

MESOZOIC INSECTS OF QUEENSLAND.

No.1. PLANIPENNIA, TRICHOPTERA, AND THE NEW ORDER
PROTOMECOPTERA.

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(Plates vii.-ix., and seven Text-figs.)

INTRODUCTION.

The present paper deals with a portion of the very interesting fossil insects recently obtained from the Ipswich Beds by Mr. B. Dunstan, Chief Government Geologist of Queensland, to whom I am much indebted for the opportunity of studying such fine and, in many respects, unique material. This collection may be looked upon as the *third* collection of insect fossils made at Ipswich. The first, or Simmonds Collection, was made in 1890 by Mr. T. H. Simmonds, of Brisbane, and the specimens were described by Etheridge and Olliff in the same year.* In 1909, Mr. Dunstan made a second collection of insects from the same locality. These were sent to me for study in 1913, together with some fossil insects from other beds in Queensland and New South Wales. All these were dealt with in a paper published last year by the Queensland Geological Survey.† In this paper,

* The Mesozoic and Tertiary Insects of New South Wales [and Queensland]. Geol. Survey of N.S.W. Memoirs, Palæontology, No.7, pp.9-22, two plates, 1890.

† Mesozoic and Tertiary Insects of Queensland and New South Wales. Queensland Geol. Survey, Publication No.253, pp.1-47, nine plates, six text-figs, 1916. (Stratigraphical Features, by B. Dunstan, pp.1-13).

the total of *named* Ipswich fossils was brought up to twenty-two, representing the following Orders:—

Order.						Genera.	Species.
Blattoidea	1	1
Protorthoptera	2	2
Coleoptera	5	14
Odonata	1	1
Mecoptera	1	1
Lepidoptera	1	1
Protohemiptera	1	1
Hemiptera	1	1
Total, 8	13	22

In dealing with the stratigraphy of the Ipswich Beds,* Mr. Dunstan places the fossil insect bed as most probably Upper Triassic. The assemblage of insects so far revealed from these beds comprises a series of forms which, judged by the succession of strata in the Northern Hemisphere, range from Upper Carboniferous to Jurassic; some of the latter differing very little from forms still living in Australia to-day. It would seem to be useless to discuss, at present, the question of the exact age of the Ipswich fossil insect bed, since the data required for correlation with beds of known age are not yet available. What is of importance to entomologists, however, is the fact that the Ipswich Insects are undoubtedly, in most respects, more specialised than the Upper Carboniferous and Permian Insects of the Northern Hemisphere; while, at the same time, they are, on the whole, undoubtedly more archaic than the assemblage of forms known from the Lower Lias. To give a striking example, the dragonfly *Mesophlebia antinodalis* Tillyard, from Ipswich, is intermediate between the Carboniferous Protodonata, in which no nodus was formed, and the Liassic Odonata, in which the same structure of the wing was completely formed. In other words, the intermediate condition of nodus-formation, seen in

* *Op. cit.*, No.253, pp.1-13.

Mesophlebia, is the condition that would be expected to be found in Triassic dragonflies from the Northern Hemisphere, if such were available. Similarly, it will be seen that the Caddis-flies described in this paper are definitely more archaic than the known Liassic forms. The value of the Ipswich fossils, therefore, lies in this, that they are gradually filling up the gaps left in Insect Phylogeny, by the unfortunate hiatus in the Trias of the Northern Hemisphere. Whether we designate these fossils as Triassic or Trias-Jura matters little, in comparison with the fact that they contain, amongst their number, forms which, if they were ever present in the Northern Hemisphere, could only have been Triassic.

Chiefly as a result of the interest attached to the specimens described by me from Mr. Dunstan's 1909 collection, further work was carried on at Ipswich in 1915-16. Owing to the sharp angle of dip, the fossil bed cannot be followed down very far without removing a great deal of overburden. Under Mr. Dunstan's close supervision, this has been carefully carried out by Mr. Wilcox, the shale being removed in large pieces to the Geological Survey in Brisbane, where it was delaminated with great care. The rock taken from some distance below the originally exposed surface has proved hard, and not easily delaminable. It would also appear to be much poorer in insect fossils than the rock nearer the surface; but this may be, in reality, only due to the difficulty of splitting it up sufficiently. The result of the examination of a considerable quantity of this rock has been the formation of the new collection of Ipswich fossil insects, which I hope to deal with in this series of papers. Mr. Dunstan informs me that the total number of specimens approaches two hundred. Most of these, however, are either Coleopterous elytra, Blattoid tegmina, or fragments of wings that do not merit a name; so that the number of recognisable new forms will be very much smaller. The study of these forms is a matter of great difficulty, requiring much care and maturity of thought. With an entirely new type of wing, it is much wiser to withhold publication for at least a year, while the peculiarities of the venation can be turned over and over in one's

mind, and a matured judgment given. Thus I have found it impossible to offer a complete account of these fossils in a single paper, without serious delay in the writing of it. The alternative is to deal with each Order separately, and to publish the results in a series of shorter papers. This I have determined to do. The present paper, dealing with the Orders Planipennia and Trichoptera, and the new Order Protomecoptera, is the first of this series.

Order NEUROPTERA PLANIPENNIA.

Family PROHEMEROBIDÆ Handlirsch.

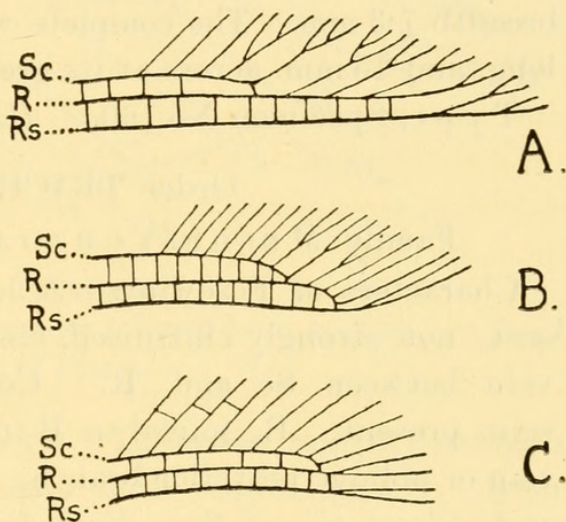
Genus PROTOPSYCHOPSIS, n.g. (Plate vii., fig.3).

Wings broad, moderately pointed, with a large number of forked apical veins. Costal margin moderately broad (not as broad as in *Psychopsis*), with numerous costal cross-veins, some forked. Sc and R separated by cross-veins; distally, Sc and R approach close to one another some little distance before the apex, and are there joined by the last of a series of cross-veins; at this point, the end of Sc turns obliquely upwards as a slanting forked vein to the costal border, while R runs almost straight on, to end somewhat above the apex. R and Rs more widely separated than are Sc and R; numerous cross-veins traverse the space between them, and continue well beyond the last cross-vein from Sc to R. Rs gives off at least twelve branches (S_1 - S_{12}), running longitudinally through the wing at a slight inclination from Rs, and subparallel to one another. The cross-veins between these branches of Rs are exceedingly delicate, and only discernible in strong oblique light. There are two rows of gradate veins arranged into almost complete transverse lines across the wing; the more distal series lies below the extreme ending of Sc on the wing-margin, and runs from R down to S_{12} ; the more proximal series lies twice as far from the apex as does the former series, and runs from S_3 to S_{12} . Between these lies an intermediate series, forming a set of steps from S_2 to below S_{12} ; this series starts close to the outer series, then curves away from it, and ends up below S_{12} very close to the inner series.

Some other scattered cross-veins are present, but are not easily discernible. [Rest of wing missing].

G e n o t y p e, *Protopsychoptis venosa*, n.sp.

