



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

Palaeodisparoneura cretatica sp. nov., a new damselfly
(Odonata: Zygoptera: Platycnemididae) from mid-Cretaceous
Burmese amber



Palaeodisparoneura cretatica sp. nov., une nouvelle demoiselle
(Odonata : Zygoptera : Platycnemididae) de l'ambre birman du Crétacé
moyen

Daran Zheng^{a,b,*}, Bo Wang^{a,c}, Su-Chin Chang^{b,*}

^a State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, 210008 Nanjing, China

^b Department of Earth Sciences, The University of Hong Kong, Hong Kong Special Administrative Region, China

^c Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, 1, Beichen West Road, 100101 Beijing, China

ARTICLE INFO

Article history:

Received 27 March 2016

Accepted after revision 15 August 2016

Available online 30 September 2016

Handled by Annalisa Ferretti

Keywords:

Platycnemididae
Zygoptera
Odonata
Cenomanian
Cretaceous
Burmese amber

Mots clés :

Platycnemididae
Zygoptera
Odonates
Cénomaniens
Crétacé
Ambre birman

ABSTRACT

Abundant odonatanans have been discovered from mid-Cretaceous Burmese amber, and Burma has played an important role in early damselfly diversification during the mid-Cretaceous. In this paper, a new damselfly, *Palaeodisparoneura cretatica* sp. nov., is described from Burmese amber. It is the second species of the extinct genus *Palaeodisparoneura* Poinar, Bechly et Buckley, 2010. *P. cretatica* sp. nov. differs from *P. burmanica* Poinar, Bechly et Buckley, 2010 in having more postnodal and postsubnodal crossveins, the base of IR1 being more cells distal of the base of RP2, a hyaline pterostigma and a longer RP3/4. Our find increases the diversity of damselflies during the mid-Cretaceous.

© 2016 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

D'abondants Odonates ont été découverts dans l'ambre birman du Crétacé moyen, et la Birmanie a joué un rôle important dans la diversification précoce des demoiselles pendant le Crétacé moyen. Dans cet article, une nouvelle demoiselle, *Palaeodisparoneura cretatica* sp. nov., est décrite dans l'ambre birman. C'est la seconde espèce du genre éteint *Palaeodisparoneura* Poinar, Bechly et Buckley, 2010. *P. cretatica* sp. nov. diffère de *P. burmanica* Poinar,

* Corresponding author. State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, 210008 Nanjing, China.

E-mail addresses: dranzheng@gmail.com (D. Zheng), suchin@hku.hk (S.-C. Chang).

Bechly et Buckley, 2010 par l'existence d'un plus grand nombre de veines croisées post-nodales et postsubnodales, la base d'IR1 ayant plus de cellules éloignées de la base de RP2, un perostigma hyalin et un plus long RP3/4. Notre découverte augmente la diversité des demoiselles au cours du Crétacé moyen.

© 2016 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

Platycnemididae [Yakobson and Bianki, 1905](#), currently consists of over 400 species and is widely distributed in the Old World ([Dijkstra et al., 2014](#); [Orr and Kalkman, 2010](#); [Schorr and Paulson, 2015](#); [Theischinger et al., 2015](#)). Adults of this family are characterized by a laterally expanded head and the tibiae bearing dense long spines ([Carle et al., 2008](#); [Dijkstra et al., 2014](#); [Rehn, 2003](#)). Platycnemididae is divided into six extant subfamilies after a recent molecular phylogeny of [Dijkstra et al., 2014](#): Allocnemidinae [Dijkstra et al., 2014](#), Calicnemiinae [Fraser, 1957](#), Disparoneurinae [Fraser, 1957](#), Idiocnemidinae [Dijkstra et al., 2014](#), Onychargiinae [Dijkstra et al., 2014](#), and Platycnemidinae [Yakobson and Bianki, 1905](#). A fossil subfamily Palaeodisparoneurinae Poinar, Bechly et Buckley, 2010 (type species: *Palaeodisparoneura burmanica* Poinar, Bechly et Buckley, 2010) was attributed to Platycnemididae based on a well-preserved damselfly from mid-Cretaceous Burmese amber; however, this subfamily was out of consideration of the molecular results provided by [Dijkstra et al. \(2014\)](#). *P. burmanica* cannot be attributed to any recent taxa since it possesses the following unique autapomorphies: the mid-fork (the base of RP3/4) originates midway between the arculus and nodus, the pterostigma is of rectangular shape, RP1 is strongly kinked at the pterostigmal brace, and IR1 originates below the pterostigma. It is attributed to Platycnemididae by the presence of a special shape of the short male terminalia (superior appendages shaped like the hammer of a revolver), which is shared by Disparoneurinae and Caconeurinae ([Poinar et al., 2010](#)).

