HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2021.1998035

The first mimarachnid planthopper (Hemiptera: Fulgoromorpha: Mimarachnidae: *Saltissus*) from the Wealden (Lower Cretaceous) of southern England

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ABSTRACT
The second species of *Saltissus*, as the first mimarachnid planthopper, is herein described from the upper Weald Clay Formation, Smokejacks brickworks, England. *Saltissus fennahi* Luo, Liu et Jarzembowski sp. nov. can be distinguished from the type species *Saltissus eskovi* Shcherbakov, 2007 due to the tegmen being more than 20 mm long, stem Pc+CP merged with margin at less than 1/10th of tegmen length, stem ScP+R forked beyond the fusion of Pcu+A_1, and branch A_1 curved strongly at base. The distribution and tegminal colour pattern of Mimarachnidae are briefly discussed.

ARTICLE HISTORY
Received 13 October 2021
Accepted 19 October 2021

KEYWORDS
Planthopper; Mimarachnidae; new species; Mesozoic; Palaeogeography

Introduction

The Order Hemiptera is the most diverse group among hemimetabolous insects and is one of the Big Five insect orders, after Coleoptera, Diptera, Hymenoptera and Lepidoptera, inhabiting all terrestrial and some marine habitats (Szwedo 2018). Planthoppers (Fulgoromorpha) comprise one of six hemipteran suborders divided into three superfamilies: Permian Coleoscytoidea Martynov, 1935, Permian and Triassic Surijokocixioidea Shcherbakov, 2000 and Fulgoroidea Latreille, 1807 with earliest fossils recorded in the Triassic (Szwedo 2018; Zhang et al. 2021). At present, the superfamily Fulgoroidea includes 13 extinct families and 21 extant ones (Bourgoin 2021). The extinct families include one Triassic family: Szeiiniidae Zhang, Jiang, Szwedo et Zhang, 2021 in Zhang et al. (2021); two Jurassic families: Fulgoridiidae Handlirsch, 1939 and Qiyangiricaniidae Szwedo, Wang et Zhang, 2011 in Szwedo et al. (2011); nine Cretaceous families: Dorytocidae Emeljanov et Shcherbakov, 2018 in Emeljanov and Shcherbakov (2018), Inoderbidae Shcherbakov et Emeljanov, 2021 in Shcherbakov and Emeljanov (2021), Jubisentidae Zhang, Ren et Yao, 2019 in Zhang et al. (2019), Katlasidae Luo, Jiang et Szwedo, 2020 in Luo et al. (2020a), Lalacidae Hamilton, 1990, Mimarachnidae Shcherbakov, 2007 in Shcherbakov (2007b), Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007 in Shcherbakov (2007a) and Yetkhatidae Song, Szwedo et Bourgoin, 2019 in Song et al. (2019); and one Eocene family Weiwoboidae Lin, Szwedo, Huang et Stroinski, 2010 in Lin et al. (2010).

Mimarachnidae Shcherbakov, 2007, is a small family placed in the group of ‘cixiid-like’ planthoppers (Bourgoin and Szwedo 2008; Szwedo and Ansorge 2015). It was first established based on two genera from the Zaza Formation, Baissa, Russia (145–125 Ma) (Shcherbakov 2007b), then a species from the Kuwajima Formation in Japan (129–121 Ma) (Fujiyama 1978) was transferred from Fulgoridae to Mimarachnidae, and attributed to a new genus in Szwedo (2008). Several years later, two new genera were discovered in the La Pedrera de Rubies Formation, Spain (130.0–125.5 Ma) (Szwedo and Ansorge 2015). Since 2015, eight genera and 15 species have been described from mid-Cretaceous Kachin amber (Shcherbakov 2017; Jiang et al. 2018, 2019, 2020; Zhang et al. 2018, 2021a, 2021b; Fu et al. 2019; Fu and Huang 2020, 2021; Luo et al. 2020b). At present, the family includes 13 genera and 20 species with some undescribed specimens assigned to this family reported from the Early Cretaceous (earliest Cretaceous of Turga, Chita Region; Aptian of Bon-Tsagan, Mongolia; Albian of Khetana, Khabarovsk Region) and the Late Cretaceous (Turonian of Kzyl-Zhar, Kazakhstan) (Shcherbakov 2007b) (Table 1).

