A New Jurassic Kempynine Species With Notes on Historical Distributions of Kempyninae Integrated Both Fossil and Extant Taxa (Neuroptera: Osmylidae)

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The extant kempynines, a strict "southern group," are confined to South America and Australia, while their most fossil relatives are abundantly recorded in the Northern Hemisphere. This pattern of the biogeographic distribution implies the complicated evolutionary scenario of Kempyninae. Herein, a new northern species *Arbusella platyptera* Ma *et* Wang, sp. nov. is described from the Jiulongshan Formation in Daohugou, Inner Mongolia, China. Additionally, a key to the extinct species and extant genera of Kempyninae is provided. Integrating all extant and most fossil genera of Kempyninae, we conducted phylogenetic analyses to explore the inner relationships of Kempyninae for the first time. The results corroborate the monophyly of Kempyninae and retrieve three clades within the subfamily, namely, two northern fossil genera (†*Arbusellla* + †*Jurakempynus*), constituting the basalmost clade and three other northern fossil genera (†*Sauktangida* + †*Mirokempynus* + †*Ponomarenkius*), forming a monophylic clade, which is sister to the third clade that includes all extant southern genera and the southern fossil genus of †*Euporismites*. Also, the extant kempynines were hypothesized to evolve independently from their northern Mesozoic relatives. The Dispersal-vicariance (DIVA) analysis revealed a northern and prepangean origin of Kempyninae, and the northern ancestral kempynines first colonized the Southern Hemisphere before the split of Pangea. Our results expose a more complicated evolutionary scenario of the insects with a long evolutionary history and provide new insights into the formation of distribution patterns in current relictual insects.

Keywords: new species, phylogeny, evolution, fossil, biogeography, DIVA

INTRODUCTION

Kempyninae, a subfamily of Osmylidae, currently comprises 11 genera, including three extant genera, namely, *Kempynus* Navás, 1912; *Australysmus* Kimmins, 1940; and *Euosmylus* Krüger, 1913, and eight fossil genera, namely, †*Euporismites* Tillyard, 1916; †*Cretosmylus* Makarkin, 1990; †*Jurakempynus* Wang et al., 2011b; †*Kempynosmylus* Makarkin, 2014; †*Sauktangida*

Khramov, 2014a; †*Arbusella* Khramov, 2014b; †*Ponomarenkius* Khramov et al., 2017; and †*Mirokempynus* Ma et al., 2020a (Winterton et al., 2019; Ma et al., 2020a). The extant Kempyninae, as an absolute "southern group," is restricted to Australia, New Zealand, Argentina, and Chile in South America (Kimmins, 1940; New, 1983; Martins et al., 2016), of which most genera are confined to a single area except for the genus *Kempynus*, occurring in all areas. Contradictory to the extant lineages, the fossil kempynines were almost entirely documented from the Northern Hemisphere in the Mesozoic, with the exception of one Cenozoic fossil species *Euporismites balli* from Queensland, which appears to be more closely related to the extant species in distribution (Lambkin, 1987; Makarkin, 1990, 2014; Wang et al., 2011a; Khramov, 2014a,b; Khramov et al., 2017; Ma et al., 2020a). The distribution pattern of fossil and extant lineages indicates the evolutionary process, and the historical biogeographic dynamics of Kempyninae may be more complicated (Wang et al., 2011b). Furthermore, the recent phylogenetic study of Osmylidae proposed the northern subfamily Osmylinae be sister to the other four southern subfamilies, i.e., Kempyninae, Eidoporisminae, Porisminae, and Stenosmylinae, instead of the current northern distributed groups, i.e., Protosmylinae and Spilosmylinae (Winterton et al., 2017). These results implied an earlier pre-Pangaea origin of Osmylidae and introduced a more complicated evolutionary scenario, and as a result, the current distributions of extant Kempyninae should not be simply attributed to the Gondwanan biogeographic events. To address the issues regarding the historical vicariance biogeographic distributions of Kempyninae, it is essential to study the phylogeny of Kempyninae by combining all fossil and extant lineages.

Herein, we describe a new species, *Arbusella platyptera* Ma *et* Wang, sp. nov., from the Middle Jurassic Jiulongshan Formation in Daohugou, Inner Mongolia, China. This new species can be assigned to Kempyninae based on the following apomorphic characters: The M space in the hind wing is extremely broad and sinuate cross-veins are arranged in the intramedial area to produce two rows of irregular cells, which are regarded as an apomorphy of Kempyninae (Winterton et al., 2019; Ma et al., 2020a). To investigate the inner relationships of Kempyninae, we conducted a phylogenetic analysis including all extant and most fossil genera. The phylogenetic results corroborated the monophyly of the subfamily, and the historical biogeography of Kempyninae was outlined by using the DIVA analysis. This study first investigated the historical biogeography of Kempyninae under the phylogenetic framework, and then promoted our understanding of this particular insect group.

MATERIALS AND METHODS

Material
The type specimen was collected from the Jiulongshan Formation of the Middle Jurassic at Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China, and deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing (CNUB; Dong Ren,

Curator). The specimen was observed and photographed by using a stereoscopic microscope, Nikon SMZ25 with an attached Nikon DS-Ri2 digital camera system. The line drawing was produced using the Adobe Photoshop CC and Adobe Illustrator CC software. The terminology for wing venation and genitalia follows Breitkreuz et al. (2017) and Winterton et al. (2019).

