Available online at www.sciencedirect.com
ScienceDirect
Progress in Natural Science 18 (2008) 59–64
Progress in Natural Science

New dragonflies (Insecta: Odonata: Gomphaeschnidae) from the Yixian Formation in Inner Mongolia, China

Binglan Zhang [a], Dong Ren [a,*], Hong Pang [b]

[a] College of Life Science, Capital Normal University, Beijing 100037, China
[b] State Key Laboratory of Biocontrol and Institute of Entomology, Sun Yat-sen University, Guangzhou 510275, China

Received 25 April 2007; received in revised form 17 July 2007; accepted 27 July 2007

Abstract

Two fossil dragonflies from the Upper Jurassic to Lower Cretaceous Yixian Formation in Liutiaogou Village, Ningcheng County, Inner Mongolia, China are described and illustrated. They are assigned to two new genera and species, i.e., *Sophoaeschna frigida* gen. et sp. nov. and *Falsisophoaeschna generalis* gen. et sp. nov. within the family Gomphaeschnidae Tillyard & Fraser, 1940. This is the first report of Odonata from Yixian Formation in Inner Mongolia and the second record of fossil Gomphaeschnidae from China.

Keywords: Odonata; New genus; Upper Jurassic to Lower Cretaceous; Yixian Formation; China

1. Introduction

The family Gomphaeschnidae Tillyard & Fraser, 1940 (sensu Bechly [1]) is a relict group maybe containing one extant genus, *Oligoaeschna* Selys, 1889 with 32 extant species occurring in South-east Asia [2,3]. Fossils of Gomphaeschnidae are represented by 23 species belonging to 10 genera. Up to now, they are all described from Cretaceous or Tertiary of Europe, Asia or America: eight genera and fourteen species from Lower Cretaceous of Brazil, England, Russia, Buryat Republica, Mongolia and China [3–7]; one genus and three species from Lower Palaeocene of Canada [3]; one genus and two species from Lower Tertiary of Denmark [4]; one genus and three species from Oligocene of England, USA and France [3,8,9], and one genus and one species from Upper Pliocene of Japan [10].

In 2001, Bechly et al. described one genus and species *Sinojagoria imperfecta* Bechly et al. 2001 from Beipiao City, western Liaoning Province, China [4]. It is the only fossil report of family Gomphaeschnidae from China prior to this study. Recently, we collected two fossil specimens of this family from Yixian Formation in Liutiaogou Village, Ningcheng County, Inner Mongolia, China. They are assigned to two new genera and species: *Sophoaeschna* gen. et sp. nov. and *Falsisophoaeschna* gen. et sp. nov.

Inner Mongolia has provided abundant fossil insect groups, such as Blattaria, Ephemeroptera, Odonata, Orthoptera, Plecoptera, Heteroptera, Homoptera, Neuroptera, Tricoptera, Coleoptera, Hymenoptera and Diptera [11–15]. Up to present, seven genera and nine species of Odonata have been described from Inner Mongolia, including six genera and eight species from Jiulongshan Formation and one genus and species from Shahai Formation [16–19]. This study is the first report of dragonflies from Yixian Formation in Inner Mongolia, China.

2. Material and methods

This study is based on three (one pair of part/counterpart and one part) specimens housed in the fossil insect

* Corresponding author. Tel.: +86 10 68901757; fax: +86 10 68980851.
E-mail address: rendong@mail.cnu.edu.cn (D. Ren).

1002-0071/$ - see front matter
doi:10.1016/j.pnsc.2007.07.005

collection of the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Science, Capital Normal University, Beijing, China (CNUB; Dong REN, Curator). Specimens were examined using a Leica MZ12.5 dissecting microscope, illustrated with the aid of a drawing tube and software Adobe Illustrator CS2.

We follow the wing venation nomenclature of Riek [20] and Riek and Kukalová-Peck [21], as amended by Kukalová-Peck [22], Nel et al. [23], Bechly [24] and Bechly et al. [4]. Structure nomenclature (except wing) is based on the work of Zhao [25]. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly [1,24]. The classification of the Aeshnoptera is based on the work of Bechly et al. [4].

3. Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys in Selys & Hagen, 1854

Family Gomphaeschnidae Tillyard & Fraser, 1940

Genus Sophoaeschna gen. nov.

