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A new collection of insects from the Upper Triassic of South Africa

by

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SYNOPSIS

A second collection of insect fossils from Bird's River and a single specimen from Mount Fletcher are described and illustrated. Meganisoptera, Odonata, Plecoptera and Lepidoptera are recorded for the fauna, bringing the number of orders known to 11. Meganisoptera are rarely recorded from strata as late as the Triassic. Lepidoptera have not previously been recognized in strata older than the Cretaceous. Large cicada-like Homoptera were a feature of the fauna. A cercopoid homopteran has unique lobes on the margin of the clavus that would produce a cryptic pattern when the wings are folded. The known fauna of 33 species from the Molteno Formation is listed.

INTRODUCTION

Fourteen species and a nymph have been described from the Molteno Formation (Zeuner 1939; Riek 1974, 1975). A new collection of 38 specimens from Bird's River (C-Dt II) and one specimen from Mount Fletcher (C-MFI) includes 18 new species, and provides additional data on two described species. Mount Fletcher is a new locality in the Molteno for insect fossils. Insects are now known from nine localities in the Formation.

Meganisoptera, Odonata, Plecoptera and Lepidoptera are recorded for the fauna, bringing the number of orders known to 11.

The dragonfly-like Meganisoptera are rarely recorded from strata as late as the Triassic. The specimen is fragmentary, but this is not unusual with insect wings of large size. Large cicada-like Homoptera were diverse: they are represented by five species referred to three families. A dysmorphoptilid cercopoid has a unique lobed margin to the clavus that would produce a cryptic pattern when the wings were folded but the function of the lobes is not known. Lepidoptera have not previously been recognized in strata older than the Cretaceous. The Mesopsychidae, also known from the Upper Triassic of Australia, which are now referred to the Lepidoptera, have had a chequered career. They have previously been referred to a separate order Paratrichoptera, to the Trichoptera, to the Mecoptera, or considered closely related to Diptera.

Most insects from the fauna are of moderate to large size but there are also a few small Homoptera, Mecoptera and Coleoptera.

The fauna is closely similar to that of the Upper Triassic of Australia although there are some notable additions especially Ephemeroptera, Meganisoptera and Protozygopterous Odonata. The Plecoptera, Blattodea, Orthoptera, Homoptera, Coleoptera and Lepidoptera are so similar to those of the Australian Upper Triassic that, unless informed of the country of origin, one would readily accept them as part of the Australian fauna of the period.

INSECTS KNOWN FROM THE MOLTENO FORMATION

Ephemeroptera: Xenophlebioidea	
Xenophlebiidae	*Xenophlebia optata* Riek in press
Meganisoptera	
Paralogidae	*Triassologus biseriatus* gen. et sp. nov.
Odonata: Protozygoptera	
Triassoneuridae nov.	*Triassoneura andersoni* gen. et sp. nov.
	T. heidiae sp. nov.
	T. regularis sp. nov.
Plecoptera	
?Gripopterygidae	
Euxenoperlinae	*Euxenoperla clara* sp. nov.
Blattodea	
Poroblattinidae	*Triassoblatta natalensis* (Zeuner) 1961
	T. robusta Riek 1974
	T. simplex sp. nov.
Mesoblattinidae	*Samaroblatta parvula* sp. nov.
	Samaroblattella revelata gen. et sp. nov.
?Mantodea	
Mesorthopteridae	*Mesorthopteron similis* Riek 1974
Orthoptera	
Haglidae	*Hagla contorta* Riek 1974
Proparagryllacrididae	*Dordrechtia robusta* gen. et sp. nov.
Geinitziidae	*Fletchitzia picturata* gen. et sp. nov.
Hemiptera: Homoptera	
Mesogereonidae	*Triassogereon distinctum* gen. et sp. nov.
Dunstaniidae	*Fletcheriana magna* sp. nov.
	Dunstania petrophila sp. nov.
Cicadoprosbolidae	*Prosbolomorpha clara* Riek 1974
	Leptoprosbole lepida gen. et sp. nov.
Scytinopteridae	*Scytinoptera distorta* sp. nov.
Dysmorphoptilidae	*Tennentsia* gen nov. *protuberans* Riek 1974
Protopsyllidiidae	nymph
Megaloptera	
Euchauliodidae	*Euchauliodes distinctus* Riek 1974
Mecoptera	
Mesopanorpodidae	*Afristella delicatula* Riek 1974

Lepidoptera: Paratrichoptera	
Mesosetidae nov.	*Mesoses optata* gen. et sp. nov.
	M. magna sp. nov.
Coleoptera	
Cupedidae	*Moltenocupes townrowi* Zeuner 1961
Permosynidae	*Ademosyne speciosa* Riek 1974
	A. prisca Riek 1974
	A. reducta sp. nov.
	Umkomaasia depressa Zeuner 1961
?Silphidae	*Pseudosilphites natalensis* Zeuner 1961

SYSTEMATICS

ORDER *MEGANISOPTERA*

The order is recorded from the Upper Carboniferous of Europe and North America, Lower Permian of North America and the Urals, the Permian of the Archangel area, the Upper Permian of Australia and the Triassic of France, and possibly from the Triassic of Germany although assignment of the very incomplete wing of *Reisia gelasii* (Reis) remains in doubt (Carpenter 1931). A species is recorded from the Upper Triassic of southern Africa.

The largest known insects were Meganisoptera. Some species, however, were of a moderate size comparable with Recent Odonata. The Meganisoptera have a rather primitive basic wing venation although there are basal fusions between the veins MP and CuA, and Cu and anal stem. The dominant two families, Paralogidae and Meganeuridae, are distinguished on the branching of Rs and MA. The Triadotypidae have unusual branching of the cubito-anal field.

The new species resembles Paralogidae in the open venation, in which the arms of the first forking of Rs are divergent and MA is not expanded into a large sector before the middle of its length. The precostal field is short with Sc ending about level with or before the first forking of Rs, as in Paralogidae but also in Typhinae (Meganeuridae). The precostal field is long in Meganeurinae.

Family Paralogidae

Diagnosis. Venation open. Arms of the first forking of Rs divergent. MA not expanded into a large sector before the middle of the wing. Precostal field short, with Sc ending at or before the level of the first forking of Rs.

Genus **Triassologus** gen. nov.

Type species. Triassologus biseriatus sp. nov.

Diagnosis. Similar to *Oligotypus* and *Paralogus* as far as can be ascertained from the preserved portion of the wing but with a distinct double row of cells between the uppermost two branches of Rs, lower branch of Rs distinctly forked, and MA and MP subparallel until well after the first forking of Rs.

The genus resembles *Oligotypus* more than *Paralogus.*

Triassologus biseriatus sp. nov. (Fig. 1; Plate 1, fig. 5)

Type. C-Dt. II 764, in Bernard Price Institute.

Description. Apical half of wing but very incomplete caudally. Length as preserved *c.* 40 mm, indicating a wing length of *c.* 95 mm. Costal margin thickened, with a distinct median channel. Subcostal space narrowing apical with R very close to margin. Rs preserved only just distally of the first forking, the lower branch forking apparently before its middle and with the two branches divergent. Area between intercalated vein and upper branch of Rs with a double row of cells and area below with a single row. One cross-vein from R to the upper branch of Rs very much more oblique than the others. Cross-veins between MA and MP simple at least until the level of the forking of the lower branch of Rs. Cubital field only fragmentarily preserved but branches curving strongly to posterior margin.

ORDER *ODONATA*

Suborder Protozygoptera

The Protozygoptera differ from Zygoptera in not having a completely formed nodus, the discoidal cell is not closed basally and the subnodus is either not developed or not fully aligned with the incipient nodus.

The discoidal cell is not closed basally in the fore wing of the Recent species *Hemiphlebia mirabilis* Selys and *Chorismagrion risi* Morton but the nodus and subnodus are fully formed. The discoidal cell is not closed basally in *Permagrion falklandicum* (Tillyard 1928) from the Upper Permian of the Falkland Islands and as the nodus is not completely formed it is preferable to refer the Permagrionidae to the Protozygoptera although Tillyard had considered it as the oldest representative of the Zygoptera.

