

A new damsel-dragonfly of the small family Selenothemistidae from the Late Jurassic of China (Odonata, Isophlebioptera)

Diyang Huang,^{1*} Chenyang Cai,² and André Nel^{3*}

¹State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China (dyhuang@nigpas.ac.cn)

²CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China (cycai@nigpas.ac.cn)

³Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 – CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP 50, Entomologie F-75005, Paris, France (anel@mnhn.fr)

Abstract.—*Sinothemis difficilis* new genus new species, youngest and first accurate Chinese representative of the small family Selenothemistidae, is described and illustrated. It is closely related to the genus *Turanothemis*, known from the Karatau outcrop in Kazakhstan. The genus *Caraphlebia*, known from the Middle Jurassic of Antarctica, seems to strongly differ from the other representatives of this family and may belong to another family. The fossil was collected from the Upper Jurassic (157.3 ± 1.5 Ma; near Oxfordian/Kimmeridgian boundary) Guancaishan locality, Jianping County, Western Liaoning, NE China. It belongs to the late assemblage of the Yanliao biota, while the early assemblage is represented by the putatively close damsel-dragonfly *Paraliassophlebia* from the Jiulongshan Formation of northern Hebei Province.

UUID: <http://zoobank.org/8b11b148-852e-4079-a9fb-1884bf4b6d94>

Introduction

The large Mesozoic odonatan clade Isophlebioptera Bechly, 1996 comprises no less than 11 families (Bechly, 1996; Nel et al., 2009; see also Phylogenetic Systematics of Odonata, <https://bechly.lima-city.de/system.htm>), recorded between the Late Triassic and the Late Cretaceous. Some are very diverse (e.g., Campteropteroptera Handlirsch, 1920 and Isophlebiidae Handlirsch, 1920), while others are very poorly documented (e.g., the small family Paragonophlebiidae Nel, 2009; note that the genus *Mongolothemis* Pritykina and Vasilenko, 2014 is a junior synonym of *Paragonophlebia* Nel, 2009, as these authors ignored Nel's paper and erroneously attributed this fossil to the Euthemistidae Pritykina, 1968). Among these damsel-dragonflies, the small Jurassic family Selenothemistidae Handlirsch, 1939 comprises only three (or four) genera for a very wide distribution, as it is known from Western Europe, Antarctica, Kazakhstan, and maybe China, with the enigmatic taxon *Paraliassophlebia* Hong, 1982 (see Bechly, 1996; see also Phylogenetic Systematics of Odonata, <https://bechly.lima-city.de/system.htm>). Here we describe the first accurate Chinese representative of this family, which is closely related to the Oxfordian representative from Kazakhstan.

Geologic settings

The new damsel-dragonfly comes from the Guancaishan locality near the Muyingzi Village, Shaha Township, Jianping

County, Western Liaoning Province, NE China. The holotype was collected by one of us (C.C.) in 2013. The Guancaishan locality has yielded very rich fossils, including various insects, bivalves, plants, and especially abundant salamanders (Gao and Shubin, 2012; Wang et al., 2015). The fossil insect was preserved in a black shale layer with a rich associated fossil entomofauna. A volcanic ash layer located less than 1 meter above the black shale was dated as 157.3 ± 1.5 Ma (U-Pb SIMS), indicating that the insect lived in a period around the boundary of Oxfordian and Kimmeridgian (Huang, 2016) (Fig. 1).

The new fossil can be attributed to the Linglongta biota, which belongs to the late assemblage of the famous Yanliao biota, while the early assemblage is represented by the Daohugou biota (Huang, 2016). Huang (2015) suggested that the age of the Linglongta biota correlates with that of the Karatau biota. The studied fossil has been collected near the upper-most layer of the Linglongta beds at Guancaishan, indicating a possible slightly later age than that of Karatau, the latter being suggested as Oxfordian. Contrasting with the Daohugou biota represented by a very diverse and well-described entomofauna, the Linglongta biota (Tiaojiashan Formation) has yielded numerous fossil insects but only one species (Coleoptera, Ommatidae) has been formally described based on a well-preserved compression from Daxishan, Jianchang County, Liaoning Province (Cai and Huang, 2017). The new fossil damsel-dragonfly described here represents the first described fossil insect from the Guancaishan locality and the second fossil described from the Tiaojiashan Formation.

