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New Upper Permian insects from Natal, South Africa

by

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SYNOPSIS

An additional 19 species of insects are described from the *Daptocephalus* reptile zone of the Middle Beaufort Series, Natal, bringing the known insect fauna from the zone to 32. The orders Megasecoptera, Protoblattodea, Protelytroptera, Orthoptera and Neuroptera are recorded for the first time. The fauna is dominated by Paraplecoptera, Plecoptera and Homoptera. Miomoptera and Mecoptera are also present. The family Permosialidae is transferred from Megaloptera to Miomoptera. The known fauna is listed and family relationships indicated.

The affinities of the fauna are divided between those of similar age in Australia and Eurasia. The relationships seem to indicate that the climate of this north-eastern part of the Karoo Basin was intermediate between the warm climate of Angara and the cold climate of eastern Australia.

INTRODUCTION

Thirteen species of insects have been recorded from four localities in the *Daptocephalus* reptile zone of the Middle Beaufort Series in Natal (Riek 1973, 1974). Single specimens were recorded from two localities at Estcourt and from Loskop, which is near Estcourt. Most of the specimens were from one locality near the Mooi River. An additional 19 species are described in this paper. Almost all are from the same productive locality near the Mooi River but there are a number of specimens from Bulwer, two specimens from Lidgetton and a single specimen from near Empangeni.

Unless otherwise indicated, all specimens on which the following systematics is based are from the locality near the Mooi River. Specimens prefixed with NM are in the Natal Museum whereas those with N–MN are in the Bernard Price Institute.

As was the case with the earlier collection, most of the species are referred to the Paraplecoptera and Homoptera. The most common species are *Mioloptera stuckenbergi* (Paraplecoptera) and the species of *Euxenoperla* (Plecoptera). These species had wings of moderate size. However, wings of small size, represented by species of Mecoptera and Homoptera, do occur in the fauna. The orders Megasecoptera, Protoblattodea, Protelytroptera, Orthoptera and Neuroptera are recorded for the fauna for the first time.

Protoblattodea have not previously been recorded from the southern hemisphere unless one accepts the transfer by Sharov (1968) of *Xenogryllacris reductus* (Riek, 1955), from the Upper Triassic of Australia, to the order. However, I maintain that the species is an orthopteron most probably referable to the Gryllacrididae. Protelytroptera are common in, and Neuroptera and Megasecoptera, also, are recorded from, the Upper Permian of Belmont, but Orthoptera are first recorded in Australia in the Triassic.

The Homopterous families Scytinopteridae, Prosbolidae and Pereboriidae are recorded in the fauna for the first time. Scytinopteridae were common, and Pereboriidae and Prosbolidae may have been present, in the Upper Permian fauna of Australia. Cockroaches are still unknown for the fauna.

The new fossils have enabled clarification of the systematic position of the Permosialidae which, it is now known, are not related to Recent Sialidae (Megaloptera) but should be referred to the Miomoptera. Also, a more complete fore wing of *Dysmorphoscartella lobata* has confirmed placement in the Eoscartarellidae.

The affinities of the fauna are divided between faunas of similar age in Australia and Eurasia. The Miomoptera, some Homoptera and some Mecoptera are common to all regions. The Plecoptera, Protelytroptera, most Mecoptera, some Homoptera and a Neuropteron indicate affinity with Australia whereas the Paraplecoptera, Orthoptera and the other Neuropteron show affinity with the faunas of Europe and Angara. These relationships seem to indicate that the climate of this north-eastern part of the Karoo Basin was intermediate between the warm climate of Angara and the cold climate of the Belmont area of eastern Australia.

Total List of Fossil Insects

Megasecoptera	
Scytohymenidae	*Karoohymen delicatulus* gen. et sp. nov.
Paraplecoptera	
Liomopteridae	*Mioloptera stuckenbergi* Riek 1973
	Mioloptoides andrei gen. sp. nov.
	Liomoptoides similis Riek 1973
	Liomopterina clara Riek 1973
	Miolopterina tenuipennis gen. et sp. nov.
	Neoliomopterum picturatum gen. et sp. nov.
Protoblattodea	
Paoliidae	*Paolekia perditae* gen. et sp. nov.
Orthoptera	
Tettavidae	*Protettavus exilis* gen. et sp. nov.
Locustopsidae	*Eolocustopsis primitiva* gen. et sp. nov.
Plecoptera	
?Gripopterygidae	*Euxenoperla simplex* Riek 1973
	Euxenoperla similis Riek 1973
	Euxenoperla oliveri sp. nov.
	Euxenoperlella jacquesi gen. et sp. nov.
Miomoptera	
Permosialidae	*Permonka bifida* Riek 1973
Protelytroptera	
Protocoleidae	*Phyllelytron acuminatum* sp. nov.
Permophilidae?	gen. et sp. indet.
Hemiptera: Homoptera	
Ignotalidae	*Ignotala mirifica* Riek 1973
	Megoniella multinerva Riek 1973

Pereboriidae?	*Perissovena heidiae* gen. et sp. nov.
Scytinopteridae	*Orthoscytina dubitata* sp. nov.
Prosbolidae	*Beaufortiscus dixi* gen. et sp. nov.
Cicadoprosbolidae	*Neurobole ramosa* gen. et sp. nov.
	Austroprosboloides vandijki Riek 1973
Eoscartarellidae	*Dysmorphoscartella lobata* Riek 1973
	gen. et sp. indet.
Uninervidae	*Redactineura acuminata* Riek 1973
Protopsyllidiidae	*Protopsyllidium lynae* sp. nov.
Permaleurodidae	*Aleuronympha bibulla* Riek 1974
Family?	nymph gen. et sp. indet.
Mecoptera	
Agetopanorpidae	*Agetochoristella similis* Riek 1973
Permochoristidae	*Mesochorista* aff. *australica* (Tillyard) 1917
	Mesochorista channingi sp. nov.
Mesopanorpodidae	*Prochoristella hartmani* sp. nov.
Nannochoristidae?	gen. et sp. indet.
Neuroptera	
Palaemerobiidae	*Sismerobius pusillus* gen. et sp. nov.
Archeosmylidae	gen. et sp. indet.

SYSTEMATICS

The wings of all specimens are illustrated with the apex to the right.

ORDER *MEGASECOPTERA*

Suborder Protohymenoptera

Family Scytohymenidae

The Protohymenoptera are characterized by the very narrow costal and subcostal spaces of the wing with Sc and R crowded close to the costal margin, and with the basal sections of the stems of the main veins, with the exception of the anal vein, all crowded close to the fore margin. In the Scytohymenidae, MA touches or anastomoses with Rs for a short distance, M and CuA are anastomosed for a short distance, MP is simple, and R ends regularly, close to the wing apex. The family is distinguished from the Protohymenidae mainly on the structure of the apex of R.

The family is recorded from the Lower and Upper Permian of the Urals. The two included genera differ only in details of the cross venation. In both *Scytohymen* and *Tshekardohymen* MA and Rs just touch and the stem of MA is very oblique before this point. A new genus is recorded from the Upper Permian of southern Africa.

Genus **Karoohymen** gen. nov.

Derivation: A protohymenopteron from the Karoo Basin.
Gender: Masculine.
Type species: *Karoohymen delicatulus* sp. nov.

Diagnosis. Similar to *Scytohymen* and *Tshekardohymen* but MA and Rs anastomosed for a short distance and the stem of MA short, and the combined costal plus sub-

costal space widened for a short distance at apex. Cross-veins forming a single gradate series, as in *Tshekardohymen*, except that there is no cross-vein in the 'pterostigma' or between the branches of Rs. Sc is clearly defined only basally to the origin of Rs, and there is no indication of Sc in the 'pterostigma'.

Karoohymen delicatulus sp. nov. (Fig. 1; Plate 1, fig. 1)

Type. N–MN 9 a, b, in Bernard Price Institute.

Description. Fore wing, except for most of posterior margin. Length as preserved *c*. 17 mm, indicating a wing length of *c*. 20 mm. Branches of Rs slightly longer than the foot-stalk to the point of anastomosis with MA. Rs and MA anastomosed for a distance about equal to the free stem of MA. Free stem of MA almost perpendicular to MP, and subequal to the free stem of Rs.

ORDER *PARAPLECOPTERA*

Family Liomopteridae

The family is well represented in the fauna. Three species were recorded by Riek (1973). Six species are now recognized, three based on fore wings and three on hind wings. There is no obvious correlation between the fore and hind wings, which differ noticeably in venation. Also, one hind wing is very much larger and one fore wing very much smaller than the wings of the other four species.

There are numerous specimens of the fore wing of *Mioloptera stuckenbergi* (Riek 1973) but no hind wing which is surprising as hind wings of other species of the family are recorded from the same horizon. This is a primitive species of the Paraplecoptera for, although the archedictyon is reduced to simple cross-veins over most of the wing, CuA 2 is not sharply differentiated from CuA 1 even though it is simple as in the more highly evolved species. CuA 2 is clearly differentiated in *Mioloptoides* gen. nov. However, the two genera are similar in most other respects, including the distinctive, reduced branching of Rs.

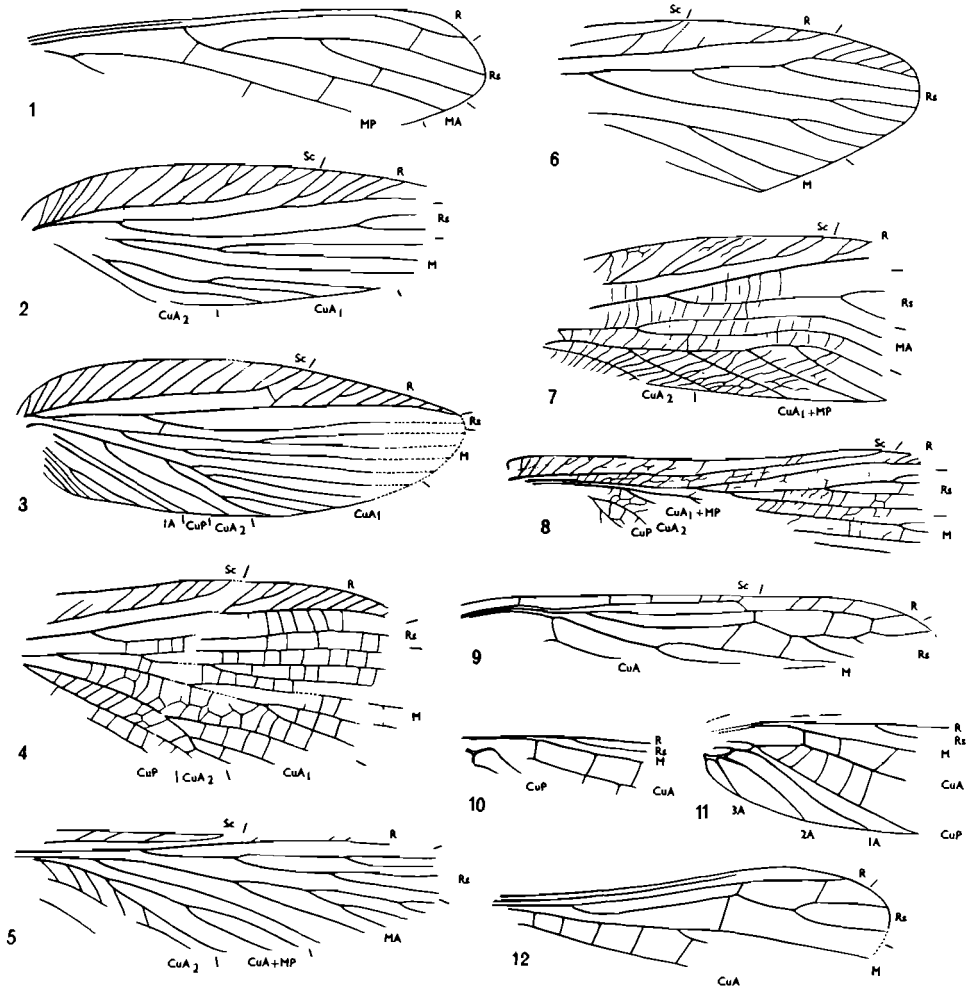
Liomoptoides (Riek 1973) is known from only the extreme apex of a hind wing. It is possible that *Miolopterina* gen. nov. is based on a more completely preserved hind wing of the same species but, as the apex of the wing is not preserved, it is not possible to make a direct comparison. *Liomopterina* (Riek 1973) is based on the well-preserved basal half of a hind wing that is very much larger than the wings of all other species. *Neoliomopterum* is based on a wing only about half the size of the other known fore wings.