Here we describe a new species of *Palaeodisparoneura*, *P. cretatica* sp. nov., from Burmese amber.

2. Material and methods

The specimen described herein was collected from the Hukawng Valley of Kachin Province, Myanmar (locality in [Kania et al., 2015](#): fig. 1). The age of Burmese amber is radiometrically dated at 98.79 ± 0.62 Ma (Earliest Cenomanian; [Cohen et al., 2013](#)) based on U–Pb zircon dating of the volcanoclastic matrix ([Shi et al., 2012](#)).

The amber containing the damselfly is yellow and transparent. Photographs were taken using a Zeiss Stereo Discovery V16 microscope system and Zen software. In most instances, incident and transmitted light were used simultaneously. All images are digitally stacked photomicrographic composites of approximately 40 individual focal planes obtained using the free software Combine ZP for a better illustration of the 3D structures. The line drawings were prepared from photographs using image-editing

software (CorelDraw X7 and Adobe Photoshop CS6). The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of [Riek \(1976\)](#) and [Riek and Kukalová-Peck \(1984\)](#), as modified by [Nel et al. \(1993\)](#) and [Bechly \(1996\)](#). The higher classification of fossil and extant Odonatoptera, as well as family and generic characters followed in the present work, are based on the phylogenetic system proposed by [Bechly \(1996\)](#) and [Dijkstra et al. \(2014\)](#) for the phylogeny of extant Zygoptera. Wing abbreviations are as follows: Cr, nodal crossvein; CuA, cubitus anterior; DC, discoidal cell; IR, intercalary radial veins; MA, median anterior; MP, median posterior; N, nodus; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Sn, subnodal crossvein. All measurements are given in mm.

3. Systematic palaeontology

Order Odonata [Fabricius, 1793](#)

Suborder Zygoptera [Selys-Longchamps, 1854](#)

Family Platycnemididae [Yakobson and Bianki, 1905](#)

Subfamily Palaeodisparoneurinae Poinar, Bechly et Buckley, 2010

Genus: *Palaeodisparoneura* Poinar, Bechly et Buckley, 2010

Type species. *Palaeodisparoneura burmanica* Poinar, Bechly et Buckley, 2010

Palaeodisparoneura cretatica sp. nov. (Figs. 1–6)

Etymology. After the age of the species.

Material. Holotype. NIGP164075, four wings associated with a fragmentary abdomen and fragmentary legs, gender feminine; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Type stratum and locality. Hukawng Valley, Kachin Province, Myanmar; Lowermost Cenomanian, lowermost Upper Cretaceous.

Diagnosis. Eight postnodal crossveins and eight post-subnodal crossveins present before Pt, well aligned; IR1 seven or eight cells distal of base of RP2; RP3/4 long, ending on posterior wing margin two or three cells distal of base of IR1; Pt hyaline; tarsi armed with dense spines.

Description. All wings with basal part somewhat absent. Abdomen with basal five segments preserved, 13.39 mm long; gender feminine in absence of male accessory genitalia on ventral side of segment 2. Right forewing most completely preserved (Figs. 2B, 3). Wing length 7.88 mm, maximum width 2.25 mm; length from base of RP3/4 to Pt base 5.61 mm, from Pt base to wing

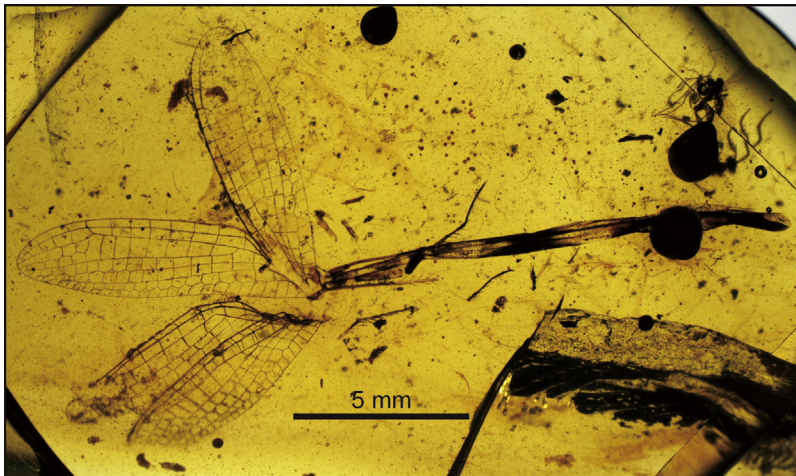


Fig. 1. *Palaeodisparoneura cretacica* sp. nov., holotype, NIGP164075, photomicrograph of specimen.
Fig. 1. *Palaeodisparoneura cretacica* sp. nov., holotype, NIGP164075, microphotographie de l'échantillon.