This genus would appear to be very closely allied to *Brongniartiella* Handlirsch, and *Mesopsychoptis* Handlirsch, both Jurassic forms, but differs from them in possessing a broader costal field apically, and in the presence of the three gradate series. It is also undoubtedly closely allied to our Australian genus *Psychoptis*, which is one of the most archaic forms of Planipennia still existing. The arrangement of the gradate series, some as complete straight lines across the wing, and some as step-veins, is exactly that found in *Psychoptis*. *Protopsychoptis*, however, differs from *Psychoptis* in not having the costal field unduly widened, and in lacking (as far as we can see in the fragment preserved) the multiple forkings of the costal cross-veins, and their breaking up by cross-veinlets, which is characteristic of *Psychoptis*. Also, in *Psychoptis*, Sc and R stand further apart, and there is a linking-up of Sc, R, and Rs distally by two strong cross-veins, which close off the closely-veined marginal area



Text-fig. 1. *

from the three strong main veins with their intermediate cross-veins. In *Psychoptis illidgei*, however, this arrangement remains only partially completed, so that *Protopsychoptis venosa*, *Psychoptis illidgei*, and *Ps. elegans*, for instance, form (for this character) a phylogenetic series, as shown in Text-fig. 1.

There can be little doubt that our recent genus *Psychoptis* is a direct descendant from a form similar to *Protopsychoptis*.

* Phylogeny of the distal ends of Sc, R, and Rs in *Protopsychoptis* and *Psychoptis*. A, oldest stage (*Protopsychoptis venosa*, n.g. et sp.). B, intermediate stage (*Psychoptis illidgei* Froggatt). C, final stage (*Psychoptis elegans* Guér.), with the three veins strongly linked together by cross-veins.

That being so, it becomes questionable whether Handlirsch's family *Prohemerobiidæ* ought to be retained, especially as the name is misleading, and suggests that they were ancestors of the *Hemerobiidæ*, with which they almost certainly had nothing to do. All these forms might well be classed as *Psychopsidæ*.

PROTOPSYCHOPSIS VENOSA, n.sp. (Plate viii., fig.3).

Characters as for the genus. [Only the apical portion of the wing preserved]. All the venation beautifully preserved, except for the more basal portion above Sc, which is indistinct. The furrows between the sectors are very clearly shown, but have not been drawn in the plate, in order to keep the venational scheme quite obvious.

Measurements of fragment: greatest length 9.5 mm., greatest breadth 7.3 mm. The complete wing would probably be 30 mm. long, and 15 mm. across at its greatest width.

Type, Specimen No.160a. (Coll. Queensland Geol. Survey).

Order TRICHOPTERA.

Family MESOPSYCHIDÆ, fam.nov. (Plate vii.).

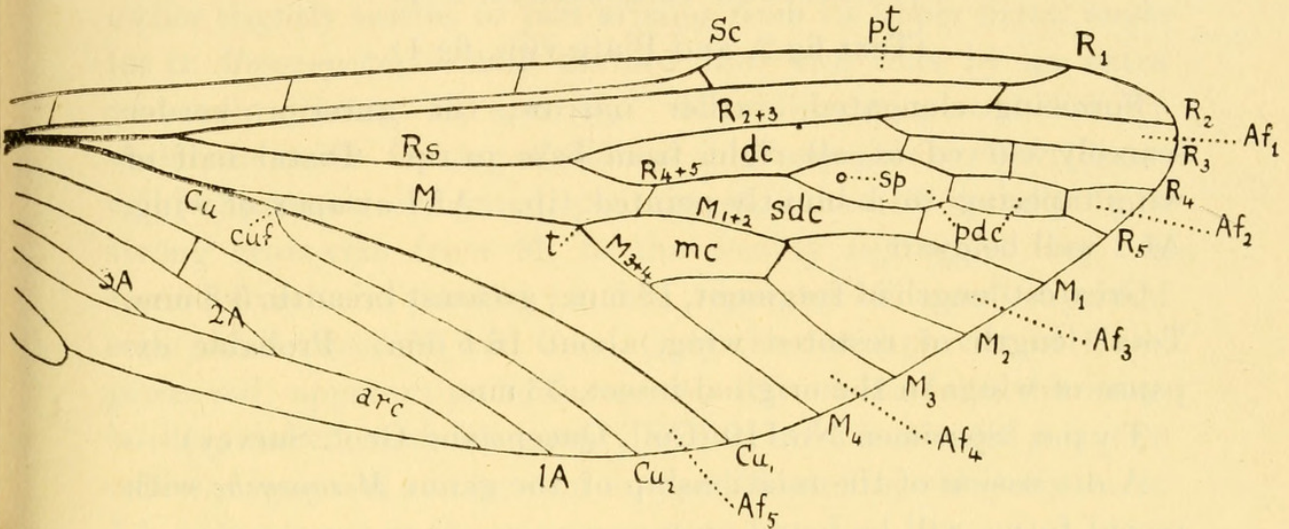
Characters of Forewing.—A long pterostigmatic region present, not strongly chitinated, closed off proximally by a cross-vein between Sc and R. Costal space with extra cross-veins present. R_1 joined to R_2 near apex by means of a cross-vein or oblique posterior branch. All five apical forks present, *and at least one of them divided into two or more separate cells, by cross-veins not present in recent forms.* Apical fork 2 with wing-point present. Discoidal and median cells present, completely closed, separated by an extra closed (subdiscoidal) cell between R_5 and M_1 . Thyridium-cell present or absent. Cubital veins variable. [Anal area not preserved].

With the above definition of the family, the two beautiful forewings represented in the present collection may be placed in two separate genera as follows:—

- | | |
|---|---------------------------------|
| Thyridium-cell absent; apical fork 2 divided into three polygonal cells, by means of two cross-veins and zig-zagging of R_4 and R_5 | Genus MESOPSYCHE, n.g. |
| Thyridium-cell present; apical fork 3 divided into two cells. | Genus TRIASSOPSYCHE, n.g. |

Genus *MESOPSYCHE*, n.g. (Text-fig.2, and Plate vii., fig.1).

To the characters of the family, as given above, we add the following generic characters:—Two costal cross-veins preserved (probably three or more in complete wing). Sc and R run parallel and very close together. Pterostigmatic region long and narrow, the proximal cross-vein descending obliquely from Sc at its distal end. R_1 joined to R_2 by a single backwardly



Text-fig.2.

Restoration of forewing of *Mesopsyche triareolata*, n.g. et sp., ($\times 7$) For lettering, see Explanation of Plates.

slanting cross-vein above Af.1. Discoidal cell (*dc*) elongated, hexagonal, with Af.1 and Af.2 both sessile upon it. Beyond distal side of *dc*, an extra cross-vein connects R_3 with R_4 . In Af.2, three separate cells (Text-fig.2, *pdc*) are formed by means of two connecting cross-veins and weak zig-zagging of R_4 and R_5 . Wing-point (*sp*) placed in Af.2 not far from the forking of R_4 from R_5 . Subdiscoidal cell (*sdc*) elongated, hexagonal. Median cell (*mc*) an irregular pentagon, with Af.4 strongly sessile upon it, Af.3 just arising from its upper distal angle. Thyridium (*t*) placed directly under the main forking of R_s . Thyridium-cell (*t'*) absent. Cu apparently fused with M basally, *cu_f* placed well basad (under second costal cross-vein) and consequently Af.5 of great length.

So much of this wing is preserved, with the details of venation beautifully clear, that there is no difficulty in restoring it to

its complete form. This I have done in Text-fig.2. The only doubtful point is as to the form of the anal area, which I have restored on the typical Trichopterous plan of a long curved arculus (*arc*), with veins 2A and 3A falling obliquely upon it from above.

G e n o t y p e, *Mesopsyche triareolata*, n.sp.

MESOPSYCHE TRIAREOLATA, n.sp.

(Text-fig.2, and Plate viii., fig.1).

