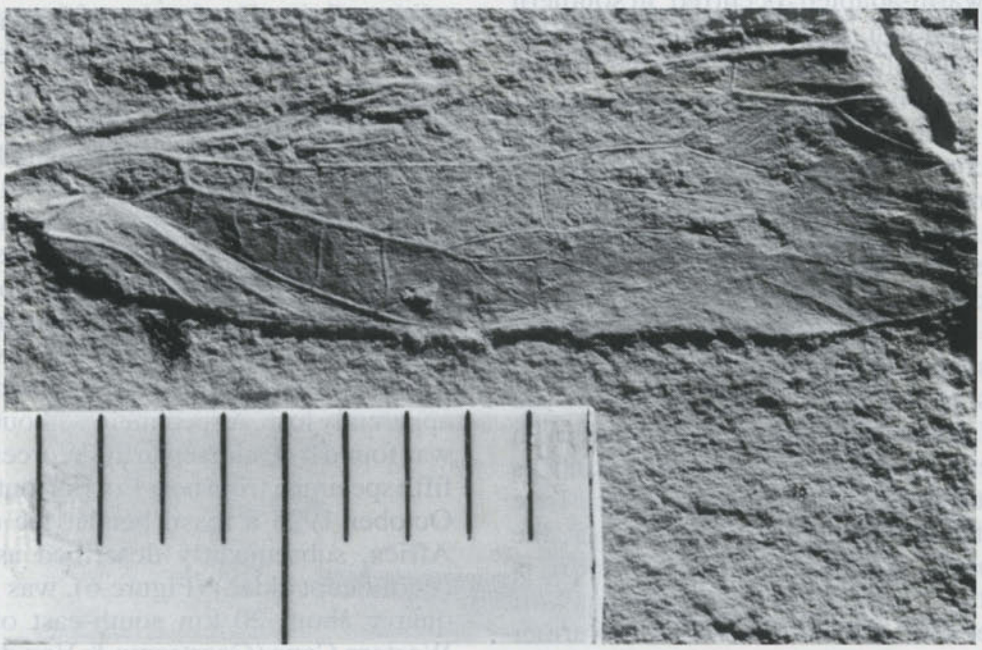

Figure 4. Wing of plecopteran from Bulwer, KwaZulu-Natal.

TABLE 1
Permian Insects From The Beaufort Group: KwaZulu-Natal

Order	Genus	Species	Other
Megasecoptera*	1	2	
Odonata			2
Protorthoptera*	7	7	
Protelytroptera*	1	1	
Plecoptera	2	4	
Blattaria	1	1	
Orthoptera	2	2	
Homoptera	13	13	
Miomoptera*	1	1	
Neuroptera	1	1	
Mecoptera	5	7	
Coleoptera			3
Trichoptera			1
*extinct	34	39	6

The Late Permian insect fauna from the *Dicynodon* Assemblage Zone of KwaZulu-Natal shows affinity to that of the Angara province of Asia (Eurasia) and to the Australian region, but there are also species unique to the African fauna. The Protorthoptera (three species), Orthoptera (two species), Miomoptera (one species) and Neuroptera (one species) are closely allied to Early Permian fauna from Europe, Angara and the Kuznetsk Basin of Russia. The Plecoptera, Protelytroptera, most Mecoptera, some Homoptera and a neuropteran indicate affinity with western Australia. Some Homoptera are related to those from the Late Triassic of Australia. Homoptera were abundant in KwaZulu-Natal (Figures 5, 8) and Australia, but most Australian species were very small, those from KwaZulu-Natal being large to very large. Mecoptera, mostly cold-adapted species with respect at least to the Recent fauna, were common in Australia and rare in southern Africa, whereas the Protorthoptera and Miomoptera, orthopteroid orders that are generally warm-adapted, occurred in southern Africa, but are unknown from the extensive Late Permian fauna of Australia. The Late Permian fauna, consisting mainly of Homoptera and Protorthoptera, of this north-eastern part of the Karoo basin suggests warmer and drier conditions, intermediate between the warm climate of Angara and the cold, moist conditions in relative close proximity to snow covered areas or glaciers of the Belmont area of Western Australia, the fauna of which is associated with colder conditions (Riek 1968).

Orthoptera are first recorded in Australia in the Triassic. Cockroaches are not recorded from the Late Permian localities of the north-eastern sector of the Karoo basin or of Australia. This suggests that even though the climate of this sector of the Karoo basin was warmer than that at Belmont in Australia during the Late Permian, it was still moderately cold. However, the primitive cockroach, *Rhodesiomylacris bondi*, is recorded from the "Lower Beaufort Series" of Zimbabwe (Zeuner 1955). This indicates that warmer conditions prevailed north of the Karoo basin during the Late Permian.

Figure 5. *Aleuronympha bibulla* Riek, 1974b. Mooi River, KwaZulu-Natal.