The Liomopteridae from this horizon are similar to those from the Lower Permian of the Kuznetsk Basin. The family is recorded, also, from the Upper Carboniferous of Europe, Lower Permian of North America, Lower Permian of Moravia, and the Upper Permian of eastern Europe and the Kuznetsk Basin of Asia (Kukalova 1964).

Genus *Mioloptera* Riek 1973

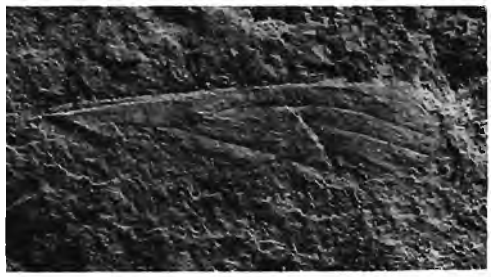
Mioloptera Riek 1973
Type species: *Mioloptera stuckenbergi* Riek 1973: 515.

Diagnosis. Now that more completely preserved wings are known, the generic diagnosis must be modified. M is 3- or 4-branched, and not at least 6-branched as given



Figs 1–12. (1) *Karoohymen delicatulus* gen. et sp. nov. Holotype; (2, 3) *Mioloptera stuckenbergi* Riek. 2. NM 904 a. 3. NM 907 a; (4) *Mioloptoides andrei* gen. et sp. nov. Holotype; (5) *Miolopterina tenuipennis* gen. et sp. nov. Holotype; (6) *Paolekia perditae* gen. et sp. nov. Holotype; (7) *Protettavus exilis* gen. et sp. nov. Holotype; (8) *Eolocustopsis primitiva* gen. et sp. nov. Holotype; (9) *Euxenoperla oliveri* sp. nov. Holotype; (10, 11) *Euxenoperla* sp. 10. NM 914 a. 11. NM 915 a; (12) *Euxenoperla jacquesi* gen. et sp. nov. Holotype.

in the original diagnosis. When M is only 3-branched Rs is usually 2-branched but when M is 4-branched, Rs is usually simple, except possibly close to the wing margin. CuA is usually 6-branched with some variation in the origin of the branches. Posterior branch of CuA simple. CuP straight, simple. Anal veins with six or more terminal branches. Costal veinlets (about 12) usually simple but occasionally one or two are forked. Humeral space not widened. Without precostal area. Cross-veins abundant over the whole wing, mostly simple, dividing the wing into more or less equal-sided areas.



1. KAROOHYMEN DELICATULUS

2. MIOLOPTERA STUCKENBERGI

3. MIOLOPTERA STUCKENBERGI

4. MIOLOPTERINA TENUIPENNIS

5. MIOLOPTOIDES ANDREI

6. LIOMOPTERINA CLARA

7. NEOLIOMOPTERUM PICTURATUM

8. PAOLEKIA PERDITAE

PLATE 1

(1) *Karoohymen delicatulus* gen. et sp. nov. Holotype. N–MN 92, reversed; (2, 3) *Mioloptera stuckenbergi* Riek. 2. NM 907 a. 3. NM 904 a; (4) *Miolopterina tenuipennis* gen. et sp. nov. Holotype. NM 909 b; (5) *Mioloptoides andrei* gen. et sp. nov. NM 852 a, reversed; (6) *Liomopterina clara* Riek. Holotype. NM 854 a, reversed. Enlargement of wing base; (7) *Neoliomopterum picturatum* gen. et sp. nov. Holotype; (8) *Paolekia perditae* gen. et sp. nov. Holotype. NM 940 a, reversed.

Mioloptera stuckenbergi Riek 1973 (Figs 2, 3; Plate 1, figs 2, 3)

Mioloptera stuckenbergi Riek 1973: 515.

This species is represented by parts of at least 17 fore wings. The hind wing is not known. NM 904 a, b (figured) is an almost complete wing (counterpart rather incomplete). NM 907 a, b (figured) is another almost complete wing (counterpart less

complete). NM 905 is the middle section of a wing in which M is 3-branched with Rs 2-branched, branching rather distally. NM 906 is the middle section of a wing. The other specimens are more fragmentary. Most are in the Natal Museum (all NM numbers) but N–NM 8 a, b, 37 a, b, and 40 a, b, are in the Bernard Price Institute.

Genus **Mioloptoides** gen. nov.

Derivation: Similar to *Mioloptera*.
Gender: Feminine.
Type species: *Mioloptoides andrei* sp. nov.

Diagnosis. Similar to *Mioloptera* but M at least 6-branched and CuA only 4-branched, with clearly differentiated, simple, straight CuA 2. Sc with numerous costal veinlets. Apex of R, beyond Sc, with numerous forward branches to margin. Rs simple, at least until close to apex. Cross-veins abundant, mostly simple and transverse, but forming a double row of cells, in part, between M and CuA.

The genus is similar to *Liomopterella* Sharov 1961 and *Kaltanella* Sharov 1961 in the structure of CuA, with clearly differentiated CuA 2, and the well-branched M but differs in the simple Rs in which character it resembles *Mioloptera* and also *Liomopterites* Sharov 1961.

Mioloptoides andrei sp. nov. (Fig. 4; Plate 1, fig. 5)

Etymology. The species is named for Master André van Dijk, a keen member of the Van Dijk family-team who together collected most of the specimens on which this study is based.
Type. NM 852 a, b, in Natal Museum. NM Type No. 1970.
Description. Apical half of a fore wing, but posterior wing margin not defined. Length as preserved *c.* 15 mm, indicating a wing length of *c.* 27 mm. Costal veinlets simple. Forward branches at apex of R simple except for first branch. Rs arising about the middle of the wing, simple except for a possible terminal twigging. CuA 1 3-branched, stem slightly up-arched, branching only beyond the middle, widely separated from M especially at first forking. CuA 2 straight, simple, approaching close to CuA 1 towards apex. CuP parallel to CuA 2.

Genus *Liomopterina* Riek 1973

Liomopterina clara Riek 1973 (Plate 1, fig. 6)

Liomopterina clara Riek 1973: 518.

The line drawing in Riek (1973), based on the counterpart (854 b) of the holotype, is incorrect in the structure of M and CuA. The wing is slightly distorted in this region, but the holotype (854 a) shows that CuA is 2-branched (as far as is preserved) and M 2-branched, with M 3+4 continuing as far as the wing is preserved but the apical preserved section is somewhat displaced (and was previously interpreted as an anterior branch of CuA). An enlargement of the well-preserved wing base is illustrated.

Genus **Miolopterina** gen. nov.

Derivation: Similar to Mioloptera.
Gender: Feminine.
Type species: *Miolopterina tenuipennis* sp. nov.

Diagnosis. Hind wing. Costal space narrow. Sc with a number of veinlets to the costal margin. R with several forward branches to margin beyond apex of Sc. Rs with at least four branches. M branching before level of origin of Rs, with a number of branches, with M 3+4 branching, at most, only distally. Median space not widened in middle. CuA branching slightly after level of branching M. CuP widely separated from CuA, the two connected by a few, long, strong, oblique cross-veins.

The wing, although similar in size, differs from the (fore) wings of *Mioloptera* and *Mioloptoides* in the distinct branching of Rs and branching of CuA but the origin of Rs, first branching of M and the abundant, mostly simple, cross-veins are similar.

The genus differs from the hind wings of *Liomopterella* and *Kaltanella* in the deeply branched CuA and almost simple M 3+4. It differs from the much larger *Liomopterina*, from the same horizon, in the branching of M and CuA 1.

Miolopterina tenuipennis sp. nov. (Fig. 5; Plate 1, fig. 4)

Types. Holotype NM 909 a, b, and paratype NM 897, in Natal Museum. NM Type no. 1971.
Type localities. Holotype from near Mooi River, paratype from Bulwer.
Description. Holotype. Hind wing complete except posteriorly. Length as preserved *c.* 21 mm, indicating a wing length of *c.* 28 mm. Sc extending level with first forking of Rs. Subcostal space not widened at level of origin of Rs. R almost straight throughout its length. Rs arising towards the base of the wing, at least 4-branched, all branches long. M at least 6-branched, with M 3+4 simple at least until close to wing margin. CuA at least 3-branched. Ano-jugal area not preserved.

It is inferred that this is a hind wing because of the narrow costal space and the very thin, somewhat crumpled wing in which the ano-jugal area is not preserved.

NM 897, from Bulwer, is a less completely preserved wing in which the crumpling of the very thin wing membrane is obvious. The forward branches of R beyond the apex of Sc are distinct.
Note. The species could possibly be based on more completely preserved wings of *Liomoptoides similis* (Riek 1973) but, as the apex of the wing is not preserved, direct comparison is not possible.

Genus **Neoliomopterum** gen. nov.

Derivation: More advanced *Liomopterum.*
Gender: Neuter.
Type species: *Neoliomopterum picturatum* sp. nov.

Diagnosis. Close to *Liomopterum* on those parts of the fore wing preserved but differing in the more distal first forking of M and, apparently, more distal forking of M 3+4. M forks slightly after the level of the origin of Rs whereas in most Paraplecoptera the forking is more basal and slightly before the origin of Rs.

Neoliomopterum picturatum sp. nov. (Plate 1, fig. 7)

Type. NM 910, in Natal Museum. NM Type no. 1972.
Type locality. Emakwezini Railway Station near Empangeni.
Description. Middle section of a fore wing. Length as preserved *c.* 6,5 mm, indicating a wing length of *c.* 14 mm. Costal space broad. Sc extending well towards apex of wing. Costal veinlets simple, sometimes interconnected by cross-veins. Rs branching, at most, beyond apex of Sc. M at least 2-branched, possibly with more branches, first forking very slightly beyond level of origin of Rs, M 3+4 apparently not forking before M 1+2. CuA strongly curved posteriorly near its origin, forking slightly before forking of M and the origin of Rs. Cross-veins simple over preserved portion of wing.
Note. Although fragmentary, the specimen is named to indicate the diversity of Paraplecoptera in the sequence and their relationships to other faunas.