Herein, we describe a new species of Mimarachnidae, tentatively attributed to *Saltissus* Shcherbakov, 2007, based on the fossil tegmen, from Smokejacks brickworks in southern England.

Material and methods

The studied specimen was discovered in the upper Weald Clay Formation at Smokejacks brickworks (NW section), near Ockley, Surrey, England (National Grid Reference TQ 112374) (see Figure 1 in Liao et al. 2017). The Weald Clay is generally interpreted as representing a variable, low-lying, muddy wetland under a Mediterranean-like climate and with hill country lying north of the quarry towards London (Allen et al. 1998). The fossil preserved in a sideritic concretion probably from the upper insect bed in the mudstone interval below British Geological Survey Bed 5 c, which is present at the top of this pit and suggests an early Barremian age for this site (Ross and Cook 1995). The insect orders recorded from Smokejacks are Ephemeroptera, Odonata, Blattodea, Isoptera, Orthoptera, Phasmatodea, Hemiptera, Coleoptera, Diptera, Hymenoptera, Mecoptera, Neuroptera, Trichoptera and Dermaptera (Ross and Cook 1995; Novokshonov et al. 2016; Austen and Batten 2018; Jarzembowski and Wang 2019; Xu et al. 2020).

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Published online 03 Nov 2021

Table 1. Fossil record of Mimarachnidae Shcherbakov, 2007.

Genus	Species	Geological formation/Locality	Period/Series/Stage/Age	References
Mimarachne Shcherbakov, 2007	*Mimarachne mikhailovi* Shcherbakov, 2007	Zaza Formation, Baissa, Buryatia, Russian	Berriasian/Barremian, Early Cretaceous, 145–125 Ma	Shcherbakov 2007b
Saltissus Shcherbakov, 2007	*Saltissus eskovi* Shcherbakov, 2007	Zaza Formation, Baissa, Buryatia, Russian	Berriasian/Barremian, Early Cretaceous, 145–125 Ma	Shcherbakov 2007b
	Saltissus fennahi Luo, Liu et Jarzembowski, 2021	Upper Weald Clay Formation, Smokejacks brickworks, England	Early Barremian, Early Cretaceous, ca. 128 Ma	This paper
Nipponoridium Szwedo 2008	*Nipponoridium matusuoi* Fujiyama 1978	Kuwajima Formation, Kaseki-kabe, Japan	Barremian/Aptian, Early Cretaceous, 129–121 Ma	Fujiyama 1978; Szwedo 2008
Mimamontsecia Szwedo et Ansorge, 2015	*Mimamontsecia cretacea* Szwedo et Ansorge, 2015	La Pedrera de Rubies Formation, La Cabrúa outcrop, Spain	Early Barremian, Early Cretaceous, 130.0–125.5 Ma	Szwedo and Ansorge 2015
Chalicoridulum Szwedo et Ansorge, 2015	*Chalicoridulum montsecensis* Szwedo et Ansorge, 2015	La Pedrera de Rubies Formation, La Cabrúa outcrop, Spain	Early Barremian, Early Cretaceous, 130.0–125.5 Ma	Szwedo and Ansorge 2015
Burmissus Shcherbakov, 2017	*Burmissus raunoi* Shcherbakov, 2017	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Shcherbakov 2017
	Burmissus szwedoi Luo, Jiang, Szwedo et Xiao, 2020	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Luo et al. 2020b
	Burmissus latimaculatus Fu et Huang, 2020	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Fu and Huang 2020
Dachibangus Jiang, Szwedo et Wang, 2018	*Dachibangus trimaculatus* Jiang, Szwedo et Wang, 2018	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Jiang et al. 2018
	Dachibangus formosus Fu, Szwedo, Azar et Huang, 2019	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Fu et al. 2019
	Dachibangus hui Zhang, Yao et Pang, 2021	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Zhang et al. 2021b
Jaculistilus Zhang, Ren et Yao, 2018	*Jaculistilus oligotrichus* Zhang, Ren et Yao, 2018	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Zhang et al. 2018
Mimaplax Jiang, Szwedo et Wang, 2019	*Mimaplax ekrypsan* Jiang, Szwedo et Wang, 2019	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Jiang et al. 2019
Ayaimatum Jiang et Szwedo, 2020	*Ayaimatum trilobatum* Jiang et Szwedo, 2020	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Jiang et al. 2020
	Ayaimatum minutum Fu et Huang, 2021	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Fu and Huang 2021
Cretodorus Fu et Huang, 2020	*Cretodorus granulatus* Fu et Huang, 2020	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Fu and Huang 2020
	Cretodorus angustus Fu et Huang, 2020	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Fu and Huang 2020
	Cretodorus rostellatus Zhang, Yao et Pang, 2021	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Zhang et al. 2021a
Mimaeurypterus Fu et Huang, 2021	*Mimaeurypterus burmiticus* Fu et Huang, 2021	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Fu and Huang 2021
Multistria Zhang, Yao et Pang, 2021	*Multistria orthotropa* Zhang, Yao et Pang, 2021	Kachin amber, northern Myanmar	Earliest Cenomanian, mid-Cretaceous, 98.8 Ma	Zhang et al. 2021b
Undescribed specimen		Kzyl-Zhar, Kazakhstan	Turonian, Late Cretaceous	Shcherbakov 2007b
Undescribed specimen		Khetana, Khabarovsk Region, Russia	Mid-Albian, Early Cretaceous	Shcherbakov 2007b
Undescribed specimen		Turga, Chita Region, East Transbaikalia in Central Siberia	Berriasian, earliest Cretaceous	Shcherbakov 2007b
Undescribed specimen		Bon-Tsagan-Nur, Mongolia	Barremian/Aptian, Early Cretaceous	Shcherbakov 2007b