* Corresponding authors

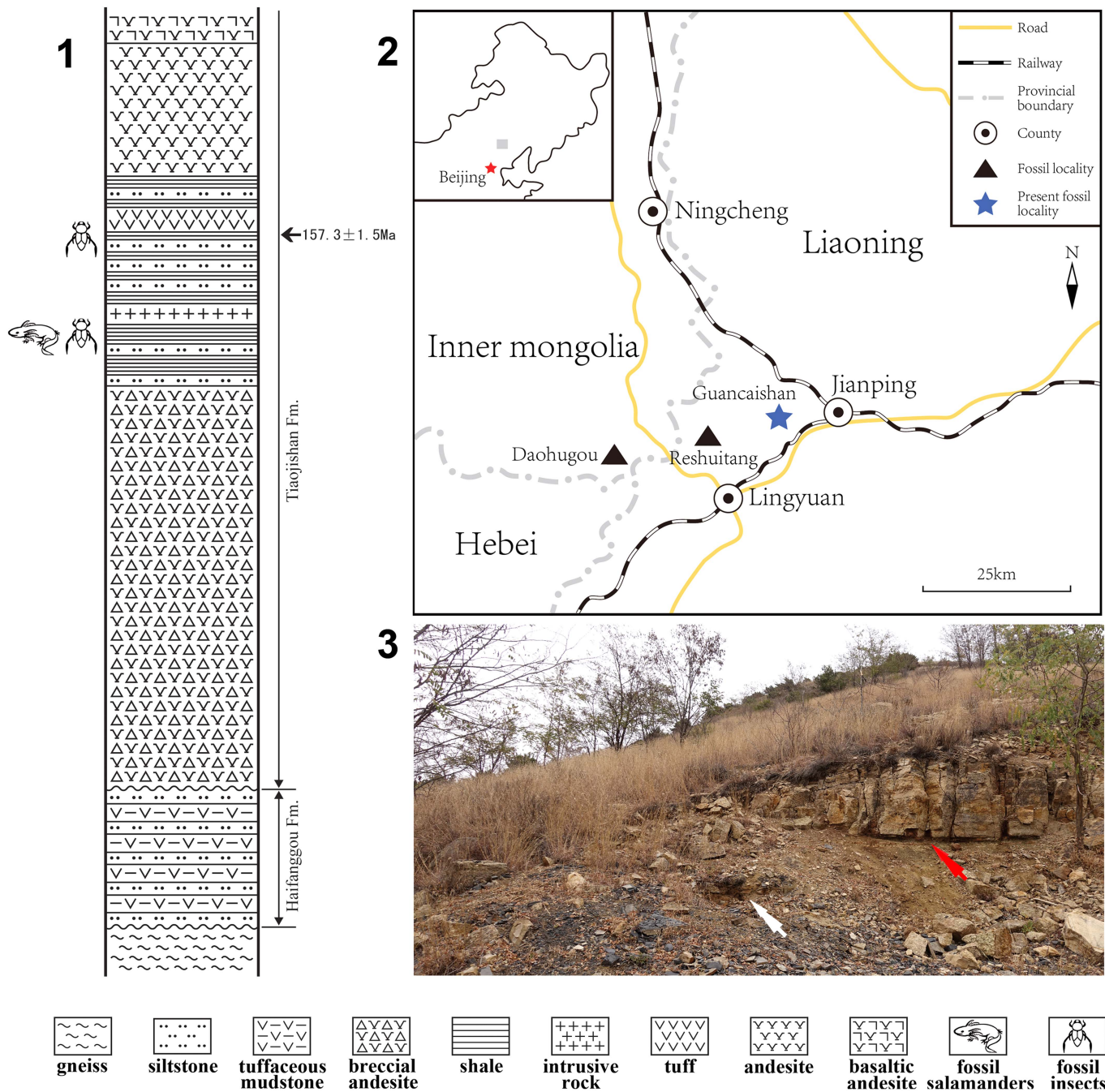


Figure 1. (1) Stratigraphic column for the Tiaojishan Formation at the Guancaishan locality, Jianping County, Liaoning Province, NE China. (2) Map showing the location of the Guancaishan locality. (3) Outcrop for fossil Odonata. White arrow indicates the black shale where the fossil was collected; red arrow indicates the volcanic ash layer slightly above the black shale (age 157.3 ± 1.5 Ma).

Materials and methods

The type specimen was prepared with a steel needle under microscope. The drawings were done using a drawing tube on a binocular microscope Nikon SMZ 1500. All images were made using a Canon 5D Mark III camera with a Canon MP-E 65 mm macro lens (F2.8, 1–5 ×); a Canon MT-24EX twin flash was used as the light source. Zerene Stacker Version 1.04 was used for image stacking. The specimen was examined with a LEO1530VP field emission scanning electron microscope (SEM), under 15.0 kV.

The nomenclature of the odonatan wing venation used in this paper is based on the interpretations of Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). The higher classification of fossil Odonatoptera, as well as family and generic characters followed in the present work, are based on the phylogenetic system proposed by Bechly (1996). Wing abbreviations are as follows: Arc = arculus; Ax = primary antenodal crossvein; C = costa; CuA = cubitus anterior; CuP = cubitus posterior; d = discoidal cell; IR = intercalary radial veins; MA = median anterior; MP = median posterior; N = nodus; 'O' = oblique vein; Pt = pterostigma; RA = radius

anterior; RP = radius posterior; sd = subdiscoidal space; Sn = subnodal crossvein. All measurements are given in millimeters.