PERMIAN INSECTS FROM THE WHITEHILL FORMATION

The Permian Whitehill Formation, formerly known as the "White Band" of South Africa, is a distinct stratigraphic unit near the base of the Ecca Group of the Karoo Supergroup in the western half of the Karoo Basin (Visser 1992). The vertebrate fauna of the Whitehill Formation has been known from as early as 1864 when the anapsid aquatic reptile *Mesosaurus tenuidens* was described (Oelofsen 1981). *Glossopteris* leaves and wood and the arthropod *Notocaris tapscotti* occur frequently (Visser 1992). Insect remains, however, are extremely scarce; only seven were reported before 1995.

Except for Oelofsen, no effort has been made to systematically collect insect fossils from the Whitehill Formation and impressions of only five specimens have been recorded (Oelofsen 1981). McLachlan & Anderson (1977) recorded the first two fossil insect finds from the southern Karoo Basin, one specimen consisting of two fragmentary mecopteran wings from Modderdrift and the second a protorthopteran wing from Krantzpoort. A coleopterid wing from the north-western part of the Karoo Basin was reported by Oelofsen (1981), but is apparently lost. A specimen, without further description, was found by Oelofsen in the Worcester outlier while the fifth specimen from near Loeriesfontein is mentioned. In October 1995 a fossil beetle, the oldest yet found in Africa, subsequently described as *Afrocupes firmae* (Permocupedidae) (Figure 6), was found in a roadside quarry about 20 km south-east of Worcester in the Western Cape (Geertsema & Van den Heever 1996). It is associated with a layer that contains numerous

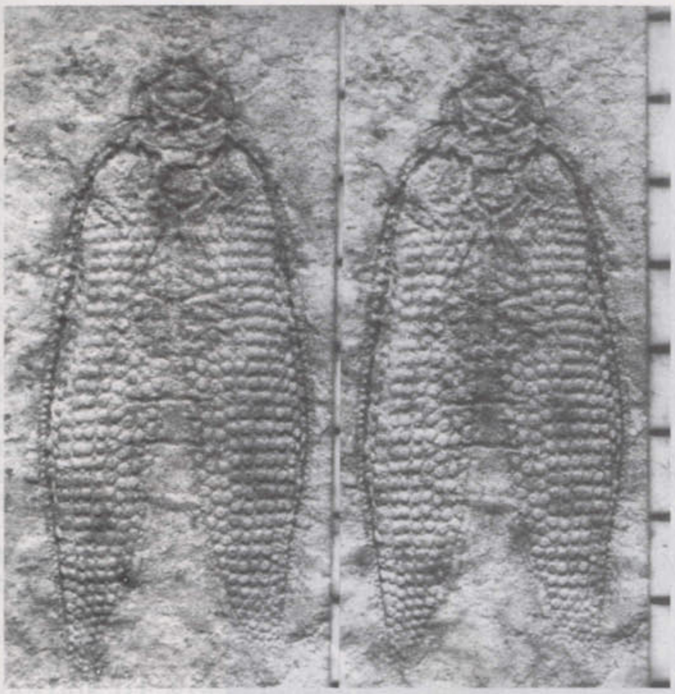

Figure 6. *Afrocupes firmae* Geertsema & Van den Heever, 1996. Worcester, Western Cape Province.

specimens of *Notocaris tapscotti*. A number of incompletely preserved *Mesosaurus* have also been recovered from the site. A similar association between fossil insects, *Mesosaurus* and crustaceans has been reported from the Irati Formation of Brazil (Pinto 1972).

The discovery of this beetle adds another insect to the list of shared insects in the Irati Formation of Brazil. Pinto (1972) pointed out the similarities of the palaeo-entomofaunas of Brazil and South Africa with those described from the Late Permian Tatarsky and Kuznetsk Formations of Russia. This association points to a possible common development of taxa in Asiatic Russia and Gondwana during the late Palaeozoic.

Fossil beetles are well-known from the Permian period. The extensive Permian Protocoleoptera and Coleoptera fauna from Moravia, the Czech Republic, Slovakia and the Ural Mountains, Russia, is well documented (Martinov 1933; Rohdendorf 1961; Kukalová 1969; Ponomarenko 1969). The Irati Formation in the Parana Basin is the temporal and lithological correlate of the Whitehill Formation and has yielded insect fossils including Homoptera, Neuroptera, Coleoptera and Mecoptera; two of the fossil beetles, *Kaltanicupes ponomarenkoi* and *Protocupoides rohdendorfi*, have been described from the Irati Formation and placed in the Permocupedidae (Pinto 1987) The beetle *Moltenocupes townrowi* was described from near Umkomaas in KwaZulu-Natal from the Late Triassic Molteno Formation and put in the Cupedidae (Zeuner 1961). An unidentified species of Late Triassic *Moltenocupes* from Mooi River was reported by Riek (1974b). Similar beetles are also recorded from the Late Permian of Australia and the Jurassic and Early Cretaceous of Central Asia (Ponamerenko 1961; Riek 1976c).