Observations were made using a Zeiss Stemi 508 microscope. The photographs were taken with a Zeiss Stereo Discovery V16 microscope system in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, and measurements were taken using Zen software. Photomicrographic composites of 10–100 individual focal planes were digitally stacked using the software Helicon Focus 6.7.1 for a better illustration of 3D structures. Photographs were adjusted using Adobe Lightroom Classic and line drawings were prepared using CorelDraw 2019 graphic software.

The venational nomenclature follows the proposals of Bourgoin et al. (2015). Vein abbreviations: CA, costa anterior; Pc+CP, precosta+costa posterior; ScP+R, subcosta posterior +radius; RA, radius anterior; RP, radius posterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; Pcu, postcubitus; A_1, first anal vein; A_2, second anal vein.

Systematic palaeontology

Class Insecta Linnaeus, 1758 Order Hemiptera Linnaeus, 1758 Suborder Fulgoromorpha Evans, 1946 Superfamily Fulgoroidea Latreille, 1807 Family Mimarachnidae Shcherbakov, 2007 in Shcherbakov (2007b) Genus *Saltissus* Shcherbakov, 2007 in Shcherbakov (2007b)

Type species

Saltissus eskovi Shcherbakov, 2007 in Shcherbakov (2007b)

Saltissus fennahi Luo, Liu et Jarzembowski sp. nov.