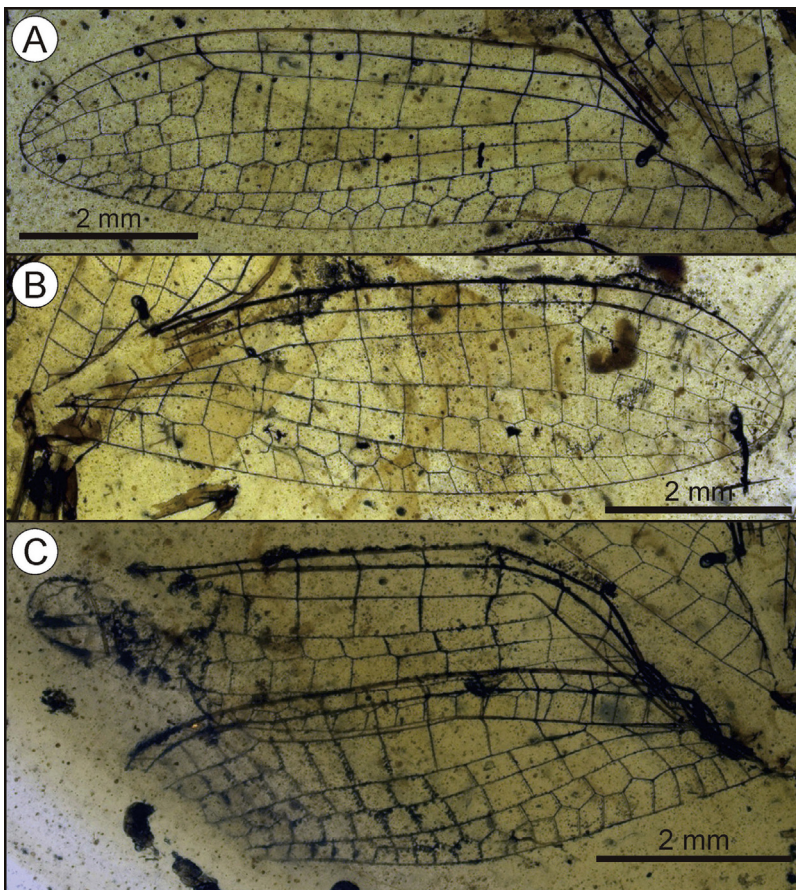


Fig. 2. *Palaeodisparoneura cretacica* sp. nov., holotype, NIGP164075. A: photomicrograph of right forewing; B: photomicrograph of right hindwing; C: photomicrograph of left forewing (upper) and hindwing (lower).
Fig. 2. *Palaeodisparoneura cretacica* sp. nov., holotype, NIGP164075. A : microphotographie de l'aile antérieure droite ; B : microphotographie de l'aile postérieure droite ; C : microphotographie de l'aile antérieure gauche (en haut) et de l'aile postérieure gauche (en bas).

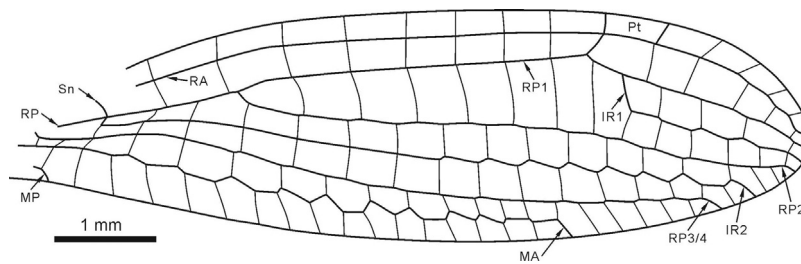


Fig. 3. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP164075, line drawing showing right hindwing venation.

Fig. 3. *Palaeodisparoneura cretacia* sp. nov. holotype, NIGP164075, dessin au trait de la venation de l'aile postérieure droite.

