A new genus of lance lacewings from the Middle Jurassic of Inner Mongolia, China

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Fossils of Osmylinae are rare, currently only one fossil genus of this subfamily is known, *Lithosmylus* which is recorded from the late Eocene Florissant Formation of USA. Herein, we report a new Osmylinae genus with two new species, *Vetosmylus tentus* gen. et sp. nov. and *Vetosmylus maculosus* gen. et sp. nov. from the Middle Jurassic Jiulongshan Formation of Daohugou Village, Inner Mongolia, China, The new genus shares many apomorphic characters with extant osmyline relatives, e.g., forked subcostal veinlets in forewing; dense cross-veins present in radial sector, usually forming one complete outer gradate series in forewing; the region between MA and MP significantly broadened in hind wing, but with only one row of cells, implying a likely morphological stasis during the evolution of Osmylinae. The new genus *Vetosmylus*, the first and earliest record hitherto of Osmylinae from the Mesozoic, enhances our understanding of the early stages of their evolution.

Key words: Insecta, Neuroptera, Osmylidae, Osmylinae, Mesozoic, Asia, China.

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Introduction

Lance lacewings (Neuroptera: Osmylidae) are an early branching family of the order, with a rich fossil record, and today comprise ca. 225 extant species in eight subfamilies that are widely distributed in all major biogeographial regions except for the Nearctic Region (Winterton et al. 2019). Among the extant Osmylidae, the subfamily Osmylinae is a typical northern temperate group that is restricted to the Palearctic, but extends into the Oriental Region (Needham 1909; Navás 1930; Makarkin 1985; Yang 1987, 1988, 1999; Xu et al. 2016). Currently, compared with other subfamilies, the Osmylinae fossils are scarce, with a single fossil genus recognized, Lithosmylus Carpenter, 1943, which is recorded from the late Eocene Florissant Formation (Cockerell 1908; Carpenter 1943). According to the phylogenetic results of Winterton et al. (2017), Osmylinae is sister to a larger clade of four extant subfamilies, Kempyninae, Eidoporisminae, Porisminae, and Stenosmylinae. Osmylinae appear to exhibit intermediate characteristic between these subfamilies as one clade and another clade comprising the remaining extant subfamilies Spilosmylinae, Gumillinae, and Protosmylinae (Winterton et al. 2017, 2019).

The Daohugou locality is well-known for the diverse Mesozoic insect fossils (Wang et al. 2010b, 2012; Gao et al. 2012; Gu et al. 2012; Ren et al. 2019), and has yielded nine genera and 15 species of Osmylidae from three subfamilies (i.e., Gumillinae, Protosmylinae, and Kempyninae) (Ren and Yin 2002; Ren and Engel 2007; Wang et al. 2009, 2010a, 2011; Yang et al. 2010; Khramov et al. 2019; Li et al. 2018; Ren et al. 2019). It is noteworthy that kempynine fossils are particularly diverse in the Daohugou locality, including five species in three genera (Wang et al. 2011; Khramov et al. 2019). Considering the phylogenetic status of Kempyninae and Osmylinae, and distributions of extant Osmylinae, the absence of fossil Osmylinae in the Palearctic Region is probably artificial. Herein, we describe the first osmylines from the Daohugou locality, representing a new genus with two new species that represent the earliest record of this subfamily.

Institutional abbreviations.—CNU, Capital Normal University, Beijing, China.

Other abbreviations.—A, anal veins; C, costa; CuA/P, anterior/posterior cubitus; MA/P, anterior/posterior branch of media; RA/P, anterior/posterior branch of radius; Sc, subcosta. The terminology for wing venation and genitalia follows Breitkreuz et al. (2017) and Winterton et al. (2019).

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:9ECE74E9-B719-42ED-BB51-9C27065A91EE

Material and methods

The new material was collected from the Middle Jurassic Jiulongshan Formation at Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. The specimens were observed and photographed with a stereoscopic microscope Nikon SMZ18, and line drawings were produced using Adobe Photoshop CC and Adobe Illustrator CC software. All type specimens of this study are deposited in the Key Laboratory of Insect Evolution and Environmental Changes at the Capital Normal University, Beijing.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Family Osmylidae Leach, 1815

Subfamily Osmylinae Leach, 1815

Genus Vetosmylus nov.