ORDER *PROTOBLATTODEA*

Family Paoliidae

The family, which includes some of the oldest known insects, is recorded from the Upper Carboniferous of North America and Europe. *Stygne roemeri* (Handlirsch 1906) and very probably *Ampeliptera limburgica* (Pruvost 1927), both from the Namurian, are referred to the family.

The fore wing of Paoliidae is similar in basic venation to primitive Paraplecoptera except for the oblique cross-connection from M to CuA and the definition of a clavus. On these attributes the family is referred to the Protoblattodea, although Kukalova (1961) transferred it to the Paraplecoptera from her earlier (1958) placement in Protorthoptera suborder Cacurgoidea. The main basis for differentiation between Paraplecoptera, Protoblattodea and Protorthoptera is the development of the cubito-anal field of the fore wing. There is an oblique cross-connection between the stem of M and CuA, representing the anastomosis of MP with CuA in Protoblattodea and Protorthoptera. The Protoblattodea differ from Protorthoptera in the development of a clavus. On the presence of a clavus, anastomosis of MP with CuA, a well-developed archedictyon and a relatively small anal field in the hind wing there can be no doubt that the Paoliidae should be referred to the Protoblattodea.

The family is represented in the Upper Permian of southern Africa by the apical half of a hind wing that is similar to the hind wing of *Zdenekia* from the Upper Carboniferous of Europe. In *Paolia*, from the Upper Carboniferous of North America, and *Pseudofouquea*, from the Upper Carboniferous of Wales, the cross-veins in the costal space are simple whereas in *Zdenekia* they are very irregular and resemble the archedictyon over the remainder of the wing.

This is a most unexpected record of the family which, otherwise, has been recorded only from the Upper Carboniferous.

Genus **Paolekia** gen nov.

Derivation: A combination from *Paolia* and *Zdenekia*.
Gender: Feminine.
Type species: *Paolekia perditae* sp. nov.

Diagnosis. Similar to the hind wing of *Zdenekia* but apical branches of Rs directed forwards as a pectinate series, and Sc slightly shorter. Archedictyon fully developed, dense and irregular over the whole wing. Sc ending well before wing apex. Uppermost branch of Rs with several branchlets directed towards anterior margin.

Paolekia perditae sp. nov. (Fig. 6; Plate 1, fig. 8)

Etymology. The species is named for Miss Perdita van Dijk, a very keen fossil hunter and discoverer of many of the interesting wings from this series.
Type. NM 940 a, b, in Natal Museum. NM Type no. 1973.
Description. Apical half of a hind wing, crumpled posteriorly so that only part of the branching of M is defined. Length as preserved *c.* 19 mm, indicating a wing length of *c.* 45 mm. R well separated from the costal margin at the apex of Sc, and with 3 or 4, not clearly defined branches to the wing margin beyond the apex of Sc. Rs with four main branches, the anterior branch with a series of five, short, anteriorly-directed pectinate branches, posterior two branches forking towards wing margin. M with three branches preserved. Posterior portion of wing crumpled and overfolded so that the venation is not distinguishable.

ORDER *ORTHOPTERA*

Family Tettavidae

The Tettavidae, recorded from the Upper Permian of Tikkie Gory (Preurals) and Lower Triassic of Fergana, are considered to be the most primitive Tettigonioidea (Sharov 1968). The long wings are similar in most respects to those of Tcholmanvissiidae except that the costal space is wider and MA has only two main branches. One of the main distinguishing attributes was said to be the anastomosis of the stems of M and CuA 1 for a short distance. In the reduced branching of MA, the family resembles the Mesozoic to Recent Haglidae but differs noticeably in the basal associations between M and CuA.

A new species from the Upper Permian of southern Africa is referred to the family even though M and CuA are not anastomosed but connected by a short slightly oblique cross connection (= stem of MP). This short cross-connection is very different from the less specialized long, oblique one present in all Haglidae but in most other respects the wing resembles that of primitive Haglidae. On the presence of the free base of MP this genus is considered less specialized than *Tettavus* and *Madygenia.*

Genus **Protettavus** gen nov.

Derivation: Ancestral to *Tettavus.*
Gender: Masculine.
Type species: *Protettavus exilis* sp. nov.

Diagnosis. Similar to *Tettavus* in the long fore wing, with wide costal space and oblique costal veinlets, with Rs arising only a short distance beyond the forking of M, with two main branches to M and with secondary branching, at most, close to wing margin, and with cross-veins dense, and somewhat irregular, especially towards wing margin but differing in that M and CuA are not anastomosed for a short distance. MP joining

CuA, only slightly obliquely and distinctly before the forking of MA. Cross-veins irregular in the costal space, and Sc ending slightly before the level of the apex of CuA 1 + MP.

Protettavus exilis sp. nov. (Fig. 7; Plate 2, fig. 1)

Type. NM 924 a, b, in Natal Museum. NM Type no. 1974.
Description. Middle section of a fore wing. Length as preserved *c.* 17 mm, indicating a wing length of *c.* 35 mm. Some details towards wing apex preserved only on the more fragmentary counterpart. Sc slightly sinuate, being deflected at the origin of each subcostal veinlet. Subcostal veinlets slightly concave proximally and slightly convex distally. Sc ending level with first forking of Rs and slightly before the apex of CuA 1 + MP. Costal space wide to apex. R almost straight at the origin of Rs, with forward branches to anterior wing margin beyond the apex of Sc, the first branch forked. MA subparallel to R and the stem of Rs, forking distinctly before the level of the origin of Rs, the two branches subparallel to at least beyond the apical fork of CuA 1 + MP. MA 3+4 curving distinctly towards posterior margin apically. CuA 1 + MP 5-branched, branches simple, subparallel, directed to posterior margin of wing. Stem of CuA 1 + MP subparallel to hind margin of wing. CuA 2 slightly curved towards CuA 1 + MP. CuP and anal veins not preserved. Cross-veins irregular between the distal branches of CuA 1 + MP.

Family Locustopsidae

The Locustopsidae (Acridoidea) were widespread in the Triassic and Jurassic. The earliest record of the family is *Praelocustopsis mirabilis* (Sharov 1968) from the Lower Triassic of Siberia. In this family, the fore wing is long and narrow, with a well developed costal vein and reduced anal field. The cross-connection from M to CuA (= stem of MP) is apparently transverse and not distinguishable from a cross-vein.

A fore wing from the Upper Permian of southern Africa is referred to the family although it does not have a long, clearly defined, costal vein. However, in other respects it resembles *Locustopsis*.

Genus **Eolocustopsis** gen. nov.

Derivation: Primitive *Locustopsis*.
Gender: Feminine.
Type species: *Eolocustopsis primitiva* sp. nov.

Diagnosis. Similar to *Locustopsis* but costal area, apparently, small and restricted to base of wing, and costal vein not clearly defined. Sc extending well towards apex of wing. R with only a few short forward branches to wing margin. Area between M and CuA wide, the cross-veins irregularly sigmoidal. Cross-veins between branches of Rs and M partly simple, slightly oblique. Cross-veins in costal and subcostal spaces irregular and interconnected.

Eolocustopsis primitiva sp. nov. (Fig. 8; Plate 2, fig. 2)

Type. NM 855, in Natal Museum. NM Type no. 1975.
Description. Fore wing, apex and posterior margin not preserved. Length as pre-

served *c.* 15 mm, indicating a wing length of *c.* 17 mm. Wing of delicate texture. Small but distinct basal precostal lobe but costal vein not clearly defined. Costal space moderately broad at base, tapering to apex, the costal veinlets irregular. R apparently with a number of short forward branches to wing margin beyond apex of Sc (two preserved). Rs arising about one-third of wing length from base, at least 4-branched, the branches diverging only slightly from R. Stem of M close and parallel to stem of R. M at least 4-branched, first branching well before level of origin of Rs, branches very long and subparallel. CuA only partly preserved, branching before the level of first branching of M. Cross-veins abundant, regular and slightly oblique between branches of Rs and M, irregular and forming an archedictyon in costal and subcostal spaces, strong and irregularly sigmoidal between M and CuA and in cubital field.

ORDER *PLECOPTERA*

Family ?Gripopterygidae

Subfamily **Euxenoperlinae** nov.

Diagnosis. Rs distinctly up-arched at the first inter-radial cross-vein and the large second radial cell distinctly widened in middle, and sometimes secondarily divided. With at least three radial cells. The first r-m cross-vein joins the upper branch of M.

The cubital field, also, is distinctive, at least in *Euxenoperla*: CuA diverges markedly from CuP at base so that CuA and CuP are widely separated, and subparallel, throughout. The stem of M is distinct to base.

Two included genera, *Euxenoperla* (Riek 1973) from the Upper Permian of southern Africa and the Upper Triassic of Australia and *Euxenoperlella* gen. nov. from the Upper Permian of southern Africa. The genera differ in the branching of Rs and development of the cross-veins. These differences would appear to be correlated with size in a similar manner to the differences in the wings of the Recent genera of Gripopterygidae.

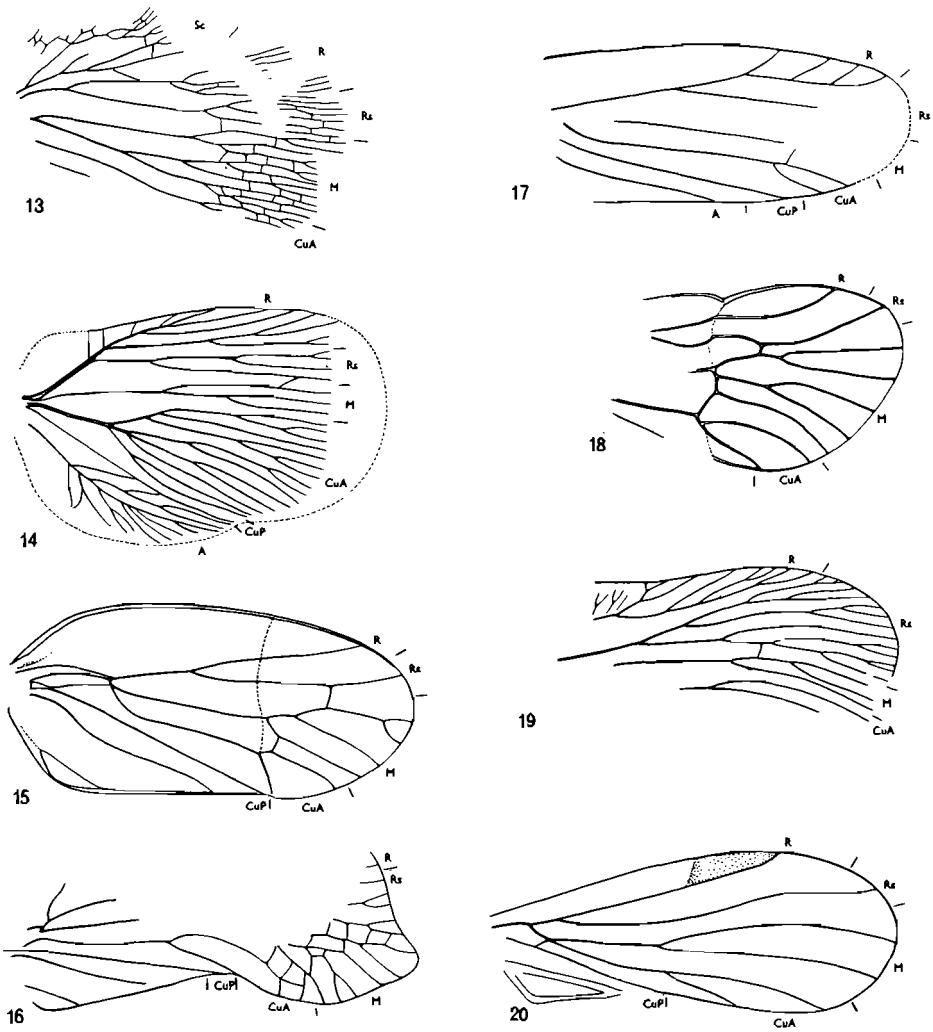
Genus *Euxenoperla* Riek 1973

Three species have been recorded, two from the Upper Permian of southern Africa and one from the Upper Triassic of Australia. A new species is described from the Upper Permian of southern Africa. The species differ in the branching of Rs and the cross-connections between both R and Sc and the costal margin.

