

**NEW PROTOMYRMELEONTID DAMSELFLIES
FROM THE TRIASSIC OF AUSTRALIA AND THE LIASSIC
OF LUXEMBOURG, WITH THE DESCRIPTION OF
TILLYARDOMYRMELEON PETERMILLERI GEN. NOV. & SPEC.
NOV. (ARCHIZYGOPTERA: PROTOMYRMELEONTIDAE)**

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Tillyardomyrmeleon petermilleri gen. n. & sp. n., the oldest known Protomyrmeleontidae is described from the Mid Triassic of Australia. A new Protomyrmeleontidae probably related to the genus *Zirzipanagrion* Zessin, 1991, is described from the Liassic of Luxembourg. An attempt of a phylogenetic analysis of the genera of Protomyrmeleontidae is proposed. A newly discovered well-preserved wing of a Liassic Protomyrmeleontidae shows that the primary antenodal crossveins of Archizygoptera are homologous to those of recent Odonata.

INTRODUCTION

The Mesozoic family Protomyrmeleontidae is known from the Upper Triassic of Australia and Italy (G. Bechly, pers. comm.), the Lower and Upper Jurassic and the Lower Cretaceous of Europe and Siberia, with 15 or 16 described species in 7 genera (ZESSIN, 1991; NEL & HENROTAY, 1992; NEL, 1992; MARTINEZ-DELCLÒS & NEL, 1996; NEL & JARZEMBOWSKI, 1997). In addition, we have discovered an undescribed genus and species from the Mid Triassic of Australia in the collection of the Natural History Museum, London, representing the oldest known record of this family. Also, further work in the Lower Jurassic in Luxembourg has led to the discovery of a very well preserved wing of Protomyrmeleontidae which adds new information concerning the venation of these curious Odonatoptera.

SYSTEMATIC PALAEOONTOLOGY

We follow the wing venation nomenclature of BECHLY (1995) based on RIEK & KUKALOVÁ-PECK (1984) and KUKALOVÁ-PECK (1991) and amended in NEL & HENROTAY's (1992) revision of the family.

Suborder Archizygoptera HANDLIRSCH, 1906 *sensu* NEL & HENROTAY, 1992

Protomyrmeleontidae HANDLIRSCH, 1906

TILLYARDOMYRMELEON GEN. N.

Type species : *Tillyardomyrmeleon petermilleri* sp. n.

E t y m o l o g y. – After Tillyard and *Myrmeleon*.

DIAGNOSIS. – This genus is characterized as follows: there is no bridge between RP'' (*sensu* BECHLY, 1996, = RP3/4 *sensu* RIEK & KUKALOVÁ-PECK, 1984) and IR2; RP''a is a long and strong vein; there is a bridge between IR2 and RP2 but the true base of RP2 on RP is clearly visible as an oblique crossvein; there is no bridge between IR1 and RP2; there is no pseudo-IR1 basad of the origin of IR1.

TILLYARDOMYRMELEON PETERMILLERI SP. N.

Figure 1

M a t e r i a l. – **H o l o t y p e:** Specimen In 46119, Tillyard coll., Natural History Museum, Palaeontology Department, London, UK.

H o r i z o n a n d l o c a l i t y. – Middle Triassic, Hawkesbury Sandstone, in a lenticular mass of shale (McKEOWN, 1937; RIEK, 1970), Beacon Hill, Brooksvale, New South Wales, Australia.

E t y m o l o g y. – After the late Dr Peter Miller, Odonata specialist.

DESCRIPTION. – The species is based on the impression of a nearly complete wing, the costal part of the base and the petiole being missing. There is no trace of colouration. Length of the preserved part, 14.5 mm, probable complete length, 20 mm; width, 3.4 mm distance from the nodus to the apex, 11.6 mm; from the nodus to the pterostigma, 8.4 mm; from the nodus to the arculus, 2.6 mm. The pterostigma is poorly preserved, only its basal side being visible; the nodal brace between ScP and RA is distinctly oblique; the subnodal crossvein is at right angles to RA and RP; there is one cross-vein in the area between RA and RP basad of the sub-nodus;

there is a crossvein in the area between RP and MA basad of the base of RP''; there is no visible pterostigmal brace; there are four visible postnodal crossveins, more or less aligned with the