Zoobank LSID: urn:lsid:zoobank.org:act:EA3D9D9B-917C-4877-A 484-1CF2FC28749D

Type species: Vetosmylus tentus sp. nov.; see below.

Species included: Vetosmylus tentus sp. nov. and *Vetosmylus maculosus* sp. nov.

Etymology: From Latin *vetus*, archaic and *osmylus*, the common generic suffix of Osmylidae; referring to the earliest of Osmylinae. Gender is masculine.

Diagnosis.—Wings oval and elongate; forewing with irregular fragmentized spots and the hind wing more hyaline. Forewing: cross-veins in RP radial sector irregularly arranged except for the outer gradate series of cross-veins (sometimes partly present); the bifurcation of M beyond origin of RP1; CuA with distinctly multiple dichotomies in distal; A1 relatively long, clearly beyond the half length of CuP; A2 closed to half length of A1, A1 and A2 with numerous oblique pectinate branches; A3 complete and terminating at the margin. Hing wing: CuA with many pectinate

branches in distal; CuP obviously shorter than CuA, about two-thirds of it, and the pectinate branches occurring near the middle of CuP; A1 long, exceeded half length of CuP.

Remarks.—Unequivocally this new genus is closely related to Kempyninae and Osmylinae due to the presence of the forked subcostal veinlets in both wings (other osmylid subfamilies commonly have the simple subcostal veinlets), as well as the elongate and pectinately branched hind wing CuP (cf. Spilosmylinae, Protosmylinae, and Gumillinae) (Winterton et al. 2019). Kempyninae and Osmylinae overlap significantly in all characteristics of the wings, especially in Kempyninae where there are exceptions in various genera which do not display the diagnostic feature for the subfamily. A feature often cited as being diagnostic for Kempyninae is the presence of an expanded area between MA and MP, which is often subdivided into multiple rows of irregular cells with sinuous crossveins (Wang et al. 2011; Khramov 2014; Winterton et al. 2017, 2019; Khramov et al. 2019). Osmylinae typically have the expanded area between MA and MP, but it contains only a single row of cells and the crossveins are not sinuous. Kempynines typically also have the distal branches of RP being rather sinuous while they are only broadly curved in Osmylinae. The exceptions to this rule in Kempyninae are Australysmus Kimmins, 1940, Euosmylus Krüger, 1913, which display the typical Osmylinae states for each character. Unfortunately, to conclusively discriminate between Osmylinae and Kempyninae examination of the male and/or female genitalia is required, and most fossils comprise only wing venation characters. There are several examples of fossil genera being transfered between Kempyninae and Osmylinae based on differing subjective interpretations of the wings, especially where the venation is incomplete. While the female terminalia of Vetosmylus maculosus sp. nov. is preserved in this fossil, the important discrimination features (i.e., the shape and position of sternite 8 and gonopophysis 9) are still obscured. Based on the observable features at hand, we believe that Vetosmylus gen. nov. should be excluded from Kempyninae due to its single row of cells between MA and MP in both fore- and hind wings. Kempyninae typically have more than one row of cells between MA and MP. Therefore, the new genus can be attributed to Osmylinae as the earliest record of this subfamily.