Forewing elongated, rather narrow, the anterior border scarcely curved at all right from base to tip. Distal half of wing tapering to a bluntly pointed tip. Af.1 at apex of wing, Af.2 well below it.

Greatest length of fragment, 13 mm.; greatest breadth, 5.8 mm. Total length of restored wing, about 16.5 mm. Probable expanse of wings in the original insect, 33 mm.

T y p e, Specimen No.110 (Coll. Queensland Geol. Survey).

A discussion of the relationship of the genus *Mesopsyche* with recent forms will be found on p. .

Genus TRIASSOPSYCHE, n.g. (Text-fig.3, and Plate vii., fig.2).

To the characters of the family *Mesopsychidae*, we add the following:—Numerous costal cross-veins present (three preserved distally in a short space). Sc and R not close together, subparallel. Towards its distal end, Sc throws off an oblique cross-vein to C, and takes a short sharp bend downwards to the point at which it is connected to R₁ by a cross-vein; it then continues in a gentle curve onward, finally uniting with C at a point lying nearly half-way along the total length of the pterostigmatic region (as measured from the proximal cross-vein to apex of R₁). Consequently, pterostigmatic region very long, of irregular shape, narrowed proximally and broadened out in middle. R₁ connected with R₂ by a cross-vein descending from middle of *pt* on to *dc*. R₁ also forks distally, the lower branch running slantingly into R₂ well before the margin of the wing. Discoidal cell (*ac*) elongated, hexagonal, distinctly broader than in *Mesopsyche*, but of very similar general shape, with Af.1 and Af.2 both sessile

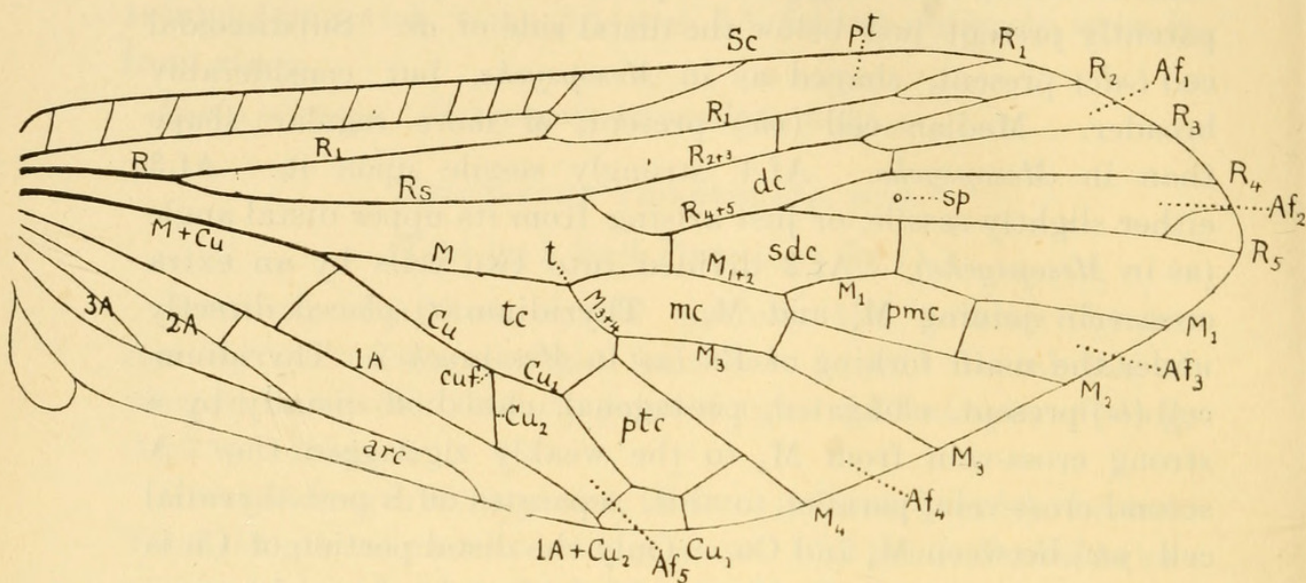
upon it. Apparently a small extra apical forking of R_5 in Af.2. Beyond dc , no extra cross-vein between R_3 and R_4 . No cross-veins in Af.2; the wing-point (sp) not clearly shown, but apparently present just below the distal side of dc . Subdiscoidal cell (sdc) present, shaped as in *Mesopsyche*, but considerably broader. Median cell (mc) present, of more regular shape than in *Mesopsyche*. Af.4 strongly sessile upon it. Af.3 either slightly sessile, or just arising from its upper distal angle (as in *Mesopsyche*). Af.3 divided into two cells by an extra cross-vein joining M_1 and M_2 . Thyridium (t) placed directly under the main forking of R_s (as in *Mesopsyche*). Thyridium-cell (tc) present, elongated, pentagonal, closed off distally by a strong cross-vein from M_4 to the weakly zig-zagged Cu_1 . A second cross-vein, parallel to this, separates off a post-thyridial cell (ptc) between M_4 and Cu_1 . Only the distal portion of Cu is preserved; apparently Cu_2 fuses with 1A not far from the wing-border, and the very irregularly formed Af.5 is divided into two cells by means of a cross-vein dropped from Cu_1 obliquely on to 1A + Cu_2 almost at the wing-margin.

G e n o t y p e, *Triassopsyche dunstani*, n.sp.

Though not so well preserved as the wing of *Mesopsyche*, yet this fossil shows most of the details necessary for a reconstruction to be possible. Several of the cross-veins are not completely preserved (see Plate vii., fig.2). There is a roughly raised linear mark extending between $M-M_4$ and $Cu-Cu_1$, which at first sight looks as if it might be covering a main vein. Fortunately, as Cu_1 is always a well-marked convex vein, it was possible to determine this question definitely. For, in the fossil, the vein marked Cu_1 is definitely convex, and hence there can be no main vein between it and $M-M_4$. The vein marked 1A is so determined because, at the point where it is broken off proximally in the fossil, it is definitely *diverging proximad* from Cu . Had it been converging, it would have been determined as Cu_2 , and the vein marked Cu_2 in the figures would have been considered a specialised cross-vein.

In Text-fig.3, I have attempted the restoration of this fine wing, which must be reckoned among the largest Trichopterous

wings known to have existed outside the *Phryganeidae* and *Limnephilidae*. The provisional restoration of the missing anal area is drawn on the same lines as that for *Mesopsyche*.



Text-fig. 3.

Restoration of forewing of *Triassopsyche dunstani*, n.g. et sp., ($\times 5\frac{3}{4}$).

For lettering, see Explanation of Plates.

TRIASSOPSYCHE DUNSTANI, n.sp. (Text-fig. 3, and Plate vii., fig. 2).