Euxenoperla similis Riek 1973

Euxenoperla similis Riek 1973: 522

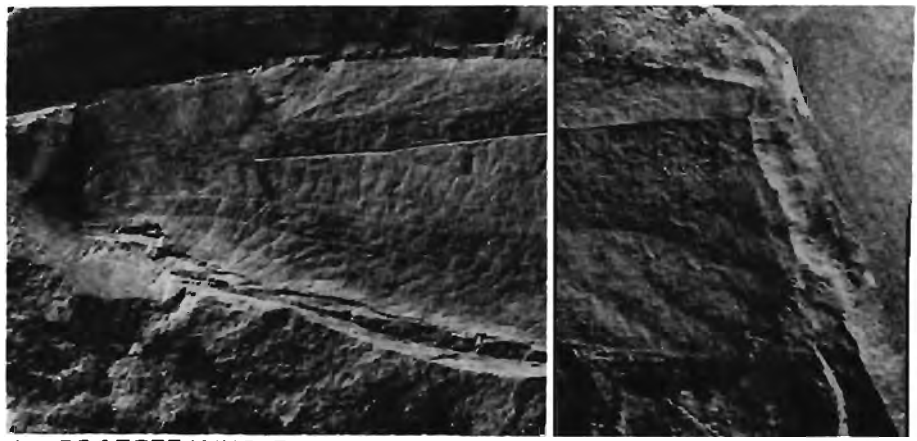
Several additional specimens of this species are recorded. NM 859, is the anterior part of a fore wing showing the branching of Rs and the cross-vein from the first branch to the upper branch of M. There are three cross-veins from R to the costal margin. There are five or more cross-veins over the preserved length of Sc, with two distinct ones towards the apex of Sc, and the others less distinct and more widely spaced. NM 860 a, b, is a crumpled fore wing showing the branching of Rs and parts of M and CuA. NM 898, consists of crumpled fore and possibly hind wing that may



Figs 13–20. (13) *Megoniella multinerva* Riek. NM 871 a; (14) *Perissovena heidiae* gen. et sp. nov. Holotype; (15) *Beaufortiscus dixi* gen. et sp. nov. Holotype; (16) *Dysmorphoscartella lobata* Riek. NM 893; (17) *Orthoscytina dubitata* sp. nov. Holotype; (18) *Austroprosboloides vandijki* Riek. NM 889 a; (19) *Neurobole ramosa* gen. et sp. nov. Holotype; (20) *Protopsyllidium lynae* sp. nov. Holotype.

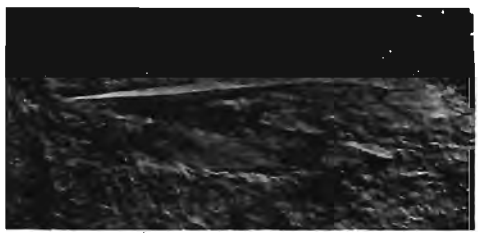
be a specimen of this species. There are several cross-veins from Sc to the costal margin. NM 895 from Bulwer, is the distal two-thirds of a fore wing; the anals are not preserved and only the distal part of CuA is preserved. NM 892, from Bulwer, is a poorly preserved apex of a wing that can probably be referred to *similis* on the branching of Rs.

The additional specimens indicate that there were several cross-veins from Sc to the costal margin and three cross-veins from R to the costal margin. There were fewer indicated in the holotype.



1. PROTETTAVUS EXILIS

2. EOLOCUSTOPSIS PRIMITIVA



3. EUXENOPERLA SIMPLEX

4. EUXENOPERLA SP.

5. EUXENOPERLA OLIVERI

PLATE 2

(1) *Protettavus exilis* gen. et sp. nov. Holotype. Combined NM 924 a and b; (2) *Eolocustopsis primitiva* gen. et sp. nov. Holotype; (3) *Euxenoperla simplex* Riek. N–MN 58 a, reversed; (4) *Euxenoperla* sp. NM 915 a; (5) *Euxenoperla oliveri* sp. nov. Holotype. NM 923 b.

Euxenoperla simplex Riek 1973 (Plate 2, fig. 3)

Euxenoperla simplex Riek 1973: 521

There are many additional specimens of this species, all from near Mooi River. NM 862 a, b, is a fore wing preserving most of the base, including CuP and two anals but most of the apex of the wing is missing. However, the first branch of Rs is distinctly after the cross-vein from Rs to the upper branch of M.

NM 863 a, b, is the apex of a fore wing with branching of Rs. There are two cross-veins from R to the costal margin. NM 864 is a very crumpled fore wing but the critical area of Rs is distinct. There are two cross-veins from R to the costal margin.

N–MN 69 a, b, 60 a, b, 22 a, b, 49 a, b, 29 a, b, and 54 a, b, all in the Bernard Price Institute, preserve the distinctive apical section of the fore wing with 3-branched Rs, with the first branching arising about the middle of the second radial cell. N–MN 69 a, b, in addition, shows three cross-veins from R to the wing margin and three radial cross-veins. N–MN 58 a, b (Plate 2, fig. 3) is a variant wing with Rs only 2-branched. It also shows three cross-veins from R to the wing margin and four cross-veins between Sc and the costal margin.

Euxenoperla oliveri sp. nov. (Fig. 9; Plate 2, fig. 5)

Etymology. The species is named for Mr. John Oliver who collected the holotype specimen during a visit to the locality with the Van Dijk family.

Type. NM 923 a, b, and paratype NM 861, in Natal Museum. NM Type no. 1976.

Type locality. Holotype from Lidgetton, and paratype from near Mooi River.

Description. Holotype. Anterior half of a fore wing, from base to apex, preserving all of Rs and M and base of CuA, but with slight wrinkling of wing membrane in median field. Length *c.* 20 mm. Similar to previously described species but second radial cell divided by a cross-vein slightly beyond middle of cell, so that there are four instead of three radial cells. Five cross-veins from Sc to costal margin. Sc ending slightly before the first inter-radial cross-vein. Humeral cross-vein slightly closer to level of basal cross connection between M and CuA than to base. Cross-vein between upper branch of M and Rs before the basal inter-radial cross-vein.

NM 861 is a fore wing showing most of the wing but the apical third is bent at right angles to the basal portion.

Notes. It is possible that these wings represent only variants of *simplex* but, as there are two specimens showing this unusual wing development, for the present, they are referred to a separate species distinguished on the presence of the additional cross-vein between R and Rs. There are three cross-veins between R and the costal margin in *oliveri* whereas there are usually two, but sometimes three or possibly only one, in *simplex*. There are three, also, in *similis* but the branching of Rs is distinct in that species. The position of the first inter-radial cross-vein is different from that in any known specimens of *simplex* and *similis*, occurring after both the apex of Sc and the first cross-vein between Rs and M.

Euxenoperla spp. indet. (Figs 10, 11; Plate 2, fig. 4)

NM 915 a, b (figured) and NM 914 a, b (figured) preserve most of the wing base and basal association of the main veins, but it is not possible to place them to species

because the branching of Rs, R and CuA are not preserved. The wing base is similar to that in Recent species of Austroperlidae and most Gripopterygidae with the stem of M distinct to base, 2A and 3A arise from a common stem and are widely separated from 1A. The base differs, however, in the very wide separation of CuA and CuP which are also subparallel almost to base. The cross-vein between the anal veins is from 1A to 2A, as in Austroperlidae and not to the stem of 2A + 3A as in most Gripopterygidae.

It would appear that the following fragments should be referred to *Euxenoperla*. All are from near Mooi River.

NM 857 a, b consists of the mesonotum and metanotum and crumpled hind wings. NM 858 is a thorax of similar form. NM 916 a, b, NM 917, NM 918, NM 919 a. b. NM 920 a, b, NM 921, NM 912 a, b, and NM 913 are fragments of fore wings and NM 865 is part of a hind wing.

N–MN 21 a, b, is a poorly preserved hind wing in which the first inter-radial cross-vein is very oblique. N–MN 20 a, b is a poorly preserved hind wing. N–MN 48 a, b is very probably a hind wing but it is only indefinitely preserved. N–MN 73 a, b is the base of one wing and the crumpled fore part of another wing. N–MN 26 consists of fragments of a fore and a hind wing in the region of the apex of Sc.

Genus **Euxenoperlella** gen. nov.

Derivation: Small *Euxenoperla*.
Gender: Feminine.
Type species: *Euxenoperlella jacquesi* sp. nov.

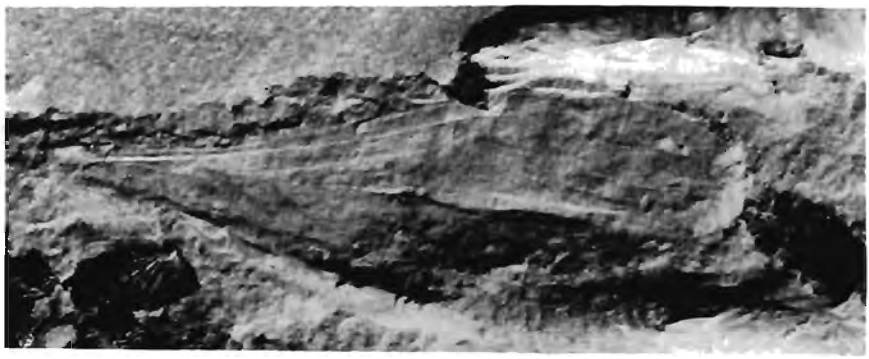
Diagnosis. Similar to *Euxenoperla* in the up-arching of the stem of Rs at the first inter-radial cross-vein and the second radial cell very wide at the point of branching of Rs but Rs only 2-branched, M branching more distally and M and CuA very widely separated before the forking of M.

Although the venation resembles that of the Taeniopterygidae and other Recent families of the Nemouroidea in some respects, the up-arching of the stem of Rs at the first inter-radial cross-vein, the wide second radial cell and the development of a third radial cell would seem to relate the genus closely to *Euxenoperla*.