Comparing with the known osmyline genera of *Osmylus* Latreille, 1802, and *Sinosmylus* Yang, 1992, *Vetosmylus* gen. nov. is distinctly different for the absence of inner gradate series in forewing, as these genera have at least two complete gradate series (Wang and Liu 2009). The new genus can also be distinguished from the other extant genus *Parosmylus* Needham, 1909 due to the relatively long A1 that exceeds half the length of CuP (cf. A1 is commonly about half the length of CuP in osmyline genera). It is noteworthy that the new genus shows the high similarity with the only fossil osmyline genus *Lithosmylus* (~34 Mya, Eocene), and in fact only several species-level differences between them can be detected, i.e., the relatively long A2 with about

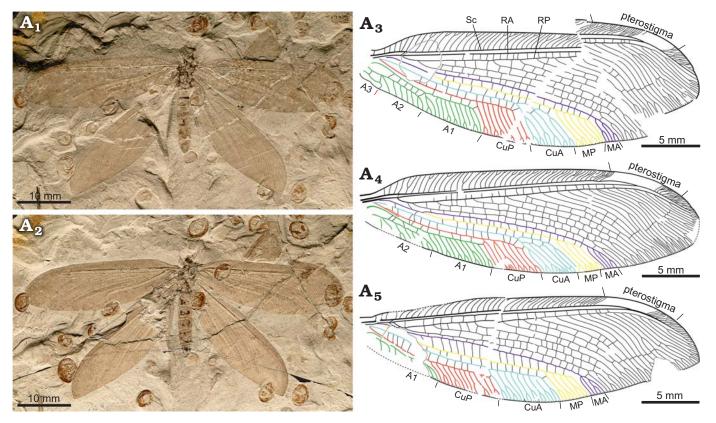


Fig. 1. Lance lacewing *Vetosmylus tentus* gen. et sp. nov. (holotype, CNU–NEU–NN2019001P/C) from Aalenian–Bajocian boundary (Middle Jurassic) of Jiulongshan Formation of Daohugou, China. Photographs of part (A_1) and counterpart (A_2). Line drawings of left forewing (A_3), right forewing (A_4), left hind wing (A_5). Abbreviations: A, anal veins; CuA/P, anterior/posterior cubitus; MA/P, anterior/posterior branch of media; RA/P, anterior/posterior branch of radius; Sc, subcosta.

half of CuP length in the new genus (cf. shorter than half of CuP in *Lithosmylus*, especially in hind wing) and A3 ending at the margin in the new insect (cf. A3 relict and partly coalescent with the proximal branch of A2 in *Lithosmylus*). Considering the huge gap of occurrence times of the fossil genera (~130 Mya), we feel it is appropriate to erect a new genus for the new Middle Jurassic insects, instead of assigning them to the much younger *Lithosmylus*.

Stratigraphic and geographic range.—Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Vetosmylus tentus sp. nov.

Fig. 1.

Zoobank LSID: urn:lsid:zoobank.org:act:30620AD1-7A74-4989-8F8A-81660E7449A5

Etymology: From Latin *tentus*, outstretched; refers to the spreaded four wings of the new species.

Holotype: CNU-NEU-NN2019001P/C, a completely preserved male specimen with fully spreaded wings and visible structures (Fig. 1A₁, A₂). *Type locality*: Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type horizon: Jiulongshan Formation, Aalenian–Bajocian boundary, Middle Jurassic.

Diagnosis.—Forewing with many scattered fuscous spots; CuP about three-fourths of CuA, forming neatly arranged pectinate branches; anal region well-developed, 2–3 crossveins between A2 and A3; A3 single; hind wing speckless; cross-veins in radial sector arranged irregularly, only the outer gradate series present; A1 well-developed, parallel with posterior margin, pectinately branched.

Description.—Head laterally compressed and deformed; antenna filiform and incompletely preserved; presence of thorax and abdomen well-developed; four wings spreaded. Forewing about 28.18 mm long as preserved, 9.53 mm wide. Hind wing about 28.36 mm long as preserved, 8.59 mm wide.

Forewing (Fig. 1A₃, A₄): Elongate with rather rounded apex; nygmata undetected; pterostigma fuscous; trichosors well-defined along the entire margin; subcostal veinlets forked distally, becoming denser towards trichosors; cross-vein sc-ra single and oblique; cross-veins ra-rp numerous, forming many square cells; RP with more than 15 branches, each broadly curved toward margin, with complicated distal forks; M forked close to the wing base, MA and MP forming several simple branches distally; CuA forked near the middle of the wing; CuP with 7–9 pectinate branches; A1 long, with 8–10 pectinate branches; A2 with 7 distal pectinate branches.