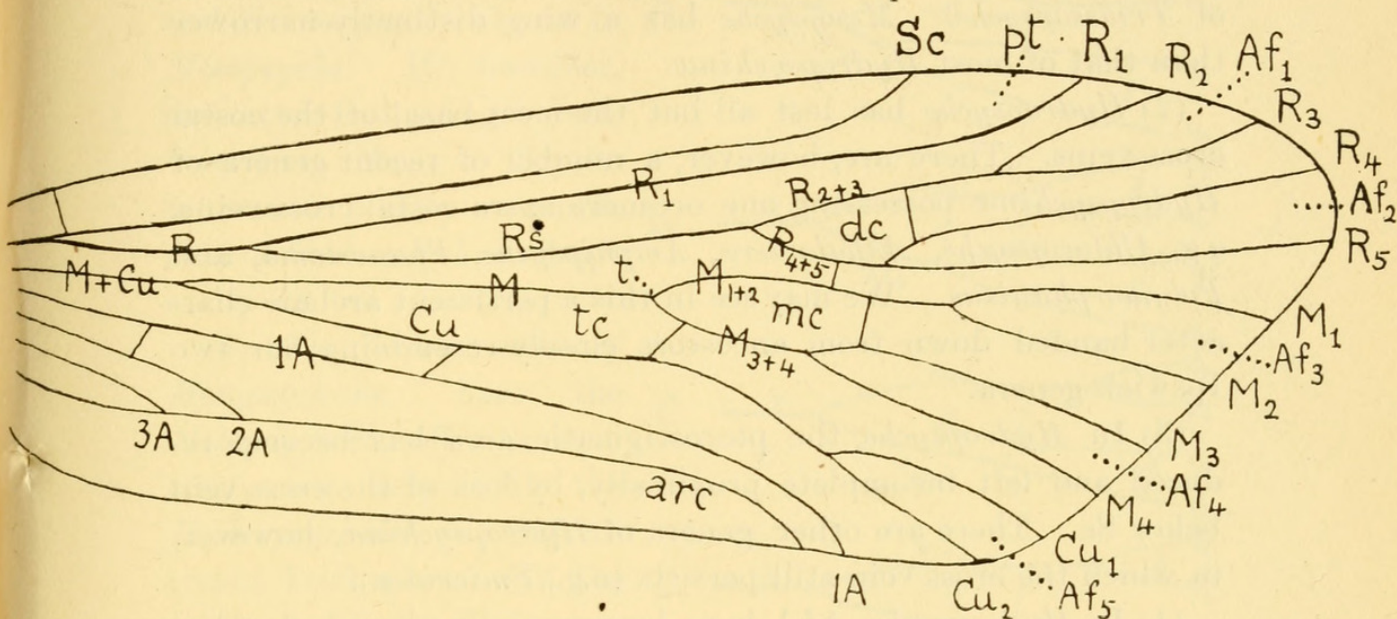
Forewing elongated, moderately broad, both anterior and posterior borders well curved distally. Apex moderately pointed. Af. 2 at apex of wing, Af. 1 placed well before it.

Greatest length of fragment, 13.5 mm.; greatest breadth, 6.8 mm. Total length of restored wing, about 19 mm. Probable expanse of wing in the original insect, 40.5 mm.

Type, Specimen No. 128a. (Coll. Queensland Geol. Survey).

These two fossil wings, *Mesopsyche* and *Triassopsyche*, are of very great interest, not only because they are the oldest fossil Trichoptera yet discovered, but also because they are, in actual wing-venational structure, very much more archaic than anything yet discovered in this Order. The Liassic *Necrotauliidae*, described from the beds of Dobbartin (Mecklenburg) and Aust (England), are a series of very small wings, ranging from 3 mm. to 7 mm. in length, the forewings possessing either four or five apical forks, the hindwings four. Most of these wings have no cross-veins, and, consequently, no closed cells of any kind. One

or two, however, have a closed discoidal cell, and one of the largest forms, *Necrotaulius major* Handlirsch, probably possessed a median cell as well. This latter form would come nearest to our Ipswich fossils, since it agrees with them in having both Af.1 and Af.2 sessile upon *dc*, and Af.4 sessile upon *mc*, while Af.3 appears to be just sessile upon the upper distal end of the same cell. In all other respects, the *Necrotauliidae* must be considered as considerably specialised by reduction, and loss of the archaic cross-venation inherited from Panorpoid ancestors.



Text-fig.4.

Forewing of *Hydropsyche* sp., for comparison with Text-figs. 2 and 3.

(After Ulmer).

Thus our new fossils are seen to stand in a much closer ancestral relationship with some of the more archaic present-day families than they do with the Liassic *Necrotauliidae*; and it seems exceedingly probable that we have in Australia, alive to-day, genera directly descended from them. Unfortunately, the Australian Trichopterous fauna, though both abundant and remarkable, has so far been hardly touched,* so that we are compelled to make a more general comparison with known forms from other parts of the world. On these lines, I must indicate

* Only thirteen species have, so far, been described from Australia and Tasmania; but I have, in my own collection alone, nearly a hundred species, many being closely related to New Zealand forms.

the *Hydropsychinae* as being the closest existing relatives of the *Mesopsychidae*, both in the general shape of the forewing, the relationships of the main veins and branches *inter se*, and, in particular, the structure of the discoidal and median cells (cf. Text-figs. 2, 3, 4).

If we compare the forewings of *Mesopsyche* and *Triassopsyche* with that of *Hydropsyche* (Text-fig. 4), we shall notice the following resemblances and differences:—

(1) The general shape of *Hydropsyche* closely resembles that of *Triassopsyche*. *Mesopsyche* has a wing distinctly narrower than that of most *Hydropsychinae*.

(2) *Hydropsyche* has lost all but the most basal of the costal cross-veins. There are, however, a number of recent genera of *Hydropsychinae* possessing one or more extra costal cross-veins, e.g., *Chloropsyche*, *Æthaloptera*, *Amphipsyche*, *Phanostoma*, and *Polymorphanisus*. We may see in this a persistent archaic character handed down from ancestors closely resembling our two Ipswich genera.

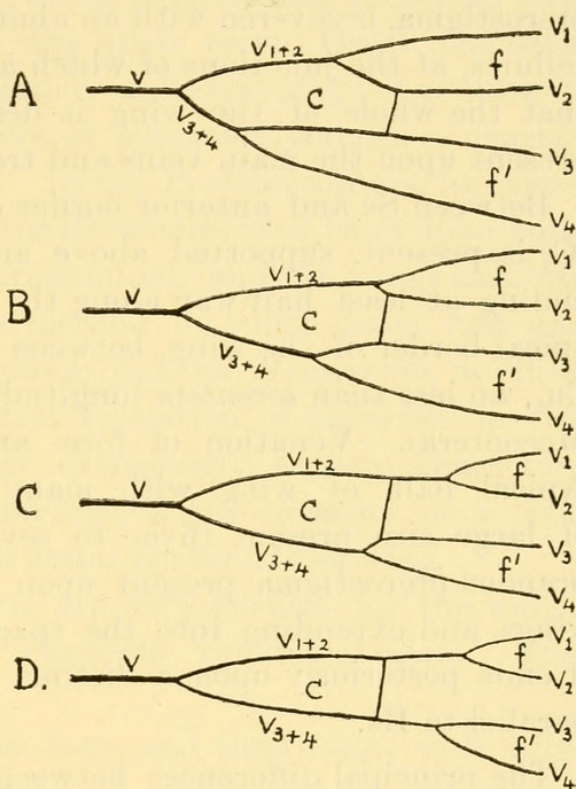
(3) In *Hydropsyche*, the pterostigmatic area has become reduced and left incomplete proximally, by loss of the cross-vein below Sc. There are other genera of *Hydropsychinae*, however, in which the cross-vein still persists (e.g., *Smicridea*).

(4) In *Hydropsyche*, Af.1 is no longer sessile upon *dc*, but has become distinctly stalked. Similarly, Af.3 is stalked from *mc*. Af.2 and Af.4 remain sessile upon *dc* and *mc* respectively, but not so completely as in the *Mesopsychidae*. The character of possessing all four forks (Af.1-Af.4) sessile upon their respective cells is retained in a few recent genera, e.g., *Anisocentropus* in the *Calamoceratidae*. In this latter genus, the structure of *dc* and *mc* and the forks arising from them very closely resembles that seen in *Triassopsyche*. The importance of this character, from a phylogenetic standpoint, may perhaps be emphasised by a phylogenetic diagram (Text-fig. 5), in which all stages are shown, from the original archaic formation (A) down to the most advanced cænogenetic form (D), in which the two forks are stalked. In this diagram, the cell may be taken either as *dc* or *mc*; if the former, the upper fork is Af.1, the lower Af.2; if

the latter, the forks are Af.3 and Af.4 respectively. Besides this direct phylogenetic line, one or both of the forks may be lost at any stage of the reduction, by suppression of a branch. Thus, in the *Leptoceridæ*, *Oecetis* (N. Zealand) keeps *dc* present and Af.1 sessile, but Af.2 is completely lost; while the allied *Triplectides* (Australia) has progressed one stage further, having Af 1 strongly stalked.

