

Taxonomic review and phylogenetic inference elucidate the evolutionary history of Mesozoic Procercopidae, with new data from the Cretaceous Jehol Biota of NE China (Hemiptera, Cicadomorpha)

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Abstract

The Mesozoic family Procercopidae is widely treated as the ancient group of Cercopoidea and a transitional unit to recent lineages, but its evolution and diversity are vague due to fragmentary fossil record and confusing taxonomic history. Herein, an extensive taxonomic review of Procercopidae is presented and some new fossils are reported from the Lower Cretaceous Yixian Formation of NE China. As a result, *Chengdecercopis* Hong, 1983 is transferred from Procercopidae to Sinoalidae; *Procercopis longipennis* Becker-Migdisova, 1962 and *P shawanensis* Zhang, Wang and Zhang, 2003 are transferred to *Procercopina* Martynov, 1937, resulting in *Procercopina longipennis* (Becker-Migdisova, 1962), comb. n. and *P shawanensis* (Zhang, Wang and Zhang, 2003), comb. n.; *Luanpingia senjituensis* Hong, 1984 is transferred to *Stellularis* Chen, Yao and Ren, 2015, leading to *Stellularis senjituensis* (Hong, 1984), comb. n.; *Anthoscytina macula* Hu, Yao and Ren, 2014 is transferred to *Sinocercopis* Hong, 1982, and *Sunoscytinopterus* (Scytinoptera) and *Cathaycixius* (Cixiidae) are treated as junior homonym names of *Sinocercopis*, leading to *Sinocercopis macula* (Hu, Yao and Ren, 2014), comb. n., *S lushangfenensis* (Hong, 1984), comb. n., *S pustulosus* (Ren, 1995), comb. n., and *S trinervis* (Ren, 1995), comb. n. Additionally, two new species are erected: *Stellularis bineuris* Chen and Wang, sp. n. and *S minutus* Chen and Wang, sp. n. Our cladistic analysis based on wing (tegmen and hind wing) characteristics recovers the high-level relationships within Cercopoidea: Sinoalidae + (Procercopidae + (Cercopionidae + modern cercopoids)). Within the family Procercopidae, the cladistic analysis reveals that the Middle to Late Jurassic *Titanocercopis* and *Jurocercopis* and the Cretaceous *Cretocercopis* occupy the basal position, and a gradual change in wing venation can be recognized from the Early Jurassic *Procercopis* and *Procercopina* to the Jurassic *Anthoscytina*, and then to the Cretaceous *Stellularis* and *Sinocercopis*. The two Cretaceous genera, sharing wing traits with extant

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cercopoids, likely represent transitional forms between Procercopidae and recent Cercopoidea; however, they are very similar to their Jurassic relatives in body structures, suggesting it is applicable to attribute them to Procercopidae. Furthermore, our analysis suggests that the extinction of Procercopidae and the origin and early diversification of modern Cercopoidea approximately coincided with the rise and explosive radiation of angiosperms in the late Early Cretaceous and onwards.

KEYWORDS

phylogenetic inference, Procercopidae, *Stellularis bineuris* sp. n., *Stellularis minutus* sp. n., taxonomic review

1 | INTRODUCTION

The remarkable hemipteran Cercopoidea Leach, 1815, as the second largest superfamily of Cicadomorpha, is a worldwide distributed insect group comprising over 2,600 species and occurring in most terrestrial habitats (Bartlett et al., 2018; Chen, Wang, Zhang, Wang, & Zheng, 2015; Chen, Zhang, Wang, Zheng, & Wang, 2015; Cryan & Svenson, 2010; Paladini, Takiya, Urban, & Cryan, 2018; Soulier-Perkins, 2019). Adult cercopoids are commonly called froghoppers, because these insects possess a frog-like appearance, and more notably, they achieve their jumping supremacy by using a particular catapult mechanism: The leaping force exerted is 414 times more than their body weight and is much higher than in other jumping animals including the well-known fleas (Burrows, 2003). To provide protection from predation, parasitism and desiccation, cercopoid nymphs, known as spittlebugs or cuckoo-spit insects, cover themselves with foaming spittle or live in sap-filled tubes (Cryan & Svenson, 2010; Rakitov, 2002). Both adults and nymphs are phytophagous insects with body size ranging from 3 to 27 mm, feeding on fluid contained in xylem tissue, and many groups exhibit a strong preference for nitrogen-fixing plants (Bartlett et al., 2018; Cryan & Svenson, 2010; Hong, 1983; Thompson, 1994; Wang, Szwedo, & Zhang, 2012).