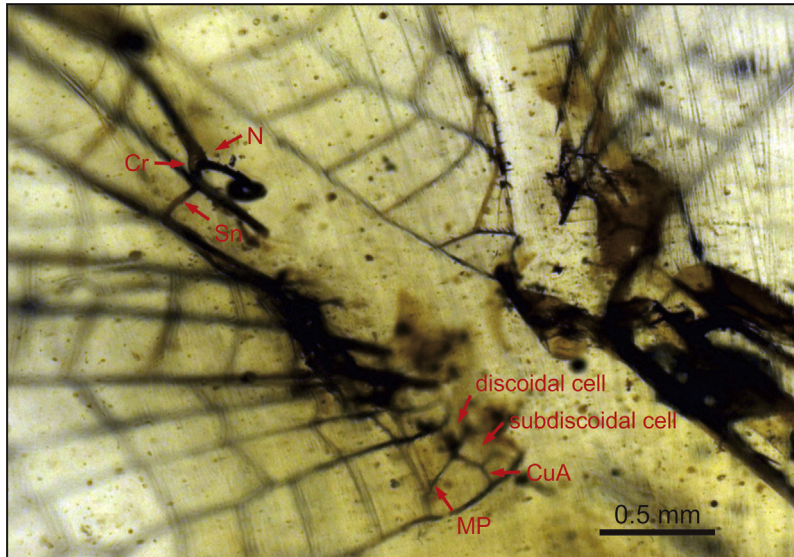


Fig. 4. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP164075, photomicrograph showing detail of basal wings.

Fig. 4. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP 164075, microphotographie montrant le détail des ailes basales.

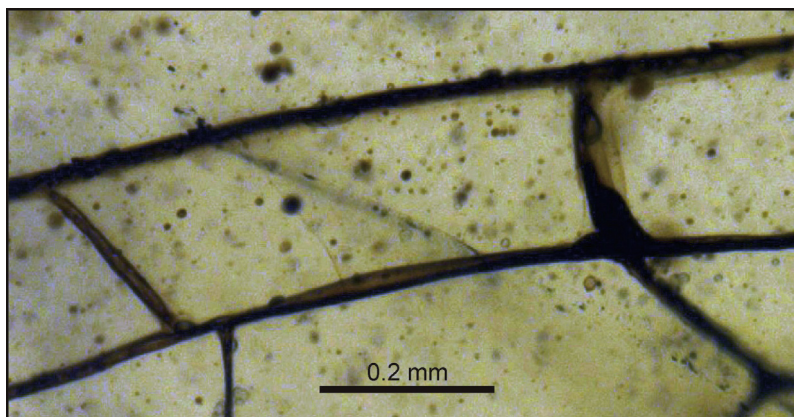


Fig. 5. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP164075, photomicrograph of right forewing pterostigma.

Fig. 5. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP164075, microphotographie du pterostigma de l'aile antérieure droite.

apex 2.03 mm. Eight postnodal crossveins and eight post-subnodal crossveins present before Pt, well aligned. Four postnodal crossveins and four postsubnodal crossveins present distal of Pt, non-aligned. Nodal structures not well preserved; Sn present and aligned with base of IR2. Midfork

one long cell and 0.66 mm basal of Sn, ending on posterior margin three cells distal of base of IR1. IR2 basally straight but distally zigzagged. Base of RP2 three cells distal of Sn, lying 1.28 mm distally, nearer to N than to Pt. Base of IR1 eight cells distal of base of RP2, lying 3.81 mm distally and



Fig. 6. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP164075, photomicrograph of legs.
Fig. 6. *Palaeodisparoneura cretacia* sp. nov., holotype, NIGP164075, microphotographie des pattes.

originating just below Pt. RP1 with a strong angle below pterostigmal brace. MA distally zigzagged and long, reaching posterior wing margin just below Pt-brace. MP curved and short. Pt one cell long, rectangular and hyaline (Fig. 5), 0.64 mm long and 0.21 mm wide, strongly braced; Pt-brace more oblique than base of Pt. All intercalary veins (except for IR1 and IR2) suppressed. Longitudinal veins RA, IR1, RP1, IR2 and RP2 strongly converging to wing apex. Other wings resemble this wing except for following differences: IR1 seven cells distal of base of RP2 in left hindwing (Fig. 2C); N well preserved (Fig. 4) in left forewing, and Sn aligned with base of IR2; MP one cell length distal of CuA, ending on posterior wing margin just below N in left hindwing (Fig. 4); CuA short and oblique in left hindwing (Fig. 4); distal part of DC and subdiscoidal cell rectangular in left hindwing (Fig. 4). Four fragmentary legs preserved (Fig. 6), paired long spines present on tibia and tarsi; tarsi armed with about 14 pairs of spines.