(5) The thyridium-cell (*tc*) is present in *Hydropsyche* and *Triassopsyche*, absent in *Mesopsyche*. If, however, the latter had a single cross-vein from M_{3+4} to Cu_1 , its *tc* would closely resemble that of *Hydropsyche* in shape and position.

(6) *The excess cells of Mesopsychidæ*: here the *Mesopsychidæ* offer a contrast, not only with the *Hydropsychinæ*, but with all recent Trichoptera. In the marine caddis-fly, *Philaniscus plebejus* Walker (Australia and N. Zealand), there is a small subdiscoidal cell which



Text-fig. 5. *

may be comparable with the large *sdc* of *Mesopsychidæ*; but, in nearly all recent genera, there is nothing comparable with it. The three post-discoidal cells (*pdc*) of *Mesopsyche*, the post-median cell (*pmc*) of *Triassopsyche*, and the complicated cell-

* Phylogeny of a principal cell in the wings of Trichoptera. A, oldest stage, with both end-forks sessile upon the cell. B-C, successive reduction-stages towards D, the cænogenetic stage, with both end-forks stalked. At any stage, the cross-vein completing the cell distally may be lost, or one of the forks may be reduced to a simple vein.—*c*, the cell; *v*, the main vein, v_{1+2} , v_{3+4} , its branches enclosing the cell basally; v_1 , v_2 , the branches enclosing the upper fork, *f*; v_3 , v_4 , the branches enclosing the lower fork, *f'*; (*c* represents either *dc* or *mc*; *v*, either *Rs* or *M*).

formation distally upon Cu_1 in the same genus, appear to be the archaic remains of an originally denser cross-venation, long since lost, and not seen in any recent forms.

Order PROTOMECOPTERA, ordo nov.

Large insects, with venation of the same type as the Mecoptera, but much denser. The whole of the wing-membrane, except the pterostigma, is covered with an abundant meshwork of polygonal cellules, at the junctions of which are developed strong hairs, so that the whole of the wing is densely hairy. Hairs are also present upon the main veins and transverse veins.

Between Sc and anterior border of wing, a strong costal vein (C) is present, supported above and below by cross-veins, and ending at least half-way along the anterior border. Upon the apical border of the wing, between the end of R and the end of Cu_1 , no less than *seventeen* longitudinal veins abut (only *nine* in Mecoptera). Venation of fore- and hindwings closely similar. Apical half of wing with many elongated polygonal cells of large size present (five- to seven-sided). A smooth membranous pterostigma present upon the distal end of R in both wings, and extending into the space between R and R_s , where it ends posteriorly upon a distinct *pterostigmatic furrow* (*ptf*), parallel to R_s .

The principal differences between the Orders Mecoptera and Protomecoptera may be best exhibited in the following table:—

	Protomecoptera.	Mecoptera.
Size	Expanse 100 mm. or over	Expanse 15-50 mm.
Costal vein... ..	present	absent
Fine polygonal network of cellules	present	absent
Hairs	present, both on veins and membrane	absent, or only very minute hairs present
Number of longitudinal veins abutting on apical portion of wing-margin, between R and Cu_1	seventeen	nine
Number of apical forks in same area	eight	five

This new Order is proposed for the reception of a very remarkable fossil from the Ipswich beds, represented by fore- and hindwings, very beautifully preserved. The insect forms the direct connecting link between the Palæozoic Palæodictyoptera on the one hand, and the recent Mecoptera on the other. The Palæodictyopterous character is seen in the primitive, almost Blattoid, scheme of venation (which is, of course, preserved also better in Mecoptera than in any other recent Order, but with great reduction), and the presence, in its last stage of evolution, of the dense reticular meshwork of polygonal cellules so characteristic of this ancient Order. In the Protomecoptera, as exemplified by this Ipswich fossil, the development of hairs upon both veins and membrane is very pronounced; and the wings exhibit, in a remarkable manner, the method by which hairs first appeared upon the wing-membrane; just as *Mesogereon*, another Ipswich fossil, exhibits the first formation of tubercles in the Hemipteroid wing. Another exceedingly archaic character, long since lost in most insect-wings, is the presence of a true *costal vein*, not fused with the costal border of the wing.

The Mecopterous characters are very obvious, for the wings are clearly built upon the Panorpid venational plan. The essentials of this are—

(1) Close similarity between fore- and hindwings, with only slight differences in venation.

(2) Symmetrical dichotomous branchings (bilateral forks) of Rs and M, as opposed to the unilateral or unsymmetrical forkings of these same veins seen in the Odonata, Neuroptera, etc.

(3) Transverse veins few, and so arranged as to support the bilateral forks. Thus are formed the typically Panorpid *elongated polygonal cells* of large size, and varying from five to seven sides. The true Mecoptera have, typically, *twelve* of these cells lying completely within the wing between Rs anteriorly and M-M₁ posteriorly, but the number may be reduced by suppression of cross-veins. In some fossil Mecoptera, the number may be greater. In the Protomecoptera, there are *twenty* of these same cells.

In view of the fact that some of the present-day Mecoptera,

(e.g., *Panorpodes*, and a new genus recently discovered in Australia) have generalised mouth-parts, with only the barest beginnings of the tendency towards the formation of the prominent *beak*, usually supposed to be typical of the Order, we may reasonably claim that the mouth-parts of the Protomecoptera were normally mandibulate, though they are not actually preserved for us in the fossil state.

It is important to bear in mind that true Mecopterous wings, allied to the Australian genus *Tæniochorista*, have already been found in the Ipswich beds. Further, I am able to state definitely that very similar forms occur in the Permo-Carboniferous strata of Newcastle, N.S.W., and are being studied by me at the present time. None of these wings show the Protomecopterous characters seen in the fossil under consideration. This is a strong argument for the erection of a new Order. For it is evident that these Protomecopterous wings are far older, evolutionarily, than are the Mecopterous wings of the Permo-Carboniferous. Since, however, the Mecoptera must have descended, by reduction, from Protomecopterous forms, it follows that our Ipswich fossil must be a representative of a much older race, that not only existed side by side with the true Mecoptera in Permo-Carboniferous times, but *preceded them* in the Carboniferous. That is, the dichotomy between Protomecoptera and Mecoptera took place in Palæozoic times. Thus the erection of a new Order is justified on palæontological as well as on morphological grounds; for the differences between the two Orders are, both in time and degree, just such as Handlirsch has relied upon in forming most of his other fossil Orders.

We must remember, too, the composite character of the Ipswich fauna. I have already shown that Protorthoptera exist there alongside forms differing scarcely at all from insects alive at the present day, and that Protohemiptera and Homoptera lived side by side. Alongside a true Dragonfly, there has recently been found another new type that is undoubtedly a Protodonate! Thus there is nothing surprising in the existence of Protomecoptera and true Mecoptera side by side in these fossil beds.

Family ARCHIPANORPIDÆ, fam.nov.

Characters as for the Order, with the following additions. Large insects, with a wing-expanse of 100 mm. or over. Pterostigma longer and narrower in hindwing than in forewing, not reaching proximally to Sc in either wing. Sc ends up on the anterior margin of the wing beyond half-way in both wings, but not so far in hindwing as in forewing. Cu₁ ends up on posterior margin a little before the level of the pterostigma in forewing, considerably before the same level in hindwing. Cu₂ probably present in both wings.

Genus ARCHIPANORPA, n.g.

(Plate viii., figs.4-6; Plate ix.)

Characters as for the family, with the following additions. Forewing broadest at or near pterostigma, hindwing broadest just before half-way, and having the apical third distinctly narrower than in forewing. Pterostigma of forewing rather short, irregularly shaped, with R arching up within it, convexly to the wing-border. Pterostigma of hindwing long and narrow, with R running almost straight through it.