Wing vein abbreviations are as follows: C, costa; Sc, subcosta; RA, anterior branch of radius; RP, posterior branch of radius; MA, anterior branch of media; MP, posterior branch of media; CuA, anterior cubitus; CuP, posterior cubitus; A, anal veins. Other abbreviations involved are as follows: J_1, Early Jurassic; J_2, Middle Jurassic; J_3, Late Jurassic; O_1, late Paleocene-early Eocene; AUS, Australia; CHN, China; KG, Kyrgyzstan; KZ, Kazakhstan; MGL, Mongolia; NZL, New Zealand; SA, South America.

Phylogenetic Analyses
Taxa Sampling
Nine genera of Kempyninae were sampled in the phylogenetic analyses, including three extant genera, namely, *Kempynus*, *Euosmylus*, and *Australysmus*, and six extinct genera, namely, †*Arbusella*, †*Euporismites*, †*Jurakempynus*, †*Mirokempynus*, †*Ponomarenkius*, and †*Sauktangida* (refer to **Table 1** for more details). Three genera are selected as outgroups, including †*Vetosmylus* (a fossil genus of Osmylinae), *Osmylus* (the type genus of Osmylinae), and *Heterosmylus* (an extant genus of Protosmylinae). Two nominal kempynine genera, *Cretosmylus* Makarkin, 1990, and *Kempynosmylus* Makarkin, 2014, from the Baissa of Lower Cretaceous were not included in the analysis due to the absence of the key features (Makarkin, 1990, 2014), and their kempynine affinity requires further investigation.

Phylogenetic Analyses
As most fossil taxa of Kempyninae were established based on the characters of wings, we primarily adopted the wing characters in the phylogenetic analysis, including ten characters for the

TABLE 1 | Species examined in the phylogenetic analysis.

Taxa	Fossil/extant	Distributions
Outgroups		
Heterosmylus wolonganus Yang, 1992	Extant	China
Osmylus fulvicephalus Scopoli, 1763	Extant	Europe
Vetosmylus tentus Ma et al., 2020b	Fossil	China
Ingroups		
Sauktangida aenigmatica Khramov, 2014a	Fossil	Kyrgyzstan
Jurakempynus sinensis Wang et al., 2011b	Fossil	China
Jurakempynus loculosus Ma et al., 2020a	Fossil	China
Mirokempynus profundobifurcus Ma et al., 2020a	Fossil	China
Ponomarenkius excellens Khramov et al., 2017	Fossil	China
Arbusella bella Khramov, 2014a	Fossil	Kazakhstan
Arbusella platyptera sp. nov.	Fossil	China
Euporismites balli Tillyard, 1916	Fossil	Australia
Australysmus lacustris Kimmins, 1940	Extant	Australia
Euosmylus stellae McLachlan, 1899	Extant	New Zealand
Kempynus incisus McLachlan, 1863	Extant	New Zealand, Australia

forewing and seven characters for the hind wing. The list of characters and character states for the phylogenetic analyses of Kempyninae are outlined as follows. The data matrix of characters used in the phylogenetic analyses is shown in **Table 2**. The missing data were coded as "?" The character matrix was edited using NDE 0.5.0 (Page, 2001). The parsimony analyses were performed with Nona/WinClada using a heuristic search that employed a TBR + TBR search strategy, holding 10,000 trees and 1,000 replicates of random additions (Nixon, 2002).

Biogeographic Analysis

To trace the historical biogeographic distributions, the ancestral distribution reconstruction of Kempyninae was conducted with RASP 4.0 using the dispersal-vicariance optimization model, which is generally used in the analyses of ancestral reconstruction (Yu et al., 2010, 2015; Liu et al., 2012). Based on the current phylogenetic analysis and the previous study (Winterton et al., 2017), the sampled tree was compiled to declare a fully resolved topology of kempynine genera. The DIVA analysis was performed with default settings except for the maximum number of areas in ancestral ranges being constrained to three, considering the widest kempynine genus *Kempynus* distributed in three areas, i.e., South America, Australia, and New Zealand.

List of Characters and Character States for the Phylogenetic Analyses

Morphological character states are scored 0–2 and ? (0 = plesiomorphic state; 1–2 = apomorphic state; ? = state unknown). As the phylogenetic analysis was conducted for fossil and extant kempynine genera, the sampled characters were primarily selected from the wings that were most shared by fossil and extant taxa.

Characters of Forewing

1. An outline of the apical margin. 0, normal or slightly convex; 1, distinctly concave. The normal outer margin occurs in the most sampled genera. State 1 exists as an apomorphy in two extant genera: *Kempynus* and *Euosmylus*, whose shape of forewings is evidently modified into the falcate shape.

2. Position of M forking. 0, proximally branched, before (or corresponding to) the RP1 point from RP; 1, distinctly beyond the RP1 point from RP, and often present in-between RP1 and RP2 from RP. The position of M fork stably occurs before RP1 among Protosmylinae, Spilosmylinae, and most fossil kempynines. Although the sampled Osmylinae outgroups *Osmylus fulvicephalus* and *Vetosmylus tentus* have the proximally branched M, state 1 is also common in some extant species, implying the distinct variation in the position of the M fork within the subfamily. Among Kemypinae, M fork commonly located at the in-between of RP1 and RP2 from RP.