Etymology: From Greek 'sopho' (clever) and the genus *Aeschna*. The gender is feminine.

Type species: *Sophoaeschna frigida* gen. et sp. nov.

Diagnosis: Discoidal triangles of all wings equal in length, two celled, longitudinal elongated and with rather curving distal sides MAb; Ax2 situated on the level of the basal side of the discoidal triangle; Pseudo-IR1 long, originating beneath the distal side of the pterostigma; Rspl and Mspl developed well, more or less parallel to IR2 and MA, respectively, with only one row of cells in between; distinctly intercalary veins appeared between Rspl and RP3/4, as well as between Mspl and MP; pterostigma covers four cells, with basal side parallel to distal side; the pterostigmal brace vein straight, aligned with the basal side of the pterostigma; in hindwing, MP and CuAa converge to each other distally, with a single row of large cells in between; anal loop four celled; compound eyes large and confluent.

Remarks: The new genus shares all important synapomorphies with Aeshnoptera, Aeshnida, Euaeshnida and Neoaeshnida, it can be assigned to the family Gomphaeschnidae by the following combination of features: presence of a "cordulegastrid gap"; no accessory cubito-anal crossveins in the submedian space between CuP-crossing and PsA; discoidal triangles only divided into two cells by a single crossvein; hypertriangles secondarily unicellular.

Within Gomphaeschnidae, *Sophoaeschna* differs markedly from all known genera in Ax2 of hind wing situated on the level of the basal side of the discoidal triangle. Based on the whole venation characters, it is most closely related to *Sinojagorini*, but differs from the latter in Ax2 situated on the level of the basal side of the discoidal triangle in all wings (vs. only in the forewing), hindwing discoidal triangle two celled (vs. four celled), anal loop four celled (vs. six or seven celled), pterostigma covering four cells (vs. two cells). Bechly regarded "only four antesubnodal crossveins between RA and RP basal of the subnodus in the forewing" as a diagnostic character of *Sinojagorini*. It is doubtful that this character is not consistent in both forewings of his material. Although no crossveins between RA and RP basal of the subnodus in both forewings of our specimen, we ignore the comparison of this character to avoid potential mistakes caused by incomplete preservation of specimens.

Sophoaeschna frigida gen. et sp. nov. (Figs. 1, 2).

Etymology: After the Latin "frigidus"= cold.

Holotype: Female, No. CNU-OD-NN2004015; specimen deposited in the College of Life Science, Capital Normal University, Beijing, China.

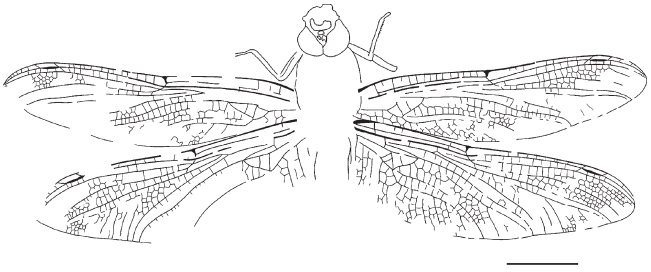

Fig. 2. Line drawing of *Sophoaeschna frigida* gen. et sp. nov., holotype, No. CNU-OD-NN2004015 (the scale bar is 10 mm).

Fig. 1. Photograph of *Sophoaeschna frigida* gen. et sp. nov., holotype, No. CNU-OD-NN2004015 (the scale bar is 10 mm).

Type locality and horizon: Liutiaogou Village, Ningcheng County, Inner Mongolia, China; Yixian Formation, Upper Jurassic to Lower Cretaceous [26–29].

Diagnosis: As for genus.

Description: A female dragonfly with four wings outspread. Head, thorax and part of legs are preserved. Basal hind part of left hindwing and several parts of detail veins are missing. There is no trace of coloration preserved, thus, the wings are probably hyaline.