Up to now, five extant families have been erected within Cercopoidea (i.e., Cercopidae Leach, 1815, Aphrophoridae Amyot & Audinet-Serville, 1843, Clastopteridae Dohrn, 1859, Machaerotidae Stål, 1866, and Epipygidae Hamilton, 2001), but their systematic position is still under controversy: Different taxonomists recognize three to five families (Dietrich, 2002, 2005; Hamilton, 2001; Soulier-Perkins, 2008). Cercopidae and Aphrophoridae are well supported as sister lineages in both recent molecular and morphological studies (Cryan & Svenson, 2010; Paladini et al., 2018), sharing some unique biological and morphological features: nymphs producing large bubbles in the "spittle" masses, antennae in shallow and open pits, or beneath prominent antennal ledges at margin of crown (Hamilton, 2001). Epipygidae bears some remarkable morphological characteristics, but is apparently nested within Aphrophoridae in a molecular phylogenetic analysis (Cryan & Svenson, 2010), suggesting that the family is the specialized descendant of Aphrophoridae. The recent molecular phylogenetic investigations indicate that both Machaerotidae

and Epipygidae are basal lineages within the five modern families, but their relationship has not been well resolved (Cryan & Svenson, 2010; Paladini et al., 2018); morphological data, however, apparently indicate that these two families constitute a monophyletic group, with a series of autapomorphies: nymphs inefficient in producing bubbles, antennae in deep circular pits, mesonotum elongate, tegmen commonly with a wide appendix, and hind wing with RP lacking terminal branch (Hamilton, 2001; Yuan & Zhang, 1999).

The extant cercopoid families were considered to rise in the mid- to Late Cretaceous (Shcherbakov & Popov, 2002; Wang et al., 2012); however, the hitherto definite earliest records of modern froghopper were from the Paleocene, represented by Cercopidae and Aphrophoridae (e.g., Piton, 1936; Zeuner, 1941). The known Mesozoic froghoppers are assigned to three extinct families (i.e., Procercopidae Handlirsch, 1906, Cercopionidae Hamilton, 1990 and Sinoalidae Wang and Szwedo, 2012). Procercopidae, widely spread in Eurasia in the Jurassic and Early Cretaceous (Figure 1), is accepted as one of the stem cercopoid lineages and the ancestral group of modern ones (Chen, Wang, et al., 2015; Shcherbakov & Popov, 2002; Wang et al., 2012). Sinoalidae, recorded in the Middle to Upper Jurassic of NE China and the mid-Cretaceous Burmese amber, is closely related to early Procercopidae and also shares some plesiomorphic characters with ancient Hylcelloidea, likely representing one of early diversifications of Cercopoidea (Chen et al., 2018; Chen, Zheng, Wei, & Wang, 2017; Fu & Huang, 2018; Wang et al., 2012). The little known Cercopionidae, with only one definite record from the mid-Cretaceous of Brazil, was likely derived from the Procercopidae in the Early Cretaceous and represents an offshoot of ancestral group of modern Cercopoidea (Chen et al., 2018; Hamilton, 1990; Wang et al., 2012).