3. Subcostal veinlets. 0, simple, no distal forks; 1, many distal forks present. Simple subcostal veinlets are present in six subfamilies of Osmylidae. State 1 occurs in some genera of the subfamilies Kempyninae and Osmylinae.

4. The number of RP branches. 0, lesser, not more than 10; 1, numerous, more than 10. Number of RP branches is variable in Osmylidae, but state 0 is common in most families of Neuroptera. State 1 occurs in Kempyninae (except *Euosmylus* and *Australysmus*) and Osmylinae.

5. Arrangement of RP cross-veins. 0, two or more gradate series are present; 1, one gradate series is present; 2, irregular, gradate series is absent. State 0 occurs in the outgroups, *Heterosmylus* and *Osmylus*. In *Vetosmylus* and most extant kempynines, RP cross-veins generally form a row of gradate series. The irregularly arranged cross-veins in the radial sector are common in the fossil kempynine species.

6. Forewing MP. 0, branched pectinately distally; 1, branched dichotomously near the middle of the wing; 2, branched proximally (near the wing base). State 0 is common in most species of Osmylidae. State 1 occurs in a few extant species of *Kempynus*. State 2 only occurs in *Ponomarenkius*.

7. Length of CuP. 0, more than three-quarters the length of CuA, approximating equal length with CuA; 1, about half the length of CuA, and less than three-quarters the

TABLE 2 | Data matrix of characters used in the phylogenetic analyses.

Taxa	Characters																
	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17
Heterosmylus wolonganus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Osmylus fulvicephalus	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1
Vetosmylus tentus	0	0	1	1	1	0	0	2	0	0	0	0	0	1	0	0	?
Sauktangida aenigmatica	?	?	?	?	?	?	?	?	?	?	0	0	2	2	1	1	2
Jurakempynus sinensis	0	0	1	1	2	0	1	2	2	0	0	0	0	1	1	1	?
Jurakempynus loculosus	?	1	1	1	2	0	1	2	2	0	0	?	0	1	1	0	1
Mirokempynus profundobifurcus	?	?	?	?	?	?	?	?	?	?	0	0	1	2	1	0	2
Ponomarenkius excellens	0	1	1	1	1	2	0	0	0	2	0	0	1	2	1	0	?
Arbusella bella	0	1	1	1	2	0	0	0	0	0	1	0	0	1	1	?	?
Arbusella platyptera sp. nov.	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	?	?
Euporismites balli	0	?	?	1	?	?	?	?	?	0	0	0	2	2	2	0	?
Australysmus lacustris	0	1	1	0	1	0	0	1	1	0	0	0	2	2	2	0	1
Kempynus incisus	1	1	1	1	1	1	0	1	1	1	0	1	2	2	2	0	1
Euosmylus stellae	1	1	0	0	1	0	0	1	1	0	0	1	2	2	0	0	1

length of CuA. State 0 commonly occurs in Kempyninae and Osmylinae. State 1 occurs in *Jurakempynus* and *Heterosmylus*.

8. Forewing CuA. 0, branched pectinately distally; 1, branched dichotomously distally; 2, branched complicatedly near the middle of the wing. The pectinately branched CuA is common in Osmylidae and is considered as a synapomorphy of the family (Winterton et al., 2019; Ma et al., 2020a). State 1 only occurs in extant species of Kempyninae. State 2 only occurs in *Jurakempynus*.

9. Length of A1. 0, approximately half the length of CuP, and less than three quarters; 1, less than or approximately half the length of CuP; 2, more than three-quarters the length of CuP. The moderate length of A1 (approximately half the length of CuP) occurs in most extant Osmylidae. In the Kempyninae, Al is distinctly beyond half the length of CuP, of which two states are detected, i.e., approximately three-quarters the length of CuP and approximately equal length of CuP. State 1 only occurs in extant species of Kempyninae. State 2 commonly occurs in most fossil kempynines.

10. Space between M branches. 0, normal or slightly dilated, with a single row of cells; 1, obviously broadened, with a single row of cells; 2, strongly broadened, with multiple rows of cells. State 0 occurs commonly in all subfamilies except Kempyninae. State 1 is distinct in some species of *Kempynus* that are apomorphies of the genus. State 2 only occurs in *Ponomarenkius*.

Characters of Hind Wing

11. The interlinked cross-veins between costal veinlets. 0, absent; 1, present. State 0 is common in Osmylidae, and state 2 only occurs in *Arbusella* within Kempyninae.

12. RP branches. 0, branched regularly, straight or slightly bent near wing margin; 1, strongly curved in distal half of RP, and slightly sinuous in distal part. State 0 occurs commonly in five subfamilies: Osmylinae, Protosmylinae, Gumillinae Porisminae and Spilosmylinae. State 1 is distinct in *Kempynus* and *Euosmylus*.

13. Pattern of MP branches. 0, branched pectinately in distal; 1, branched proximally near the wing base; 2, branched dichotomously in distal. State 0 is common in outgroups and most species of Osmylidae. State 1 only occurs in two fossil genera *Mirokempynus* and *Ponomarenkius*. State 2 generally presents in other kempynine genera.

14. Space between M branches. 0, both branches parallel, obviously un-broadened; 1, distinctly broadened from the middle; 2, gradually widened from the base to the distal. State 0 occurs in most subfamilies of Osmylidae except Kempyninae and Osmyninae. State 1 occurs in Osmylinae and some fossil genera of Kempyninae. State 2 is common in Kempyninae, which is regarded as an apomorphy of the subfamily.