Genotype, *Archipanorpa magnifica*, n.sp.

ARCHIPANORPA MAGNIFICA, n.sp. (Plate viii., figs.4-6; Plate ix.)

This species is represented by two fine fossil wings, Nos. 106*a* and 120*a*, in the Queensland Geological Survey's Collection. Of these, No.106*a* is the better preserved specimen. It shows the whole of the wing from the apex to a level slightly distad from the origin of Rs. A transverse fracture of the rock has destroyed the base. The total length of this fragment is 33 mm., its greatest breadth 13 mm. The specimen represents a *cast of a left hindwing*.

No.120*a* is not so well preserved, there being two pieces cut out from the posterior margin, and two slight cracks running across the wing. The main fracture, which appears to be the same break that cut off the base of No.106*a*, (the two wings were found very close together) has cut off this wing more obliquely, and a little further from the base (see Plate viii., figs.4-5). The

total length of the fragment is 30 mm., its greatest breadth 14 mm. It represents the *mould* of a *right forewing*.

The method of determining what wing a given specimen represents may be briefly stated as follows. In the Panorpoid wing, there are two strong and highly convex veins, viz., R and Cu₁. If such a wing became fossilised, and a cleavage of rock later on reveals it, there should be a *cast* of the wing showing R and Cu₁ as high convex ridges, and a *mould* showing them as concave furrows. In the mould, also, *all* the veins will be concave grooves *in themselves*; whereas, in the cast, they will be convex rods, quite apart from whether they stand high up on ridges of the wing (as R and Cu₁ do), or not. Now in 106a, R and Cu₁ lie upon high ridges, and all the veins are convex rods; hence it must be a *cast*; and, as the apex lies to the left, it must be a *left* wing. In No.120a, R and Cu₁ lie at the bottom of furrows, and all the veins are concave grooves; hence it must be a *mould*; and, as the apex lies to the left, it must have been formed by a *right* wing turned over, so that its underside lay uppermost.

Further, the fore- and hindwings of all Panorpid, though closely similar, differ in the following points:

(1) Sc always extends further towards the apex in the forewing than in the hindwing.

(2) In the hindwing, M tends to become fused basally with Cu₁, but this tendency is not so much in evidence in the forewing.

(3) In the forewing, Cu₁ ends up on the posterior margin of the wing somewhat beyond half-way. In the hindwing, it reaches only about half-way, or less.

Now, if we compare Nos.106a and 120a, we see at once that Sc ends up much further from the apex in 106a than it does in 120a. Further, although only a small remnant of Cu₁ is left in No.120a, yet the slant of this vein to the wing-axis is measurably less than in 106a. The measurements, carefully determined, give an angle of 23° for No.120a, 31° for No.106a. Measurements made to determine the obliquity of *corresponding* portions of Cu₁ in *Panorpa confusa* give 22° for the forewing,

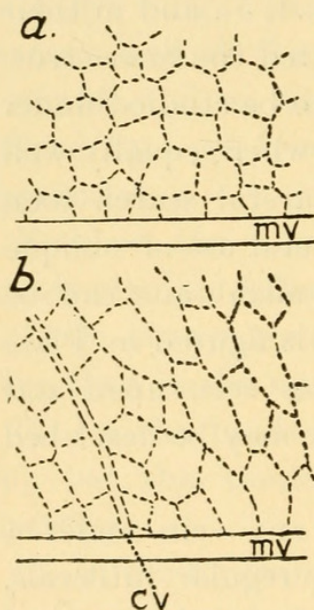
33° for the hindwing. Hence we must conclude, from the combined evidence of both Sc and Cu₁, that No.106a represents a *hindwing*, No.120a a *forewing*.

Unfortunately, not quite enough of the main stem of M is preserved to enable us to say definitely with what vein it tends to fuse basally. But, as the condition stated above in (2) is universally present in Panorpid wings (even in the archaic *Merope*, which has been claimed, with good reason, to be a Palæozoic remnant), there is no reason to suppose that the same rule did not hold for our fossil wings. Thus, in the restoration of these wings given in Plate ix., I have correlated character (2) with (1) and (3), so that fore- and hindwings are to be distinguished by three differences, as in recent Mecoptera.

The Structure and Hairiness of the Wing-membrane.—In the figures given of the two wings (Plate viii., figs.4, 5), and in their restoration (Plate ix.), I have purposely omitted the finer structure of the wing-membrane, which requires to be studied under a higher power. The structure is not everywhere equally well preserved in all parts of the wing; but a careful search soon reveals a number of places at which, by careful use of oblique light, the remarkable formation of the wing-membrane can be well studied and interpreted. Such a place is figured in Plate ix., fig.6, where I have drawn the structures seen upon and above one of the smaller main veins. These may be described as follows:—

(1) *Hairs upon the veins.*—Following up any vein under a moderate power, there will be found, at fairly regular intervals, the typical circular-based tubercles which indicate the bases of insertion of original *stiff hairs* or *bristles* upon the veins. A comparison with a cleared and mounted wing of *Myrmeleon* shows that these tubercles in *Archipanorpa* closely resemble those of *Myrmeleon* in size and position; if anything, those of *Archipanorpa* are the larger in proportion to the size of the veins, and of the wing as a whole. Thus we see that *Archipanorpa* had *hairy veins*, as in the Planipennia. Recent Mecoptera also possess these hairs, but they are not usually so large as in Planipennia, and they are generally more abundant and closely set.

(2) *Polygonal meshwork of the wing-membrane* — Turning from the vein to the membrane alongside it, we notice at once that this is not smooth, but is thrown into innumerable pits and ridges, with tubercles appearing upon the latter in many places. In places where this structure is well-preserved, it will be seen that the ridges form an *irregular polygonal meshwork*, enclosing sunken areas or *cellules* (shaded in Plate viii., fig.6). The large tubercles, which resemble those of the veins, are seated principally upon the swollen junctions of the ridges. The ridges are not as well-defined as actual veinlets would be, except here and there (Text-fig.6*b*, *cv*), where a particularly strong and straight ridge may be seen running out for some distance from a main vein. Nor are their tubercles usually as well-defined as are those of the main veins.



Text.fig.6.*

The area shown diagrammatically in Plate viii., fig.6, was selected from near one of the main veins on the basal portion of the preserved part of the wing. It is a typical unspecialised meshwork. But, in most parts of the wing, and especially towards the distal end, the polygons of the meshwork tend to become stretched out transversely and somewhat obliquely to the main veins. This is represented diagrammatically in Text-fig.6*b*, whereas Text-fig.6*a* corresponds with the unspecialised portion shown in Plate viii., fig.6.

The only conclusion that I can come to, from a study of these peculiar structures, is that the ridges represent *the original Palæodictyopterous meshwork of veinlets in a degenerating stage*. The

* Diagrams of the Palæodictyopterous meshwork upon the membrane of the wing of *Archipanorpa magnifica*, n.g. et sp.,—*a*, from near base of preserved portion of wing (corresponding with Plate viii., fig.6); *b*, from distal portion of wing, showing tendency of the mesh to become stretched transversely and somewhat obliquely across the wing, ($\times 20$); *cv*, a strong cross-vein, not yet obliterated; *mv*, main vein, with macrotrichia omitted. The figure is intended to show only the *position*, and not the *structure* of the meshwork.

most probable cause of degeneration would be the using-up of the veinlet-chitin in the formation of the accumulated masses or tubercles in which the hairs are inserted. Thus *Archipanorpa* would illustrate an intermediate stage in the evolution of a *wing with a hairy membrane* from an *ancient net-veined* or *Palæodictyopterous* wing-type, and would give us the clues both as to the method whereby an open-veined wing, such as that of the Lepidoptera or Diptera, has been evolved from a closely-veined type, and also as to the method whereby the hairs (or, later on, the scales) become seated upon the membrane as well as upon the main veins.