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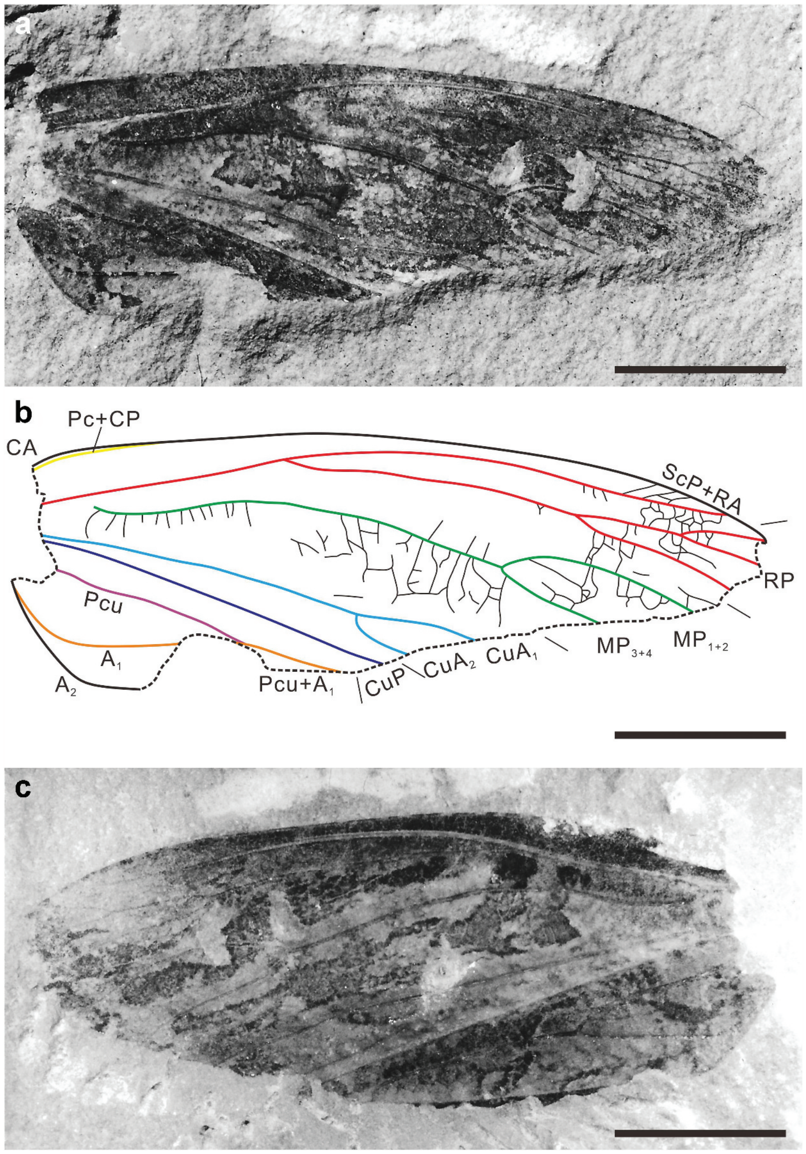

Figure 1. Photographs and line drawings of *Saltissus fennahi* Luo, Liu et Jarzembowski sp. nov., holotype. (a) Tegmen, part (BMB 014919). (b) Line drawing of a. (c) Tegmen, counterpart (NHM UK In 64637). Scale bars = 5 mm.

Etymology

The specific name is after Prof. Dr. Ronald Gordon Fennah (1910–1987) in appreciation of his contribution to the study of Fulgoroidea.

Material

Holotype BMB 014919 (part), NHM UK In 64637 (counterpart) deposited in the Booth Museum of Natural History and The Natural History Museum, respectively. Holotype: compression incomplete, only tegmen preserved and the base and apex of the tegmen is missing.

Locality and horizon

Upper Weald Clay Formation below BGS Bed 5 c, Lower Cretaceous (lower Barremian), Smokejacks brickworks, Surrey, England.

Diagnosis

Tegmen more than 20 mm long. Stem Pc+CP merged with margin at less than 1/10th of tegmen length, stem ScP+R forked beyond fusion of Pcu+A_1, branch RP with three terminal branches, stem MP with two terminal branches, stem CuA forked much later than fusion of Pcu+A_1, CuA_2 indistinct basally, and A_1 strongly curved at base.