15. Arrangement of cells between M branches. 0, a single row of cells present; 1, multiple rows of cells occupying the entire area; 2, multiple rows of cells present in distal half of MP. Multiple rows of cells only occur in Kempyninae, which is an apomorphy of this subfamily. State 1 occurs in

almost all fossil species of Kempyninae. State 2 only occurs to *Kempynus*, *Euosmylus* and *Euporismites*.

16. Length of A1. 0, about equal to or less than half the length of CuP; 1, more than half the length of CuP. State 0 occurs in most species of Osmylidae. State 1 only occurs to *Sauktangidas*, *Jurakempynus* and *Heterosmylus*.

17. Pattern of A3. 0, A3 simple, directly reaching the margin; 1, A3 fused with the first branch of A2 and forming a small loop; 2, A3 well-development, with some pectinated branches. State 0 occurs in the outgroup of Heterosmylus and also occurs in a few genera of Gumilinae. State 1 is present in Osmylinae and Kempyninae (e.g., *Euosmylus*). State 2 is common within the fossil osmylids.

RESULTS AND DISCUSSION

Systematic Paleontology

Order NEUROPTERA Linnaeus, 1758
    Family OSMYLIDAE Leach, 1815
    Subfamily KEMPYNINAE Carpenter, 1943
    Genus ARBUSELLA Khramov, 2014b
    Type species. Arbusella bella Khramov, 2014b
    Included species. Arbusella bella Khramov, 2014b; *Arbusella magna* Khramov et al., 2017; Arbusella platyptera Ma et Wang, sp. nov.

Keys to the Extinct Species and Extant Genera of Kempyninae

1. HW: MP proximally branched and forming deep forking............2
 - HW: MP forked at the middle or in distal half of wing..............3

2. HW: MA and MP forming the similar deep branches, three rows of regular cells present in medial region............. †*Ponomarenkius* Khramov et al., 2017 (CHN, J2)
 - HW: The branches of MA and MP are different: MA branched distally, and MP proximally forked.................... †*Mirokempynus* Ma et al., 2020a (CHN, J2)

3. HW: cross-veins between MA and MP sinuous, and forming multiple rows of cells before branching of MP.........................4
 - HW: cross-veins between MA and MP relatively straight, only forming a single row of cells before branching of MP....................13

4. HW: MP forked close to the middle, each branch of MP with pectinated or dichotomous branches.....................†*Sauktangida* Khramov, 2014a (KG, J1)
 - HW: MP only forming the distal branches.......................5

5. HW: the presence of an additional row of gradate series between the subcostal veinlets .... 6 (†*Arbusella* Khramov, 2014b)
 - HW: the absence of the gradate series between the subcostal veinlets...................................... 8 (†*Jurakempynus* Wang et al., 2011b)

6. Presence of large eye spots in hind wing................. 7

- Absence of large eye spots in the hind wing; the presence of three tint longitudinal stripes in the forewing....... †*Arbusella magna* Khramov et al., 2017 (CHN, J2)

7. HW: Presence of two large eye spots, CuA forming more pectinate branches (ca. 12)............. †*Arbusella bella* Khramov, 2014b (KZ, J3)

- HW: Presence of three large eye spots, CuA with less pectinate branches (ca. 6)....... *Arbusella platyptera* Ma *et* Wang, sp. nov. (CHN, J2)

8. HW: M region with two relatively regular rows of quadrangular cells; CuP with deeply dichotomic branches............... †*Jurakempynus bellatulus* Wang et al., 2011b (CHN, J2)

- HW: M region with 2–3 irregular rows of cells; CuP with many pectinated branches....... 9

9. HW: CuP with relatively few branches, only forming 4–5 branches.............. †*Jurakempynus sinensis* Wang et al., 2011b (CHN, J2)

- HW: CuP with numerous branches, more than 9 branches............ 10

10. HW: M region relatively narrow with an additional short and narrow row of cells............. †*Jurakempynus sublimis* Khramov, 2014b (MGL, J3)

- HW: M region without an additional short and narrow row of cells............ 11

11. HW multi-row cells appeared only in distal half of the M widened region............. †*Jurakempynus epunctatus* Wang et al., 2011b (CHN, J2)

- HW multi-row cells occupied almost all the M widened regions before MP distal fork....... 12

12. FW: A2 with relatively few and short branches; A2 shorter than half of A1........................ †*Jurakempynus arcanus* Khramov, 2014b (KZ, J3)

- FW: A2 with relatively numerous and long branches; A2 longer than half of A1.............. †*Jurakempynus loculosus* Ma et al., 2020a (CHN, J2)

13. HW: MP deeply forked at the mid-length of wing; gradate series absent from both wings.................. †*Euporismites* Tillyard, 1916 (AUS, P1)

- HW: MP with dichotomous branched beyond the mid-length of wing; outer gradate series distinct on both wings.................. 14

14. HW: M branches widely forked, cross-veins between them somewhat sinuous........................ *Kempynus* Navás, 1912 (AUS, NZL, and SA)

- HW: M branches normally forked, cells between them relatively quadrate..................15

15. Forewings distinctly falcate, membrane strongly patterned; relative small insect (wingspan ca. 20–30 mm)............*Euosmylus* Krüger, 1913 (NZL)

- Forewings not or slightly falcate, membrane-less patterned and scattered with sporadic spots; relatively large insect (wingspan > 40 mm).................. *Australysmus* Kimmins, 1940 (AUS)

Arbusella platyptera Ma and Wang, sp. nov. (**Figure 1**).