(3) *Hairs upon the wing-membrane*.—In those places where the structure of the tubercles of the wing-membrane can be most clearly made out, they are seen to be very closely similar to those upon the wing-veins, both in size and form. We can distinguish an outer raised rim (indicated by the outer circles in Plate viii., fig.6), and an inner depression or hollow (indicated by the inner circles in the same figure). There can be no doubt that these structures represent the tubercular bases of insertion of stiff bristle-like hairs; for the insertions of such hairs in the wings of recent Planipennia are exactly similar to them. I propose to call these hairs *macrotrichia*.

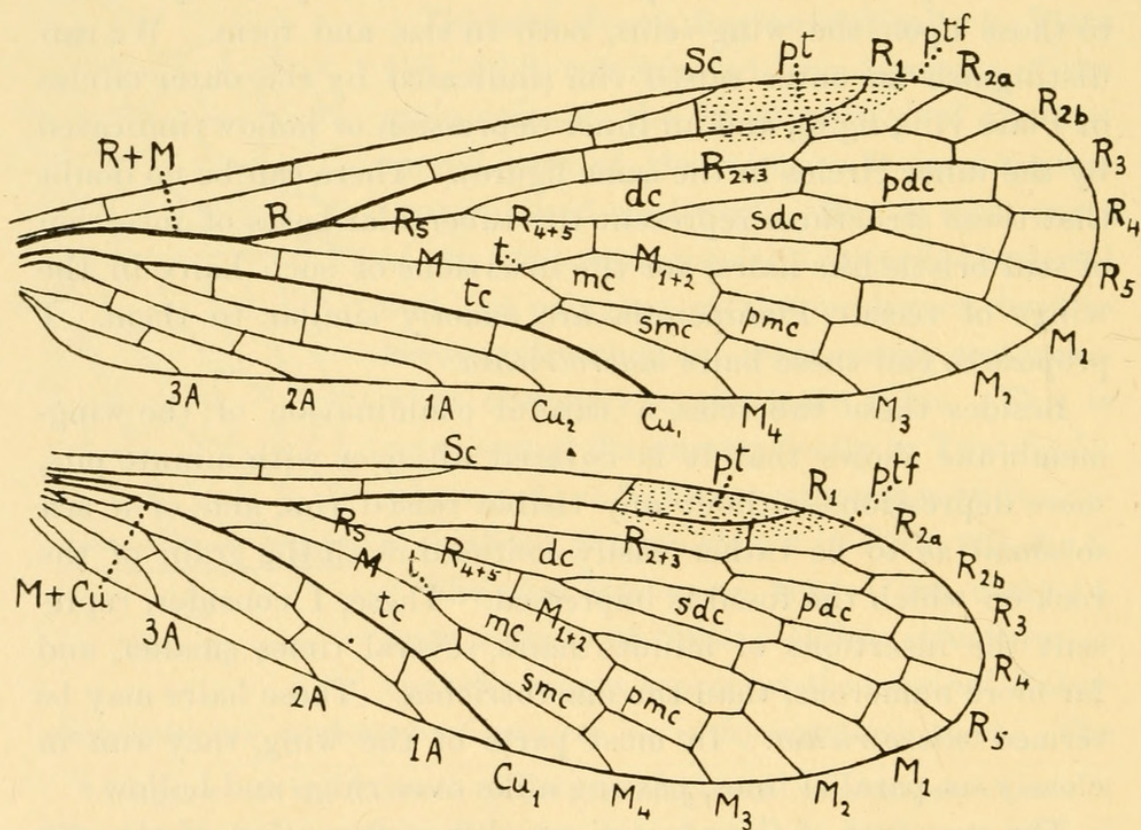
Besides these tubercles, a careful examination of the wing-membrane shows that it is covered all over with minute pits, mere depressions without any visible raised rim, and of a size so small as to be rather easily confused with the grain of the rock on which the fossil is impressed. These, I consider, represent the insertions of minute hairs, several times smaller, and far more numerous, than the *macrotrichia*. These hairs may be termed *microtrichia*. In most parts of the wing, they run in closely-set parallel lines, passing alike over ridge and hollow.

The structure of the pterostigma differs from that of the rest of the wing-membrane only in lacking the polygonal ridges, and in being of a single thickness throughout. This makes it appear very smooth in comparison with the rest of the wing. On examination under a moderate power, both *macrotrichia* and *microtrichia* can be seen to be present upon it.

The polygonal meshwork of ridges is absent from all recent Mecoptera. Microtrichia, however, are abundant all over the wing-membrane, though excessively minute in some genera (e.g., *Panorpodes*). Macrotrichia are present only towards the distal end of the wing, especially in the pterostigmatic region. In the polygonal cells formed between R_s and Cu_1 , there may be seen, in certain genera (e.g., *Panorpa*), two or three irregular rows of macrotrichia.

In the figures given in Plates viii.-ix., I have purposely shaded-in the pterostigma, in order to distinguish it from the rest of the wing-membrane. In the actual fossils, it is not darkened in colour.

Type, forewing, Specimen No.120a; hindwing, Specimen No.106a (Coll. Queensland Geol. Survey).



Text-fig.7.

Wings of *Panorpa confusa* Westwood, with colour-pattern omitted, to show venational scheme, ($\times 9$). For lettering, see p.200.

Corrigenda: for M_4 read $M_4 + Cu_{1a}$, and for Cu_1 read Cu_{1b} .

In Text-fig.7, I have drawn the wings of *Panorpa confusa* Westwood, (omitting colour-pattern), for comparison with those

of *Archipanorpa magnifica*. The pterostigma is shaded in, as in the figures of *Archipanorpa*. A comparison of the two forms enables us at once to fix the limits of the main veins in *Archipanorpa*, and to name the principal cells of the wing. The steps of the determination may be briefly outlined as follows:—

(1) The radius (R) is a strongly-built, highly convex vein running *through* the pterostigma (*pt*). Therefore I searched first of all for the pterostigma, which was easily located, both from its smoothness compared with the rest of the wing-membrane, and because of the *pterostigmatic furrow* (*ptf*) bordering it posteriorly. Having found it, the radius was at once determined. There were then *two* other veins ending up on the anterior wing-border between the radius and the base of the wing; whereas, in *Panorpa*, as in all recent insects, there is only *one* (the subcosta, Sc). It became clear, therefore, that *Archipanorpa* possessed not only a subcostal vein, Sc, but also an archaic costal vein, C, separated from the costal or anterior border, as in some of the larger Carboniferous fossils (e.g., the *Meganeuridae* of the Order Protodonata).

(2) Turning next to the area of the wing below R, in specimen No.106a (hindwing), the cubitus, Cu₁, is easily determined as a strongly convex, obliquely-running vein, ending about half-way along the posterior border. Between this and R, basally, there lie two main stems, of which the upper must be the radial sector, Rs, (its point of union with R is not preserved in the fossil), and the lower must be the media, M.

(3) The first forking of Rs is preserved in the fossil. Here Rs divides into R₂₊₃ above, and R₄₊₅ below. The cell enclosed between these two veins basally is the *discoidal cell* (*dc*). R₂₊₃ again forks into R₂ and R₃, R₄₊₅ into R₄ and R₅, and both are sessile upon *dc*, as in the two Trichopterous wings already dealt with. The area enclosed between R₂ and R₃ would be, in Trichoptera, the *first apical fork* (Af.1 in Text-figs.2-4). But, in most Mecoptera, R₂ forks again into R_{2a} and R_{2b} (Text-fig.7). This occurs in *Archipanorpa*; but, above and beyond this, R_{2b} forks a second time into R_{2b} and R_{2b}. Moreover, R₃, which remains unforked in both Trichoptera and Mecoptera, in *Archip-*

panorpa divides into R_{3a} and R_{3b} , and each of these again divides* before reaching the wing-border.