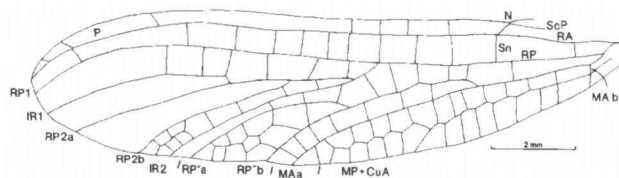


Fig. 1. *Tillyardomyrmeleon petermilleri* gen. n. & sp. n., wing venation of the holotype. – [Scale = 2 mm]

corresponding subpostnodal crossveins between RA and RP1. There are nine subpostnodal crossveins, so there were probably about nine postnodal crossveins originally. The base of vein RP is midway between the base of RP + MA and the posterior branch MAb of MA; the base of RP'' is 3.2 mm distad of the base of RP; RP'' seems to be obliquely branched on MA rather than on RP and the anterior branch RP''a (RP3 *sensu* NEL & HENROTAY, 1992) and posterior branch RP''b (RP4 *sensu* NEL & HENROTAY, 1992) are 2.9 mm apart distally; RP''a is a long and strongly arched vein, 4.1 mm long; there is no bridge between RP'' and the base of IR2; IR2 branches directly from RP1/2, 5.4 mm distad of the base of RP; there is a short bridge between IR2 and RP2 which seems to be secondarily branched on IR2; the true base of RP2 is an oblique vein between RP1 and the bridge, 1.4 mm distad of the base of IR2; RP2 separates into two long branches RP2a and RP2b 0.4 mm distally; width of area between RP2a and RP2b along the posterior wing margin, 1.6 mm; the base of IR1 is 2.1 mm distad of that of RP2; IR1 seems to be branched on RP2 because it is basally weakly "oblique with a pronounced angle between its basal and distal portions; IR1 is not zigzagged; MAb is strong and distally closes the basally open discoidal space; MAa is gently curved; veins MP and CuA are never separated; MP + CuA is basally straight and distally zigzagged; vein AA is fused with AP.

DISCUSSION. – The attribution of *Tillyardomyrmeleon petermilleri* gen. n. & sp. n. to the Protomyrmeleontidae is based on the following synapomorphies: RP2 has two branches; there is a bridge between IR2 and RP2 (although this character was convergently acquired by the Zygophlebioidea); RP'' seems to begin on MA rather than RP. It differs from other Protomyrmeleontidae in the following plesiomorphies: IR1 is not basally recessed in a long zigzagged pseudo-IR1; there is no bridge between IR1 and RP2; the true base of IR2 on RP is present; there is a bridge between IR2 and RP2 but the true base of RP2 on RP is very clear as an oblique crossvein; there is no bridge between IR2 and RP''. *Tillyardomyrmeleon* gen. n. has two autapomorphic characters, viz. the base of RP is midway between vein MAb and the base of MA + RP in the arculus (acquired convergently with *Protomyrmeleon cretacicus* NEL & JARZEMBOWSKI, 1997 and the more recent Zygoptera); RP''a is a very strong, not zigzagged vein.

ZIRZIPANAGRION ZESSIN, 1991 (?)

Type species : *Zirzipanagrion quadriordinum* ZESSIN, 1991

SPECIES UNDETERMINED

Figure 2

Material. – Specimen IB0010027, Henrotay coll., deposited in the Muséum national d'Histoire Naturelle, Paris, France.

Horizon and locality. – Lower Toarcian, Upper Liassic, Bascharage, Luxembourg.