As an ancient lineage of Cercopoidea and a transitional unit to extant groups with a high bio-diversity, Procercopidae is vitally significant in revealing the early evolutionary history of Cercopoidea. The first fossil specimen of Procercopidae, an isolated hind wing, was reported from the Lower Jurassic of Germany and originally attributed to the type genus of modern Cercopidae (*Cercopis* Fabricius, 1775) (Geinitz, 1884). Handlirsch (1906) erected the Procercopidae to accommodate the genus *Procercopis* Handlirsch, 1906 with the species described in Geinitz (1884) and two new species on the basis of a tegmen and hind wing, respectively. Additional genera and species,

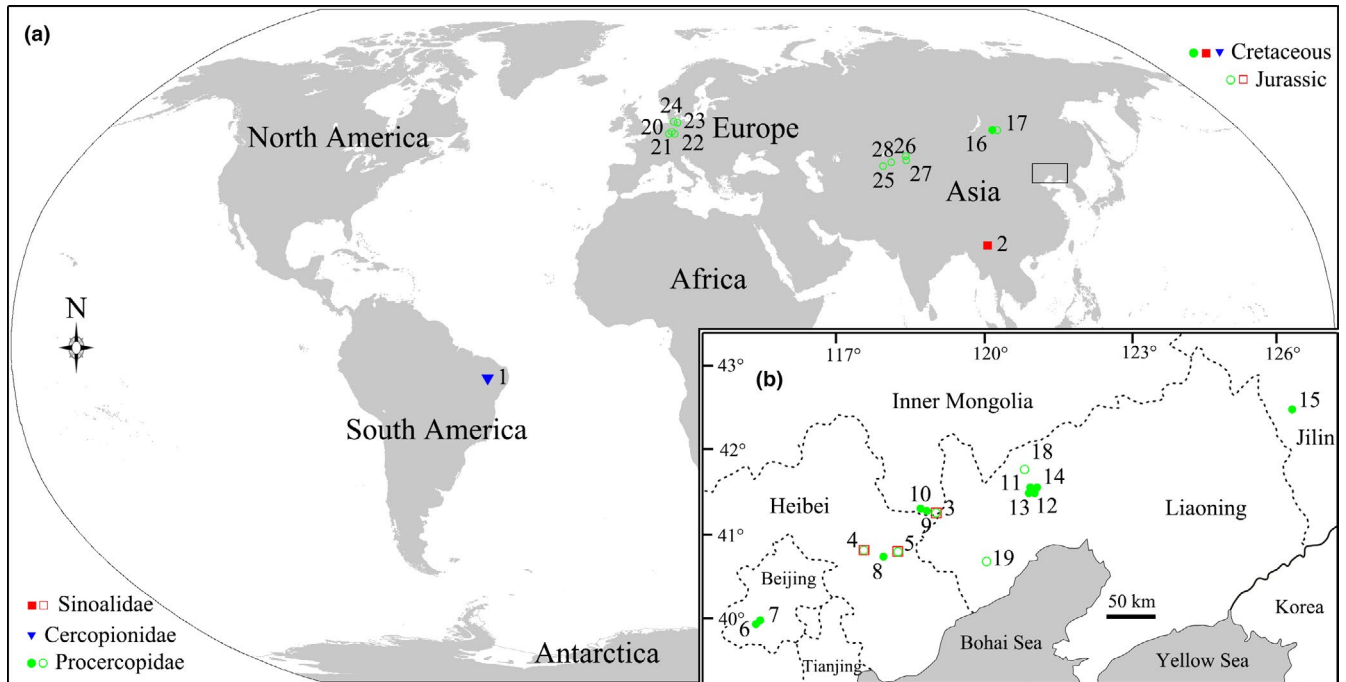


FIGURE 1 Locations of Mesozoic fossils ascribed to the superfamily Cercopoidea. (a) World map and (b) map of northeastern China. See Table 1 for the detailed information on geographical and stratigraphical distribution of each fossil locality

erected based on isolated tegmina or hind wings from the Lower Jurassic of Germany and Central Asia, were subsequently added to this family by Martynov (1937), Bode (1953), and Becker-Migdisova (1962). The first whole-bodied procercopid (the holotype of *Sinocercopis liaoyuanensis* Hong, 1982) was described and illustrated from the Early Cretaceous Jehol Biota of NE China, and originally placed in the modern Cercopidae (Hong, 1982). Subsequently, some nearly complete procercopids with both body structures and wings preserved were reported from the Middle and Upper Jurassic and the Lower Cretaceous of northeast Asia (NE China and Siberia of Russia) (Chen, Wang, et al., 2015; Chen, Yao, & Ren, 2015; Chen, Zhang, et al., 2015; Hong, 1983, 1984; Hu, Yao, & Ren, 2014; Ren, 1995; Ren, Cai, & Xiu, 1998; Shcherbakov, 1988; Wang & Zhang, 2009; this study).