Diagnosis. Large hind wing with length exceeding 40 mm and width exceeding 15 mm; membrane with three large eye spots, one located at proximal one-third of wing, and the other two closely spaced and located at distal one-third of wing; numerous and sinuate cross-veins arranged in the two-third of radial region forming densely distributed cells with irregular sizes and shapes, and the outer well-defined gradate series; MP with irregularly arranged pectinated branches in the distal, and the first branch forming dichotomous branches; CuA with 6 pectinated branches.

Etymology. From the Greek combination of *platy-* and *-ptera*, referring to the broad wing.

Type material. Holotype CNU-NEU-NN2020005. Only the hind wing is preserved.

Type locality and age. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Aalenian/Bajocian boundary, Middle Jurassic.

Description. Hind wing *ca.* 43.8 mm in length, 16.6 mm in width. The proximal part of the hind wing is incompletely preserved.

Hind wing (**Figure 1**): membrane nearly transparent except for three distinct eye spots; trichosors well-developed along the margin; subcostal veinlets dichotomously forked from the pterostigma region to the apex; subcostal cross-veins regularly arranged and forming a row of gradate series in-between subcostal veinlets; RP with more than 25 branches, and each RP branch with irregular distal bifurcations; the region between MA and MP dilated visibly in the middle, with two rows of irregular cells in-between; MA only forming three simple primary branches in distal; CuP with 11 pectinated branches; A1 relatively straight and long, about one-half of CuP.

Remarks. The hind wing is significant to the generic taxonomy of Kempyninae, and many fossil genera were established based on the characters of the hind wing (Winterton et al., 2019). The genus *Arbusella* was first erected by Khramov based on a species from the Late Jurassic of Kazakhstan, which was most characterized by the presence of a row of gradate series in-between subcostal veinlets (Khramov, 2014a). In spite of the absence of forewing, the new specimen can be clearly assigned to the genus of *Arbusella* for sharing this character. It is noted that the hind wing length of the new specimen exceeds 40 mm long as preserved, which is the hitherto known largest fossil kempynine. Although the hind wings of two other *Arbusella* species are preserved partially, it can still be concluded that the two species are distinctly smaller than the new specimen according to the lengths of their forewings, i.e., 22.5 mm long in *A. bella* and *ca.* 37 mm long in *A. magna*. Comparing two *Arbusella* species, the new specimen can be easily distinguished from *A. bella* by three eye spots in the hind wing and CuA with 6–7 branches (*cf.* two large eye spots and 12 branches in *A. bella*). As only the partial hind wing of *A. magna* was preserved, the new specimen was just separated from the latter species by one apomorphic character, i.e., a large eye spot present in the middle of the hind wing vs. distinctly absent in *A. magna* (**Figure 1**, Khramov, 2017: figure 4B). Considering the significant differences between the new specimen and the known *Arbusella* species, we established a new species for it, and it is hoped
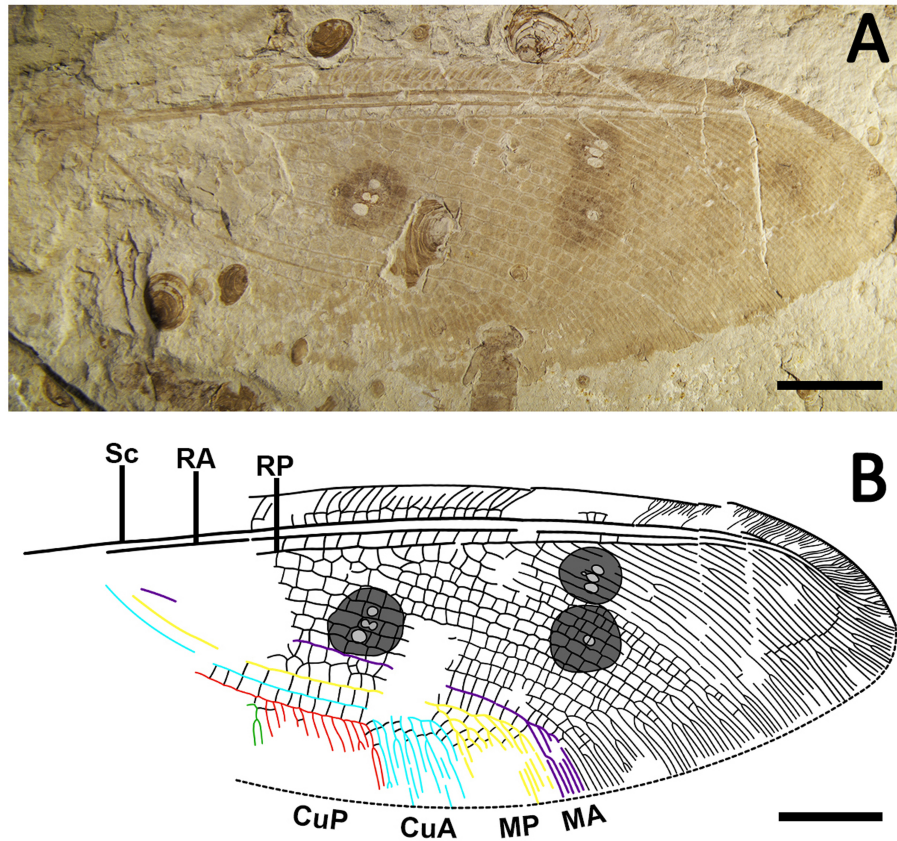
FIGURE 1 | Lance lacewing *Arbusella platyptera* Ma and Wang, sp. nov. (holotype, CNU-NEU-NN2020005) from the Middle Jurassic of Jiulongshan Formation in Daohugou, China. **(A)** Photograph of the hind wing. **(B)** Line drawing of the hind wing. Scale bars are 10 mm.