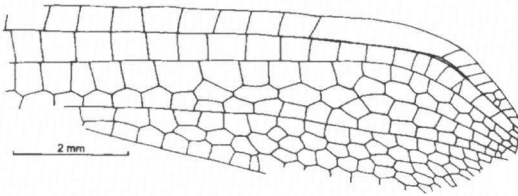


Fig. 2. *Zirzipanagrion*(?) species undetermined, wing venation of specimen IB0010027. – [Scale: 2 mm]

DESCRIPTION. – This is the costo-apical part of a hyaline wing. Length of the fragment 9.3 mm, width 3.1 mm; the pterostigma is very long and distally recessed towards the apex of the wing 2.6 mm long and 0.5 mm wide, distance

from the pterostigma to the apex 1.9 mm; the pterostigma covers six cells; the pterostigmal brace is very weak and not oblique; 9 postnodal crossveins are preserved, nearly all aligned with the subpostnodal crossveins; length of the preserved part of the postnodal area basad of the pterostigma 5.3 mm; there are four rows of cells in the broad area between RP1 and RP2; IR1 is very zigzagged in its basal part but it is only a curved vein in its distal part; the two branches of RP2, RP2a and RP2b are very long and straight veins, with four rows of small cells between them.

DISCUSSION. – This wing fragment, although incomplete, has two of the main venational synapomorphies of the Protomyrmeleontidae: (1) the bifurcation of RP2 into two branches; (2) the very long postnodal area crossed by numerous postnodal veins which are well aligned with the corresponding subpostnodal veins. This specimen has two synapomorphies of the monospecific genus *Zirzipanagrion* Zessin, 1991; (3) there are four rows of cells between RP1 and RP2a opposite the pterostigma; (4) there are four rows of small cells in the area between RP2a and RP2b. Nevertheless, it differs from *Z. quadriordinum* Zessin, 1991 in its very long pterostigma, covering six cells, instead of four in *Z. quadriordinum*. The attribution of this new specimen to *Zirzipanagrion* remains uncertain because of the lack of information concerning the structures of its wing base.

LIST OF DESCRIBED PROTOMYRMELEONTIDAE

TRIASAGRION TILLYARD, 1922

T. australiense Tillyard, 1922

Upper Triassic of Australia

PROTOMYRMELEON GEINITZ, 1885

P. brunonis Geinitz, 1885 (*P. bascharagensis* Nel & Henrotay, 1992)

Upper Liassic of Germany and Luxembourg

ANSORGE (1996) synonymized *P. bascharagensis* and *P. brunonis*. However, specific variability in the genus is still not well established and the synonymy of the two species remains dubious because the holotype of *P. brunonis* seems to be a very poorly preserved specimen, as already noted by NEL & HENROTAY (1992).

P. handlirschi Martynov, 1927

Upper Liassic of Turkestan

P. angustivenosus Martynov, 1927

Upper Liassic of Turkestan

- P. pascholdi* Zessin, 1992
Upper Liassic of Germany
- P. anglicanus* Tillyard, 1925
Lower Liassic of England
- P. grasselensis* (Bode, 1953)
Upper Liassic of Germany
- P. jurassicus* Nel, 1992
Upper Jurassic of Germany
- P. cretacicus* Nel & Jarzembowski, 1997 (in press)
Lower Cretaceous of England
- OBOTRITAGRION** ZESSIN, 1991
- O. petersi* Zessin, 1991
Upper Liassic of Germany
- O. tenuiformum* Zessin, 1991
Upper Liassic of Germany
- ZIRZIPANAGRION** ZESSIN, 1991
- Z. quadriordinum* Zessin, 1991
Upper Liassic of Germany
- Z. (?)* species undetermined (this paper)
Upper Liassic of Luxembourg
- SAXOMYRMELEON** NEL & JARZEMBOWSKI, 1997
- S. keatingei* Nel & Jarzembowski, 1997
Lower Cretaceous of England
- MALMOMYRMELEON** MARTÍNEZ-DELCLÒS & NEL, 1996
- M. viohli* Martínez-Delclòs & Nel, 1996
Upper Jurassic of Germany
- TILLYARDOMYRMELEON** GEN. N. (this paper)
- T. petermilleri* gen. n. & sp. n. (this paper)
Mid Triassic of Australia
- Protomyrmeleontidae** gen. et sp. indet. Nel & Jarzembowski, 1997
Lower Cretaceous of England
- Malmagrion eichstaettense* (Hagen, 1862) from the Upper Jurassic of Germany is an Odonatoptera incertae sedis (NEL, 1992).