The fossil data on Procercopidae have been significantly updated in recent decades, but the taxonomy of this family is somewhat confusing and some fossil records apparently need an exhaustive reinvestigation (Wang & Zhang, 2009). The chaotic situation hampers our understanding of morphological disparity and evolutionary history of Mesozoic procercopids as well as the rise and early diversity of modern froghoppers. We herein report some new fossil procercopids from the Lower Cretaceous Yixian Formation (Jehol Biota) of NE China. Moreover, to shed light on the evolutionary history of the Mesozoic Cercopoidea, an extensive taxonomic review and phylogenetic analyses were executed.

2 | MATERIAL AND METHODS

2.1 | Fossil material

The new fossil materials were collected from the Yixian Formation (Lower Cretaceous of Inner Mongolia and Liaoning, China) (Table 1)

and are housed in the Institute of Geology and Paleontology, Linyi University and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences in Nanjing, China. The Yixian Formation, widespread across Liaoning, Hebei, and Inner Mongolia of NE China, yields diverse feathered dinosaurs, primitive birds, mammals, angiosperms, and abundant insects belonging to the well-known Jehol Biota (e.g., Shi, Béthoux, Shih, & Ren, 2012; Sun, Dilcher, Zheng, & Zhou, 1998; Xu, Makovicky, Wang, Norell, & You, 2002), which contributes significantly to our understanding of the transformations of terrestrial ecological system in the late Mesozoic (Lloyd et al., 2008). The geological age of Yixian Formation was under great controversies in the last century, varying from the Late Jurassic to Early Cretaceous. As indicated from recent studies in biostratigraphy and isotopic geochronology, the age of fossiliferous beds of this formation is now widely regarded as the Barremian to Aptian (Chang, Gao, Zhou, & Jourdan, 2017).

Fossil materials described herein were examined and photographed dry or under alcohol, using a VHX 5000 digital microscope platform. Illustrations and line drawings were prepared with software programs CorelDraw 12.0 and Adobe Photoshop CS3. In the line drawing, faintly seen and hypothesized regions are indicated by dotted lines, while the edges of missing regions are indicated by thin solid lines. All measurements were made in the software ImageJ 1.42q (Wayne Rasband; National Institutes of Health).

2.2 | Venational terminology

The venational terminology used herein follows Chen et al. (2018), which is slightly modified from Nel et al. (2012). In Nel et al. (2012), a new interpretation of wing venation pattern for all Paraneoptera was

TABLE 1 Mesozoic geographical and stratigraphical distribution of the superfamily Cercopoidea