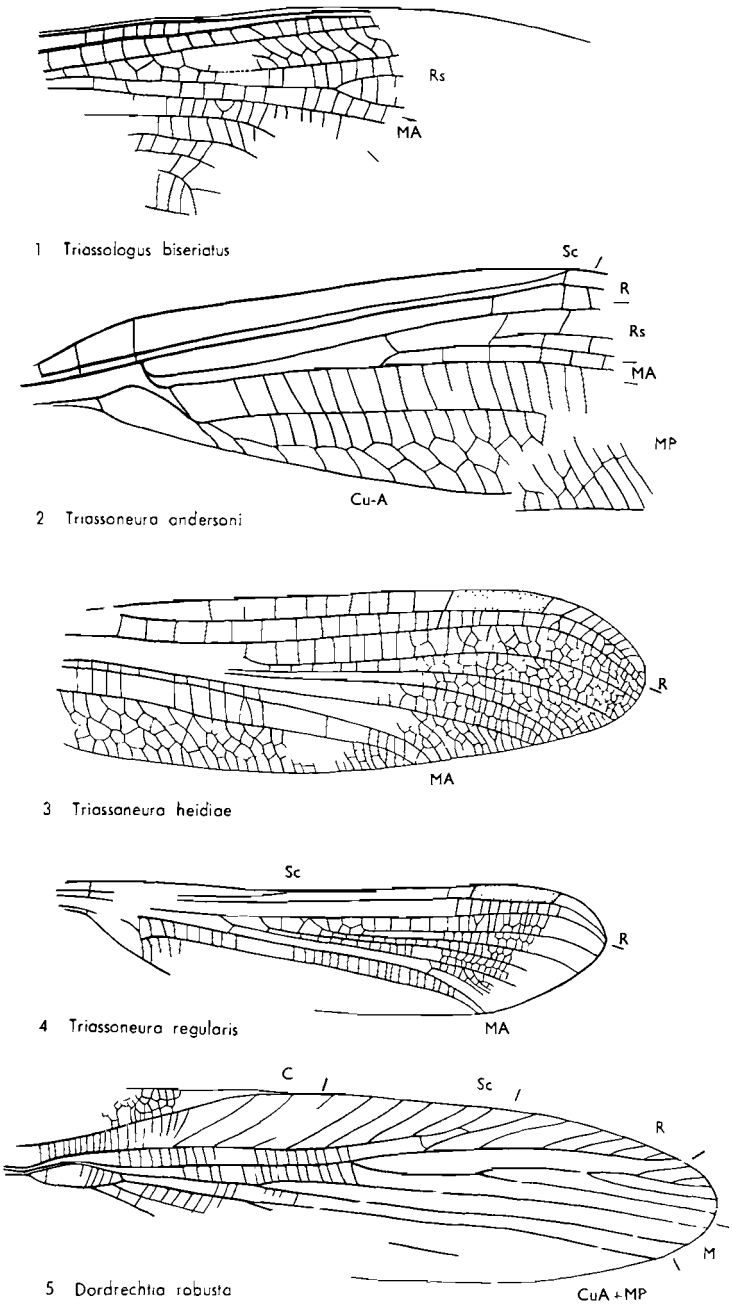
Species from the Upper Triassic of southern Africa resemble *Permagrion falklandicum* in many characters, including the open discoidal cell, but the nodus and subnodus are even less defined. However, the basal venation is even more reduced than in many Recent species. The species are referred to a separate family of the Protozygoptera.

Family **Triassoneuridae** fam. nov.

Protozygoptera with Sc extending almost to the middle of the wing. The two antenodals situated towards the base of the costal space. Postnodals not in line with the cross-veins behind them. Subnodus not developed, the cross-vein more or less transverse. Cu+A free from MP only from the lower corner of the discoidal cell.

It would appear that the stem of Cu+A is anastomosed with MP, to the discoidal cell, and not with the hind margin of the wing. This is similar to the condition in typical Protozygoptera and in *Permagrion* except that the anastomosis is more extensive distally.

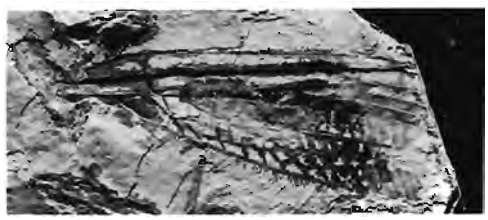
The family differs from the Permagrionidae in the more distal position of the incipient node, the non-development of a subnodus, the non-alignment of the postnodals with the cross-veins behind them and the anastomosis of Cu+A with MP to the lower corner of the discoidal cell.



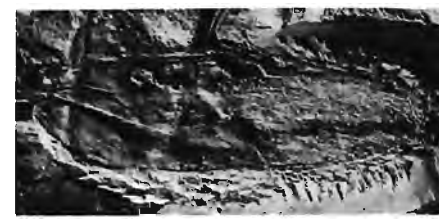
Figs 1–5. (1) *Triassologus biseriatus* gen. et sp. nov. Holotype C-Dt II 764; (2) *Triassoneura andersoni* gen. et sp. nov. Holotype C-Dt II 763 b; (3) *Triassoneura heidiae* sp. nov. Paratype C-Dt II 762 a; (4) *Triassoneura regularis* sp. nov. Holotype C-Dt II 760 a; (5) *Dordrechtia robusta* gen. et sp. nov. Holotype C-Dt II 792 b, reversed and two folds in wing flattened.

1 Triassoneura heidiae

5 Triassologus biseriatus



2 Triassoneura andersoni



6 Leptoprosbole lepida

3 Triassoneura heidiae

7 Scytinoptera distorta

4 Triassoneura regularis

8 Protopsyllidiid nymph

PLATE 1

(1) *Triassoneura heidiae* gen. et sp. nov. Holotype C-Dt II 791 b reversed; (2) *Triassoneura andersoni* gen. et sp. nov. Holotype C-Dt II 763 b; (3) *Triassoneura heidiae* gen. et sp. nov. Paratype C-Dt II 762 a; (4) *Triassoneura regularis* gen. et sp. nov. Holotype C-Dt II 760 a; (5) *Triassologus biseriatus* gen. et sp. nov. Holotype C-Dt II 764; (6) *Leptoprosbole lepida* gen. et sp. nov. Holotype C-Dt II 790 a reversed; (7) *Scytinoptera distorta* sp. nov. Holotype C-Dt II 782 b; (8) Protopsyllidiid nymph. C-Dt II 786 a and b.

Genus **Triassoneura** gen. nov.

Type species. Triassoneura andersoni sp. nov.

Diagnosis. Postnodals numerous. Costal space distinctly widened at second antenodal. MA and MP widely separated at base and subparallel over basal half, converging at wing margin, connected only by simple cross-veins. Arculus and distal margin of discoidal cell not aligned. Subquadrilateral area very broad, with

MP + Cu + A distinctly bent at the level of the arculus. A median line of polygonal cells between MP and hind margin.

The genus is represented by three species in the Upper Triassic of southern Africa. The species differ in the development and form of the cross-veins, and in size.

Triassoneura andersoni sp. nov. (Fig. 2; Plate 1, fig. 2)

Etymology The species is named for John Anderson in appreciation of his help and interest in fossil insects from this series.
Type. C-Dt. II 763 a, b, in Bernard Price Institute.

Description. Basal half of wing to and including the incipient node. Wing narrowing gradually towards base and then abruptly narrowed at level of first antenodal. Venation clear almost to base but basal swellings of veins not preserved. Length as preserved along R *c.* 34 mm indicating a wing length of *c.* 70 mm. Cross-vein from Sc to R slightly before apex of Sc, and transverse. Cross-vein from R to Rs at apex of Sc transverse. Rs and MA distinctly closer to one another near base than R and Rs. Rs with two branches or intercalated veins before the apex of Sc. Cells between MA and MP about twice as high as wide. Cu+A with 6 branches to hind margin before the first polygonal cell. MP distally with 4–5 cells between the branches to the hind margin. Spicules, represented by pits, dense on all cross-veins and some intercalated veins, more openly spaced but regular on all other veins and posterior margin. Costal margin with spicules fine.

Triassoneura heidiae sp. nov. (Fig. 3; Plate 1, figs 1, 3)

Etymology. The species is named for Heidi Anderson for her enthusiastic and material support in my study of fossil insects from southern Africa.
Types. C-Dt. II 791 a, b and paratypes 762 a, b and 759 a, b in Bernard Price Institute.

Description. Holotype. An almost complete wing preserving the narrowed base and hind margin. The nodal area is distinct only on the counterpart. Length as preserved *c.* 47 mm, indicating a wing length of *c.* 50 mm. Similar to *andersoni* basally except in much smaller size, and development of cross-veins especially in posterior section of wing. Node, as in *andersoni*, not fully formed and without subnodus, only a transverse cross-vein. MA and MP only moderately separated over basal half, the cells between them only a little higher than wide. Area between MP and hind margin similar to *andersoni* but with less defined single line of polygonal cells. Distal half of wing with pterostigma very distinct, very much longer than wide. R strongly curved subparallel to margin at apex. Rs with 5 main terminal branches. Cells irregular between all branches towards margin, posterior branch with a subpectinate series of short branches to margin. MA simple to wing margin. MP and MA widest apart slightly beyond the middle, distinctly converging at apices and connected by simple cross-veins to the margin. MP almost straight, with an extensive series of short, subpectinate branches to the margin, with cross-veins forming irregular cells. Cu+A only about half as long as MP. Spicules dense on the cross-veins.

C-Dt. II 762 a, b is the distal half of a wing from the region of the nodus. Nodus preserved but obscure. Length as preserved *c.* 52 mm, width *c.* 10 mm.

C-Dt. II 759 a, b is the distal half of a wing from the nodus. It is clear only towards apex and at nodus, but shows the distal convergence of MA and MP and the absence

of a defined subnodus. Length as preserved *c.* 34 mm, width *c.* 10 mm. Length from nodus to apex *c.* 30 mm.

C-Dt. II 758 a, b is a poorly preserved whole wing with some parts missing or obscure, that can probably be referred to the species. C-Dt. II 794, 793, 871 and 757 are small fragments that are only doubtfully referred to the species.

Triassoneura regularis sp. nov. (Fig. 4; Plate 1, fig. 4)

Type. C-Dt. II 760 a, b, in Bernard Price Institute.