PHYLOGENETIC ANALYSES

PHYLOGENETIC POSITION OF *TILLYARDOMYRMELEON* GEN. N.

NEL & HENROTAY (1992) considered that the phylogenetic relationships of Protomyrmeleontidae, Protozygoptera and recent Odonata were unsolved. BECHLY (1995) included Protomyrmeleontidae and Protozygoptera in the same group. He (1996) proposed a sister-group relationship between Protomyrmeleontidae and

Table I
Character score in the Protomyrmeleontidae

Taxa / Character score	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Malmomyrmeleon</i>	2	0	1	0	1	1	0	0	1	1	1	1	0	1
<i>Tillyardomyrmeleon</i>	0	0	1	0	1	1	1	0	0	1	0	?	0	0
<i>Saxomyrmeleon</i>	?	0	1	1	1	1	0	0	0	1	?	0	0	0
<i>Triassagrion</i>	1	0	0	0	0	0	0	1	1	1	0	0	0	1
<i>Protomyrmeleon</i>	2	0	1	1	1	0/1	0/1	0	1	1	2	0/1	1	1
<i>Obotritagrion</i>	2	1	1	1	0	0	0	0	0	1	2	0	1	1
<i>Zirzipanagrion</i>	2	0	1	1	1	1	0	0	1	1	2	1	1	1
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Batkeniidae (*sensu* BECHLY, 1996, = [*Batkenia* Pritykina, 1981 + *Terskeja* Pritykina, 1981] + *Voltzialestes* NEL et al., 1997) because they share the following synapomorphies: the base of IR1 closely approaches RP2 or is fused with it; RP2 closely approaches IR2 or is fused with it; IR2 closely approaches on RP'' or is fused with it; MA and RP'' are distinctly curved towards the posterior wing margin, so that both veins are distinctly shortened. BECHLY (1996) stated that IR1 apparently originates on RP2 but IR1 in *Tillyardomyrmeleon* gen. n. and *Batkenia* does not originate on RP2 and only closely approaches RP2 near its base.

We have attempted a phylogenetic analysis of protomyrmeleontid genera using the computer-software PAUP 3.1.1 and MACCLADE 3.0 on a Macintosh Computer, choosing Batkeniidae (*sensu* BECHLY, 1996) as the outgroup for the primary polarisation of the characters. The characters were unordered and a Branch and Bound search was completed. The result is two minimal trees (Figures 3-4, length, 24 steps; Consistency Index (CI), 0.750; Retention Index (RI), 0.684; CI excluding uninformative characters, 0.636; Rescaled Consistency Index (RC), 0.513). The strict consensus tree is given in Figure 5. The various indices show that, even if there are some homoplasies affecting characters 4, 5, 6, 9, 13 and 14, the global degree of homoplasy remains acceptable for a study only based on the wing venational characters which are subject to numerous homoplasies within the Odonoptera. The Protomyrmeleontidae are a monophyletic group, characterized by the synapomorphic characters 10. *Malmomyrmeleon*, *Protomyrmeleon* and *Zirzipanagrion* appear as a monophyletic group, characterized by the synapomorphic characters 11 and 13. Although older, *Tillyardomyrmeleon* gen. n. is in a less basal position than *Triassagrion*. This, together with the already advanced condition of the wing venation of these Triassic taxa, suggest that the Protomyrmeleontidae appeared well before the Mid Triassic, perhaps during the Upper Permian. Further collecting are needed to support this hypothesis.

Table II
Characteristics of the characters

Character	Type	Weight	States	Steps	CI	RI	RC
1	unordered	1	3	2	1.00	1.00	1.00
2	unordered	1	2	1	1.00	0.0	0.0
3	unordered	1	2	1	1.00	1.00	1.00
4	unordered	1	2	2	0.50	0.67	0.33
5	unordered	1	2	2	0.50	0.50	0.25
6	unordered	1	2	3	0.67	0.50	0.33
7	unordered	1	2	1	1.00	0.0	0.0
8	unordered	1	2	1	1.00	0.0	0.0
9	unordered	1	2	2	0.50	0.67	0.33
10	unordered	1	2	1	1.00	0.0	0.0
11	unordered	1	3	2	1.00	1.00	1.00
12	unordered	1	2	2	1.00	1.00	1.00
13	unordered	1	2	2	0.50	0.50	0.25
14	unordered	1	2	2	0.50	0.50	0.25