Hind wing (Fig. 1E): Without any large fuscous spots; trichosors well-developed along the entire margin; subcostal veinlets simple, with few forks; sc-ra single; presence of sigmoid vein joined the base of RP; the region between MA and MP expanded obviously, with one row of cells; MA

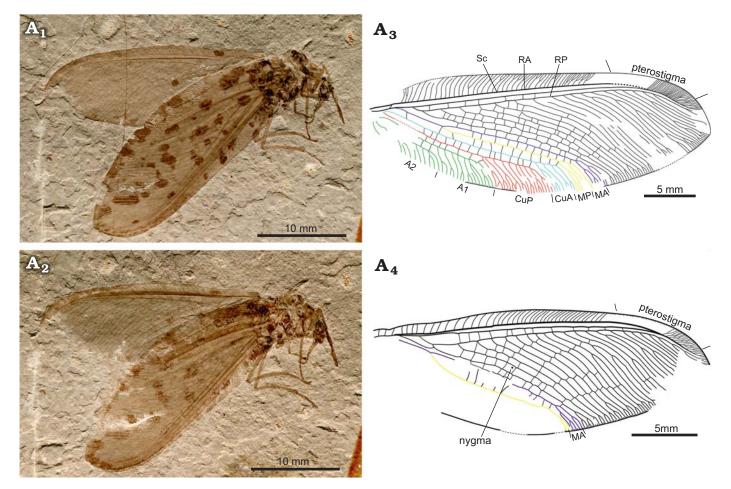


Fig. 2. Lance lacewing *Vetosmylus maculosus* gen. et sp. nov. (holotype, CNU–NEU–NN2019002P/C) from Aalenian–Bajocian boundary (Middle Jurassic) of Jiulongshan Formation of Daohugou, China. Photographs of part (A₁) and counterpart (A₂). Line drawings of forewing (A₃), hind wing (A₄). Abbreviations: A, anal veins; CuA/P, anterior/posterior cubitus; MA/P, anterior/posterior branch of media; RA/P, anterior/posterior branch of radius; Sc, subcosta.

forming simple distal branches; MP with 4–5 distal pectinate branches; CuA long, forming 9 pectinate branches; CuP with 10 pectinate branches; A2 and A3 poorly preserved.

Remarks.—Vetosmylus tentus is separated from the other species by the following characters: forewing with many fragmentary fuscous spots, and the hind wing immaculate rather than distributed with large spots; the outer gradate series present in forewing; MP forming several pectinate distal branches instead of simple branches in forewing.

Stratigraphic and geographic range.—Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Vetosmylus maculosus sp. nov.

Figs. 2, 3.

Zoobank LSID: urn:lsid:zoobank.org:act: 0AF432C0-B8AB-4663-BC 27-8B1A1B686044

Etymology: From Latin *maculosus*, spotted; refers to many brown round spots on forewings of the new species.

Type material: Holotype: CNU-NEU-NN2019002P/C, a completely preserved specimen with three wings overlapped, one hind wing spreaded with visible structures (Figs. 2A₁, A₂). Paratype: CNU-NEU-

NN2019003P/C, a completely preserved specimen with clear structure of genitalia (Figs. $3A_1, A_2$) from the type locality and horizon.

Type locality: Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type horizon: Jiulongshan Formation, Aalenian/Bajocian boundary, Middle Jurassic.

Diagnosis.—Forewing with many brown round spots; RP branches numerous, more than 18; hind wing with numerous radial cross-veins, arranged regularly and forming 3–4 rows of gradate cross-veins; radial region with slender cells.

Description.—Compound eyes large and round; antennae linear, clearly segmented. Forewing about 27.88 mm long as preserved, 9.80 mm wide. Hind wing about 24.63 mm long as preserved, 9.18 mm wide (Fig. 2).