Description. An almost complete wing but all areas not clearly preserved, and a small area of hind margin near wing base and a small area in the region of the discoidal cell not preserved. The counterpart preserves only two small fragments in the region of the pterostigma. Length as preserved *c.* 50 mm, width *c.* 10 mm, from nodus to apex *c.* 25 mm. With regular double row of cells between the branches of Rs. A distinct long marginal intercalary between posterior branch of Rs and MA as well as a series of short posterior branches from Rs to wing margin. MP slightly up-arched at origin from point slightly below discoidal cell. Distal branches of MP to wing margin interconnected by 4 or 5 cross-veins. Apparently without a line of polygonal cells between middle of MP and the wing margin. Spicules, represented by fine pits or tubercles, present on all cross-veins, 25 to 30 per mm. Slightly larger and much more openly spaced spicules on main veins, 3 to 5 per mm.

Note. The species is similar to *heidiae* except for the more regular cellular development of the cross-veins and a more defined intercalated vein between the posterior branch of Rs and MA. The two species are similar in size.

ORDER *PLECOPTERA*

Family ?Gripopterygidae

Subfamily Euxenoperlinae Riek 1975

This subfamily was established for *Euxenoperla* recorded from the Upper Permian of southern Africa and the Upper Triassic of Australia and *Euxenoperlella* from the Upper Permian of southern Africa. The genera differ in the branching of Rs and development of the cross-veins. The subfamily is distinguished by the up-arching of Rs at the first inter-radial cross-vein, the large second radial cell widened in the middle or at apex when there are four radial cells, and the presence of at least three radial cells.

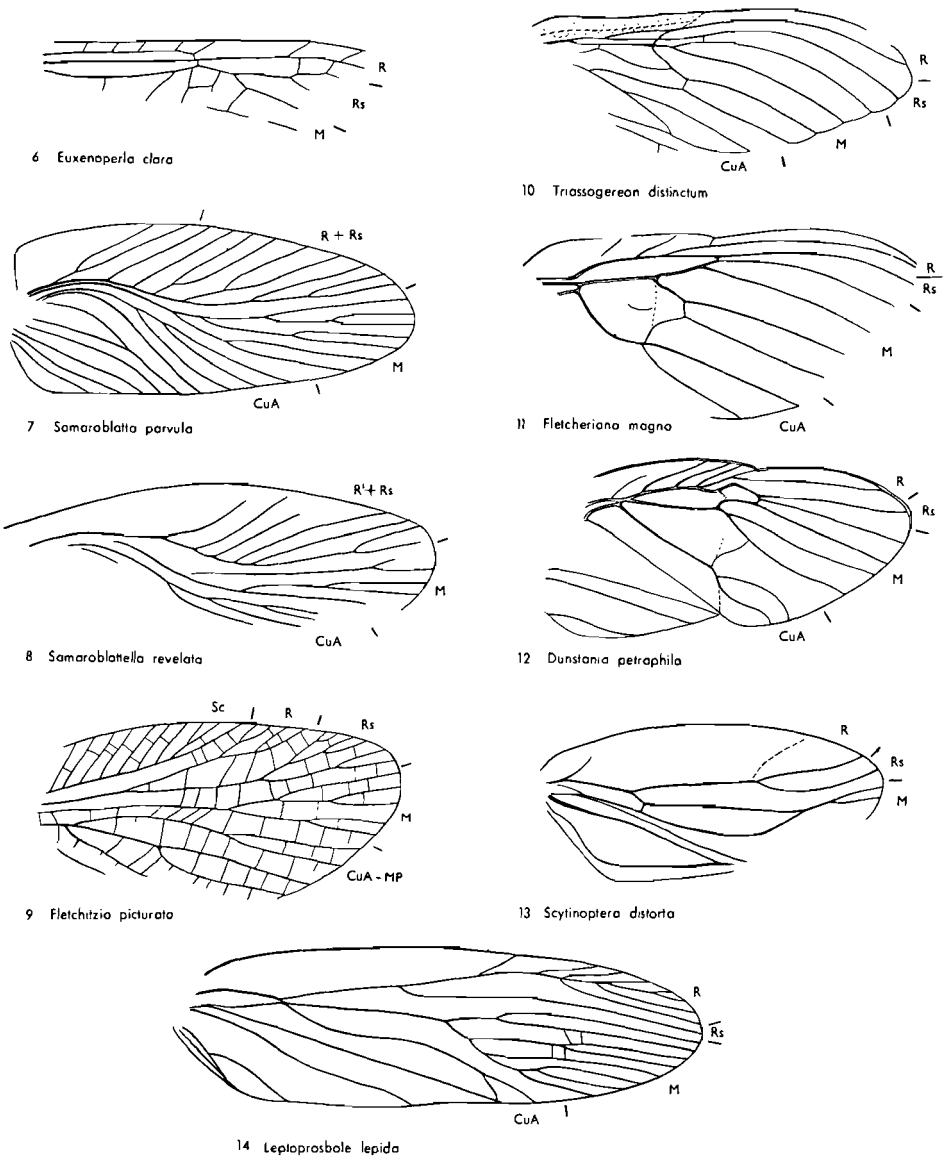
A species from the Upper Triassic of southern Africa is referred to *Euxenoperla.*

Euxenoperla clara sp. nov. (Fig. 6; Plate 2, figs 1, 2)

Type. C-Dt. II 773 a, b in Bernard Price Institute.

Description. Distal three-quarters of fore wing with extreme apex and posterior portion missing. The counterpart shows portion of an underlying wing. Length as preserved *c.* 18 mm indicating a wing length of *c.* 28 mm. Sc with numerous cross-veins to wing margin, apical one very oblique. R with at least two short branches to wing margin. Rs 3-branched, with two branches arising from the second radial cell. Second radial cell very long, widest close to apex at origin of second branch of Rs.

Four radial cells. At least four cross-veins between Rs and M, the first very oblique and well before the first inter-radial cross-vein, second and third interconnected by a transverse cross-vein. Cu and anal veins not preserved.



Figs 6–14. (6) *Euxenoperla clara* sp. nov. Holotype C-Dt II 773 a, b; (7) *Samaroblatta parvula* sp. nov. Holotype C-Dt II 765 a, b; (8) *Samaroblattella revelata* gen. et sp. nov. Holotype C-Dt II 766 a, b; (9) *Fletchitzia picturata* gen. et sp. nov. Holotype C-M-FI 256; (10) *Triassogereon distinctum* gen. et sp. nov. Holotype C-Dt II 783 a; (11) *Fletcheriana magna* sp. nov. Holotype C-Dt II 784 a, b; (12) *Dunstania petrophila* sp. nov. Holotype C-Dt II 781 b; (13) *Scytinoptera distorta* sp. nov. Holotype C-Dt II 782 b; (14) *Leptoprosbole lepida* gen. et sp. nov. Holotype C-Dt II 790 a reversed.

1 Euxenoperla clara

5 Triassoblatta simplex

2 Euxenoperla clara

6 Triassoblatta simplex

3 Triassoblatta simplex

7 Triassoblatta simplex

4 Samaroblatta parvula

8 Samaroblatta parvula

PLATE 2

(1) *Euxenoperla clara* sp. nov. Holotype C-Dt II 773 a; (2) *Euxenoperla clara* sp. nov. Holotype C-Dt II 773 b; (3) *Triassoblatta simplex* sp. nov. Holotype C-Dt II 770 b; (4) *Samaroblatta parvula* sp. nov. Holotype C-Dt II 765 b; (5) *Triassoblatta simplex* sp. nov. Paratype C-Dt II 769 b; (6) *Triassoblatta simplex* sp. nov. C-Dt II 353 a; (7) *Triassoblatta simplex* sp. nov. Paratype C-Dt II 352 b; (8) *Samaroblatta parvula* sp. nov. Holotype C-Dt II 765 a.

Note. The species differs from the Upper Permian species of southern Africa in having more cross-veins in the costal space, the more oblique apex of Sc, second radial cell widest towards apex, radial space with two cross-veins to the apical branch of Rs and irregular cross-veins between Rs and M. The last character may be an individual variation: it is not usual for these cross-veins to be irregular in Plecoptera but they are irregular in some (Recent) Eustheniidae.

ORDER *BLATTODEA*

Two families, Poroblattinidae and Mesoblattinidae, are represented in the fauna. They differ in the development of Sc. The archedictyon has been replaced by cross-veins in both families.

Family Poroblattinidae

Sc is distinct, and distinctly branched, although relatively short. The family occurs commonly in the Permian and early Mesozoic but is also recorded from the Upper Carboniferous.

Genus *Triassoblatta* Tillyard 1919

Two species were recorded in an earlier paper (Riek 1974) from the Upper Triassic of southern Africa. A third species is recorded from Bird's River. Each of the three recorded species is from a different locality in the Molteno Formation. The clavus appears to be the most diagnostic area of the wing in differentiating between the species. Fortunately, the clavus is attached to most of the preserved wings.

The genus is recorded also from the Upper Triassic of Australia.

Triassoblatta simplex sp. nov. (Plate 2, figs 3, 5–7)

Types. C-Dt. II 770 a, b and paratypes 352 a, b, 768 a, b and 772 a, b in Bernard Price Institute.