LIST OF POLARISED CHARACTERS (for the distribution cf. Tab. I):

- (1) 0. Vein IR1 commences on the main branch of RP1, even if it is very near to RP2 at its beginning;
 1. IR1 branches from RP2, the original branching of IR1 on RP being reduced to an oblique crossvein;
 2. The original branching of IR1 on RP is indistinct (Fig. 2).
- (2) 0. The original branching of RP2 on RP is present, even if looks like an oblique crossvein;
 1. The original branching of RP2 is completely indistinct (Fig. 2).
- (3) 0. There is no bridge between IR2 and RP2;
 1. There is a distinct bridge between IR2 and RP2 (Fig. 2).
- (4) 0. There is no bridge between RP" and IR2, IR2 being basally completely independent of R:";
 1. There is a distinct bridge between RP" and IR2, so that IR2 seems to be basally fused with RP" (Fig. 2).
- (5) 0. RP" is not divided into two well-defined branches;
 1. RP" is divided distally into two well-defined branches (RP"a and RP"b) (Fig. 2).
- (6) 0. RP"a is a weak, more or less zigzagged vein;
 1. RP"a is a strong, not zigzagged vein.
- (7) 0. The base of RP is nearer to MAb than to the base of RP + MA;
 1. The base of RP is midway between that of RP + MA and MAb.
- (8) 0. AA and AP are completely fused;
 1. AA is an independent vein.
- (9) 0. There are less than fifteen postnodal crossveins;
 1. There are more than fifteen postnodal crossveins.
- (10) 0. Vein RP2 is not divided into two branches;
 1. Vein RP2 is divided into two branches.
- (11) 0. IR1 begins distad of the free part of RP2;
 1. IR1 seems to begin basad of the free part of RP2 but distad of the base of IR2;
 2. IR1 seems to begin basad of the free part of IR2 (Fig. 2).
- (12) 0. There are less than two longitudinal secondary branches between RP2a and RP2b;
 1. There are more than two longitudinal secondary branches between RP2a and RP2b.

- (13) 0. IR2 is a straight vein;
 1. IR2 is a zigzagged vein in its distal part.
- (14) 0. There is no basal pseudo-IR1;
 1. There is a basal more or less zigzagged pseudo-IR1 (Fig. 2).

PRIMARY ANTENODAL CROSSVEINS OF PROTOMYRMELEONTIDAE AND ODONATA

ZESSIN (1991) considered that the primary antennodal crossveins are absent or very reduced in Protomyrmeleontidae. NEL & HENROTAY (1992) indicated that these veins are very faint but present in the holotype of *Protomyrmeleon bascharagensis*. Another specimen figured by ANSORGE (1996) shows the two primary antennodals. We figure a very well preserved new wing of *P. bascharagensis* from the Toarcian of Luxembourg which clearly shows the two primary antennodals

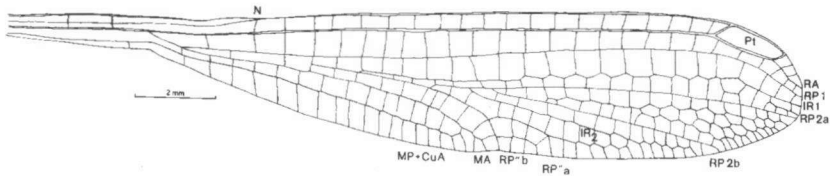


Fig. 3. *Protomyrmeleon brunonis* (*P. bascharagensis*), wing venation of specimen IB00962a.— [Scale = 2 mm]

(specimen IB 00962a, Henrotay coll., Lower Toarcian, Upper Liassic, Bascharage, Luxembourg, Fig. 3). These veins are clearly basal to the arculus, confirming the assumption of BECHLY (1996) that this is a plesiomorphic condition shared by the Archizygoptera and Zygoptera, the apomorphic condition present in “Anisozygoptera” + Anisoptera being an arculus lying between the two primary antennodals. Furthermore, these primary antennodal crossveins are clearly aligned