Repositories and institutional abbreviations.—NIGP: Nanjing Institute of Geology and Palaeontology CAS, Nanjing, China.

Systematic paleontology

Superorder Odonatoptera Martynov, 1932
Order Odonata Fabricius, 1793
Clade Isophlebioptera Bechly, 1996
Family Selenothemistidae Handlirsch, 1939

Type genus.—*Selenothemis* Handlirsch, 1920. Other genera: *Turanothemis* Pritykina, 1968, *Sinothemis* new genus, *Caraphlebia* Carpenter, 1969, *Paraliassophlebia* Hong, 1982.

Genus *Sinothemis* new genus

Type species.—*Sinothemis difficilis* n. sp.

Etymology.—Named after *Sinica*, Latin name for China, and the suffix *Themis* (ancient Greek Titaness, personification of the divine order), frequently employed for taxa in this family. Gender masculine.

Remark.—*Sinothemis* shares some characters with *Selenothemis* and others with *Turanothemis*. Its exact affinities will need a phylogenetic analysis to be solved.

Sinothemis difficilis new species
Figures 2–4

Holotype.—NIGP167785, stored at the Nanjing Institute of Geology and Palaeontology CAS, Nanjing, China.

Diagnosis (for genus and species).—Hindwing characters only. Wing ~41 mm long; base of RP2 not aligned with subnodus; only one oblique vein 'O'; only one row of cells between RP3/4

and MAa well distal (five cells) of nodus level; only one row of cells between IR2 and RP3/4 well distal (three cells) of oblique vein.

Occurrence.—Guancaishan, Jianping County, Liaoning Province, NE China; late Oxfordian to early Kimmeridgian.

Description.—A thorax with nearly complete abdomen, fragments of legs, a nearly complete hindwing plus fragments of another attached.