Description. Holotype. Complete tegmen except for apex, parts of distal margins and posterior part of clavus. Length as preserved *c.* 15 mm indicating a wing length of *c.* 19 mm. Costal space narrow, with an oblique groove from base that does not cross any definitive branch of Sc. Sc 4-branched, branches simple, with faint indications of more proximal branches in the thickened basal area of the costal space. Sc extending slightly beyond the level of the apex of the clavus. Clavus with simple, subparallel veins, the distance between the first two veins only slightly greater than that between the other veins. R sigmoidally curved only over basal portion. Both M and CuA branching towards base, with M branching slightly more distally than CuA. CuA with subpectinate branching of main branches.

C-Dt. II 352 a, b is complete except for base and apex. Length as preserved *c.* 12 mm. Sc has four distinct terminal branches but there are faint indications of more basal ones. Clavus with 7 or 8 simple subparallel veins.

C-Dt. II 772 a, b consists of a complete fore wing and part of a hind wing but the specimen is weathered and the venation partly obscured by an overlying deposit of fine mud.

C-Dt. II 768 a, b is a complete fore wing except for the extreme base. The branching of Sc is not completely preserved but on the branching of M and CuA it is referred to this species.

C-Dt. II 353 a, b differs from the above specimens in the branching of Sc. Although Sc is 4-branched the branches arise on two stems, as in *natalensis* (Zeuner) from Upper Umkomaas. However, although the clavus is crumpled, it would appear that the veins are simple and subparallel.

C-Dt. II 769 a, b is a complete but slightly weathered wing.

Notes. The species resembles *natalensis* in general shape but differs noticeably in the structure of the clavus and, usually, to a less extent in the branching of Sc. In the latter character it resembles the Australian species of the genus. This species differs noticeably from *robusta* Riek from Askeston both in wing shape and structure of the clavus.

Family Mesoblattinidae

This is one of the dominant families of Blattodea in the Mesozoic but it is recorded even as early as the Upper Carboniferous. It is more specialized than the Poroblattinidae in that Sc is very reduced and usually not clearly separable from R+Rs which together form a series of forward branches to the costal margin.

A species from the Upper Triassic of southern Africa is referred to the family and placed in *Samaroblatta*, a genus recorded from the Upper Triassic of Australia. A second species is referred to a new genus with no known close relatives.

Genus *Samaroblatta* Tillyard

Samaroblatta Tillyard 1919: 373.
Striatotegmen Haughton 1924: 334 **(syn. nov.)**
Type species. Samaroblatta reticulata Tillyard 1919: 374.

Diagnosis. Humeral area broad at base, no longer than clavus. Sc not clearly distinguishable from R+Rs. Stem of Sc + R + Rs strongly sigmoidally curved. Clavus with most of veins simple and ending on wing margin.

Tillyard (1919) named five species from the Upper Triassic of Ipswich, Australia.

Haughton (1924) described *Striatotegmen africanum* from the Upper Triassic Cave Sandstone (Stormberg Series) from a nearly complete specimen. *Striatotegmen* was said to differ from *Samaroblatta* in the shorter and narrower humeral (=costal) space and in that the distal portion of R probably reached the wing apex. The difference in R, if in fact it is valid, is not significant, and the narrow costal space in *Striatotegmen* is almost certainly due to distortion in preservation.

Samaroblatta parvula sp. nov. (Fig 7; Plate 2, figs 4, 8; Plate 3, fig. 5)

Type. C-Dt. II 765 a, b in Bernard Price Institute.

Description. Tegmen complete except for wing margin postero-apically. Length *c.* 8 mm. Wing rather broad, broad at base, apex rounded. Humeral space very wide at base, short, ending well before the level of the apex of the clavus. First distinct branch of Sc+R+Rs 3-branched, the following branches simple. Sc+R+Rs ending well before wing apex. M occupying a large area at wing apex. CuA only 3-branched. CuP not strongly curved at margin. Clavus with veins simple and ending on wing margin, except for looping (anastomosis) of first and second about the middle of their lengths. First vein in clavus widely separated from CuP and first and second widely separated near base. With interlacated veins between the venation less defined on clavus, and most distinct between branches of M and CuA.

C-Dt. II 785 is the basal half of a slightly smaller wing, apparently of this species. Length as preserved *c.* 5 mm indicating a wing length of *c.* 6,5 mm. Intercalated veins and dense cross-connections to venation well developed over whole wing, including clavus.

The species differs from Australian species in the shorter humeral (costal) space, less branched CuA and looping of the first two veins in the clavus. In the distinct intercalated veins and three branches to the basal branch of Sc+R+Rs it resembles the Australian species *intercalata* Tillyard. As the clavus is not preserved in *intercalata* it is not known whether the two species were similar also in the short humeral space.

Genus **Samaroblattella** gen. nov.

Type species. Samaroblattella revelata sp. nov.

Diagnosis. Wing rather narrow. Costal space not widened at base, but with distinct long groove extending to wing margin beyond the level of the apex of the clavus. Sc not defined. R+Rs distinctly sigmoidally curved, with only a few branches. M with few branches. CuA subpectinately branched, branches directed distally towards wing apex. Clavus not preserved. Intercalated veins between the venation and connected to it by dense somewhat irregular cross-veins.

The genus resembles *Samaroblatta* in the sigmoidally curved stem of Sc+R+Rs and *Samaroblatta intercalata* in the development of intercalated veins but in most other respects it is very distinct. Sc+R+Rs has very few branches and the costal space is very narrow, and not at all widened at base.

Samaroblattella revelata sp. nov. (Fig. 8; Plate 3, fig. 6)

Type. C-Dt. II 766 a, b in Bernard Price Institute.

Description. Tegmen, complete except for clavus. Length *c.* 14 mm. Costal space narrow, widest at and beyond middle. R+Rs with six branches, the basal ones almost transverse. M with three main branches, the upper two branching again near margin. CuA 5-branched.

BLATTODEA GEN. ET SP. INDET.

C-Dt II 870 a, b is the abdomen and metanotum of a nymphal cockroach.

ORDER *ORTHOPTERA*

Family Proparagryllacrididae Riek

Riek (1956) described *Proparagryllacris crassifemur* from the Upper Triassic of Australia and referred the species to a new subfamily of Gryllacrididae. Sharov (1968) described a number of species from the Lower Triassic of Madygen and raised the group to family status. He was of the opinion that the Proparagryllacrididae are not related to Gryllacrididae but was undecided on the affinities of the family. The Lower Triassic species had long filiform antennae, the legs were long and said to be cursorial but the hind legs were considerably longer than the other legs, and the tarsi were 5-segmented. The ovipositor was broad, knife-shaped and serrated on the ventral valves which shows, according to Sharov (1968), that the eggs were laid into plant tissue. The Australian Upper Triassic species is very imperfectly known but the hind leg was large and the femur distinctly enlarged basally. Although Sharov (1968) was of the opinion that the structure of the costal vein differed from that in

the Gryllacrididae I fail to see any significant difference between the two for in neither family do the proximal branches of Sc cross the costal vein into the precostal space.

The tarsi are 5-segmented, with a well developed arolium, as in Oedischioidea, and there is certainly a distinct similarity between the Proparagryllacrididae and the Tcholmanvissiidae (Oedischioidea) in venation and probably a greater similarity in leg structure, especially the hind leg, than indicated by Sharov. Proparagryllacrididae differ from Tcholmanvissiidae in the reduced branching of the veins and the more transverse alignment of the stem of MP before it anastomoses with CuA 1.

Proparagryllacrididae differ from Gryllacrididae in venation only in the 2-branched MA. They differ in body structure in having 5-segmented tarsi and only a moderately enlarged hind leg. The family is referred to the Gryllacridoidea as a primitive family, retaining 5-segmented tarsi.

A species from the Upper Triassic of southern Africa is referred to the family. It may be closely related to *Proparagryllacris* from the Upper Triassic of Australia but as that genus is so imperfectly known, it seems preferable to establish a new genus for this almost complete wing.

Genus ***Dordrechtia*** gen. nov.

Type species. Dordrechtia robusta sp. nov.

Diagnosis. Pre-costal area large and filled with irregular cellules. Sc ending well before wing apex, with a number of forward branches to wing margin. R extending to wing apex, with a number of forward branches to wing margin. Rs arising distally, with several branches. M 2-branched, upper branch not deflected towards Rs. Stem of MP short and almost transverse. CuA 1 + MP at least 2-branched. CuA 2 and CuP parallel at least basally. Stem of M deflected towards R near base and Cu away from it to form a distinct widened area between the stems of M and Cu close to wing base.

Dordrechtia robusta sp. nov. (Fig. 5; Plate 3, fig. 2)

Type. C-Dt. 11 792, a, b in Bernard Price Institute.

Description. Almost complete fore wing except for anal field and base of pre-costal area, with posterior half of wing folded forward over anterior half. Length *c.* 68 mm. Pre-costal space large, with C extending more than one third of length of wing. Sc with eight main branches, the apical six to the wing margin. Costal space broad. R with a series of seven forward branches to wing margin. Rs arising beyond the middle of R, 5-branched. M branching distinctly before the origin of Rs. CuA 1 + MP with first forking level with forking of M. Apices of CuA 2 and CuP not preserved. Cross-veins well developed and simple over most of wing.