Forewing: Length 41.3 mm; width at nodus 10.0 mm; distance from nodus to pterostigma 15.2 mm; Ax1 and Ax2 slightly stronger than the secondary antenodal crossveins; only one secondary antenodal crossvein between Ax1 and Ax2 preserved in the first row; Ax2 situated on the level of the basal side of the discoidal triangle; distal of Ax2 there are twelve secondary antenodal crossveins between the costal margin and ScP; except Ax1 and Ax2, nearly no antenodals crossveins between ScP and RA preserved; no antesubnodal and postsubnadal crossveins appeared near the subnodus, thus the ''cordulegastrid gap'' and ''libellulid gap'' present; pterostigma 2.7 mm long and 0.8 mm wide, covers four cells; the pterostigmal brace vein straight, aligned with the basal side of the pterostigma and with the same lean; costal margin and RA thickened along the pterostigma; two-celled discoidal triangle is longitudinal elongated, with a rather curving distal side MAb; length of anterior side 4.0 mm, of basal side 1.8 mm, of distal side MAb 4.1 mm; unicellular subdiscoidal triangle well defined; Pseudo-IR1 long and distinct, originating beneath the distal side of the pterostigma; base of RP2 aligned with subnodus; Rspl long and slightly undulated, strong tendency to with only one row of cells between it and IR2, at least two intercalary veins are visible in the area between Rspl and RP3/4; IR2 slightly undulated, bending to the hind margin distally; MA rather undulated with a sudden bending to the hind margin distally; Mspl long, with a single row of cells between it and MA; postdiscoidal area distally strongly widened; two row of cells in the postdiscoidal area immediately distal of the discoidal triangle; MP ends far distal of the level of nodus; at least five weakly defined and zigzagged posterior branches originated on CuAa.

Hindwing: Length 41.5 mm; width at nodus 12.8 mm; distance from base to arculus 4.8 mm, from arculus to nodus 11.8 mm, from nodus to pterostigma 16.6 mm; Ax1 and Ax2 slightly stronger than the secondary antenodal crossveins; Ax2 situated on the level of the basal side of the discoidal triangle; only two secondary antenodal crossveins between costal margin and ScP preserved, not aligned with the visible single antenodal crossvein between ScP and RA; eight postnodal crossveins visible, not aligned with the ten postsubnodal crossveins; pterostigma 3.2 mm long and 0.8 mm wide, covers four cells and distinctly braced by a very oblique crossvein that is aligned with its basal side; costal margin and RA thickened along the pterostigma; origins of RP and MA are separated at the arculus which is angled; none (left wing) or two (right wing) antesubnodal crossvein preserved in the antesubnodal area and there might be a ''cordulegastrid gap''; median space and submedian space free of crossveins; unicellular hypertriangle long, with the costal side slightly vaulted; subdiscoidal triangle well defined, divided by one crossvein; two-celled discoidal triangle is longitudinal elongated, with a sigmoid curved distal side MAb; length of anterior side 4.0 mm, of basal side 2.6 mm, of distal side MAb 4.0 mm; RP1 and RP2 basally relatively paralleled, with only one row of cells between them up to the 2/3 distance from nodus to pterostigma; Pseudo-IR1 long and slightly zigzagged, originating beneath the distal side of the pterostigma, with two rows of cells between it and RP1 and three rows of cells between it and RP2; RP2 and IR2 with a single row of cells in-between up to the midway between nodus and pterostigma, about three rows of cells distally; bridge-crossveins Bqs not preserved; base of RP2 aligned with subnodus; oblique vein ''O'' 0.7 mm distal of the subnodus; IR2 rather straight, slightly bending to the hind margin distally; Rspl long and slightly undulated, nearly parallel to IR2, strong tendency to with only one row of cells between it and IR2; six intercalary veins visible in the area between Rspl and RP3/4; MA rather undulated; Mspl long, strong tendency to with only one row of cells between it and MA; at least three intercalary veins in the area between Mspl and MP; postdiscoidal area distally widened (with near discoidal triangle 3.9 mm, width at wing margin 7.0 mm); two row of cells in the postdiscoidal area immediately distal of the discoidal triangle; MP ends far distal of the level of nodus with a single row of large cells between it and CuAa; six posterior branches originated on CuAa; anal loop well-defined, divided into four cells by Y-shaped crossveins; the area between MP and CuAa with only one row of cells, basal part wider than distal part.

Head about 7.0 mm long and 7.4 mm wide; compound eyes very large, meeting dorsally for a distance about 1.1 mm long; three ocelli large and distinct.