that more evidence could be found to further corroborate the taxonomic status of the new species.
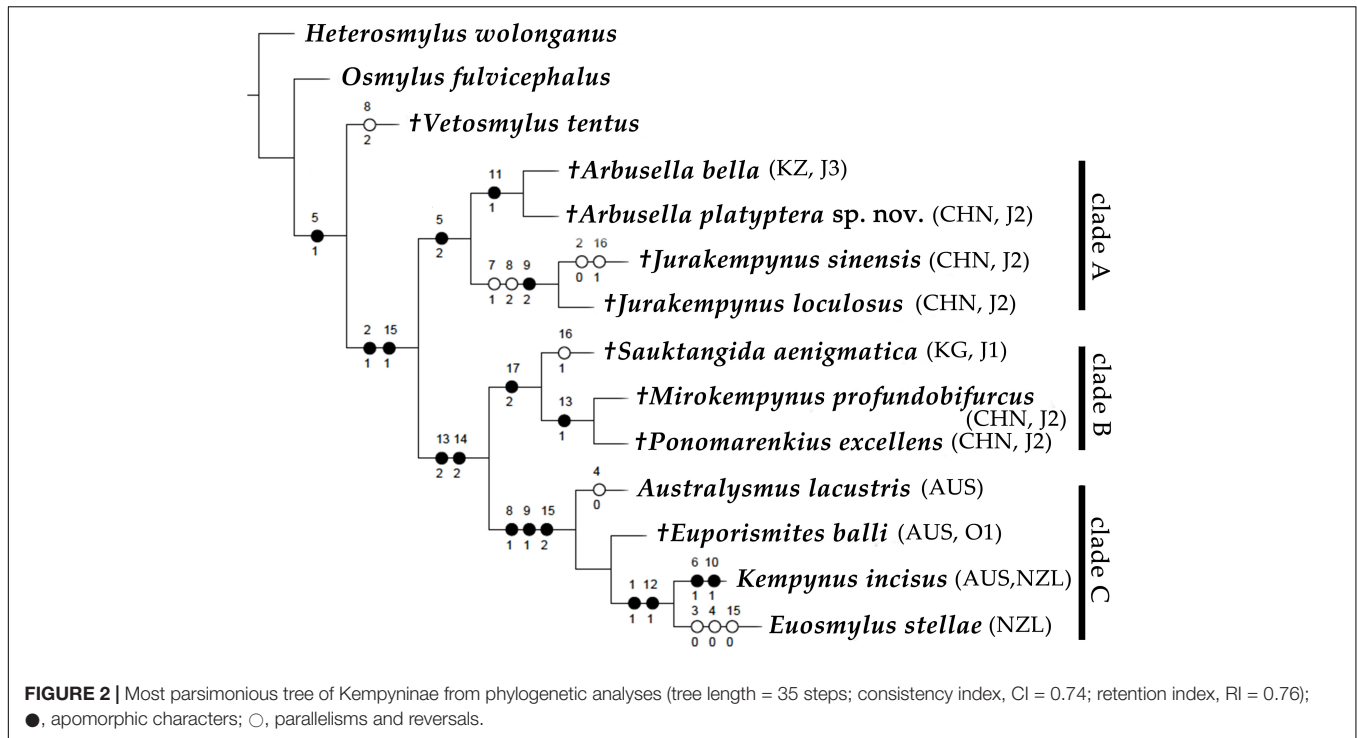
Phylogenetic Results

The phylogenetic analyses resulted in one most parsimonious tree (tree length = 35; consistency index = 0.74; retention index = 0.76), which is shown in **Figure 2**. Based on the phylogenetic results, all fossil and extant kempynine genera were well grouped as a monophyly, which was supported by two synapomorphic characters: the distal branched M in the forewing (Cha. 2: 1) and multiple rows of cells between M branches in the hind wing (Cha. 15: 1). The latter character has been considered as a diagnostic feature of Kempyninae (Winterton et al., 2019; Ma et al., 2020b). The Kempyninae was divided into two primary clades, namely, clade A, consisting of two fossil genera *Arbusella* + *Jurakempynus*, and clade B + C, consisting of the other genera (**Figure 2**). The grouping of *Arbusella* and *Jurakempynus* was anticipated for their homologous venation, which was supported by one synapomorphy: the absence of gradate series in the forewing (Cha. 5: 2). The other kempynine genera were well grouped, which was supported by two apomorphic characters of the hind wing: distal branched MP (Cha. 13: 2) and the gradually divergent M branches (Cha. 14: 2). Two clades were identified in this grouping, namely, clade