Euxenoperlella jacquesi sp. nov. (Fig. 12; Plate 3, fig. 1)

Etymology. The species is named for Master Jacques van Dijk who has been very successful in collecting stonefly wings, as well as others of this interesting fauna.
Type. NM 922, in Natal Museum. NM Type no. 1977.
Description. Anterior two-thirds of a fore wing. Length as preserved *c.* 5,5 mm, indicating a total length of *c.* 6 mm. Sc extending at least almost to level of first inter-radial cross-vein. R without obvious branches to wing margin beyond apex of Sc. Rs 2-branched, with the branches about as long as the foot-stalk to the first inter-radial cross-vein. Two inter-radial cross-veins defining three inter-radial cells. Second inter-radial cell widest at point of forking ot Rs. First r-m cross-vein slightly distal to first inter-radial cross-vein. Four cross-veins between M and CuA before the forking of M. Stem of M arising from or close to wing base.

The wing is only about one quarter the length of the wings of *Euxenoperla* spp. but it is very similar in basic venation.

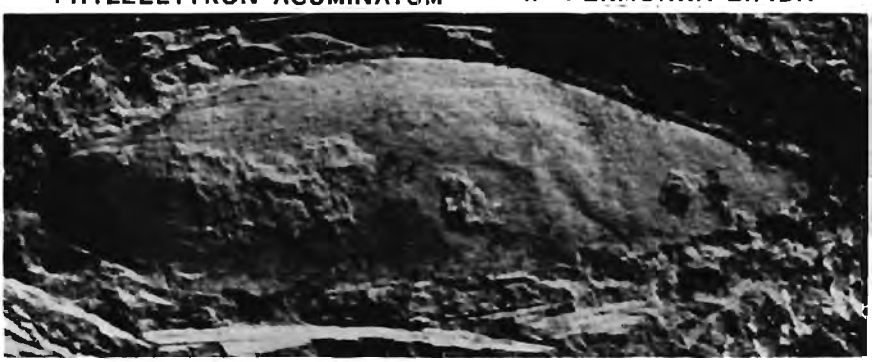


1. EUXENOPERLELLA JACQUESI

2. PERMONKA BIFIDA

3. PHYLLELYTRON ACUMINATUM

4. PERMONKA BIFIDA



5. PHYLLELYTRON ACUMINATUM

PLATE 3

(1) *Euxenoperlella jacquesi* gen. et sp. nov. Holotype. Reversed; (2) *Permonka bifida* Riek. NM 866; (3) *Phyllelytron acuminatum* sp. nov. Holotype; (4) *Permonka bifida* Riek. NM 866. Reversed lighting; (5) *Phyllelytron acuminatum* sp. nov. N–MN 71.

ORDER *MIOMOPTERA*

Family Permosialidae

The small, broad-winged species of *Permosialis*, from the Upper Permian of north-eastern Europe (Martynov 1928) and Upper Permian of Australia (Riek 1968), resemble Recent sialids only in basic venation. There is a series of openly-spaced cross-veins in the broad costal place, Sc and R are separate at their apices and M appears to arise as a forward branch of CuA. Martynov (1928) noted that *Permosialis* is more specialized in some attributes than Recent Sialidae. He was of the opinion that the Permosialidae were an extinct side-branch of the sialoid stem. Carpenter (1954) placed the family in Megaloptera with some doubt, and Riek (1968) expressed doubts as to its affinities. In most respects the wings are similar to the fore wings of other Miomoptera.

Sharov (1953) described a larva, from the Upper Permian of Kargala (Preurals), that he referred to *Permosialis*: it is undoubtedly that of a corydaloid, but not sialoid, megalopteron. On this basis alone, it is not closely related to *Permosialis*.

Riek (1973) described *Permonka bifida* from hind wings from the Upper Permian of southern Africa, and placed the species in the Permembiidae in the expanded sense of the family as reinterpreted by Kukalova (1963) to include several species from the Lower Permian of Czechoslovakia as well as *Permembia delicatula* (Tillyard 1928) from the Lower Permian of Kansas. The hind wing of *Permonka bifida* is similar to that of *Permonikia permoniki*, also known from only the hind wing. The fore wing of *Permonka bifida* is now known: it differs markedly, especially in wing shape, from the fore wings of Permembiidae but is similar to the fore wings of *Permosialis*. Both *Permonka bifida* and *Permonikia permoniki* are transferred to the Permosialidae.

The family embraces three genera, *Permosialis* known only from fore wings, *Permonikia* known only from the hind wing and *Permonka* known from both fore and hind wings and parts of the body. It is possible that *Permonikia* is based on the hind wing of *Permosialis*. Also, *Permosialis belmontensis* (Riek 1968) differs from other species of *Permosialis* and, also, *Permonka* in the forking of CuA, and may be generically distinct but, until better preserved material is available, the species is retained in *Permosialis*.

Genus *Permonka* Riek 1973

Re-diagnosis. Fore wing. Similar to *Permosialis* but Rs arising more distally, CuA deeply forked and CuP distinctly kinked towards CuA at the cross-vein about the middle of the veins.

Hind wing. Similar to fore wing in basic venation, but costal margin almost straight, costal space narrow, Rs arising very close to wing base, at the very distinct kink in the stem of R, and CuP widely separated from CuA. All anals arising from close to base, with four stems. Cross-veins irregular, especially in cubital and anal fields.

Permonka bifida Riek 1973 (Fig. 24; Plate 3, figs 2, 4)

Permonka bifida Riek 1973: 520.

NM 866 is more complete than the holotype. The mesothorax as well as the metathorax, and presumably abdomen. are preserved in this specimen. Whereas the

folded hind wings were preserved in the holotype both the folded fore and hind wings are preserved in the second specimen but the hind wing venations are obscured by that of the fore wings. Head missing and abdomen not visible through the folded wings.

Fore wing. Both fore wings complete but anal areas not clearly defined. Length *c.* 9,5 mm. Costal margin decidedly convex, the broad wing rounded at apex. Costal space widest in middle, with at least three costal veinlets to the margin, the most distal branch very oblique, veinlets widely spaced. R almost straight almost to base and not decidedly kinked near base as in hind wing. Rs either 3-branched or 2-branched and M 2-branched or 3-branched when Rs is only 2-branched. CuA forking before forking of M, about the middle of its length. CuP simple, subparallel to CuA, decidedly kinked in middle and there with a cross-vein to CuA 2 near its origin.

Hind wing. Very different in shape from fore wing with anal area markedly expanded and costal space much narrower. Basic venation similar to that of fore wing except that the main veins are distinctly kinked near the wing base.

Mesonotum and metanotum of similar form but metanotum somewhat smaller than mesonotum. Nota similar to those in Recent Endopterygota and Psocoptera. Mesonotum with parapsides large, clearly defined, not quite meeting at meson. Praescutum not quite as large as scutellum. Scutellum somewhat produced posteriorly but rounded at apex, with a distinct transverse groove across middle differentiating apparently, a heavily sclerotized apical half from a lightly sclerotized basal half. Metanotum with parapsides relatively larger than in mesonotum, praescutum slightly smaller but with clearly defined lateral area anterior to parapsides. Scutellum similar and with a transverse groove but, apparently, uniformly sclerotized.

NM 925, from Bulwer, is a fragment of the basal half of a hind wing, preserving the deep forking of CuA, forking of M and stems of Sc and R. The anal margin is not preserved but the anal field is large and expanded at base, and apparently similar to that in the holotype. 1A is strong over its basal half.

ORDER *PROTELYTROPTERA*

Family Protocoleidae

Venation of the fore wing dense, but irregular, over the whole tegmen. Homologies of the veins not clear except in the anal field. Costal projection at wing base rounded and prominent, and subcostal space extremely broad. Tegmen rather flat. The archedictyon reduced to dense granulation.

The family is recorded from the Upper Permian of Australia. A species from the Upper Permian of southern Africa is referred to the family, and placed in a known genus.

Genus *Phyllelytron* Kukalova 1966

Type species: *Phyllelytron folium* Kukalova 1966: 94.

Diagnosis. Venation distinct over whole wing but irregular. Sutural margin narrow. Apex of wing pointed. Cross-veins irregular. Costal expansion subcircular, strongly projecting.

Four Australian species have been referred to the genus. They differ in surface granulation of the tegmen, development of the cross-veins, development of the basal costal projection and, to some extent, in wing shape.

Phyllelytron acuminatum sp. nov. (Plate 3, figs 3, 5)

Type. N–MN 52 and paratype N–MN 71, in Bernard Price Institute and paratype NM 867, in Natal Museum.

Description. N–MN 52 preserves the basal one-third of a tegmen with the venation somewhat indistinctly preserved. Sculpture entirely, finely, reticulate-tuberculate, with a superimposed finer shagreening, especially medianly. The basal costal swelling not preserved.

N–MN 71 preserves the outline of the tegmen, which is somewhat pointed at apex. Venation present over whole tegmen but less distinctly preserved in anal field. Base of cubito-anal area raised. Basal costal swelling not preserved.

NM 867 is a tegmen with part of the base missing. The venation is somewhat indistinctly preserved.

The species differs from the Australian species in the type of sculpture which, in some respects, resembles that of *Protocoleus mitchelli* (Tillyard 1924). However, the venation, especially the wide basal separation of Sc and R, places the species in *Phyllelytron*.

Family Permophilidae?

NM 927 a, b is a poorly preserved specimen, with parts of the body including the pronotum. The left fore wing, slightly displaced at base, shows the expanded costal margin at base, somewhat pointed wing apex and a few strong basal stems of the veins over the posterior basal portion.

The poor preservation makes it difficult to place the specimen but it can be referred to either the Permophilidae or Stenelytridae on the general shape of the elytriform fore wing. The two families differ in the amount of venation retained in the sclerotization process, with the venation defined only at base in Permophilidae and continued to wing apex, but fine, in Stenelytridae.

The specimen is much smaller than the three tegmina of *Phyllelytron acuminatum*.

ORDER *HEMIPTERA*

Suborder Homoptera

Family Ignotalidae Riek 1973

Ignotala mirifica Riek 1973

Ignotala mirifica Riek 1973: 522.

NM 869 a, b is the apical portion of a fore wing and NM 870 is the middle section of a fore wing. Both N–MN 13 a, b and N–MN 45 a, b preserve the clavus, very probably of this species. N–MN 45 a, b shows the fine, closely spaced tubercles on the surface of the clavus. Clavus with three veins, 2A and 3A arising on a common

stem, 3A joining claval margin close to base, 2A curved, subparallel to hind margin, with short cross-veins to hind margin distally. Apex of clavus not preserved.

Megoniella multinerva Riek 1973 (Fig. 13; Plate 4, fig. 1)

Megoniella multinerva Riek 1973: 526.

NM 871 a, b, recorded in the original description, is figured. The line drawing is based on 871 a, reversed and the photograph on 871 b. Estimated length of wing *c.* 45 mm. Wing margin vaguely indicated, with costal margin very convex. The wing was, probably, only about $1\frac{1}{2}$ times as long as broad, although the width of the clavus, which is not preserved, is not known.

NM 872 is a small fragment of a large wing; it may be referable to *Megoniella*. N–MN 10 a,b is a very fragmentary portion of a wing that is probably referable to this species.

Superfamily Fulgoroidea

Family Pereboriidae?