Hindwing probably hyaline, 40.8 mm long, 10.0 mm wide at nodus; distance between base and arculus 5.4 mm, between arculus and nodus 11.7 mm, between nodus and pterostigma 15.0 mm, between pterostigma and apex 5.8 mm; wing very shortly petiolate; cells of anal area irregular, some being very small and others being very large, a large cell below CuP; median space free; submedian space with a curved vein CuP; a curved crossvein separating submedian and subdiscoidal spaces; subdiscoidal space posteriorly closed and very broad, with AA making a right angle in its basal part; discoidal cell free, basally closed, basal side 0.7 mm long, costal side 1.2 mm long, posterior side 1.5 mm long, distal side 2.0 mm long; RP

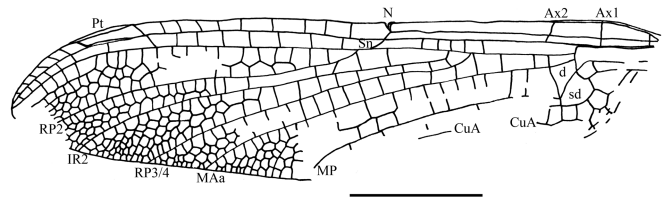


Figure 3. *Sinothemis difficilis* n. gen. n. sp., holotype NIGP167785, reconstruction of hindwing. Ax = primary antenodal crossvein; CuA = cubitus anterior; d = discoidal cell; IR = intercalary radial veins; MAa = median anterior; MP = median posterior; N = nodus; Pt = pterostigma; RP = radius posterior; sd = subdiscoidal space; Sn = subnodal crossvein. Scale bar = 8 mm.

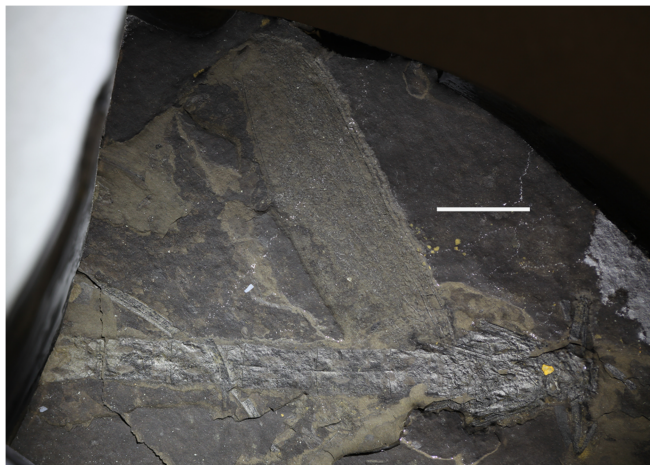


Figure 2. *Sinothemis difficilis* n. gen. n. sp., holotype NIGP167785, photograph of general habitus. Scale bar = 10 mm.

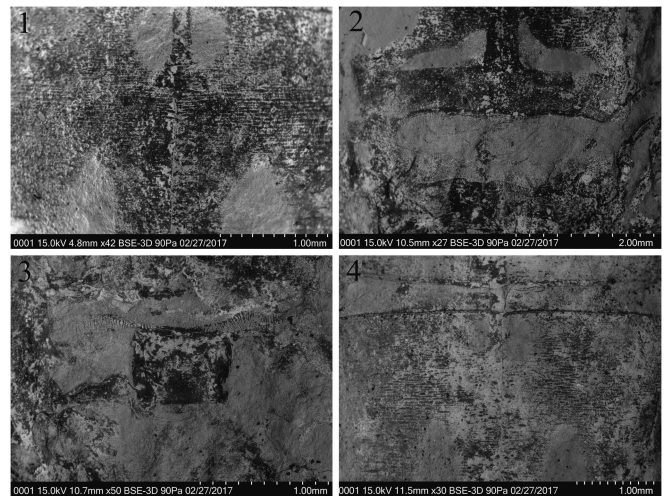


Figure 4. *Sinothemis difficilis* n. gen. n. sp., SEM scans showing the details on body surface (pattern and setae). (1) Detail of anterior part of third segment; (2) posterior part of first segment and anterior part of second; (3) detail of anterior part of first segment; (4) detail of anterior part of fifth segment.