B, comprising three other Mesozoic fossil genera, *Sauktangida*, *Mirokempynus*, and *Ponomarenkius*, and clade C, comprising the only Cenozoic genus of *Eupoismites* and all extant genera (**Figure 2**). In clade B, the genus *Sauktangida* from the Early Jurassic is sister to *Mirokempynus* and *Ponomarenkius*, which is supported by one synapomorphy: well-developed A2 with several pectinated branches (Cha. 17:2). The grouping of two Middle Jurassic genera, *Mirokempynus* and *Ponomarenkius* was also anticipated for sharing the distinct pattern of MP branches in the hind wing (Cha. 13: 1). The four southern genera were well grouped (clade C), which was supported by three apomorphic characters: distally dichotomously branched CuA (Cha. 8: 1), A1 approximately the half the length of CuP (Cha. 9: 1); the multiple rows of cells present in the distal half of MP (Cha. 15: 2). However, the inner relationships of these southern genera were not well resolved except for the grouping of *Kempynus* and *Euosmylus* that were supported by two apomorphic characters: the modified outer margin of the forewing (Cha. 1: 1) and distinctly curved RP branches (Cha. 12: 1) (**Figure 2**).

Discussion

Considering the distribution pattern of extant lineages, Kempyninae unequivocally belongs to a typical Gondwanan group, especially for the occurrence of the Cenozoic genus
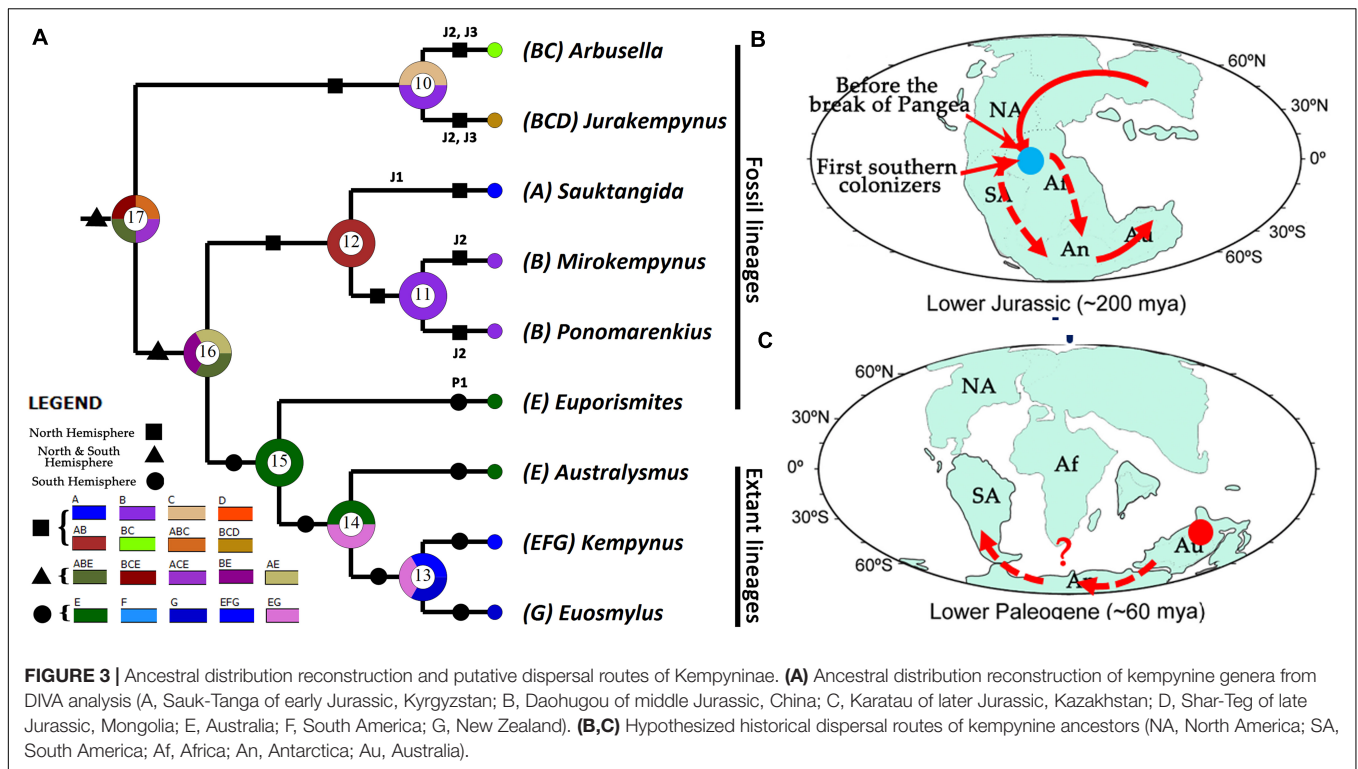
FIGURE 2 | Most parsimonious tree of Kempyninae from phylogenetic analyses (tree length = 35 steps; consistency index, CI = 0.74; retention index, RI = 0.76); ●, apomorphic characters; ○, parallelisms and reversals.

Euporismites, also from Australia. However, the occurrences of diverse fossil kempynines from the Northern Hemisphere imply that the evolution of this group should have a more complicated scenario. Based on the results of phylogenetic analyses (**Figure 2**), the northern Mesozoic kempynines occupied the earliest divergence of the group (**Figure 2**: Clades A, B), which strongly implies an earlier and northern origin of this subfamily. Two questions have arisen: how and when the northern ancestors migrated to the austral areas, and how the extant kempynines shaped the current distribution pattern.