Forewing (Fig. 2A₃): Pterostigma fuscous; trichosors well-developed along the entire margin; subcostal veinlets forked distally; areas between Sc and RA, RA and RP equally spaced; cross-veins sc-ra single and close to the wing base; cross-veins in radial sector arranged irregularly, the outer gradate series residually present (putatively due to the poor preservation); MA and MP forming some

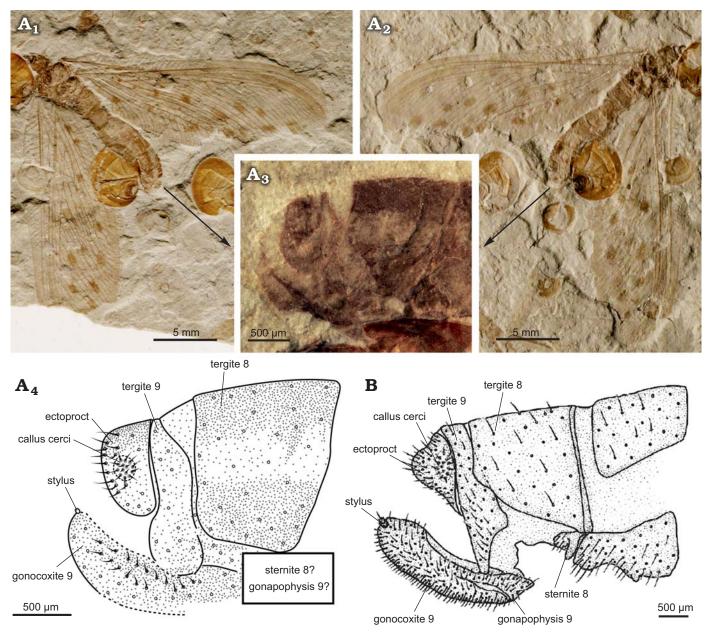


Fig. 3. Female lance lacewing *Vetosmylus maculosus* gen. et sp. nov. (paratype, CNU–NEU–NN2019003P/C) from Aalenian–Bajocian boundary (Middle Jurassic) of Jiulongshan Formation of Daohugou, China (**A**) and extant *Parosmylus tibetanus* Yang, 1988 (**B**). **A**. Photographs of part part (A₁) and counterpart (A₂); terminalia in lateral view, a combination of photos of part and counterpart under dry condition (A₃) and line drawing (A₄), sternite 8 and gonapophysis 9 cannot be clearly observed. **B**. Line drawing of terminalia in lateral view.

simple pectinate branches in distal; CuP shorter than CuA, pectinately branched approximately at middle of the wing, with 10 pectinate branches; A1 and A2 well-developed; A1 with 8 pectinate branches; A2 with at least 6 branches; A3 incompletely preserved.

Hind wing (Fig. 2A₄): Only with several sporadic fuscous spots; only a middle nygma distinct; subcostal veinlets simple; presence of a longer curved vein fused with RP1; M forked close to the separation of RP1 from RA; the region between MA and MP dilated visibly, only a single row of cells present.

Female genitalia (Fig. 2A₃, A₄): Tergite 8 large, approximately quadrate; tergite 9 narrow, gonocoxite 9 stout and

knife-shaped, slightly bent at the middle; gonostylus 9 short and attached to gonocoxite 9 distad; ectoproct large, callus cerci round.

Remarks.—*V. maculosus* can be easily distinguished from *V. tentus* by the presence of the numerous fuscous spots in forewing. Besides, the cross-veins in the radial sector of the two species are distinctly different, i.e., presence of multiple gradate series in *V. maculosus* vs absence of gradate series in *V. tentus*.