and MA strongly separated at arculus; MAb more than twice as long as basal side of discoidal cell, MAb well aligned with distal free part of CuA; CuA divided into CuAa and CuAb; CuAb short, directed toward posterior wing margin and distally lost; only fragments of CuAa preserved, but CuAa and MP clearly parallel for a long distance, at least till below level of nodus, with probably one row of cells between; MP weakly curved, reaching posterior margin not far distal of nodus level, 24.0 mm from wing base; MAa nearly straight, more or less parallel to MP, with one row of cells in basal part of postdiscoidal area, 1.7 mm wide, this area being quite broader near posterior wing margin with 14 rows of small cells present; Ax0 visible, very near to wing base; two primary antenodal veins very strong, Ax1 1.5 mm basal of arculus and Ax2 1.7 mm distal of arculus, Ax1 nearly perpendicular to ScP and R + MA, Ax2 distinctly oblique; no secondary antenodal crossvein visible; five preserved antesubnodal crossveins between arculus and subnodus; base of RP3/4 6.5 mm distal of arculus, closer to nodus than to arculus; base of IR2 very close to that of RP3/4, 1.4 mm distally, originating distinctly from RP; nodal crossing and subnodus oblique; nine postnodal crossveins between C and RA not strictly aligned with the seven postsubnodal crossveins between RA and RP1; an oblique pterostigmal brace vein; only one crossvein below pterostigma; pterostigma not basally recessed, 4.3 mm long and strong, 0.9 mm wide; C and RA thickened along pterostigma; area between C and RA distal of pterostigma with six crossveins; RP2 not aligned with subnodus; two visible bridge crossveins; one oblique vein "O," and one cell 1.3 mm distal of base of RP2; RP2 nearly straight; area between RP1 and RP2 with two rows of cells basal of pterostigma; base of IR1 three cells distal of subnodus, IR1 strongly zigzagged; base of pseudo-IR1 below distal side of pterostigma; pseudo-IR1 short and straight; area between MAa and RP3/4 widened distally; area between RP3/4 and IR2 strongly widened distally; area between IR2 and RP2 distally widened, with six to seven rows of cells along posterior wing margin; area between RP2 and IR1 progressively widened, with four rows of cells along posterior wing margin; area between pseudo-IR1 and RP1 not distally widened.

Abdomen parallel-sided, stout, and rather smooth (no setae or spines appear), with apex not preserved, at least 41.0 mm long, 4.5 mm wide; transverse carina visible (sensu Asahina 1954); no secondary genital apparatus visible (female); complex pattern of coloration preserved (see Figs. 2, 4).

Thorax stout, about 14.0 mm long and 8.0 mm wide; dorsal, ventral, and internal parts are heavily compressed and difficult to interpret. Fragments of legs are visible but incomplete. Nevertheless, they look strong. Head absent.

Etymology.—Named *difficilis* for the very delicate preparation of the holotype, before study.

Remark.—The pattern of coloration of the abdomen of this taxon is simpler than those of many extant Odonata but similar to those of the Epiophlebiidae.

Discussion

This fossil belongs to the clade Isophlebioptera Bechly, 1996 for the hindwing subdiscoidal space strongly expanded with a bulged posterior margin. Furthermore, it has all the characters of the family Selenothemistidae Handlirsch, 1939: hindwing distal side (MAb) of discoidal cell about twice as long as basal side; unique shape of hindwing subdiscoidal cell, with AA making a right angle and with a broad cell below CuP in anal area; postdiscoidal space not narrowed and RP3/4 not parallel to IR2 (Bechly, 1996). This family currently comprises the three genera *Selenothemis* Handlirsch, 1920 (Toarcian, Germany), *Turanothemis* Pritykina, 1968 (Oxfordian, Karatau, Kazakhstan), and *Caraphlebia* Carpenter, 1969 (early Middle Jurassic of Antarctica, after Towrow, 1967; Shen, 1994), and possibly *Paraliassophlebia* Hong, 1982 (Jiulongshan Formation, Middle Jurassic, North Hebei Province, China).