It is noted that the ancestral distribution reconstruction from DIVA analysis acquired multiple ancestral distributions, in which Australia was consistently aligned with the Northern distributions (**Figure 3A**: node 17). The genus *Sauktangida*, as the earliest fossil record of Kempyninae, in the phylogenetic tree (**Figure 2**), is not the most basal clade of Kempyninae, and instead, along with two Middle Jurassic genera, constitutes a derived clade that is sister to the southern lineages. The results strongly implied an earlier and prepangean origin of Kempyninae, and the ancestors first migrated to the future Gondwana before the breakup of Pangea [no later than 174 Mya (Dietz and Holden, 1970; Cox, 2000)]. This point partly agrees with the results of molecular dating that concluded the divergence time of major clades of Osmylidae was before the breakup of Pangaea (Early to Mid-Triassic, 247 Mya) (Winterton et al., 2017). In this hypothesis, the northern and southern kempynines are considered to evolve independently after the separation of Laurasia and Gondwana. As Laurasia was an intact landmass (Dietz and Holden, 1970; Cox, 2000), the northern kempynine ancestors were able to achieve a widespread distribution by an early dispersal over land (**Figure 3A**: nodes 10,

12), resulting in the remarkable diversity of Kempyninae in North Hemisphere. Although we could not determine the origin place of Kempyninae, it is evident that the early colonization had been proceeding, considering the widespread distribution of Jurassic kempynines in the Northern Hemisphere. It is noteworthy that no convincing Cretaceous kempynines were reported except for several equivocal records (Makarkin, 1990, 2014). Also, it is still an enigma for the ultimate disappearance of these kempynine antiques in the Northern Hemisphere. Considering the stable Laurasia landmass, the extinction of kempynines in the Northern Hemisphere was possibly not related to the plate drift but more possibly to the subsequent climate changes.

It is bewildering that the absence of the Mesozoic fossil kempynines in the Southern Hemisphere (Khramov, 2017), which hindered our understanding to further trace the history of Kempyninae. It is noted that the youngest known kempynine fossil is from the Redbank Plains Formation of the late Paleocene-early Eocene in Australia [ca. 55 Mya (Tillyard, 1916; Rozefelds et al., 2016)], and it means that the ancestors of Kempyninae should have reached the southern destination no later than this time. Based on the current analyses, it is noted that all southern kempynines are grouped into a single clade (**Figure 2**), which shared a common ancestral distribution in DIVA analysis, i.e., Australia (**Figure 3A**: node 15). Considering the prepangean origin of Kempyninae, it is easy to conclude that the first southern colonizers could disperse southerly through South America or Africa to the southernmost destination (**Figure 3B**). It means that the extant kempynines should have no direct ancestor-descendent relationships with their northern Mesozoic relatives, but instead descended from the "first southern ancestors." It should be mentioned that the most

FIGURE 3 | Ancestral distribution reconstruction and putative dispersal routes of Kempyninae. **(A)** Ancestral distribution reconstruction of kempynine genera from DIVA analysis (A, Sauk-Tanga of early Jurassic, Kyrgyzstan; B, Daohugou of middle Jurassic, China; C, Karatau of later Jurassic, Kazakhstan; D, Shar-Teg of late Jurassic, Mongolia; E, Australia; F, South America; G, New Zealand). **(B,C)** Hypothesized historical dispersal routes of kempynine ancestors (NA, North America; SA, South America; Af, Africa; An, Antarctica; Au, Australia).

widespread genus *Kempynus* [occurs in Australia, New Zealand, and South America (Argentina and Chile)] and a New Zelanian endemic genus *Euosmylus* were placed in the most derived clade (**Figure 2**). If considering the northern origin of Kempyninae, it is easy to deduce that the northerly American lineages should represent the earlier divergence, and the Australian lineages should be a more derived clade. If so, the *Kempynus* should be the basalmost lineage of Kempyninae. Herein, an alternative hypothesis is proposed to explain this contradiction: the extant kempynines of Southern America should derive from Australia, which means that the extant kempynines possibly re-dispersed to South America following their Mesozoic ancestors' route, representing a recent Paleocene-Eocene dispersal event (**Figure 3C**). Nevertheless, this hypothesis is far from being supported just based on the current evidence. It is hoped that a future phylogeny of extant kempynines, especially for the inclusion of all *Kempynus* species, could provide a deep insight into this question.

As the relic of ancient lineages, it is vital to trace the history by combining both fossil and extant groups. Although it is far from eventually revealing the evolutionary history of Kempyninae due to the currently limited evidence, the results still exposed a more complicated scenario of Kempyninae, which could direct the future research to the insects.

CONCLUSION

In this study, we described a new species *Arbusella platyptera* Ma *et* Wang, sp. nov. from the Jiulongshan Formation in Daohugou,

Inner Mongolia, China. A key to the extinct species and extant genera of Kempyninae is provided. Combining all extant and most fossil genera, we performed phylogenetic and dispersal-vicariance analyses to trace the history of Kempyninae for the first time. The results corroborated the monophyly of Kempyninae and revealed a northern and prepangean origin for the subfamily. Our results also indicated that the Mesozoic kempynine and the extant lineages had no direct ancestor-descendent relationships. The results expose a more complicated evolutionary scenario of the relic insects and provide new insight into understand the historical evolution of insects that have a long history.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

YM contributed to conceptualization, formal analysis, and writing—original draft. CS contributed to writing—original draft. DR contributed to funding acquisition, investigation, resources, supervision, and writing—original draft. YW contributed to conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, and writing—original draft. All authors contributed to the article and approved the submitted version.

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