Family Geinitziidae Handlirsch 1908

The family is recorded from the Lower Jurassic of Germany. Handlirsch (1906–8, 1925) was of the opinion that the family was related to Mantodea. Martynov (1937) and Bode (1953) placed the family in Protoperlaria (=Paraplecoptera in part), and Sharov (1962, 1968) and Fujiyama (1973) placed it in Protoblattodea (in which they included Paraplecoptera). Zeuner (1939) referred the subfamily Geinitziinae provi-

sionally to the Prophalangopsidae (=Haglidae) (Orthoptera) and Carpenter (1954) synonymized it with Prophalangopsidae (=Haglidae). Sharov (1968) excluded the Geinitziidae from the Orthoptera on the apparent absence of a precostal field and a

1 Fletchitzia picturata

5 Samaroblatta parvula ?

6 Samaroblattella revelata

2 Dordrechtia robusta

3 Mesoses optata

7 Ademosyne reducta

4 Mesoses magna

8 Ademosyne reducta

PLATE 3

(1) *Fletchitzia picturata* gen. et sp. nov. Holotype C-M-FI 256; (2) *Dordrechtia robusta* gen. et sp. nov. Holotype C-Dt II 792 a reversed; (3) *Mesoses optata* gen. et sp. nov. Holotype C-Dt II 774 a; (4) *Mesoses magna* gen. et sp. nov. Holotype C-Dt II 789 b; (5) *Samaroblatta parvula*? C-Dt II 785; (6) *Samaroblattella revelata* gen. et sp. nov. Holotype C-Dt II 776 b reversed; (7) *Ademosyne reducta* sp. nov. Holotype C-Dt II 780 b reversed; (8) *Ademosyne reducta* sp. nov. Paratype C-Dt II 777 a.

costa, and the double row of cells between CuA 1 and CuA 2. However, the Geinitziidae have the orthopteroid and protoblattodean character of fusion of a posterior branch of M (=MP) with CuA. A clavus is not developed as it is in Protoblattodea. Even though M is at least 5-branched, the family is referred to the Orthoptera rather than Protorthoptera because of the development of a distinct Cun, but relationship within the Orthoptera is not clear.

Sharov (1962) referred *Shurabia ovata* (Martynov 1937) from the Jurassic of central Asia to the family. The base of the wing is not preserved so the relationship between M and CuA is not known. Therefore there is some doubt as to whether the species should be referred to the Orthoptera or Paraplecoptera, but on the forking of M more basally than the origin of Rs the species should probably be referred to the Paraplecoptera.

A wing from the Upper Triassic of southern Africa is similar to *Geinitzia* in most respects and is referred to the family.

Genus **Fletchitzia** gen. nov.

Type species. Fletchitzia picturata sp. nov.

Diagnosis. Wing of broad, oval form. Sc long and costal space wide, with numerous branches from Sc to wing margin. R and Rs branched dichotomously at apex. MA with several branches, first forking distinctly distal to origin of Rs. Stem of MP oblique but short. CuA occupying a large area of the wing. Cross-veins between CuA 1 and CuA 2 simple.

The genus differs from *Geinitzia* in the broader form, the dichotomic branching of Rs, distal branches of MA and the simple cross-veins between CuA 1 and CuA 2.

Fletchitzia picturata sp. nov. (Fig. 9; Plate 3, fig. 1)

Type. C-M.F.I 256 in Bernard Price Institute.
Type locality. Mount Fletcher.

Description. An almost complete fore wing but base, CuP and anals not preserved. Length as preserved *c.* 18 mm indicating a wing length of *c.* 22 mm. Sc extending well past middle of wing. Costal veinlets mostly simple. R with 4 dichotomic terminal branches. Rs with 6 terminal branches. MA 5-branched, branching distally, almost level with first branching of Rs. MP oblique but relatively short. CuA 1 + MP with 4 terminal branches. CuA 2 arising very slightly after (and not, as usual, before) the anastomosis of MP with CuA. Cross-veins openly spaced over whole wing. Wings patterned, with dark areas bordering the cross-veins, tending to produce narrow transverse fasciae.

ORDER *HEMIPTERA*

Suborder Homoptera

Superfamily Cicadoidea

Two families represented in the Recent fauna, Cicadidae and Tettigarctidae, are referred to the superfamily as well as a number of families with only fossil representation.

The Prosbolidae is certainly the most primitive family of the Cicadoidea. There is usually a nodal break in the fore margin and usually a nodal line across the middle of the fore wing, and M and CuA have deep forks arising on the nodal line and usually almost in line with the origin of Rs. The fore margin of the hind wing is deeply emarginate and the anal field is markedly expanded. The Cicadoprosbolidae are transitional between Prosbolidae and Cicadidae. They are sometimes combined with the Tettigarctidae from which they differ mainly in the basal associations of the veins, in the extension of CuA 2 beyond the nodal line and in the somewhat more distal origin of Rs but Rs arises well before the nodal line and in this respect differs from Prosbolidae. The Cicadoprosbolidae may also represent the base line leading to the 'palaeontinoid complex', a group of three families, Palaeontinidae, Dunstaniidae and Mesogereonidae, sometimes separated from the Cicadoidea as a distinct superfamily because of their specialized wing venation but they are all obviously derivatives of the Prosbolidae. The wings are broad, with the costal space expanded in Palaeontinidae and Dunstaniidae and very long and narrow with almost linear costal space in Mesogereonidae. There is a node on the fore margin and a transverse nodal line at least anteriorly in all three families.

The Cicadoprosbolidae have been recorded previously from this fauna (Riek 1974). The Dunstaniidae and Mesogereonidae are added to the fauna, together with a second genus of Cicadoprosbolidae. As these families become better known it is increasingly difficult to define the differences between them.

Family Mesogereonidae

The Mesogereonidae, from the Upper Triassic of Australia, were very specialized Cicadoidea. The wings are markedly elongate, and there is an ambient vein extending over most of the wing margin. The ambient vein is widely separated from the wing margin posteriorly but is close to the margin anteriorly. Contrary to the statement by Becker-Migdisova & Wootton (1965), R and Rs are not united with the costa although all three veins are very close to one another. This part of the wing is comparable with that in *Palaeontinodes* (Palaeontinidae) except that the costal space is much narrower in *Mesogereon* than in *Palaeontinodes*. Both Becker-Migdisova (1949, 1961, 1962) and Evans (1956, 1963) referred the Mesogereonidae to Homoptera to a position close to Palaeontinidae. Becker-Migdisova & Wootton (1965) considered that the Mesogereonidae was a specialized family of the Palaeontinoidea, a superfamily that they separated from the Cicadoidea, and to which they referred the Palaeontinidae, Dunstaniidae and Mesogereonidae. Although the species referred to these families are very specialized in some attributes they are all derivatives of the Prosbolidae and related to Tettigarctidae and Cicadidae: they are all referred to the Cicadoidea.

A marginal node and a nodal line between R and Rs is present in *Mesogereon* although Evans (1956) considered that 'a transverse line of weakness is not to be expected in *Mesogereon* in a wing which has a very small area situated proximally of the position of where a nodal line would lie if present, as in such a position it would be a hindrance and not an asset for flight purposes'.

The family differs from Palaeontinidae in the development of an ambient vein,

in the elongated form of the wing with very narrow costal space, and in the more or less longitudinal alignment of the two cross-veins between M and CuA. It differs from Dunstaniidae in which, also, there is an ambient vein, in wing shape and absence of veinlets in the costal space.

A genus from the Upper Triassic of southern Africa in which the wing is of less elongated form than in *Mesogereon* is referred to the family. This genus shows the origin of Rs from about the middle of the costal space, as in Dunstaniidae and Cicadoprosbolidae. Rs arises from the same point as M in Palaeontinidae.

Genus **Triassogereon** gen. nov.

Type species. Triassogereon distinctum sp. nov.

Diagnosis. Wing similar to that of *Mesogereon* but less elongated, with the node only slightly before the middle of the wing and the nodal line extending from fore margin to the basal fork of M and then sharply angled to continue for a short distance along M 3+4 to the point of origin of the first cross-vein to CuA. M 1+2 forking before M 3+4. Rs arising from R about the middle of the costal space.

Triassogereon distinctum sp. nov. (Fig. 10; Plate 4, fig. 1)

Type. C-Dt. II 783 a, b in Bernard Price Institute.

Description. Fore wing complete, except for most of clavus. Length *c.* 35 mm. Costal space deeply longitudinally grooved and closely rather coarsely punctate (? insertions of dense setae). Cross-vein from Rs to M1 level with node. Lower branch of fork of M 3+4 appearing as a cross-vein. Distal cross-vein between M 3+4 and CuA subparallel to CuA for most of its length, basal one somewhat sigmoidally curved and also connected to stem of M by a short cross-vein, proximal origins from CuA not preserved. Clavus very small, apparently heavily sclerotized. Wing margin widely separated from ambient vein (preserved only in the region of CuA).

Family Dunstaniidae

The family is recorded from the Upper Triassic of Australia and the Triassic of central Asia, and probably Permian of Siberia (Becker-Migdisova 1961). The fore wing has a distinct prosbolid form even though the costal space is markedly expanded. The family is most probably ancestral to the Palaeontinidae. Rs arises only some distance closer to the base than the nodal line and not close to the base as in Palaeontinidae. Rs arises similarly in Cicadoprosbolidae, which are more generalized species than Dunstaniidae. Rs arises about in line with the node in most Prosbolidae.