Wing fragments of a mecopteran and a protorthopteran were reported from the Whitehill Formation by McLachlan & Anderson (1977). They considered that these wings were transported passively or actively from their usual abode to the site of fossilization and might have floated in the sea for some distance, similar to twig and leaf fragments, but regard wind as a probable dispersal agent. The beetle *A. firmae* from the Whitehill Formation was almost intact and found in close association with *Notocaris*, suggesting an intertidal zone or shore line as habitat or burial site (Geertsema & Van den Heever 1996).

An orthopteran insect, in the collection of the late Roy Oosthuizen, was collected in mudstone of the Early Permian Laingsburg Formation (Karoo Sequence, Ecca Group) by Oelofsen and his team. This insect was recently described as *Afrodoeschia oosthuizeni* (Figure 7) and is the only member of the Oedischiidae known in the southern Hemisphere, and probably the oldest long-horned orthopteran in the southern hemisphere (Geertsema & Van Dijk 1999). Orthoptera date from the Carboniferous. Oedischiidae are generally considered the most primitive of the known Orthoptera.

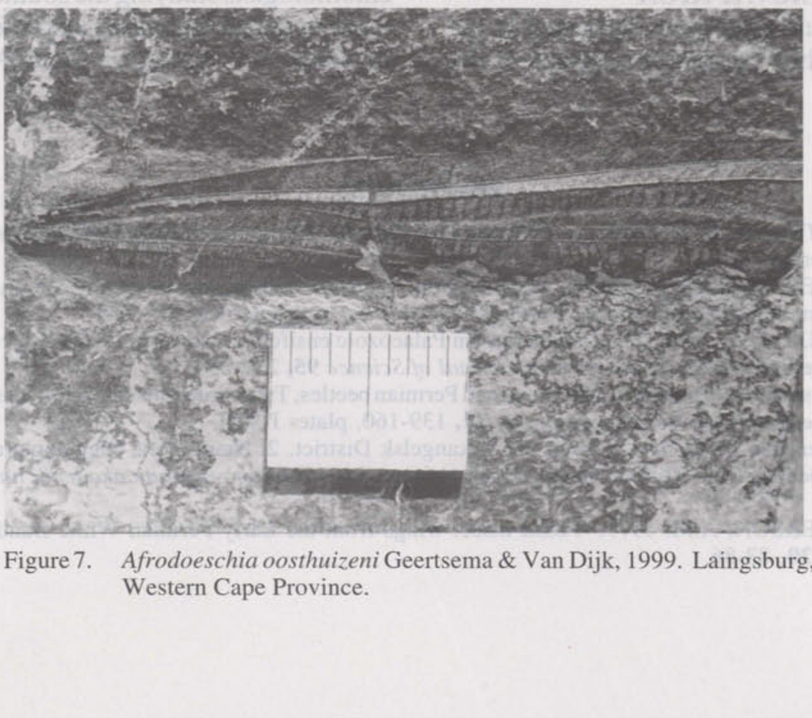

Figure 7. *Afrodoeschia oosthuizeni* Geertsema & Van Dijk, 1999. Laingsburg, Western Cape Province.

Figure 8. Hemipteran from Lidgetton, KwaZulu-Natal.

Thirteen genera of this family have been described so far, ranging from the Late Carboniferous and Permian of Europe, the Permian of European and Asian Russia and of Kansas in the USA (Carpenter 1992). *Proedischia* (Proedischiidae) has been described from the Late Carboniferous of Brazil (Pinto 1972). The earliest ensiferan Orthoptera described from South Africa is from the Late Permian of KwaZulu-Natal.

Several additional insect fossils have recently been found from the Worcester site and await description. Most of these are poorly preserved, probably because of deep water fossilization, deterioration of the material occurring when the fossil-bearing sediments are exposed. In contrast, *A. firmae* from the same site was very well preserved (Figure 6).

PAUCITY OF PERMIAN INSECTS FROM SOUTHERN AFRICA

Few insect fossils would have been deposited in the main basin of the Whitehill Formation because of the distance of most of these deposits from the shore line. Although they would have been well-preserved in the anoxic black muds, exposure and oxidation of these deposits would have destroyed the majority of these fossils (Visser 1992). The continuous erosion of fossil-bearing mudstone beds of most Permian sites removes a source of material for study. Road construction has been responsible for the elimination of the Mooi River site (Van Dijk 1997); more recently, the construction of a dam has destroyed a promising fossil insect site at Lidgetton. A quarry near Bulwer, one of the more promising fossil sites, is presently utilized as a ready source of road gravel. It is estimated that to date only 10 square meters of fossiliferous material from Bulwer has been inspected for insect remains and that more than 5000 sq m has already been removed in the form of gravel. Presently there is an acute shortage of palaeo-entomologists studying the southern African fossil insect fauna and with dwindling institutional support, the future of palaeo-entomology in South Africa looks bleak.

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