Stratigraphic and geographic range.—Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Discussion

The venation of Vetosmylus gen. nov. is very similar to the extant osmylines, especially in having cross-veins forked distally in forewing and the expansion of the region between MA and MP displaying a single row of cells in hind wing. Among the Osmylinae, Vetosmylus gen. nov. shows similarities to Parosmylus due to the absence of the inner gradate series of cross-veins. The generic status of *Parosmylus* had been questioned by some authors (e.g., Banks 1913 and Nakahara 1914). Wang and Liu (2009) proposed two apomorphic characters of Parosmylus to distinguish it from other genera, i.e., presence of a single gradate series of cross-veins (or absence) and boat-like gonocoxite 9 of female genitalia (Fig. 3A). Remarkably, the well-preserved female genitalia of Vetosmylus maculosus sp. nov. (paratype, CNU-NEU-NN2019003) (Fig. 3A₃, A₄) show high similarities with those of the extant Parosmylus (Fig. 3B), and both genera are characterized by a pair of distinctly boat-like gonocoxite 9, which is very different from other finger-like gonocoxite 9 in other osmyline genera (Martins et al. 2016).

Conclusions

The fossil Osmylinae are particularly rare; only one unambiguously fossil genus was found from the late Eocene Florissant Formation. Herein we described a new genus with two new species of Osmylinae from the Middle Jurassic of China, representing the first and oldest osmylines from the Mesozoic. The new genus shares many apomorphic characters with the extant representatives of Osmylinae, which corroborates its osmyline affinity. The occurrence of the new osmylines from the Mesozoic implies a much longer and intricate evolutionary history of the group.

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References

- Banks, N. 1913. Synopses and descriptions of exotic Neuroptera. *Transactions of the American Entomological Society* 39: 201–242.
- Breitkreuz, L.C.V., Winterton, S.L., and Engel, M.S. 2017. Wing tracheation in Chrysopidae and other Neuropterida (Insecta): a resolution of the confusion about vein fusion. *American Museum Novitates* 3890: 1–44.
- Carpenter, F.M. 1943. Osmylidae of the Florissant shales, Colorado (Insecta-Neuroptera). American Journal of Science 241: 753–760.
- Cockerell, T.D.A. 1908. Fossil Osmylidae (Neuroptera) in America. Canadian Entomologist 40: 341–342.
- Gao, T., Shih, C.K., Xu, X., Wang, S., and Ren, D. 2012. Mid-Mesozoic flea-like ectoparasites of feathered or haired vertebrates. *Current Biology* 22: 732–735.
- Gu, J., Montealegre, Z.F., Robert, D., Engel, M.S., Qiao, G., and Ren, D. 2012. Wing stridulation in a Jurassic katydid (Insecta, Orthoptera) produced low-pitched musical calls to attract females. *Proceedings of the National Academy of Sciences of USA* 109: 3868–3873.
- Khramov, A.V. 2014. Lacewings of the family Osmylidae (Insecta: Neuroptera) from the Upper Jurassic of Asia. *Paleontological Journal* 48: 300–309.
- Khramov, A.V., Liu, Q., and Zhang, H. 2019. Mesozoic diversity of relict subfamily Kempyninae (Neuroptera: Osmylidae). *Historical Biology* 31: 938–946.
- Li, Q., Ren, D., and Wang, Y. 2018. Revision of the gumilline genus *Nilionympha* with a new species from the Middle Jurassic of China (Neuroptera: Osmylidae). *Zootaxa* 4399: 146–150.
- Makarkin, V.N. 1985. Review of the family Osmylidae (Neuroptera) of the fauna of the USSR. *In*: P.A. Lehr and Y.S. Storozhenko (eds.), *Taxonomy and Ecology of Arthropods from the Far East*, 35–47. Far Eastern Scientific Centre, Vladivostok.
- Martins, C.C., Ardila-Camacho, A., and Aspöck, U. 2016. Neotropical osmylids (Neuroptera, Osmylidae): Three new species of *Isostenosmylus* Krüger, 1913, new distributional records, redescriptions, checklist and key for the Neotropical species. *Zootaxa* 4149: 1–66.
- Nakahara, W. 1914. On the Osmylinae of Japan. Annotationes Zoologicae Japonenses 8: 489–518.
- Navás, L. 1930. Insectos del museo de París. 5.a série. Brotéria (Zoológica) 26: 5–24.
- Needham, J.G. 1909. Notes on the Neuroptera in the collection of the Indian Museum. *Records of the Indian Museum*, *Calcutta* 3: 185–210.
- Ren, D. and Engel, M.S. 2007. A split-footed lacewing and two epiosmylines from the Jurassic of China (Neuroptera). *Annales Zoologici* 57: 211–219.
- Ren, D. and Yin, J. 2002. A new Middle Jurassic species of *Epiosmylus* from Inner Mongolia, China (Neuroptera: Osmylidae). Acta Zootaxonomica Sinica 27: 274–277.
- Ren, D., Shih, C.K., Gao, T., Wang, Y., and Yao, Y. 2019. *Rhythms of Insect Evolution—Evidence from the Jurassic and Cretaceous in Northern China*. 710 pp. Wiley Blackwell, New York.
- Wang, Y. and Liu, Z. 2009. Two new species of *Parosmylus* Needham (Neuroptera, Osmylidae) from China, with a key to Chinese species. *Zootaxa* 1985: 57–62.
- Wang, Y., Labandeira, C.C., Shih, C.K., Ding, Q.L., Wang, C., Zhao, Y.Y., and Ren, D. 2012. Jurassic mimicry between a hangingfly and a ginkgo from China. *Proceedings of the National Academy of Sciences USA* 109: 20514–20519.
- Wang, Y., Liu, Z., and Ren, D. 2009. A new fossil lacewing genus and species from the Middle Jurassic of Inner Mongolia, China. Acta Palaeontologica Polonica 54: 557–560.
- Wang, Y., Liu, Z., Ren, D., and Shih, C. 2010a. A new genus of Protosmylinae from the Middle Jurassic of China (Neuroptera: Osmylidae). *Zootaxa* 2480: 45–53.
- Wang, Y., Liu, Z., Ren, D., and Shih, C. 2011. New Middle Jurassic kempynin osmylid lacewings from China. Acta Palaeontologica Polonica 56: 865–869.