Tillyard (1916) placed the Dunstaniidae in Lepidoptera. Meyrick (1916) suggested that it should be referred to the Homoptera. Later, Tillyard (1918) redescribed the original specimen as a fore and not a hind wing, described an additional two genera and species, and transferred the family to Heteroptera (Hemiptera). This placement was accepted by Handlirsch (1937–9), Jeannel (1947, 1949), Evans (1950), Laurentiaux (1953), Carpenter (1954) and Oberberger (1958). Subsequently, Tillyard (1926) stated that the family was ancestral to Pentatomoidea. Tillyard (1918) presented a reconstruction of *Dunstania pulchra* based on a composite of the three described species of the Dunstaniidae. All three wings are fragmentary but most essential

features are preserved in '*Dunstaniopsis triassica*': the three wings are probably those of one slightly variable species.

Becker-Migdisova (1949, 1950, 1962) disagreed with placement in Heteroptera and referred the Dunstaniidae to a position close to the Palaeontinidae (Cicadomorpha). Evans (1956) described *Fletcheriana triassica* from fore and hind wings from the Upper Triassic of Brookvale, Australia, and referred the species to the Cicadomorphidae (=Palaeontinidae). He compared the genus with *Pseudocossus*, from which it differs significantly in the more distal origin of Rs. *Fletcheriana* is transferred to the Dunstaniidae on the relatively distal origin of Rs in which it resembles *Cicadoprosbole* and differs from Palaeontinidae. Becker-Migdisova & Wootton (1965) described two genera and species of Dunstaniidae from the Triassic of central Asia, and confirmed Becker-Migdisova's placement of the Dunstaniidae in Homoptera as a family closely allied to the Palaeontinidae.

Two species from the Upper Triassic of southern Africa are referred to the family. One very large wing resembles *Fletcheriana triassica* and a somewhat smaller wing can be compared with *Dunstania pulchra*.

Genus *Fletcheriana* Evans

Fletcheriana Evans 1956: 224.
Type species. Fletcheriana triassica Evans 1956: 225.

Diagnosis. Fore wing broad. Costal space markedly expanded and with a series of costal veinlets from R to the wing margin. Rs arising from an intermediate position between the origin of M and the node. M 4-branched, first branching at the nodal line. CuA markedly deflected towards the caudal margin at its base. CuA 2 extending to wing margin beyond the nodal line. With only one distinct cross-vein between M and CuA.

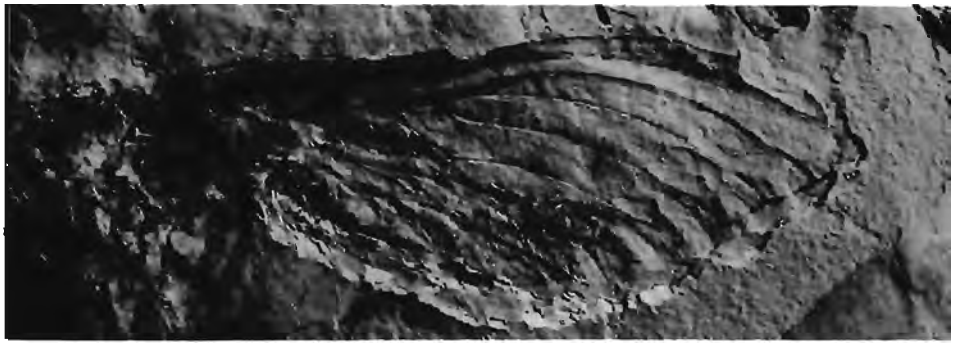
Hind wing broad, shorter than fore wing. Costal space markedly expanded over basal half. Fore margin distinctly emarginate in middle.

Fletcheriana magna sp. nov. (Fig. 11; Plate 4, fig. 2)

Type. C-Dt. II 784 a, b in Bernard Price Institute.

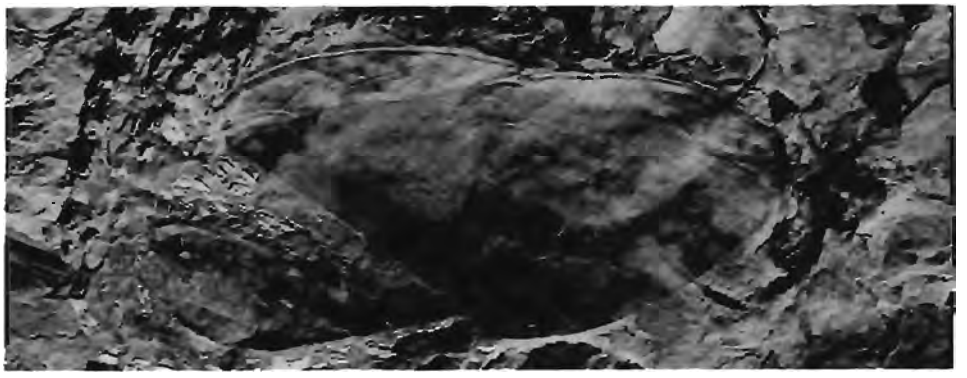
Description. Fore wing, mostly complete except for clavus and wing apex. Length as preserved *c.* 70 mm, indicating a wing length of *c.* 75 mm. Costal space not as expanded as in *triassica*, with indications of three cross-veins, in the distal half, surface with fine, close punctures in posterior half bordering R. Rs arising only a very short distance basal to the nodal line, and only slightly kinked at the nodal line. M arising from the thickened basal stem of R, but CuA connected to this common stem by a short cross-vein. Stem of CuA regularly, but strongly, curved. Nodal line almost straight from forking of M to forking of CuA. A short transverse ridge from middle of this section of the nodal line and directed to wing base. Wing membrane basal to nodal line rather smooth but with dense fine tubercles over most of the surface, membrane distal to nodal line appearing to be less heavily sclerotized but with tubercles slightly larger, more grouped in certain areas between the venation proximally and becoming regular and more openly spaced distally.

The species differs from *triassica* in the less expanded costal space, slightly more distal origin of Rs and more regularly curved CuA.



1 Triassogereon distinctum

2 Fletcheriana magna



3 Dunstania petrophila

4 Tennentsia protuberans

[*Caption on opposite page*]

Genus *Dunstania* Tillyard

Dunstania Tillyard 1916: 31.
Type species. Dunstania pulchra Tillyard 1916: 32.

Diagnosis. Costal space broad, with costal veinlets. Rs arising basal to nodal line but only slightly so. M arising from R, stem deflected forwards to nodal line. CuA almost straight after cross-connection to R+M. M and CuA very widely separated at nodal line. Clavus with two anals, both well developed, looped only close to apex.

The genus is recorded from the Upper Triassic of Australia. A species from the Upper Triassic of southern Africa is referred to the genus.

Dunstania petrophila sp. nov. (Fig. 12; Plate 4, fig. 3)

Type. C-Dt. II 781 a, b in Bernard Price Institute.

Description. Fore wing complete (part b), with clavus partly detached. Counterpart (part a) preserving only the apex. Length *c.* 28 mm. Similar to *pulchra* as far as can be ascertained from the imperfect preservation of that species with the exception, mainly, of the cross-vein from M to CuA. Costal space broad, with at least four oblique, curved cross-veins from R to wing margin, the first arising from the basal stem of R + M. Node clearly defined and wing margin slightly emarginate at this point. Distal branch of R widely separated from wing margin. Rs arising beyond the midpoint of the stem of R over the length from the separation of M to the node. Rs strongly deflected anteriorly at the nodal line. M separating from R slightly beyond the cross-connection between R and CuA, deflected slightly towards fore margin, branching slightly before nodal line and upper branch strongly deflected anteriorly. M 1 strongly angled at cross-vein to Rs. Branches of M deflected posteriorly at their origins, especially M3 and M4. CuA diverging strongly from M so that the two are separated by almost half the wing width at the nodal line. The m-cu cross-vein from M4 to CuA strongly deflected posteriorly near CuA, with the nodal line following the cross-vein. CuA 2 distinctly curved posteriorly at the margin. Clavus large, with two veins distinct. 1A subparallel to CuP. 2A separating from margin close to base, long and subparallel to 1A for most of its length, very close to margin distally and looped at apex onto 1A. Wing surface, including clavus, with dense very fine tubercles. Fore margin of wing distinctly thickened. Hind margin with a very narrow ambient space.

This is the most completely known wing of the Dunstaniidae.

Family Cicadoprosbolidae

The family is recorded from the Upper Permian of Australia and southern Africa and the Upper Triassic of Russia and southern Africa. R is 2-branched in the Australian *Austroprosbole* and the African *Austroprosboloides* and *Prosbolomorpha* but there are several forward branches in *Cicadoprosbole*. Rs is simple and M is 4-branched in all four genera although there may be a fifth branch of M in *Austroprosboloides*.

PLATE 4

(1) *Triassogereon distinctum* gen. et sp. nov. Holotype C-Dt II 783 a; (2) *Fletcheriana magna* sp. nov. Holotype C-Dt II 784 a; (3) *Dunstania petrophila* sp. nov. Holotype C-Dt II 781 b; (4) *Tennentsia protuberans* (Riek) C-Dt II 787 a.