A large hind wing with much branched venation is referred to the Fulgoroidea on similarity in basic venation with Achilidae, and tentatively placed in the Permian family Pereboriidae. Unfortunately, hind wings of Homoptera are rarely preserved as fossils so it is not possible to make direct comparisons with other species. Cixiidae are also recorded from the Permian but this hind wing differs markedly from the hind wings of that family.

The wing could possibly be the hind wing of *Megoniella multinerva* (Riek 1973) which has dense venation, is of large size and only somewhat larger than one would expect to match this hind wing. However, until direct association can be established it seems preferable to consider the two as distinct species.

The family Pereboriidae is recorded from the Lower Permian of the Kuznetsk Basin and from a number of Upper Permian localities in Russia. Some Australian species referred to the Scytinopteridae could almost as readily be referred to the Pereboriidae except that a basal pentagonal cell is not developed.

Genus **Perissovena** gen. nov.

Derivation: Abundant veins.
Gender: Feminine.
Type species: *Perissovena heidiae* sp. nov.

Diagnosis. Hind wing. Veins densely branched, especially R, CuA and the ano-jugal area. R with a series of branches to the costal margin, as well as several long, posterior, terminal branches. Rs with 3 or 4 branches. M branching before middle, with three terminal branches. CuA branching before middle, fan-wise, with numerous terminal branches. CuP simple. Anals, and apparently jugal, veins forming a much-branched complex arising from a common stem.

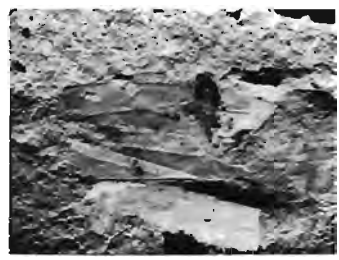
Perissovena heidiae sp. nov. (Fig. 14; Plate 4, fig. 2)

Etymology. The species is named for Heidi Anderson in appreciation of her interest and co-operation in this study.

Type. N–MN 50 a, b, in Bernard Price Institute.

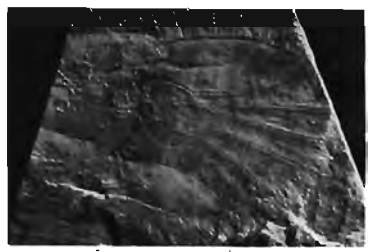
1. MEGONIELLA MULTINERVA

2. PERISSOVENA HEIDIAE



3. ORTHOSCYTINA DUBITATA

4. NEUROBOLE RAMOSA



5. AUSTROPROSBOLOIDES VANDIJKI

PLATE 4

(1) *Megoniella multinerva* Riek. NM 871 b; (2) *Perissovena heidiae* gen. et sp. nov. Holotype. N–MN 50 a; (3) *Orthoscytina dubitata* sp. nov. Holotype. NM 873 a; (4) *Neurobole ramosa* gen. et sp. nov. Holotype; (5) *Austroprosboloides vandijki* Riek. NM 889 a, reversed.

Description. Hind wing, complete except for extreme base and apex, wing very broad, only slightly longer than wide. Length as preserved *c.* 20 mm, indicating a total length of *c.* 27 mm. Costal margin at least slightly concave in middle. Combined

costal and subcostal space apparently very wide towards base, narrowed towards apex. Cross-veins from R to costal margin almost transverse before middle, very oblique at apex. Stem of R very stout over basal one-third, distinctly curved posteriorly beyond this point except close to margin. R branching slightly before the middle with at least 6 terminal branches. Rs arising well before middle of R, branching early, with at least four terminal branches. M arising from R close to base, branching slightly before the middle, all branches long. Cross-connection between Rs and M very oblique. CuA arising from base, branching towards base, fan-wise with at least 15 terminal branches. CuP simple, lying in a groove (along which the wing folds), straight except close to wing margin where it is slightly curved towards apex of wing. A large complex anal vein behind CuP, widely separated from CuP, branching fan-wise as in CuA, and at about the same distance from wing base, the more basal, anteriorly-directed branches ending on CuP, and with more than 10 terminal branches.

Family Scytinopteridae

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 Triassic of Australia. They have been considered ancestral to or as primitive Fulgoroidea, Cicadelloidea or Cercopoidea, with recent opinion favouring the family as being ancestral to Cicadelloidea (Becker-Migdisova 1962; Evans 1963) or ancestral to both Cercopoidea and Cicadelloidea (Evans 1964).

Scytinopteridae differ from Prosbolidae, the other dominant family of the Upper Permian, in the absence of both a nodal break in the fore margin (as in Cicadidae) and a transverse nodal line across the middle of the fore wing. The fore margin of the hind wing is not deeply emarginate, as in Prosbolidae.

It is sometimes difficult to distinguish the fore wings of Scytinopteridae from those of Fulgoroidea, especially the early (Permian) family Pereboriidae. There is a tendency towards a basal pentagonal cell in Pereboriidae and the venation is usually more densely branched than in Scytinopteridae. The Pereboriidae are amongst the most primitive known Hemiptera, and the family very probably arose from a primitive protoblattodean-like ancestor.

A species from the Upper Permian of southern Africa is referred to the Scytinopteridae. It is similar to species from the Upper Permian of Australia. Although the median field is imperfectly preserved the species is referred tentatively to the Australian genus *Orthoscytina*.

Genus *Orthoscytina* Tillyard 1926

The genus is recorded from the Upper Permian of Australia. Tillyard described and gave nine separate specific names to tegmina that he referred to the genus, Evans (1943) was of the opinion that all these tegmina could equally have been regarded as representatives of a single species. He figured, but did not name, another ten tegmina none of which corresponded exactly with those described by Tillyard. R has a number of branches and CuA usually has more than two branches in all

these tegmina. The branching of M, too, is somewhat variable but it is usually 4-branched.

Owing to variability in the fore wings of *Orthoscytina* it is difficult to ascertain any specific difference that may be present between the wing from southern Africa and those from Australia. However, it is considered preferable to distinguish this wing specifically from the Australian species.

The wing from southern Africa resembles *subcostalis* Tillyard 1926 in the 2-branched CuA but R differs in being 4-branched.

Orthoscytina dubitata sp. nov. (Fig. 17; Plate 4, fig. 3)

Type. NM 873 a, b in Natal Museum. NM Type no. 1979.

Description. Fore wing except for base and apex. Length as preserved *c.* 8 mm, indicating a total length of *c.* 10 mm. R with 4 branches. Apex of Rs and branching of M not preserved. CuA 2-branched. The m-cu cross-vein to the upper branch of CuA. Clavus with 1A only slightly curved. Fore margin of tegmen thickened towards base.

Family Prosbolidae

The family is similar to Scytinopteridae except that, as indicated above, there is either or both a nodal break in the fore margin and a nodal line across the middle of the fore wing. M and CuA have deep forks arising almost in line with the origin of Rs except in a few species in which Rs arises more basally. When the node on the fore margin is well developed, the branch of R to the node is distinctly curved forward.

The family is well represented in the Permian of Russia and Europe and may occur in the Upper Permian of Australia but *Permodipthera robusta* (Tillyard 1925) is imperfectly preserved and *Mitchelloneura permiana* (Tillyard 1921) is based on a hind wing of which the fore margin is not adequately preserved: the venation suggests that it should be referred to the Scytinopteridae in preference to Prosbolidae.

The placement of a few species presents some problems. In *Permocicada borealis* from the Upper Permian of Russia, a distinct node is not developed on the fore margin but there is a faint nodal line across the wing. R appears as a straight vein with the posterior branch, and not the anterior branch, forming the main apical section of the vein continuing straight to the wing margin, and Rs arises more basally than the branching of M and CuA.

A wing from the Upper Permian of southern Africa is similar to *Permocicada borealis* except in the branching of CuA in which CuA 2 is more transverse and lies on the nodal line. In this respect, and in the proximal origin of Rs, the wing resembles *Austroprosbole* but there are marked differences. The wing is referred to a new genus of Prosbolidae.

Another wing from the Upper Permian of southern Africa is referred to the Prosbolidae: it resembles the Permian genus *Neuropibrocha* (Becker-Migdisova 1961) in the much-branched venation and slight emargination on the fore margin suggesting an incipient node. Becker-Migdisova referred *Neuropibrocha* to the Pereboriidae. The wings do resemble *Pereboria*, and also Recent Fulgoroidea, to a con-

siderable extent, but the incipient node suggests a closer relationship with Prosbolidae, although the venation is much nore dense than in typical Prosbolidae. *Neuropibrocha* and the new species from southern Africa are referred to the Prosbolidae and considered very primitive representatives of the family.

Genus **Beaufortiscus** gen. nov.

Derivation: From the Beaufort Series.
Gender: Masculine.
Type species: *Beaufortiscus dixi* sp. nov.

Diagnosis. Fore wing tegminous, distinctly sculptured anteriorly and on clavus. Nodal line distinct but without defined node on anterior margin. R almost straight at apex, with posterior branch of R continuing the line to the margin. Rs arising distinctly before the nodal line. CuA 2 almost transverse and forming part of the nodal line. Clavus with three anal veins, stem of 2A + 3A distinct towards base. M and CuA anastomosed for a short distance at base.

Beaufortiscus dixi sp. nov. (Fig. 15; Plate 5, figs 1, 2)

Etymology. The species is named for Mr Owen Dix who found the very fine holotype specimen.
Type. NM 950 a, b, and paratype NM 928 a, b, in Natal Museum. NM Type no. 1980.
Type locality. Lidgetton, Natal.
Description. Holotype. Complete tegmen. Length *c.* 12,5 mm. Rs arising about half way between nodal line and origin of M, curving slightly anteriorly at margin. The r-m cross-vein half-way from nodal line to wing margin. M 4-branched, M 3 + 4 simple and M 1 branched. The m-cu cross-vein to CuA 1 close to its origin. 1A sigmoidally curved. 2A + 3A with basal stem diffuse but as long as the veins before they re-anastomose. Costal space and clavus with dense fine pits, appearing as tubercles in the obverse mould. Similar pits on each side of the main veins.

NM 928 a, b is the distal half of a wing. The anterior branch of M does not have an end-twigging and M 3 + 4 and CuA 1 diverge from one another at the wing margin.

Genus **Neurobole** gen. nov.

Derivation: A combination from *Neuropibrocha* and *Prosbole*.
Gender: Feminine.
Type species: *Neurobole ramosa* sp. nov.

Diagnosis. Similar to *Neuropibrocha* in having a much-branched fore wing venation and a slight emargination of the fore margin at the apex of R but with the cross-veins more regular. Rs arising well before apex of R. M apparently deeply forked.

Neurobole ramosa sp. nov. (Fig. 19; Plate 4, fig. 4)

Type. N–MN 32, in Bernard Price Institute.
Description. Anterior apical half of a fore wing. Length as preserved *c.* 9 mm, indicating a wing length of *c.* 15 mm. Costal space broad, apparently with irregularly developed, branched cross-veins. R with 6 or 7 terminal branches, the short basal

branch to the margin, at a slight emargination, directed basally. Rs with 11 or more terminal branches, forking only after the forking of R. One stout cross-vein between Rs and M some distance from wing margin. M apparently branching well before the branching of Rs but vein not fully preserved. Cu and anal veins not preserved.