- Wang, Y., Liu, Z.Q., Wang, X., Shih, C.K., Zhao, Y.Y., Engel, M.S., and Ren, D. 2010b. Ancient pinnate leaf mimesis among lacewings. *Proceedings of the National Academy of Sciences of the United States of America* 107: 16212–16215.
- Winterton, S.L., Martins, C.C., Makarkin, V., Ardila-Camacho, A., and Wang, Y. 2019. Lance lacewings of the world (Neuroptera: Archeosmylidae, Osmylidae & Saucrosmylidae): a review of living and fossil genera. *Zootaxa* 4581: 1–99.
- Winterton, S.L., Zhao, J., Garzón-Orduña, I., Wang, Y., and Liu, Z. 2017. Phylogeny of lance lacewings (Neuroptera: Osmylidae). Systematic Entomology 42: 555–574.
- Xu, H., Wang, Y., and Liu, Z. 2016. Three new species of *Osmylus* Latreille from China (Neuroptera, Osmylidae). *Zookeys* 589: 107–121.
- Yang, C. 1987. Neuroptera. In: S. Zhang (ed.), Agricultural Insects, Spiders, Plant Diseases and Weeds of Xizang. Vol. 1, 191–220. Xizang Renmin Press House, Xizang.
- Yang, C. 1988. Neuroptera: Osmylidae, Dilaridae, Hemerobiidae, Chrysopidae, Mantispidae, Myrmeleontidae, Ascalaphidae, Corydalidae. *In:* F.S. Huang (ed.), *Insects of Mt. Namjagbarwa Region of Xizang*, 193–216. Science Press, Beijing.
- Yang, C. 1999. Osmylidae. In: B. Huang (ed.), Fauna of Insects in Fujian Province of China. Vol. 3, 96–98. Fujian Science & Technology Publishing House, Fuzhou.
- Yang, Q., Makarkin, V.N., and Ren, D. 2010. Remarkable new genus of Gumillinae (Neuroptera: Osmylidae) from the Jurassic of China. Annals of Entomological Society of America 103: 855–859.