Thorax about 11.0 mm long and 9.3 mm wide, jumbled and rather indiscernible.

Genus Falsisophoaeschna gen. nov.

Etymology: From 'falsi-' (pseudo) and the genus *Sophoaeschna*. The gender is feminine.

Type species: *Falsisophoaeschna generalis* gen. et sp. nov.

Diagnosis: Similar to *Sophoaeschna* but different in the following characters: anal loop much larger (seven celled vs. four celled); discoidal triangle in fore wing longer (by 8 percent) than that of hind wing (vs. equal in length); RP2 more curved with four rows of cells between it and Pseudo-IR1 (vs. less curved, three rows of cells); CuAa basally strongly curved, thus the area between CuAa and MP with a distinct broader basal part than that of *Sophoaeschna*; wings, especially hind wings slightly broader, correlated with the broader area between IR2 and RP3/4.

Remarks: This new genus is similar to *Sophoaeschna* especially in discoidal triangles of all wings two celled, longitudinal elongated and with rather curving distal sides

MAb; Ax2 situated on the level of the basal side of the discoidal triangle. We propose it a new genus because of the marked difference aforementioned.

Falsisophoaeschna generalis gen. et sp. nov. (Figs. 3 and 4).

Etymology: After the Latin ''generalis''= general.

Holotype: Female, part and counterpart, No. CNU-OD-NN2004065-1, CNU-OD-NN2004065-2; specimens deposited in the College of Life Science, Capital Normal University, Beijing, China.

Type locality and horizon: Liutiaogou Village, Inner Mongolia, China; Yixian Formation, Late Jurassic to Early Cretaceous.

Diagnosis: As for genus.

Description: Part of a female dragonfly with all four wings outspread. Head, thorax and part of legs are preserved. A majority of left wings, apex of right wings and hind margin of right hind wing are missing. There is no trace of coloration preserved, thus, the wings are probably hyaline.

Forewing: Length at least 39.7 mm; width at nodus 10.6 mm; distance from base to arculus 4.2 mm, from arculus to nodus 14.6 mm, from nodus to pterostigma 15.5 mm; Ax1 and Ax2 slightly stronger than the secondary antenodal crossveins; only one secondary antenodal crossveins in the first row poorly preserved between Ax1 and Ax2; Ax2 situated on the level of the basal side of the discoidal triangle; distal of Ax2 there are at least eleven secondary antenodal crossveins between the costal margin and ScP; only four antenodals crossveins between ScP and RA partly preserved; pterostigma 2.7 mm long and 0.9 mm wide, covers four cells and distinctly braced by a very oblique crossvein aligned with its basal side; costal margin and RA thickened along the pterostigma; two celled discoidal triangle is longitudinal elongated, with a slightly curving distal side MAb; length of anterior side 4.3 mm, of basal

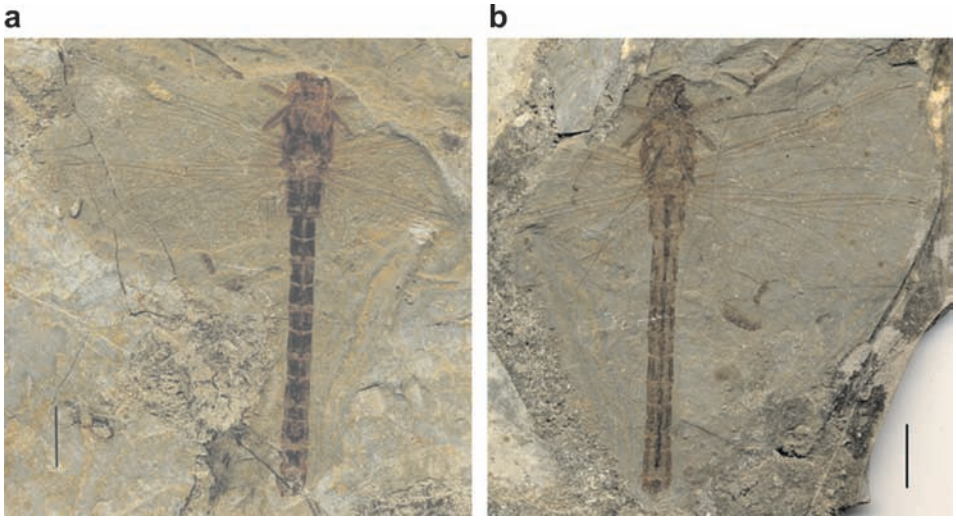

Fig. 3. Photographs of *Falsisophoaeschna generalis* gen. et sp. nov. (a) Holotype, No. CNU-OD-NN2004065-1, part; (b) holotype, No. CNU-OD-NN2004065-2, counterpart (the scale bar is 10 mm).