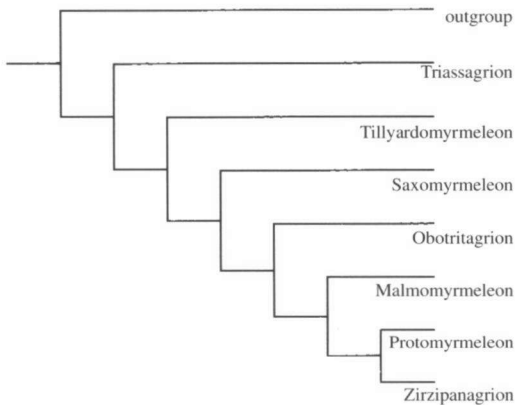


Fig. 4. Minimal phylogenetic tree.

with the primary subantennodals, i.e. complete, and are enforced by a chitinous bracket. Thus they do not show any morphological difference with the Ax1 and Ax2 of the Recent Odonata, unlike the hypothesis of BECHLY (1996) who supposed that the primary antennodal crossveins of the Archizygoptera could not be homologous with those of Recent Odonata.

PROBLEM OF THE RADIUS POSTERIOR OF THE ODONATA

NEL & HENROTAY (1992) proposed a nomenclature of the wing venation of Protomyrmeleontidae based on RIEK & KUKALOVÁ-PECK's (1984) theory. ZESSIN (1991) and ANSORGE (1996) followed another nomenclature which differs in the following point: they consider that vein RP2 is in fact RP2 + RP3 and that RP3/4 (*sensu* RIEK & KUKALOVÁ-PECK, 1984) is RP4. NEL & HENROTAY (1992) previously discussed about this problem and concluded that there is no evidence favoring ZESSIN's opinion. They added that the division of vein RP2 into two branches is a synapomorphy of Protomyrmeleontidae (convergently present in Triadophlebiidae; BECHLY, 1995). BECHLY (1995) considered that the exact nature of vein RP3/4 (= RP4 *sensu* ZESSIN, 1991) is not clear at all and proposed to name it RP". He added that there is no argument supporting the hypothesis of the fusion of RP2 and RP3 in the ground-plan of the Odonatoptera.

If we follow the hypothesis of NEL & HENROTAY (1992), the bifurcation of vein RP2 into two branches RP2a and RP2b needs to be considered as a synapomorphy of the Protomyrmeleontidae (convergently present in Triadophlebiidae). If we follow the hypothesis of ZESSIN (1991), the bifurcate condition of 'RP2/3' in Protomyrmeleontidae would rather be the result of apomorphic reversion than a plesiomorphic condition of this group which would imply that the supposed complete fusion of 'RP2' and 'RP3' in 'RP2/3' would have been achieved convergently in Recent Odonata and all other Permian and Triassic families of Odonatoptera. Also, the distal division of RP" into RP"a and RP"b is more likely to be a synapomorphic condition of the Protomyrmeleontidae than a plesiomorphic condition of an unachieved fusion of RP3 and RP4 into RP3/4. Thus, both Zessin's and Nel & Henrotay's hypotheses imply that the bifurcations of veins RP2 (= RP2/3 *sensu* Zessin) and RP" (= RP4 *sensu* Zessin) are synapomorphies of Protomyrmeleontidae.

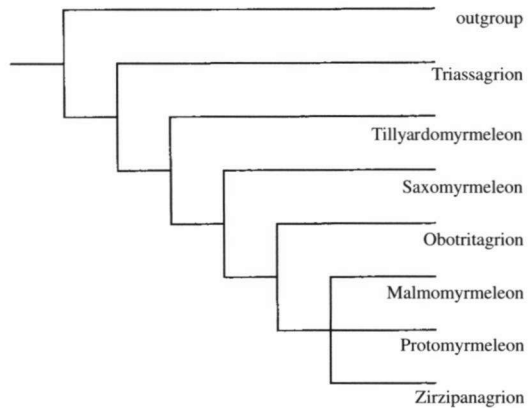


Fig. 5. Strict consensus phylogenetic tree.

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