4. Discussion

P. cretacia can be attributed to the subfamily Palaeodisparoneurinae Poinar, Bechly et Buckley, 2010 by sharing the characters provided by Poinar et al. (2010): small damselfly species characterized by greatly shortened veins MP (only one cell long) and CuA (only an oblique crossvein); aligned postnodal and postsubnodal crossveins; rectangular and distinctly braced Pt; RP1 strongly kinked at pterostigmal brace; very short IR1 originating beneath Pt. *Palaeodisparoneura* Poinar, Bechly et Buckley, 2010 is also characterized by a rectangular discoidal cell, a well-developed sub-rectangular subdiscoidal cell being not fused to the wing margin, the midfork being situated halfway between the arculus and subnodus, and the male terminalia being short. These characters are poorly

discernible in *P. cretacia*. However, the rectangular distal parts of the discoidal cell and subdiscoidal cell further support the attribution.

Although *P. cretacia* shares the diagnosis of *P. burmanica*, some obvious differences can be observed between these two species. Specifically, *P. cretacia* has more postnodal crossveins and postsubnodal crossveins (eight instead of five in *P. burmanica*) before the pterostigma, the base of IR1 is seven or eight cells distal of the base of RP2 instead of five rows in *P. burmanica*, the pterostigma is hyaline instead of dark colour, a long RP3/4 ends on the posterior wing margin three cells distal of the base of IR1 instead of one cell in *P. burmanica*. In view of the above differences, we suggest a new species for the new specimen.

The recently described odonatan in Burmese amber help us understand the role of Burma in odonatan diversification during the mid-Cretaceous. The damselfly group is represented by some extant families, viz., Platycnemididae, Platystictidae, Hemiphlebiidae and Perilestidae (Huang et al., 2015; Poinar et al., 2010; Zheng et al., 2016a, b, c). Besides *P. burmanica*, *Cretadisparoneura hongii* Huang, Azar, Cai et Nel, 2015 is the third representative of Platycnemididae (Huang et al., 2015). *Burmalindenia imperfecta* Schädel and Bechly, 2016 is the first true dragonfly from Burmese amber (Schädel and Bechly, 2016). *Burmaphlebia reifi* Bechly and Poinar, 2013 is the first damsel-dragonfly from amber (Bechly and Poinar, 2013). *Burmahemiphlebia zhangii* Zheng et al., 2016a is the first member of the Hemiphlebiidae in Burmese amber and may be the most common damselfly in these deposits, since about 40 specimens have been observed by the present authors (Zheng et al., 2016a). *Palaeodysagrion cretacia* Zheng et al., 2016a represents the second Cretaceous dysagrionid damselfly (Zheng et al., 2016a). *Mesosticta burmatica* Huang, Azar, Cai et Nel, 2015 and *Mesosticta electronica* Zheng et al., 2016b are

the earliest fossil platystictid damselflies, which puts the origin of Platystictidae to at least mid-Cretaceous (Huang et al., 2015; Zheng et al., 2016b). *Palaeoperilestes electronicus* Zheng et al., 2016c is the first fossil representative of perilestid damselfly (Zheng et al., 2016c).

5. Conclusions

Abundant extant damselfly families have been discovered from mid-Cretaceous Burmese amber, indicating the important geological position of these tropical forests for early damselfly diversification. In the present paper, a new platycnemid damselfly, *P. cretacica* sp. nov., representing the second species of the extinct subfamily Palaeodisparoneurinae Poinar, Bechly et Buckley, 2010, is described from Burmese amber.

Acknowledgements

This research was supported (grant numbers in parentheses) by the National Basic Research Program of China (2012CB821900), National Natural Science Foundation of China (41572010, J1210006), Youth Innovation Promotion Association of Chinese Academy of Sciences (2011224), and the HKU Seed Funding Program for Basic Research (201210159058). We offer our sincere gratitude to Sandrine Fléché and Dr. Annalisa Ferretti for editing, and two anonymous reviewers for the very useful comments on the earlier version of the manuscript.

References

Bechly, G., 1996. *Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta: Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata*. *Petalura* 2, 1–402.

Bechly, G., Poinar Jr., G., 2013. *Burmaphlebia reifi* gen. et sp. nov., the first anisozygoteran damsel-dragonfly (Odonata: Epiophlebioptera: Burmaphlebiidae fam. nov.) from Early Cretaceous Burmese amber. *Hist. Biol.* 25, 233–237.