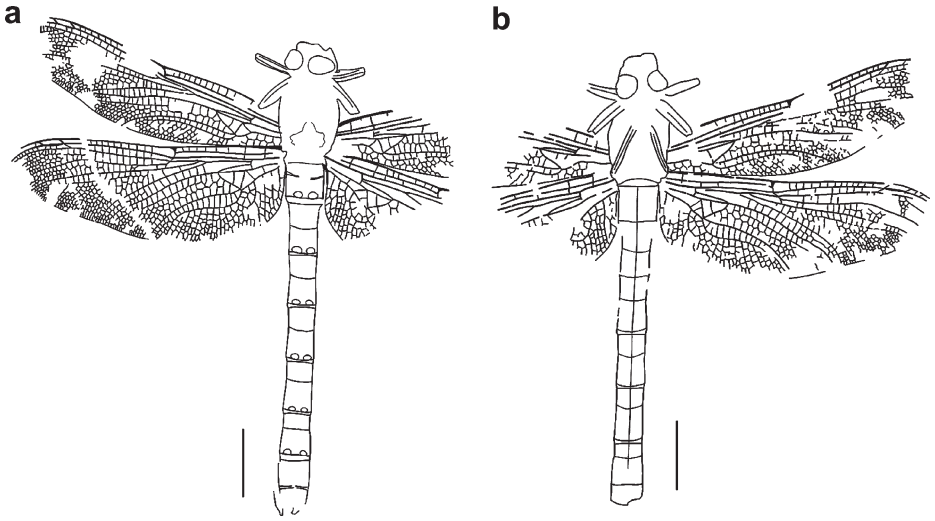

Fig. 4. Line drawings of *Falsisophoaeschna generalis* gen. et sp. nov. (a) Holotype, No. CNU-OD-NN2004065-1, part; (b) holotype, No. CNU-OD-NN2004065-2, counterpart (the scale bar is 10 mm).

side 2.1 mm, of distal side MAb 4.3 mm; subdiscoidal triangle unicellular; Pseudo-IR1 distinct, originating beneath the distal side of the pterostigma; Rspl and IR2 rather straight and parallel to each other, with only one row of cells in between, at least three intercalary veins in the area between Rspl and RP3/4; MA rather undulated; Mspl long, with a single row of cells between it and MA; postdiscoidal area distally strongly widened; two row of cells in the postdiscoidal area immediately distal of the discoidal triangle; MP ends distal of the level of nodus; four zigzagged intercalary veins visible between the Mspl and MP; six weakly defined and zigzagged posterior branches originated on CuAa.

Hindwing: Length at least 40.7 mm; width at nodus 14.3 mm; distance from base to arculus 4.8 mm, from arculus to nodus 11.6 mm, from nodus to pterostigma 16.7 mm; Ax1 and Ax2 slightly stronger than the secondary antenodal crossveins; six secondary antenodal crossveins between costal margin and ScP preserved, not aligned with the visible two antenodal crossvein between ScP and RA; thirteen postnodal crossveins visible, not aligned with the nine postsubnodal crossveins; pterostigma 3.1 mm long and 0.7 mm wide, distinctly braced by a very oblique crossvein aligned with its basal side; costal margin and RA thickened along the pterostigma; none antesubnodal crossvein preserved in the antesubnodal area thus the ''cordulegastrid gap'' present; hypertriangle long and free of crossveins; subdiscoidal triangle and discoidal triangle divided by a vaulted vein respectively; discoidal triangle with a smoothly curved distal side MAb, length of anterior side 4.0 mm, of basal side 2.8 mm, of distal side MAb 4.1 mm; RP1 and RP2 basally relative paralleled, with only one row of cells in between up to the 3/4 distance from nodus to pterostigma; RP2 hump up rather acutely right before the pterostigma; Pseudo-IR1 long, originating beneath the distal side of the pterostigma, with four rows of cells between it and RP2; RP2 and IR2 with a single row of cells in between up to the middle from the nodus to pterostigma and about three rows of cells distally; bridge-crossveins no preserved; base of RP2 aligned with subnodus; oblique vein ''O'' 0.6 mm distal of subnodus; Rspl long and slightly undulated, with only one row of cells between it and IR2; at least four intercalary veins in the area between Rspl and RP3/4; IR2 rather straight, slightly bending to the hind margin distally; MA strongly undulated; Mspl long, with a single row of large cells between it and MA; postdiscoidal area distally widened (with near discoidal triangle 4.2 mm, width at wing margin about 6.8 mm); two row of cells in the postdiscoidal area immediately distal of the discoidal triangle; MP reach posterior margin distal of the level of nodus; seven posterior branches originated on CuAa; anal loop well-defined, divided into seven cells; the area between MP and CuAa with only one row of cells, basal part much wider than distal part.