In all genera Rs arises distinctly proximal to the nodal line and the vein is slightly kinked where it crosses the nodal line, and in *Prosbolomorpha* and *Cicadoprosbole* there is a break in the vein and a thickening at this point.

A new genus is described from the Upper Triassic of southern Africa. It is distinct from *Prosbolomorpha* from the same horizon, and all other genera, in having more than four branches to M. The wing is of decidedly longer and narrower form than in the other genera.

Genus **Leptoprosbole** gen. nov.

Type species. Leptoprosbole lepida sp. nov.

Diagnosis. Fore wing of long narrow form but node and nodal line slightly beyond the middle of the length of the wing. R with a number of forward branches to the costal margin and posterior branches to the wing apex. Rs simple. M with more than four branches. CuA 2-branched, with CuA 2 following the nodal line. Clavus with 2A and 3A arising on a common stem.

The genus resembles *Cicadoprosbole* in the extra branching of R and *Austroprosbole* in the strongly curved CuA 2 lying on the nodal line.

Leptoprosbole lepida sp. nov. (Fig. 14; Plate 1, fig. 6)

Type. C-Dt. II 790 a, b in Bernard Price Institute.

Description. Fore wing complete. Length *c.* 37 mm. Wing 3½ times as long as wide. Costal space moderately wide, narrowing regularly to node. R almost straight to wing margin. Node not clearly preserved. R with four forward and two posterior branches. Rs arising before middle of wing and distinctly before nodal line, simple, only slightly up-arched at the nodal line. M 8-branched, upper branches long, M4 4-branched. Cross-vein (not shown in fig. 14) from M to CuA from just after the first forking of M4 to CuA 1, just beyond the nodal line. CuA 2-branched, branching only close to margin, CuA 2 strongly downcurved. Nodal line not clearly preserved except posteriorly on the stem of M3+4, across to CuA slightly before the forking and along CuA2 to the margin. (The chipping of the matrix to expose the venation has obscured details of the wing surface.) 1A sigmoidally curved. Stem of 2A+3A as long as the free distal portion of 2A. Claval margin thickened at base, parallel to the stem of 2A+3A so that there appears to be a fourth anal vein. Wing membrane with rather dense and fine punctures at least over basal half, more crowded on clavus.

Superfamily ?Cicadelloidea

Family Scytinopteridae

The Scytinopteridae have neither a nodal break on the fore margin nor a nodal line in the fore wing and, on these attributes, are readily separated from Prosbolidae. The fore wing has a large, distinctly defined clavus and Sc is not distinguishable. The venation may be reduced with Rs simple and M 4-branched. However, there are usually additional branches to R and CuA and sometimes to Rs and M. This is particularly true of Australian species. The hind wing has only a slight emargination of the costal margin, associated with the coupling of the wings.

Scytinopteridae are the dominant Homoptera of the Upper Permian of Australia. They also occur in the Lower and Upper Permian of Russia, in the Upper Permian of North America (Mexico), and in the Upper Triassic of Australia. A species from the Upper Triassic of southern Africa is referred to the family, and placed, tentatively, in *Scytinoptera.*

Genus *Scytinoptera* Handlirsch

Scytinoptera Handlirsch 1904.
Type species. Scytinoptera kokeni Handlirsch 1904: 3.

There is considerable variation in the venation of wings referred to this genus. In the type species, R is straight almost to the wing margin and not deflected at apex towards the fore margin. The species from southern Africa has venation of this type.

Scytinoptera distorta sp. nov. (Fig. 13; Plate 1, fig. 7)

Type. C-Dt. II 782 a, b in Bernard Price Institute.

Description. Fore wing with clavus attached, complete except for apex, but postero-apical area distorted and venation obscure. Length as preserved *c.* 5,5 mm, indicating a wing length of *c.* 6 mm. Costal space broad almost to apex. Rs simple. M arising rather distant from wing base, branching only distally, only upper two branches preserved. CuA connected to M slightly after its origin from R by a distinct cross-vein. Clavus with the second anal distinct from hind margin, looped at apex onto 1A. Costal space with a distinct short groove close to base (? indicating a ventral stridulatory projection).

Superfamily Cercopoidea

Family Dysmorphoptilidae

The family is recorded from the Triassic of Australia and southern Africa and Jurassic of England and central Asia. The apex of the fore wing is strongly produced so that there is a marked re-entrant angle at the apex of R.

In *Dysmorphoptiloides* (Evans 1956) M and CuA are anastomosed for some distance near their origins. The origins of these two veins are not preserved in *Dysmorphoptila* (Handlirsch 1906). The complete fore wing of *Dysmorphoptiloides protuberans* Riek from the Upper Triassic of southern Africa shows that these two veins are not anastomosed near the base. In this respect the wing resembles Eoscarterellidae but the wing shape and development of an ambient vein indicate that the species is correctly referred to the Dysmorphoptilidae.

However, the species is referred to a new genus on the separate origins of M and CuA combined with the less produced apex to the wing.

Genus **Tennentsia** gen. nov.

Etymology. The genus is named for the Tennent family whose help and generosity were very much appreciated during field studies at Bird's River.
Type species. Dysmorphoptiloides protuberans Riek 1974: 22.

Diagnosis. Similar to *Dysmorphoptiloides* but M and CuA connected near base by a cross-vein and wing subtruncate at apex.

The claval margin is produced into three, broad, medianly-ridged processes.

Tennentsia protuberans (Riek) (Fig. 15; Plate 4, fig. 4)

Dysmorphoptiloides protuberans Riek 1974: 22.
Type. C-Dt. II 342 in Bernard Price Institute.
Other material. C-Dt. II 787 a, b a complete fore wing including clavus.
C-Dt. II 788 a, b, a fore wing complete except for most of clavus.

Description of C-Dt. II 787 a, b. Length *c.* 24 mm. (Specimen 788 a, b *c.* 28 mm.) Fore wing, with clavus attached. Distinct re-entrant angles at apex of R and CuP. Fore margin convex. Apical lobe with convexly rounded margins except that apex is subtruncate and very slightly concave in middle. Costal space with a deep groove at base towards costal margin and a short, crescentic groove just anterior to R slightly before origin of M (?representing a ventral stridulatory projection). R slightly kinked towards apex, with two forward branches to costal margin from close to apex and a long 4-branched posterior branch. Rs simple. M 5-branched, extra branch on M3+4, all branches short. CuA up-arched near base, but cross-vein to M distinct, branching about its middle. CuA 1 strongly curved posteriorly to wing margin. CuP straight and continuing the line of the stem of Cu. Clavus with second anal vein short. Claval margin thickened towards base and produced over distal half into three lobes, rounded at apex, about as broad at base as long and with a median ridge. Ambient vein distinct over distal half of wing but close to margin, apparently very narrow at wing apex. Surface of wing with dense rather coarse punctures, punctures finer and denser over apical lobe.

The function of the lobes on the margin of the clavus is unknown although they would produce a cryptic pattern in the folded tegmina.

Division Sternorrhyncha

Family Protopsyllidiidae

Protopsyllidiid nymph (Plate 1, fig. 8)

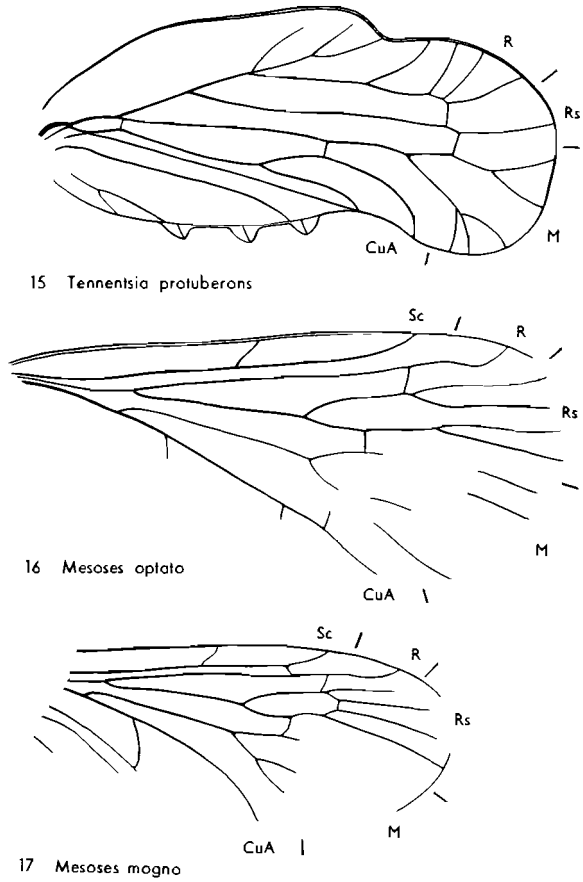
A nymph has been described previously from this formation. A second nymph, C-Dt. II 786 a, b, slightly smaller than the earlier nymph, is similar in structure.

ORDER *LEPIDOPTERA*

The earliest record of undoubted adult Lepidoptera is from the Eocene but the order was highly evolved by that time. The head capsule of a ditrysian larva has been recorded from Canadian Cretaceous amber (Mackay 1970).