Family Cicadoprosbolidae

Genus *Austroprosboloides* Riek 1973

A second fore wing referable to the genus preserves complete details of the apical two-thirds of the wing. Rs joined to the upper branch of M by a short cross-vein. As indicated in the original diagnosis the anastomosis between these two veins in the holotype of *A. vandijki* is only an aberration. CuA forked near apex, with the lower branch ending on the wing margin well beyond the apex of the claval suture and the transverse nodal line. The kink in Rs at the nodal line is very pronounced and sub-angular.

Austroprosboloides vandijki Riek 1973 (Fig. 18; Plate 4, fig. 5)

Austroprosboloides vandijki Riek 1973: 527.

NM 889 a, b, from Bulwer, is the distal two-thirds of a tegmen. Length *c.* 10 mm. Similar to and more clearly preserved than holotype, except that Rs and M 1 + 2 are connected by a short cross-vein and not anastomosed for a short distance and the spur vein posteriorly on M is continued to the wing margin so that M is 5-branched. CuA 2 ending on wing margin about half its length beyond the apex of CuP (=claval suture). Clavus detached, and not preserved. Rs thickened at the kink at the transverse claval line.

NM 929 a, b is the distal two-thirds of a fore wing of which the distal portion of the fore margin is not preserved and other parts are obscure. The wing membrane is thick and finely tuberculate. M and CuA arise from a point on R, and CuA is slightly more strongly curved than in the holotype. Rs arises slightly basal of the forking of M. M is only 4-branched. The presence of a node and nodal line cannot be ascertained because of the imperfect preservation.

NM 844 is part of a hind wing that may be referred to this species. Rs is simple, M is apparently 3-branched and CuA is deeply forked. The costal margin and anal region are not preserved.

Family Eoscartarellidae

The distinction between this family and the Dysmorphoptilidae is based mainly on wing shape. The wing margin is deeply emarginate at the apex of R in Dysmorphoptilidae and entire in Eoscarterellidae. There is a series of costal veinlets in the Dysmorphoptilidae.

Dysmorphoscartella (Riek 1973) from the Upper Permian of southern Africa was referred to the Eoscartarellidae even though the apex of the wing was not entire. However, the emargination is not at the apex of R, as in Dysmorphoptilidae. A second specimen of this genus from the same horizon shows that M and CuA are connected by a cross-vein as in other Eoscartarellidae.

Dysmorphoscartella lobata Riek 1973 (Fig. 16; Plate 5, fig. 2)

Dysmorphoscartella lobata Riek 1973: 528.

NM 893, from Bulwer, length 22 mm, preserves the posterior half of a fore wing showing clearly the basal origins of M and CuA. The clavus is attached and fully preserved. Costal area, near base, deeply grooved near the margin, as in Recent Cercopoidea. M arising from stem of R close to wing base. The branching of M differs from that in the holotype but this is considered to be individual variation, especially as there is no difference in wing shape. CuA deflected slightly towards M at its point of origin but cross-connection not distinct. A small area of the wing, discally, below the curved basal stem of R is not clearly preserved. CuA may have been connected to the stem of R as in *Eoscartarella*. Clavus with 2 distinct anal veins. 1A diverging slightly from claval suture from base to apex. Second anal at margin except at the point of greatest curvature of the clavus. The posterior margin of the clavus is regular and without lobes or processes. Clavus sculptured similar to remainder of wing.

?Eoscartarellidae gen. et sp. indet.

NM 890 a, b, from Bulwer, is the fragment of the apex of a wing that may be referred to this family. The veins are not as branched at apex as in *Dysmorphoscartella lobata*. The veins and cross-veins are bordered on each side by a row of setal insertions and there is a marginal cord to the wing. Most of the preserved portion of the wing is finely sculptured but there are distinct pits near the anterior margin.

Family Protopsyllidiidae

The family is represented in the Upper Permian and Triassic of Australia and the Permian, Triassic and Jurassic of Russia. The species have been considered as archaic Psylloidea but the fore wing differs from that of Recent psyllids in the small clavus and more basal origin of M + CuA, and often 3-branched M. The hind wing is broader, the costal space is much narrower towards its apex, and there is less fusion between M and CuA than in the fore wing.

The Protopsyllidiidae are related to the Archescytinidae and Permaphidopsidae, the other two Permian families referred to the Sternorrhyncha. The Archescytinidae are the only Homoptera in the Lower Permian of Kansas. The family is represented in the Australian Upper Permian fauna by only a few atypical species whereas the Protopsyllidiidae are abundant. The Archesytinidae differ from Protopsyllidiidae in the absence of fusion between M and CuA and the unlooped veins in the clavus. The Permaphidopsidae, recorded from the Lower Permian of the Urals and the Kuznetsk Basin, and the Upper Permian of northern Europe, differ from Protopsyllidiidae mainly in the independent origin of both M and CuA from R, and the slight reduction in the size of the clavus.

A species from the Upper Permian of southern Africa is referred to the Protopsyllidiidae and placed in *Protopsyllidium*, a genus recorded from the Upper Permian of Australia.

Genus *Protopsyllidium* Tillyard 1926

Type species: *Protopsyllidium australe* Tillyard 1926: 26.

Diagnosis. Fore wing with M 2-branched and CuA deeply forked.

Protopsyllidium lynae sp. nov. (Fig. 20; Plate 5, fig. 4)

Etymology. The species is named for Miss Lyn Smook who has joined the Van Dijk family in fossil hunting.

Type. NM 874 a, b, in Natal Museum. NM Type no. 1981.

Description. Fore wing, with clavus detached but preserved. Length *c.* 4 mm. Closely similar to *Protopsyllidium sinuatum* Davis 1942 from the Upper Permian of Belmont, Australia, but R straighter at apex, pterostigma larger and less fusion between the stems of M and CuA. M branching level with branching of CuA. Rs arising distinctly closer to origin of M than pterostigma. Clavus small, with two anals, looped at apex, 1A close and parallel to CuP, second anal close to claval margin.

Family Permaleurodidae

Aleuronympha bibulla Riek 1974

Aleuronympha bibulla Riek 1974: 272.

NM 876 a, b is the apex of an abdomen very probably of this species.

Nymph of Homoptera (Plate 5, fig. 5)

N–MN 56 a, b is the body of a nymph without head. Length as preserved *c.* 6 mm, indicating a total length of *c.* 7,5 mm. The fore wing sheath is large, apparently almost concealing the hind wing and extending to the basal segments of the abdomen so, presumably, the nymph was in the last nymphal instar. Eight or nine segments of the abdomen are visible. The abdomen is without distinct doublure.

The nymph is similar in form to the known protopsyllidiid nymphs but is distinctly larger. It is also similar to psyllid nymphs but, also, it is large for that family.

ORDER *MECOPTERA*

Family Permochoristidae

The family is dominant in the Upper Permian of Australia and occurs also in the Triassic of Australia. It is possibly represented in the Permian of Russia. Sc is 2-branched in the fore wing and the more basal branch is short and almost transverse. M is 6-branched in the fore wing but only 4-branched in the hind wing. Rs is either 4-branched dichotomic or there is a tendency to pectination of Rs 1. The hind wing differs from the fore wing in a manner comparable with that which occurs in Recent Choristidae: Sc is simple, R is forked at apex, M is only 4-branched, and there is partial fusion between CuP and 1A.

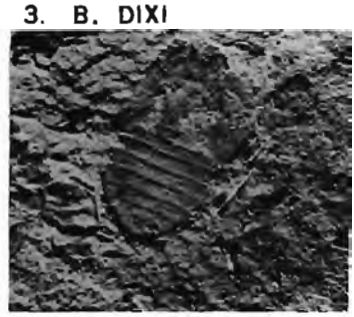
Two species from the Upper Permian of southern Africa are referred to *Mesochorista*. It is not possible on the preserved portions of the fore wings of one species to differentiate between the southern African specimens and *Mesochorista australica* (Tillyard). The second species differs from the known species but is most similar to *dubia* Riek from the Upper Permian of Belmont, Australia.

1. BEAUFORTISCUS DIXI

2. DYSMORPHOSCARTELLA LOBATA

3. B. DIXI

4. PROTOPSYLLIDIUM LYNAE



5. HOMOPTERA
NYMPH INDET.

PLATE 5

(1) *Beaufortiscus dixi* gen. et sp. nov. Holotype. NM 950 a; (2) *Dysmorphoscartella lobata* Riek, NM 893; (3) *Beaufortiscus dixi* gen. et sp. nov. Paratype. NM 928 a; (4) *Protopsyllidium lynae* sp. nov. Holotype. NM 874 a; (5) *Nymph. Homoptera.* N-MN 56 a.

Genus *Mesochorista* Tillyard 1916

Mesochorista Tillyard 1916.
Type species: *Mesochorista proavita* Tillyard 1916.

Diagnosis. Rs 4-branched, Rs 3 + 4 forking before Rs 1 + 2. Fore wing with cubito-median Y-vein variable.

The genus is recorded from the Upper Permian and Triassic of Australia and may occur also in the Upper Permian of Russia.

Mesochorista aff. *australica* (Tillyard) (Plate 6, figs 1,2)

Permochorista australica Tillyard 1917: 733.
Mesochorista australica: Riek 1953: 60.

NM 930 a, b is the distal two-thirds of a fore wing showing the forking of Sc, origin and branching of Rs and branching of M. Length as preserved *c.* 6 mm, indicating a wing length of *c.* 8 mm which is slightly smaller than Australian specimens.

NM 878 a, b is also the distal two-third of a fore wing, less completely preserved than NM 930 but showing the Y-vein connection between the stems of M and CuA, representing the fusion of MP with CuA.

Mesochorista channingi sp. nov. (Fig. 21; Plate 6, fig. 3)

Etymology. The species is named for Mr A. E. Channing who collected some of the Mecoptera fossils.

Type. NM 877 a, b, in Natal Museum. NM Type no. 1982.

Description. Similar to *dubia* in the structure of Sc and branching of Rs but wing distinctly larger and cubito-median Y-vein clearly defined. Length *c.* 12,5 mm. Sc long, continuing straight to apex, forking slightly after level of first fork of Rs and with a strong cross-vein to R shortly after the forking. Rs 1 + 2 forking only very slightly after forking of Rs 3 + 4. M apparently only 5-branched, branching not completely preserved. Cubito-median Y-vein very clearly defined, Cu arm the longer. CuA curved posteriorly towards apex. 1A and 2A simple, 3A appearing branched (representing 3A plus jugal vein).

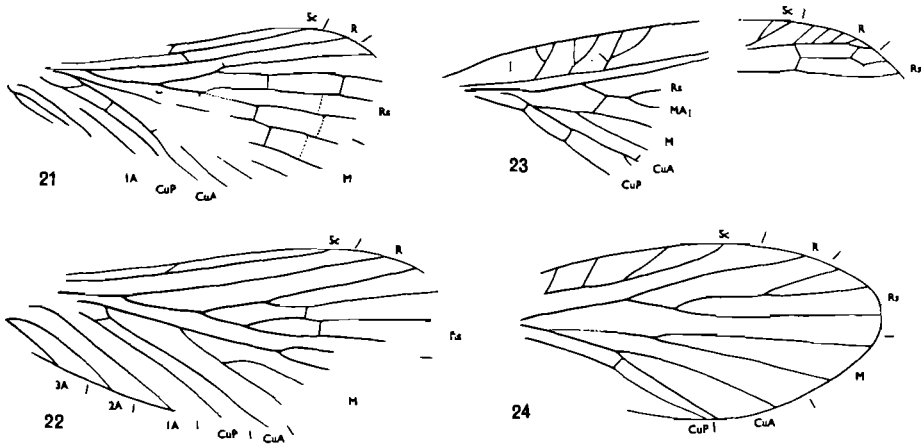
NM 901 a, b, is very probably a fragment of a wing of this species, preserving only the apex of R and branching of Rs.