Head not well preserved; compound eyes not confluent.

Thorax about 10.6 mm long and 8.8 mm wide, jumbled and rather indiscernible.

Abdomen about 53.4 mm long; dorso-longitudinal abdominal carina present; segment 2–7 slightly narrowed in middle with two round marking on dorsal–distal part and antecostalsuture (ACS), acrotergite (ATG), supplementary transverse carina (SUTC) distinctly visible.

4. Discussion

All known and newly discovered fossil Gomphaeschnids showed their widespread distribution in Europe, Asia and America from Upper Jurassic to tertiary. But extant Gomphaeschnids (species of *Oligoaeschna*, which systematic situation still questioned) were only found in South-east Asia till now. To uncover the geographic changes of this family, even the relations between *Oligoaeschna* and Gomphaeschnidae, we need further evidence, especially fossil Gomphaeschnids from Quaternary.

Acknowledgements

This work was supported by National Natural Science Foundation of China (Grant No. 30430100), Beijing Municipal Commission of Education (Grant No. KZ200410028013), the Beijing Natural Science Foundation (Grant No. 5032003), PHR Project of Beijing Municipal Commission of Education and the financial support from China Postdoctoral Science Foundation (Grant No. 20060400479). We are grateful to Dr. Shih Chungkun (College of Life Science, Capital Normal University, Beijing) for his helpful improvement on an earlier draft of this manuscript. We sincerely thank anonymous reviewers for their valuable comments on the manuscript.

References

[1] Bechly G. Phylogenetic systematics of ''Anisozygoptera''. http://www.bernstein.naturkundemuseum-bw.de/odonata/anis-opt1.htm#gomphaeschnidae [2006-03-15].

[2] Waldfrieden MS, Wolfstr ML, Paulson D. World list of Odonata (last revision November 2006). http://www.ups.edu/media/SlaterMuseum/WorldOdonataList.pdf [2006-03-12].

[3] Wighton DC, Wilson MVH. The Gomphaeschninae (Odonata: Aeshnidae): new fossil genus, reconstructed phylogeny, and geographical history. Systematic Entomology 1986;11:505–22.

[4] Bechly G, Nel A, Martínez-Delclòs X, et al. A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of numerous taxa (Insecta: Odonata: Anisoptera). Neue Paläontologische Abhandlungen 2001;4:1–219.

[5] Wighton DC. *Gomphaeschna Obliqua* spec. nov., a new species of Gomphaeschninae from the lower Cretaceous of Northeastern Brazil (Anisoptera: Aeshnidae). Odonatologica 1987;16(3):311–4.

[6] Jarzembowski EA, Nel A. New fossil dragonflies from the Lower Cretaceous of SE England and the phylogeny of the superfamily Libelluloidea (Insecta: Odonata). Cretaceous Research 1996;17(1):67–85.

[7] Pritykina LN. New dragonflies from the Lower Cretaceous deposits of Transbaiklia and Mongolia. In: Fauna, Flora, and Biostratigraphy of the Mesozoic and Cenozoic of Mongolia (in Russian). Moscow: Nauka; 1977. p. 81–93.