Sinothemis n. gen. shares with *Selenothemis* the base of RP2 not aligned with subnodus, unlike in *Turanothemis*, but *Sinothemis* has only one oblique vein 'O' as in *Turanothemis*, instead of two as in *Selenothemis*. *Sinothemis* also shares with *Turanothemis* the presence of only one crossvein below the pterostigma, unlike *Selenothemis*. *Sinothemis* differs from both *Selenothemis* and *Turanothemis* in the presence of only one row of cells between RP3/4 and MAa well distal (five cells) of nodus level, instead of zero to two as in these two genera; *Sinothemis* has only one row of cells between IR2 and RP3/4 well distal (three cells) of oblique vein, instead of zero to one cell distal of 'O' as in *Selenothemis* and *Turanothemis* (Pritykina, 1968; Nel et al., 1993). The original description and figure of *Caraphlebia* were in great part reconstructed (Carpenter, 1969); Kelly and Nel (personal communication, 2018) revised this fossil that is rather poorly preserved. It strongly differs from *Sinothemis*, *Selenothemis*, and *Turanothemis* in having the bases of RP3/4 and IR2 very distant with four cells between them (an uncommon character in the Epiproctophora). Last, *Paraliassophlebia* could belong to the Selenothemistidae on the basis of the shape of the discoidal cell, but it differs from the other taxa in this family, including *Sinothemis*, in the subdiscoidal cell not greatly widened and AA not making a right angle, after Hong (1982).

Sinothemis seems to be more closely related to *Turanothemis* than to the other Selenothemistidae, supporting the similar ages of the two outcrops Karatau and Guancaishan. Both are the youngest representatives of the Selenothemistidae. It seems that this family became extinct during the latest Jurassic, while the closely related family Campteropteroptera was still present and diverse in the Chinese Early Cretaceous (Li et al., 2012). The clade Isophlebioptera did not survive the great change in the odonatan fauna during the Cenomanian (Nel et al., 2010).

Acknowledgments

We sincerely thank two anonymous referees for their useful comments on the first version of the paper. This work was supported by the Ministry of Science and Technology (2016YFC0600406), the Strategic Priority Research Program of

the Chinese Academy of Sciences (XDB18000000 and XDPB05), and the National Natural Science Foundation of China (41688103 and 91514302). This study is a contribution to UNESCO-IUGS IGCP Project 632.