Suborder Paratrichoptera

Tillyard (1919) erected an order Paratrichoptera for a number of wings from the Upper Triassic of Australia, and considered that the order was closely related to Diptera. He also compared it with Trichoptera and Mecoptera. Riek (1956) showed that these wings should be referred to one species of Mesopsychidae (including



Figs 15–17. (15) *Tennentsia protuberans* (Riek). C-Dt II 787 a; (16) *Mesoses optata* gen. et sp. nov. Holotype C-Dt II 774 a; (17) *Mesoses magna* sp. nov. Holotype C-Dt II 789 b.

Triassopsychidae). The Mesopsychidae have most of the basic wing venation attributes of the Eumecoptera except that there are a number of costal veinlets. However, the alignment of the veins is different and very characteristic, particularly the straightness of R at the origin of Rs, a characteristic of Diptera and Lepidoptera. Several other families have been assigned to the Paratrichoptera. The Liassophilidae, from the Liassic of England, differ from Mesopsychidae in having 3A looped on to 2A, and the anal veins are all relatively longer. *Pseudodiptera gallica* (Laurentiaux, 1953), from the Triassic of France, apparently had a very reduced hind wing and this may have been an attribute of the family Pseudodipteridae. *Pseudodiptera siberica* (Kolosnitsyana and Martynova, 1961), from the Upper Jurassic of Siberia, has a rather dipterous appearance to the wing due to the probably inferred occurrence of only two anal veins, although the wing is narrowed at base. The Pseudopolycentropodidae (Handlirsch 1925, 1939), from the Jurassic of western Europe and Karatau, had a very broad fore wing and reduced hind wing. It is apparently the most specialized

family of the Paratrichoptera, although M is 5-branched and not 4-branched as in the other families.

Choristopsyche tenuinervis (Martynov, 1937), from the Lower Jurassic of central Asia, was referred to the Paratrichoptera on the development of CuP and the anal veins but on the curved stem of R at the origin of Rs (and the broad costal space with 3-branched Sc) it is apparently not closely related to the Paratrichoptera.

Martynov (1927) agreed with Tillyard (1919) that the Paratrichoptera were closely related to Diptera but was of the opinion that they represented a side-stem that arose with the Diptera from a common mecopterous ancestor. Carpenter (1954) referred the suborder to Trichoptera even though CuA was not forked, apparently basing his decision on families other than the Mesopsychidae in some of which there was partial looping of the anal veins. Martynova (1962) and Smart & Wootton (1967) combined the suborder Protodiptera with the suborder Paratrichoptera (Mecoptera). Rohdendorf (1969) recognized the Paratrichoptera as an order, and considered that it is the sister-group of the Diptera.

However, I consider that the Paratrichoptera are ancestral Lepidoptera *s. str.* The fore wing is similar, with R long and straight except at base and apex, the origin of the 4-branched Rs towards the wing base, CuP widely separated from CuA, and a strong cross-vein from M to CuA the alignment of which often results in the appearance of a forked CuA. Paratrichoptera differ from other Lepidoptera in the presence of a well-developed CuP. At present the suborder can be defined only on this plesiomorphic character.

Mesopsychidae and Liasophilidae have a number of costal veinlets which further distinguishes them from Recent Lepidoptera in which Sc is at most 2-branched.

A new family, described from the Upper Triassic of southern Africa, has a 2-branched Sc, as in Prototheoridae and Palaeosetidae, but it also has a (small and indefinite) pterostigma.

Family **Mesosetidae** fam. nov.

Diagnosis. Lepidoptera with CuP fully formed and connected to CuA by two cross-veins, Sc 2-branched, R slightly kinked at apex within the indefinite pterostigma.

One included genus.

Genus **Mesoses** gen. nov.

Type species. Mesoses optata sp. nov.

Diagnosis. Costal space broad towards base. Sc not extending to the small pterostigma. Branches of Rs strongly divergent at the first forking. M distinctly up-arched at its origin. First cross-vein between CuA and CuP oblique and distinctly distal to the level of separation of M from CuA. Costal margin distinctly thickened at base. At least fore margin and probably whole wing membrane with dense, irregularly-positioned, fine setae.

Two included species, differing markedly in size.

Mesoses optata sp. nov. (Fig. 16; Plate 3, fig. 3)

Type. C-Dt. II 774 a,b and paratype 778 a,b in Bernard Price Institute.

Description. Fore wing, complete except for anal field and part of posterior and

apical margins. Length *c.* 22 mm. Costal space broad but tapering markedly to base. Sc 2-branched, forking beyond middle, first branch almost transverse. R slightly curved towards base and before the origin of Rs, straight at the origin of Rs, decidedly sigmoidally curved close to apex. Rs arising towards wing base, first forking decidedly before middle of its length, Rs 1+2 forking slightly before Rs 3+4. A cross-vein from R to the stem of Rs 1+2 just before the forking. M arising on CuA slightly more basally than origin of Rs, curving rather abruptly away from CuA, first branching level with first branching of Rs, M 3+4 branching slightly before M 1+2, all branches long. A cross-vein from Rs 3+4 to M 1+2, and a cross-vein from M 3+4 to CuA just before the forking of M 3+4. CuA appearing to arise from wing base, close to and parallel to the stem of R at base, vein straight until the cross-vein to M 3+4 and there deflected forward, otherwise straight to wing margin. CuP appearing to arise from base, widely separated from CuA and connected to it by only two cross-veins, both distinctly beyond the separation of M from CuA. First cross-vein oblique to the veins but transverse to the wing. Second cross-vein a short distance before the cross-vein from CuA to M 3+4. Anal veins only partly preserved, 1A parallel to CuP at base, the two only about half as far apart as CuA and CuP. Basal thickening on fore margin not clearly defined but bulging slightly into the costal space, the basal thickening continuous with the remainder of the stout costal margin. Costal margin, including the basal thickening, completely covered with numerous fine setae. The iridescence on the wing membrane suggests that the whole surface was covered with very dense setae. Wrinkling of the wing membrane most pronounced in the costal and subcostal spaces. Stem of R, over its middle half, with a series of alternating transverse grooves and ridges.

C-Dt. II 778 a, b preserves only the apex of a wing, showing Sc, R and pterostigma, Rs and portion of M.

Note. There are faint indications of a second underlying wing in the holotype, and it is the fore margin of this wing that makes it difficult to interpret the outline of the basal thickening on the fore margin of the upper wing. The wrinkling along the stem of R is similar to that which occurs on a number of the veins in the wings of some Recent Lepidoptera.

Mesoses magna sp. nov. (Fig. 17; Plate 3, fig. 4)

Type. C-Dt. II 789 a, b.

Description. Anterior half of fore wing, without base. Length as preserved *c.* 30 mm indicating a wing length of *c.* 36 mm. Similar to *optata* but considerably larger and CuA and CuP apparently more widely separated. Wing membrane apparently completely covered with dense fine setae, indicated at middle of radial space (wrinkling of wing membrane at base of radial space).

ORDER *COLEOPTERA*

Family Permosynidae

The Permosynidae, including Ademosynidae, were mainly Triassic beetles although they are also recorded from the Upper Permian of Australia, and from the Jurassic

and Lower Cretaceous of Karatau and central Asia (Ponomarenko 1968, 1969).

There is a longitudinal sulcus on internal moulds of the elytra and this led Tillyard (1916) and Dunstan (1923) to refer *Ademosyne* to the Hydrophilidae. Jeannel (1947) referred the Permosynidae, and also the Permorraphidae and Sojanocoleidae, to a separate suborder, Archicoleoptera. However, Ponomarenko (1969) was of the opinion that the Permosynidae are on the cupedid-line, and are also close to the ancestor of the Polyphaga. The family is probably very closely related to the Hydrophilidae as far as can be ascertained from the elytra: other diagnostic features are not preserved in Australian or southern African species.

The genus *Ademosyne* has previously been recorded from southern Africa (Riek 1974) as well as from Australia.

Genus *Ademosyne* Handlirsch

Ademosyne Handlirsch 1906.
Type species. Ademosyne maior Handlirsch 1906: 402.

Two species have been recorded from Upper Umkomaas. A third species, of smaller size, is recorded from Bird's River.

Ademosyne reducta sp. nov. (Plate 3, figs 7, 8)

Type. C-Dt. II 780 a, b and paratypes 777 a, b, 4 and 795 in Bernard Price Institute.

Description. Holotype. External view of whole elytron but partly obscured by a fine deposit of mud deposited during weathering. Length *c.* 6,5 mm. Elytron distinctly convex in all directions, slightly pointed at apex, rounded at base laterally but slightly angular medianly (in anal field). Elytron with nine rows of pits lying in shallow longitudinal grooves, rows somewhat irregular near base and anterior rows deflected slightly towards costal margin. Pits spaced about 10 per mm. Sutural margin clearly defined but narrow. Area adjoining costal margin flattened distally and flattened zone distinctly wider than sutural margin.

C-Dt. II 777 a, b shows the pitting very clearly but the margins are only partly clear. C-Dt. II 795 is also a clear external view of an elytron. C-Dt. II 4 is an internal mould.

The species differs from those previously described from southern Africa in its smaller size and more openly-spaced pits along the venational grooves.

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