Description

Tegmen at least 22.4 mm long and 8.1 mm wide filled with meshwork of veinlets forming irregular polygonal cells. Costal margin slightly arcuate, apex of tegmen missing, postclaval margin curved. Stem Pc+CP very close to costal margin and merged with margin at less than 1/10th of tegmen length. Stem ScP+R straight at base, then forked at about 1/3rd of tegmen length, slightly distal of fusion of stem Pcu+A_1; branch ScP+RA slightly arched, then slightly downcurved, running subparallel to costal margin, single; branch RP slightly sinuate, forked at about ¾ths of tegmen length, with three terminal branches. Stem MP distinctly sinuate, forked at about ⅔rds of tegmen length; branch MP_{1+2} distinctly arched, single; branch MP_{3+4} slightly curved, single. Stem CuA almost straight, forked at less than half of tegmen length; branch CuA_1 slightly arched, single; branch CuA_2 indistinct at base, single. Stem CuP almost straight. Branch Pcu slightly sinuate; branch A_1 strongly

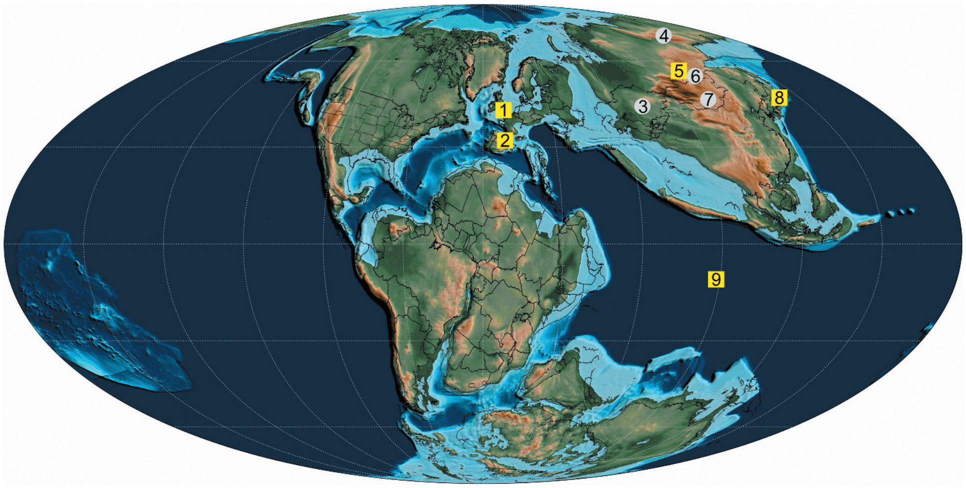

Figure 2. Distribution of Mimarachnidae during the Cretaceous Period. Palaeogeographic map (125 Ma) modified from Scotese (2021), yellow squares represent confirmed localities, grey circles represent unconfirmed localities. 1 – Smokejacks brickworks, England, upper Weald Clay Formation, lower Barremian, Early Cretaceous, ca. 128 Ma; 2 – La Cabrúa outcrop, Spain, La Pedrera de Rubies Formation, early Barremian, Early Cretaceous, 130.0–125.5 Ma; 3 – Kzyl-Zhar, Kazakhstan, Turonian, Late Cretaceous; 4 – Khetana, Khabarovsk Region, Russia, mid-Albian, Early Cretaceous; 5 – Baissa, Buryatia, Russian, Zaza Formation, Berriasian–Barremian, Early Cretaceous, 145–125 Ma; 6 – Turga, Chita Region, East Transbaikalia in Central Siberia, earliest Cretaceous; 7 – Bon-Tsagan-Nur, Mongolia, Barremian/Aptian, Early Cretaceous; 8 – Kaseki-kabe, Japan, Kuwajima Formation, Barremian/Aptian, Early Cretaceous, 129–121 Ma; 9 – Kachin amber, mid-Cretaceous, approximately 99 Ma.

curved at base, then almost straight; claval veins $Pcu+A_1$ fused at less than 1/3rd of tegmen length. Costal area extremely narrow, 2.6 mm long and less than 0.1 mm wide, cell C1 longest, 13.9 mm long and 1.02 mm wide; cell C3 at least 4.6 mm long and 1.6 mm wide; cell C5 at least 2.7 mm long and 1.02 mm wide.