[8] Cockerll TDA. Two fossil insects from Florissant, Colorado, with a discussion of the venation of the Aeshnine Dragonflies. Proceedings US National Museum 1913;45:577–83.

[9] Cockerll TDA, Andrews H. Dragonflies from the English Oligocene. Proceedings of the Biological Society of Washington 1916;29:89–92.
[10] Esaki T, Asahina S. On two Tertiary dragonfly species from the Oya-Formation in Kazusa, Nagasaki Prefecture. Kontyu 1957;25(3):82–8.
[11] Liu YS, Ren D, Sinitshenkova ND, et al. A new Middle Jurassic stonefly from Daohugou, Inner Mongolia, China (Insecta: Plecoptera). Annales Zoologici (Warszawa) 2006;56(3):549–54.
[12] Ren D, Krzeminski W. Eoptychopteridae (Diptera) from the Middle Jurassic of China. Annales Zoologici (Warszawa) 2002;52(2):207–10.
[13] Tan JJ, Ren D, Shih CK. New Cupedids from the Middle Jurassic of Inner Mongolia, China (Coleoptera: Archostemata). Annales Zoologici (Warszawa) 2006;56(1):1–6.
[14] Wang Y, Ren D, Shih CK. Discovery of Middle palaeontinids from Inner Mongolia, China (Hemoptera: Palaeontinidae). Progress in Natural Science 2007;17(1):112–6.
[15] Yao YZ, Cai WZ, Ren D, et al. New fossil rhopalids (Heteroptera: Coreoidea) from the Middle Jurassic of Inner Mongolia, China. Zootaxa 2006;1384:41–58.
[16] Hong Y. A new fossil dragonfly, *Sinaeschnidia* Hong gen. nov. (Odonata, Insecta). Acta Entomologica Sinica (in Chinese) 1965;14:171–6.
[17] Tan JJ, Ren D. Palaeoecology of insect community from Middle Jurassic Jiulongshan Formation in Ningcheng County, Inner Mongolia, China. Acta Zootaxonomica Sinica 2001;27(3):428–34.
[18] Fleck G, Nel A. The first isophlebioid dragonfly (Odonata: Isophlebioptera: Campterophlebiidae) from the Mesozoic of China. Palaeontology 2002;45:1123–36.
[19] Zhang BL, Fleck G, Huang DY, et al. New isophlebioid dragonflies (Odonata: Isophlebioptera: Campterophlebiidae) from the Middle Jurassic of China. Zootaxa 2006;1339:51–68.
[20] Riek EF. A new collection of insects from the Upper Triassic of South Africa. Annals of the National Museum 1976;22:791–820.
[21] Riek EF, Kukalová-Peck J. A new interpretation of dragonfly wing venation based upon early Carboniferoous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in Pterygote wings. Canadian Journal of Zoology 1984;62:1150–66.
[22] Kukalová-Peck J. The insects of Australia. A textbook for students and research workers. Melbourne: Melbourne University Press; 1991, p. 141–79.
[23] Nel A, Martínez-Delclos X, Paicheler JC, et al. Les "Anisozygoptera" fossiles Phylogénie et classification (Odonata) (in French). Martinia (Numéro hors-série) 1993;3:1–311.
[24] Bechly G. 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 (Boblingen) 1996;2(spec):1–402.
[25] Zhao XF. The Gomphid dragonflies of China (Odonata: Gomphidae) (in Chinese). 1st ed. Fuzhou: The Science and Technology Publishing House; 1990, p. 6–48.
[26] Ren D, Lu LW, Guo ZG. Faunae and Stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas (in Chinese). 2nd ed. Beijing: Seismic Publishing House; 1995, p. 64–73.
[27] Ren D, Guo ZG, Lu LW, et al. A further contribution to the knowledge of the Upper Jurassic Yixian Formation in Western Liaoning. Geological Review (in Chinese) 1997;43:449–59.
[28] Tan JJ, Ren D, Liu M. New ommatids from the Late Jurassic of Western Liaoning, China (Coleoptera: Archosternata). Insect Science 2005;12:207–16.
[29] Zhang BL, Ren D, Zhou CQ, et al. New genus and species of fossil dragonflies (Insecta: Odonata) from the Yixian Formation of Northeastern China. Acta Geologica Sinica 2006;80(3): 327–35.