Carle, F.L., Kjer, K.M., May, M.L., 2008. Evolution of Odonata, with special reference to Coenagrionoidea (Zygoptera). *Arthropod Syst. Phylo.* 66, 37–44.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J., 2013. The ICS international chronostratigraphic chart. *Episodes* 36, 199–204.

Dijkstra, K.-D.B., Kalkman, V.J., Dow, R.A., Stokvis, F.R., van Tol, J., 2014. Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Syst. Entomol.* 39, 68–96.

Fabricius, J.C., 1793. *Entomologia systematica emendata et aucta, secundum classes, ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*. C. G. Proft, Hafniae (= Copenhagen) 3, 1–487 and 1–349.

Fraser, F.C., 1957. A reclassification of the order Odonata, based on some new interpretations of the venation of the dragonfly wing. *R. Zool. Soc. N. S. W. Sydney* 12, 1–133.

Huang, D., Azar, D., Cai, C., Nel, A., 2015. New damselfly genera in the Cretaceous Burmese amber attributable to the Platystictidae and Platycnemididae Disparoneurinae (Odonata: Zygoptera). *Cretaceous Res.* 56, 237–243.

Kania, I., Wang, B., Szewo, J., 2015. *Dicranoptycha* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Upper Cretaceous Burmese amber. *Cretaceous Res.* 52, 522–530.

Nel, A., Martinez-Delclòs, X., Paicheler, J.C., Henrotay, M., 1993. Les 'Anisozygoptera' fossiles. *Phylogénie et classification (Odonata)*. *Martinia Num. Hors Sér.* 3, 1–311.

Orr, A.C., Kalkman, V.J., 2010. *Arrhenocnemis parvibullis* sp. nov. (Odonata: Platycnemididae), a new calicnemine damselfly from Papua New Guinea, with a description of the female of *A. amphidactylis* Lieftinck, 1949. *Aust. Entomol.* 37 (4), 137–146.

Poinar Jr., G., Bechly, G., Buckley, R., 2010. First record of Odonata and a new subfamily of damselflies from Early Cretaceous Burmese amber. *Palaeodiversity* 3, 15–22.

Rehn, A.C., 2003. Phylogenetic analysis of higher-level relationships of Odonata. *Syst. Entomol.* 28, 181–239.

Riek, E.F., 1976. A new collection of insects from the Upper Triassic of South Africa. *Ann. Natal Mus.* 22, 791–820.

Riek, E.F., Kukulová-Peck, J., 1984. A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Can. J. Zool.* 62, 1150–1166.

Schädel, M., Bechly, G., 2016. First record of Anisoptera (Insecta: Odonata) from mid-Cretaceous Burmese Amber. *Zootaxa* 4103 (6), 537–549.

Schorr, M., Paulson, D., 2015. World Odonata list, Available on the Internet at: <http://www.pugetsound.edu/> (accessed 16 March 2016).

Selys-Longchamps de, E., 1854. *Monographie des Caloptérygines*. *Mémoires de la Société royale des Sciences de Liège* 9, xi + 291 pp.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Res.* 37, 155–163.

Theischinger, G., Gassmann, D., Richards, S.J., 2015. *Macrocnemis gracilis*, a new genus and species of Idiocnemidinae (Zygoptera: Platycnemididae) from Papua New Guinea. *Zootaxa* 3990 (3), 429–437.

Yakovson, G.G., Bianki, V.L., 1905. *Orthoptera and Pseudo-Neuroptera of the Russian Empire and adjoining countries*. St. Petersburg (In Russian).

Zheng, D., Zhang, Q., Nel, A., Jarzembowski, E.A., Zhou, Z., Chang, S.-C., Wang, B., 2016a. New damselflies (Odonata: Zygoptera: Hemiphlebiidae, Dysagrionidae) from mid-Cretaceous Burmese amber. *Alcheringa*, <http://dx.doi.org/10.1080/03115518.2016.1164402>.

Zheng, D., Zhang, Q., Chang, S.-C., Wang, B., 2016b. A new damselfly (Odonata: Zygoptera: Platystictidae) from mid-Cretaceous Burmese amber. *Cretaceous Res.* 63, 142–147.

Zheng, D., Wang, B., Jarzembowski, E.A., Chang, S.-C., Nel, A., 2016c. The first fossil Perilestidae (Odonata: Zygoptera) from mid-Cretaceous Burmese amber. *Cretaceous Res.* 65, 199–205.