Family Mesopanorpodidae

This family is possibly a composite one embracing all the Permian and early Mesozoic species in which the venation is reduced to a very simple condition, with Sc 2-branched and both Rs and M 4-branched. The family is well represented in the Upper Permian, and is recorded also from the Triassic, of Australia. The cubito-median Y-vein varies from being well developed to obliterated through anastomosis of the stems of M and CuA for a short distance.

The family is distinguished from the Nannochoristidae, a family with extant species that is also recorded from the Upper Permian of Australia, by the absence or limited amount of anastomosis between the stems of M and CuA, and the 4-branched Rs.

A species from the Upper Permian of southern Africa is placed in *Prochoristella*, a genus recorded from the Upper Permian of Australia.



Figs 21–24. (21) *Mesochorista channingi* sp. nov. Holotype; (22) *Prochoristella hartmani* sp. nov. Holotype; (23) *Sismerobius pusillus* gen. et sp. nov. Holotype; (24) *Permonka bifida*. NM 866. Fore wing.

Genus *Prochoristella* Riek 1953

Prochoristella Riek 1953: 71.
Type species: *Prochoristella megaloprepia* Riek 1953: 71.

Diagnosis. Fore wing with cubito-median Y-vein variable, from arms subequal to CuA just anastomosed with M, and then M appearing to arise only gradually from CuA.

Prochoristella hartmani sp. nov. (Fig. 22; Plate 6, figs 4, 5, 7)

Etymology. The species is named for Mr G. Hartman, who has collected insects from this series with the Van Dijk family.

Type. NM 900 a, b, and paratype NM 879 a, b, in Natal Museum. NM Type no. 1983. Paratype N–MN 23 a, b, in Bernard Price Institute.

Description. NM 900 a, b. Complete fore wing except for postero-apical one-third. Length as preserved *c*. 5,5 mm, indicating a wing length of *c*. 6 mm. Similar to Australian species except in the branching of Sc and straighter Rs 1. Sc forking slightly after level of origin of Rs 1, the distal branch long and almost straight to wing margin. Rs 1 + 2 branching only slightly after Rs 3 + 4. Arms of cubito-median Y-vein only slightly unequal. Three anal veins distinct, 2A and 3A arising close together and distinctly separated from 1A.

In NM 879 a (counterpart b preserves only the branching of Rs). Sc is slightly more curved at apex and the branching is slightly more distal but in other preserved parts the wing is similar to the holotype.

N–MN 23 a, b is complete except for the anal veins and part of Cu. The branching of Sc, Rs and M is similar to that in the holotype except that both branches of Rs branch again slightly more distally. The rounded apex of the wing is preserved.

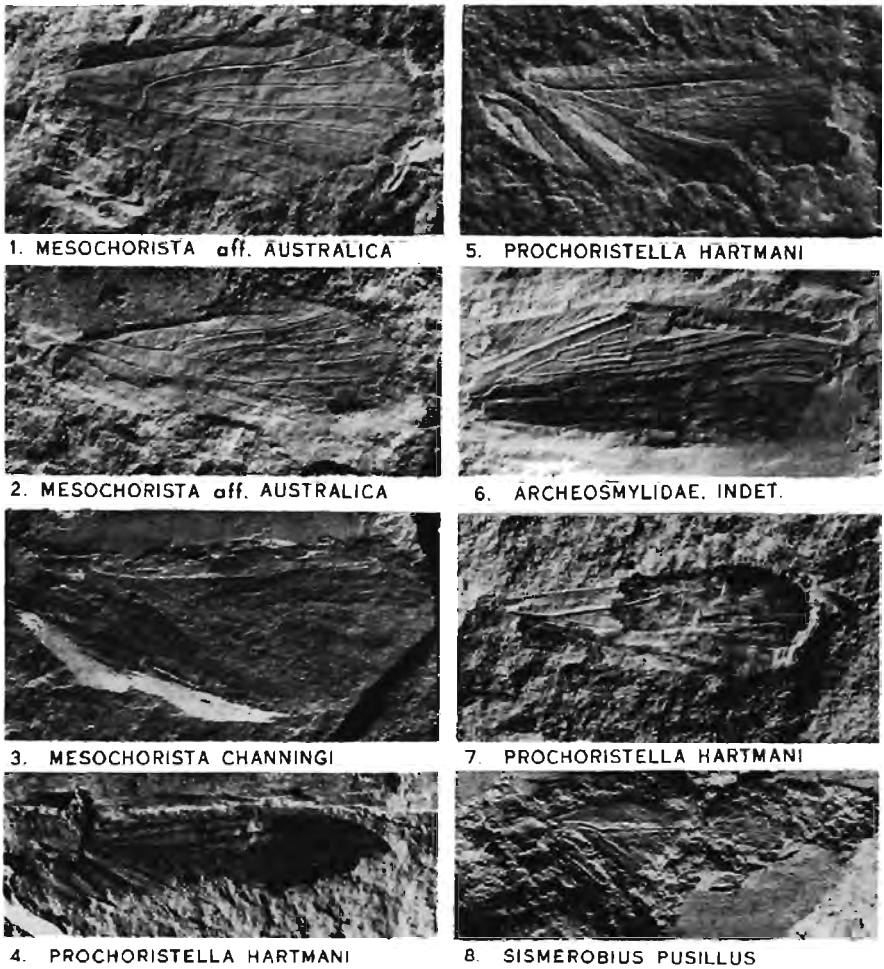


PLATE 6

(1, 2) *Mesochorista* aff. *australica* Tillyard. 1. NM 930. 2. NM 878 b; (3) *Mesochorista channingi* sp. nov. Holotype. NM 877 b; (4, 5, 7) *Prochoristella hartmani* sp. nov. 4. Paratype. NM 879 a, reversed. 5. Holotype. NM 900 b, reversed. 7. N–MN 23 b; (6) Archeosmylidae, gen. et sp. indet. NM 937 b; (8) *Sismerobius pusillus* gen. et sp. nov. Holotype. Reversed.

Prochoristella sp. indet.

NM 932 a, b is poorly preserved. It is probably a hind wing. Rs 1 + 2 forks towards the wing margin, as in *concinna* Riek from the Upper Permian of Australia.

Family Nannochoristidae?

NM 934 a, b is a very small wing, length *c.* 4 mm. Rs is possibly only 3-branched with Rs 1 + 2 simple. The bases of M and Cu are indefinite so that family placement cannot be confirmed but the reduced branching of Rs and the small size are suggestive of Nannochoristidae.

ORDER *NEUROPTERA*

Family Palaemerobiidae

The Palaemerobiidae and the Sialidopsidae (including Permosisyridae) are the earliest undoubted Neuroptera. The two families differ in the amount of end-twigging to the veins, which is more developed in Palaemerobiidae, in which the costal veinlets, too, are branched. Sc and R are separate at apex, with Sc ending on the costal margin. The pterostigma is weakly developed. The upper branch of MA is anastomosed with the stem of Rs for a short distance. The insertions of numerous stout setae are visible on the veins and costal cross-veins. The trichosors at the wing margin are of the elongated dilarid form. There is a distinct similarity between the Palaemerobiidae and Recent Dilaridae and Berothidae.

Palaemerobiidae are recorded from the Permian of Europe and Siberia. A species from the Upper Permian of southern Africa is referred to the family.

Genus *Sismerobius* gen. nov.

Derivation: A combination from *Sisyra*, a genus of small Neuroptera, and *Palaemerobius*.
Gender: Masculine.
Type species: *Sismerobius pusillus* sp. nov.

Diagnosis. Similar to *Palaemerobius* with branched costal veinlets, Sc and R separate at apex, R straight at apex and pterostigma not sharply defined, CuA strongly deflected at base to fuse for a very short distance with the stem of M, and CuP simple or almost so, but distinguished by the wide separation of M from the stem of Rs and, apparently, with fewer branches to Rs with, consequently, fewer cross-veins between R and Rs.

Sismerobius pusillus sp. nov. (Fig. 23; Plate 6, fig. 8)

Type. NM 938, in Natal Museum. NM Type no. 1984.

Description. Fore wing. Length *c.* 7 mm. Costal space widest in middle, narrowing only slightly to apex. Costal veinlets widely spaced, irregularly branched, branches deep. R with 4–5, anteriorly directed, terminal branches. Rs arising well beyond the basal curvature in R, branching not fully preserved, but apparently open, upper terminal branches widely separated. With two subapical cross-veins between R and Rs. Upper branch of MA anastomosed with stem of Rs for a distance slightly greater than the free stem of the branch. M arising from base or close to base, subparallel to R at the basal curvature, branching early and before the upper branch to Rs. Stem of Cu defined, well separated from M. CuA touching M at the level of the distal curvature of R. CuA branching only beyond its presumed middle. CuP simple at least to branching of CuA. Anals not preserved. End-twigging, apparently, not well developed. Venation with openly-spaced macrotrichia, represented by pits in obverse mould of wing. Hind wing. Only stem of R preserved.

Mesonotum and metanotum preserved. Praescutum small. Parapsides very large, meeting at meson over a long distance. Scutellum only slightly produced at apex, with distinct transverse groove about middle. Parapsides each with at least seven, large, openly-spaced, stout setae and scutellum with two stout setae (represented by deep pits in the obverse mould).

Family Archeosmylidae gen. et sp. indet. (Plate 6, fig. 6)

The family is recorded from the Upper Permian of Australia. Sc and R are fused at apex, as in Permithonidae, from the Upper Permian of Australia and Russia, but the pterostigma is very long, the main veins, especially Rs, have numerous close branches, and the trichosors are short and very distinct. The family is apparently directly ancestral to Osmylidae. The wings of the Archeosmylidae differ from those of Protosmylinae (Osmylidae) in the absence of regularly arranged gradate cross-veins and in the simpler CuP and anal veins.

NM 937 a, b, is the distorted apex of a wing, showing a long pterostigma. There are apparently only a few cross-veins between R and Rs, Rs had at least 7 and probably 9–10 branches and there were distinct macrotrichia on the veins. The specimen is referred tentatively to the Archeosmylidae.

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I wish to record my deep and sincere appreciation to Dr Eddie van Dijk without whose unflagging efforts and boundless enthusiasm the insects on which this study is based would have remained undiscovered and have been lost in the weathering of the exposed and disturbed strata. I am especially appreciative, also, of Dr Brian Stuckenberg's interest in my study of this fossil insect fauna. Study facilities were provided in the Natal Museum. My studies at the Bernard Price Institute were greatly facilitated by Heidi Anderson whom I thank most sincerely. The photographs are mainly a joint effort by Eddie van Dijk and by John Green of CSIRO Canberra. The line-drawings were prepared by Mrs Sybil Monteith from preliminary drawings by myself.

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