(4) The area enclosed between R_4 and R_5 would be, in Trichoptera, the *second apical fork* (Af.2 in Text-figs.2-4). In Mecoptera, this area is often subdivided by a cross-vein (Text-fig.6). In *Archipanorpa*, both R_4 and R_5 divide into two again before reaching the wing-border. Thus R_s , which in Trichoptera sends *four* veins to the apical wing-border, and in Mecoptera *five*, sends no less than *nine* such veins to the border in the hindwing of *Archipanorpa*, *eight* in the forewing.

(5) Turning next to the media (M), we see that the *thyridium* (*t*), or *median fork*, is clearly preserved in both wings, lying just below the first forking of R_s . As this is its position also in the two Trichopterous wings already dealt with, we are probably right in assuming that it is the archaic condition, and that a shifting of the thyridium to a level distad from the level of the first forking of the radius (as in *Panorpa*, Text-fig.7; and in many recent Caddis-flies) is a cænogenetic character. The cell below *t* is the *thyridial cell* (*tc*), and is only partially preserved in both wings. At *t*, M forks into M_{1+2} above and M_{3+4} below, and the two branches enclose between them the *median cell* (*mc*). M_{1+2} then divides into M_1 and M_2 , and M_{3+4} into M_3 and M_4 ; and the forks thus made are sessile upon *mc*, as in the two fossil Trichopterous wings already studied, and in recent Mecoptera (Text-fig.7).

(6) The area enclosed between M_1 and M_2 would be, in all Trichoptera and true Mecoptera, the *third apical fork* (Af.3, in Text-figs.2-4). In *Archipanorpa*, both M_1 and M_2 fork again; in the hindwing, the two middle branches fuse together, so that only *three* separate veins reach the wing-border, instead of *four* as in the forewing. This difference offsets the difference in the behaviour of R_3 in the two wings (see above), and makes the total number of apical end-veins the same in both wings (viz., seventeen between R and Cu_1).

(7) The area enclosed between M_3 and M_4 would be, in all Trichoptera and true Mecoptera, the *fourth apical fork* (Af.4 in Text-figs.2-4). The archaic condition of this fork is that it is

* In the hindwing; in the forewing, only the lower fork divides.

very strongly sessile upon *mc*; in other words, M_{3+4} again divides before it has passed far from *t* round the border of *mc*. M_3 continues on as the lower border of *mc*, and passes on to the wing-border without branching, in *Archipanorpa* as in all Trichoptera and Mecoptera. M_4 , in *Archipanorpa* and all Mecoptera, behaves differently from what it does in most Trichoptera (see, however, the formation in Text-fig.3). Diverging strongly from M_3 , it picks up a branch Cu_{1a} thrown out anteriorly from Cu_1 . In Mecoptera (Text-fig.7), the two fuse and continue on to the wing-border as $M_4 + Cu_{1a}$. In *Archipanorpa*, they only fuse for a short distance, and then run separately to the wing-border.

(8) Thus far, the structure of the wing is clear. Below and basad from Cu_1 , not enough is preserved for us to be sure of the structure of the anal area. In all recent Mecoptera, Cu_2 is present in the forewing (arising from Cu_1 very close to the wing-base), but absent in the hindwing. It would appear that the original *Cu* is completely altered in the hindwing, Cu_1 having become fused with *M*, and Cu_2 with *1A*. The remnants of the base of Cu_1 are to be seen as a short, weak, waved vein running in a curve from the base to join *M* a short distance beyond the base (Text-fig.7). Bearing in mind the archaic structure of *Archipanorpa*, the presence of many longitudinal veins, and especially the presence of the costal vein *C* in both wings, I think the probabilities are all in favour of a normal Cu_2 being present in the hindwing of *Archipanorpa*. I have, therefore, restored the wing on that supposition. The suggested anal area calls for no comment. The complete restoration of both wings is given in Plate ix.

With regard to the question of the wing-coupling apparatus, it has generally been assumed that the Mecoptera are descended from forms in which the wings were free and unconnected in flight. But, in a new family of the Order which I have recently discovered in Tasmania, I was surprised to find a well-developed wing-coupling apparatus present, consisting of jugal lobe on the forewing, and jugal process with frenulum on the hindwing. As in the Planipennia and in the females of most moths, the frenulum consists of two strong bristles directed obliquely outwards. Following up this discovery, I examined other genera of

Panorpids, and discovered that the frenulum is present in all forms examined by me, though only vestigial in the highly specialised *Bittacidae*. Hence it is clear that the ancestors of the Mecoptera must have possessed the wing-coupling apparatus in a well-developed form; so that its inclusion in the restoration of the wing of *Archipanorpa* (Plate ix.; *jl*, jugal lobe; *jp*, jugal process; *fr*, frenulum) needs no further apology or explanation.

WING-NOTATION USED IN PLATES AND TEXT-FIGURES.

1A, first anal vein—2A, second anal vein, or axillary vein—3A, third anal vein, or basilar vein—4A, fourth anal vein (rarely present)—Af₁, Af₂, Af₃, Af₄, Af₅, the five apical forks, or end-forks, formed between the final bifurcations of the main veins—C, costal vein—cs, costal space—Cu, cubitus—Cu₁, Cu₂, its primary branches—Cu_{1a}, upper branch of Cu₁ in Mecoptera; Cu_{1b}, continuation of Cu₁—*cuf*, cubital fork—*dc*, discoidal cell—*fr*, frenulum—*jl*, jugal lobe—*jp*, jugal process—M, media—M₁, M₂, M₃, M₄, its four main branches. (Further branchings are denoted by Cu_{1a} suffixes *a* and *b*).—*mc*, median cell—*pcs*, precostal space (in Protomecoptera)—*pdc*, post-discoidal cell—*pme*, postmedian cell—*pt*, pterostigma—*ptc*, post-thyridial cell—*ptf*, pterostigmatic furrow—R, radius; R₁, its main stem—*rf*, radial fork—Rs, radial sector; R₂, R₃, R₄, R₅, its four main branches. (Further branchings are denoted by suffixes *a* and *b*, and branchings of these by *a*, *a'*, or *b*, *b'*).—S₁—S₁₂, branches of Rs in Planipennia—Sc, subcosta—*scs*, subcostal space—*sdc*, subdiscoidal cell—*sme*, submedian cell—*t*, thyridium (=median fork)—*tc*, thyridial cell.

EXPLANATION OF PLATES VII.-IX.

Plate vii. (Trichoptera).

Fig.1.—*Mesopsyche triareolata*, n.g. et sp. Forewing; (×7·5).

Fig.2.—*Triassopsyche dunstani*, n.g. et sp. Forewing; (×7·5).

Plate viii. (Planipennia and Protomecoptera).

Fig.3.—*Protopsycheopsis venosa*, n.g. et sp. Portion of wing; (×5).

Fig.4.—*Archipanorpa magnifica*, n.g. et sp. Forewing; (×5).

Fig.5.—*Archipanorpa magnifica*, n.g. et sp. Hindwing; (×5).

Fig.6.—*Archipanorpa magnifica*, n.g. et sp. A small portion of the hindwing, showing part of a main vein carrying the basal tubercles of three macrotrichia, and the membrane above it, with its polygonal meshwork (the ridges left unshaded), basal tubercles of eleven macrotrichia (double concentric circles), and small pits for insertions of microtrichia (in black). Semi-diagrammatic; (×73).

Plate iv.

Restoration of fore- and hindwings of *Archipanorpa magnifica*, n.g. et sp.; (×4·5).



Tillyard, R. J. 1917. "Mesozoic and tertiary Insects of Queensland. 1. Plannipenia, Trichoptera and the new order Protomecoptera." *Proceedings of the Linnean Society of New South Wales* 42, 175–200.
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