References

- Asahina, S., 1954, A morphological study of a relict dragonfly *Epiophlebia superstes* Selys (Odonata, Anisozygoptera): The Japan Society for the Promotion of Science, Tokyo, v. 1954, p. 1–153.
- 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*, spec. v. 2, p. 1–402.
- Cai, C., and Huang, D.-Y., 2017, *Omma daxishanense* sp. nov., a fossil representative of an extant Australian endemic genus recorded from the Late Jurassic of China (Coleoptera, Ommatidae): *Alcheringa*, v. 41, p. 277–283.
- Carpenter, F.M., 1969, Fossil insects from Antarctica: *Psyche*, v. 76, p. 418–425.
- Fabricius, J.C., 1793, *Entomologia systematica emendata et aucta, secundum classes, ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*: C.G. Proft, Hafniae, v. 3, 1–488.
- Gao, K.-Q., and Shubin, N.-H., 2012, Late Jurassic salamandroid from western Liaoning, China: *Proceedings of the National Academy of Sciences*, v. 109, p. 5767–5772.
- Handlirsch, A., 1920, *Palaeontologie: Handbuch der Entomologie*, v. 3, p. 117–208.
- Handlirsch, A., 1939, Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, paläogeographische und allgemeine biologische Probleme. Teil 2: *Annalen des Naturhistorischen Museums in Wien*, v. 49, 1–240.
- Hong, Y.-C., 1982, Beijing zhongzhu Inoshi kunchong huashi [Middle Jurassic fossil insects in North China]: Beijing, Geological Publishing House, 223 p. [in Chinese with English summary].
- Huang, D.-Y., 2015, Yanliao Biota and Yanshan movement: *Acta Palaeontologica Sinica*, v. 54, p. 501–546. [in Chinese with English abstract].
- Huang, D.-Y., 2016, *The Daohugou Biota*: Shanghai, Shanghai Scientific and Technical Publishers, 332 p. [in Chinese].
- Li, Y., Nel, A., Ren, D., and Pang, H., 2012, A new damselfly dragonfly from the Lower Cretaceous of China enlightens the systematics of the Isophlebioidea (Odonata: Isophlebioptera: Campteropteroptera): *Cretaceous Research*, v. 34, p. 340–343.
- Martynov, A.V., 1932, New Permian Paleoptera with the discussion of some problems of their evolution: *Trudy Paleozoologicheskogo Instituta Akademii nauk SSSR, Moscow*, v. 1, p. 1–44. [in English with summary in Russian].
- Nel, A., 2009, A new Odonata family from the Jurassic of Central Asia: *Journal of Natural History*, v. 43, no. 1–2, p. 57–64.
- Nel, A., Martínez-Delclòs, X., Paicheler, J.-C., and Henrotay, M., 1993, Les ‘Anisozygoptera’ fossiles. Phylogénie et classification (Odonata): *Martinia Numéro Hors Série*, v. 3, p. 1–311.
- Nel, A., Bechly, G., Delclòs, X., and Huang, D.-Y., 2009, New and poorly known Mesozoic damselfly dragonflies (Odonata: Isophlebioidea: Campteropteroptera: Isophlebioptera): *Palaeodiversity*, v. 2, p. 209–232.
- Nel, A., Nel, P., Petrulevičius, J.F., Perrichot, V., Prokop, J., and Azar, D., 2010, The Wagner parsimony using morphological characters: A new method for palaeosynecological studies: *Annales de la Société Entomologique de France (N.S.)*, v. 46, p. 276–292.
- Riek, E.F., and Kukulová-Peck, J., 1984, A new interpretation of dragonfly wing venation based upon early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings: *Canadian Journal of Zoology*, v. 62, p. 1150–1166.
- Pritykina, L.N., 1968, Strekozy Karatau (Odonata) [Dragonflies from Karatau (Odonata)], in Panfilov, D.V., coord., *Yurskie Nasekomye Karatau* [Fossil Insects from Karatau]: Moscow, Academy of Sciences of the S.S.S.R., Nauka, p. 26–55. [in Russian].
- Pritykina, L.N., and Vasilenko, D.V., 2014, Odonata, in Ponomarenko, A.G., et al., eds., *Upper Jurassic Lagerstätte Shar Teg, Southwestern Mongolia*: *Paleontological Journal*, v. 48, p. 1641–1647.
- Shen, Y., 1994, Jurassic conchostracans from Carapace Nunatak, southern Victoria Land, Antarctica: *Antarctic Science*, v. 6, p. 105–113.
- Wang, Y., Dong, L.P., and Evans, S.E., 2015, Polydactyly and other limb abnormalities in the Jurassic salamander *Chunerpeton* from China: *Palaeobiodiversity and Palaeoenvironments*, v. 96, p. 49–59.
- Townrow, J.A., 1967, Fossil plants from Allan and Carapace Nunataks, and from the upper Mill and Shackleton Glaciers, Antarctica: *New Zealand Journal of Geology and Geophysics*, v. 10, p. 456–473.

Accepted 22 April 2018