Discussion

Saltissus fennahi sp. nov. can be easily assigned to the suborder Fulgoromorpha based on the 'Y-shape' veins on the clavus (Pcu and A_1), and it can be easily attributed to Mimarachnidae due to its simplified venation and meshwork of veinlets. The new species can be assigned to *Saltissus* Shcherbakov, 2007, based on the following characters: branch RP with three terminal branches, stem MP with two terminal branches, CuA forked much later than the fusion of $Pcu+A_1$, and CuA_2 indistinct basally. However, it is different from *Saltissus eskovi* Shcherbakov, 2007 in the following features: tegmen more than 20 mm long (9.5–13 mm long in *Saltissus eskovi* Shcherbakov, 2007), stem Pc+CP merged with margin at less than 1/10th of tegmen length (stem Pc+CP merged with margin at about ⅔rds of tegmen length in *S. eskovi*), stem ScP+R forked beyond the fusion of $Pcu+A_1$ (slightly earlier in *S. eskovi*), branch A_1 strongly curved at base (almost straight in *S. eskovi*). Based on the venation, we place the wing in *Saltissus* Shcherbakov, 2007, and establish a new species for it.

This is the second planthopper reported from Weald Clay Formation. Previously, only a cixiid species was known, tentatively referred to the genus *Cixius* half a century ago (Fennah 1961). The discovery of Mimarachnidae in England from the Early Cretaceous is not surprising because this family has been reported from Spain not too far away (Szwedo and Ansorge 2015). Mimarachnid planthoppers preserved in rock formation can only be found at the middle and high latitudes of the northern hemisphere, while in the low latitude, many specimens have been discovered from Kachin amber. The Burma Terrane was part of a Trans-Tethyan island arc at a near-equatorial southern latitude in the mid-Cretaceous (Westerweel et al. 2019), the abundant species of Mimarachnidae from Kachin amber indicate that Mimarachnidae has already adapted to the tropical environment and might has spread to Gondwana. Mimarachnidae mainly and widely distributed in Eurasian during the Cretaceous and crossed different climatic zones (Figure 2); this implies that its still unknown ancestor must have appeared (and spread) in the Jurassic.

Although the name of this family is referred to spider mimic, no robust evidence can confirm such behavior at present. Distinct colour pattern of tegmen also presents in many mimarachnid planthoppers, e.g. *Burmissus* Shcherbakov, 2017, *Dachibangus* Jiang, Szwedo et Wang, 2018, *Mimaplax* Jiang, Szwedo et Wang, 2019, *Multistria* Zhang, Yao et Pang, 2021 (Shcherbakov 2017; Jiang et al. 2018, 2019; Fu et al. 2019; Luo et al. 2020b; Zhang et al. 2021b). The spider mimicry pattern of *Mimarachne* Shcherbakov, 2007 can also be interpreted as the morphological adaptation to camouflage on tree bark like other mimarachnids, e.g. *Mimaplax ekrypsan* Jiang, Szwedo et Wang, 2019 (Jiang et al. 2019).

Conclusion

Saltissus fennahi sp. nov. is the first mimarachnid planthopper discovered in the upper Weald Clay Formation and is the 21st species of the family Mimarachnidae. The new species not only adds to the taxonomic diversity and morphological disparity of Mimarachnidae, but also extends the distribution of this family to NW Europe. Mimarachnidae was a widely distributed family during the Cretaceous and its ancestor must have appeared in the Jurassic, well before the angiosperm radiation. The colour pattern of tegmen of Mimarachnidae most likely is the morphological adaptation to camouflage on tree bark.

Acknowledgments

We express our sincere thanks to two anonymous reviewers for their thoughtful comments on the manuscript. This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), National Natural Science Foundation of China (42125201, 41688103, 31970442), and the CAS President's International Fellowship Initiative (PIFI). This is a Leverhulme Emeritus Fellowship contribution for EAJ and a contribution to UNESCO-IUGS IGCP Project 679.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the National Natural Science Foundation of China [31970442,41688103,42125201]; Strategic Priority Research Program of the Chinese Academy of Sciences [XDB26000000].

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