Horizon	Locality	Taxa	Reference
Cercopionidae			
Crato Fm., Albian (K1)	Crato Ceará ¹ , Brazil	<i>Cercopion reticulata</i> Hamilton, 1990	Hamilton (1990)
Sinoalidae			
Cenomanian (K2)	Kachin ² , Myanmar	<i>Fangyuania xiai</i> Chen, Szwedo and Wang, 2018	Chen et al. (2018)
Jiulongshan Fm., Callovian– Oxfordian (J2–J3)	Daohugou ³ , Ningcheng; Zhouyingzi ⁴ , Luanping; Xiaofanzhangzi ⁵ , Chengde, China	<i>Luanpingia longa</i> Hong, 1983; <i>L daohugouensis</i> Fu et al., 2017; <i>Chengdecercopis xiaofanzhangziensis</i> Hong, 1983; <i>Huabeicercopis yangi</i> Hong, 1983; <i>Hebeicercopis triangulata</i> Hong, 1983; <i>Sinoala parallelivena</i> Wang and Szwedo, 2012; <i>Jiania crebra</i> Wang and Szwedo, 2012; <i>J gracila</i> Wang and Szwedo, 2012; <i>Shufania hani</i> Chen et al., 2017; and <i>Stictocercopis wuhuaensis</i> Fu and Huang, 2018	Chen et al. (2017), Fu et al. (2017), Fu and Huang (2018), Hong (1983), Wang et al. (2012)
Procercopidae			
Lushangfen Fm., Albian (K1)	Chongwenshuiku ⁶ and Lushangfen ⁷ , Beijing, China	<i>Cretocercopis yii</i> Ren, 1995; <i>Sinocercopis lushangfenensis</i> (Hong, 1984); <i>S pustulosus</i> (Ren, 1995); <i>S trinervis</i> (Ren, 1995)	Hong (1984), Ren (1995)
Yixian Fm., Barremian– Aptian(K1)	Shidongzi ⁸ , Fengning; Yangshuwanzi ⁹ and Liutiaogou ¹⁰ , Ningcheng; Huangbanjigou ¹¹ , Chaomidian ¹² , Sihetun ¹³ and Jianshangou ¹⁴ , Beipiao; Xiajiajie ¹⁵ , Liaoyuan, China	<i>Stellularis</i> sp.; <i>S longirostris</i> Chen, Yao, et al., 2015; <i>S senjituensis</i> (Hong, 1984); <i>S aphthosa</i> (Ren et al., 1998); <i>S bineuris</i> Chen and Wang, sp. n.; <i>S minutus</i> Chen and Wang, sp. n.; <i>Sinocercopis liaoyuanensis</i> Hong, 1982; and <i>S macula</i> (Hu et al., 2014)	Chen, Yao, et al. (2015), Hong (1982, 1984), Hu et al. (2014), Ren et al. (1998), this study
Daya Fm., Hauterivian (K1)	Shiviya ¹⁶ , Chita, Russia	Procercopidae sp.	Shcherbakov (1988)
Glushkovo Fm., Tithonian (J3)	Daya ¹⁷ , Chita, Russia	<i>Anthoscytina daica</i> Shcherbakov, 1988	Shcherbakov (1988)
Jiulongshan Fm., Callovian– Oxfordian (J2–J3)	Zhouyingzi ⁴ , Luanping; Xiaofanzhangzi ⁵ , Chengde; Daohugou ³ , Ningcheng, China	<i>Anthoscytina liugouensis</i> (Hong, 1983); <i>A parallelica</i> Ren, 1995; <i>A perpetua</i> Li, Shih and Ren, 2013; <i>A brevineura</i> Chen, Wang and Zhang, 2015; <i>A elegans</i> Chen, Wang and Zhang, 2015; <i>Jurocercopis grandis</i> Wang and Zhang, 2009; and <i>Titanocercopis borealis</i> Chen, Zhang and Wang, 2015	Chen, Wang, et al. (2015), Chen, Zhang, et al. (2015), Hong (1983), Ren (1995), Wang & Zhang (2009)
Haifanggou Fm., Callovian– Oxfordian (J2–J3)	Yujiagou ¹⁸ , Beipiao; Sandaogou ¹⁹ , Xingcheng, China	<i>Anthoscytina longa</i> Hong, 1983; <i>A hongii</i> Chen Wang and Zhang, 2015	Chen, Wang, et al. (2015), Hong (1983)
Posidonia Shale Fm., Toarcian (J1)	Hondelage ²⁰ , Braunschweig; Grassel ²¹ , Braunschweig; Beienrode ²² , Fletchtorf, Germany	<i>Procercopis abscissa</i> Bode, 1953; <i>P completa</i> Bode, 1953; <i>P debilis</i> Bode, 1953; <i>P lacerata</i> Bode, 1953; and <i>P wunnenbergi</i> Bode, 1953	Bode (1953)
<i>Dactylioceras tenuicostatum</i> Zone, Toarcian (J1)	Klein Lehmhagen pit ²³ , Grimmen, Germany	<i>Procercopina frenzeli</i> Ansorge, 1996	Ansorge (1996)
<i>Harpoceras falciferum</i> Zone, Toarcian (J1)	Dobbertin ²⁴ , Mecklenburg of Germany	<i>Procercopis alutacea</i> Handlirsch, 1906; <i>P liasina</i> Handlirsch, 1906; <i>P coriacea</i> Handlirsch, 1939; <i>P similis</i> Handlirsch, 1939; and <i>P jurassica</i> (Geinitz, 1884)	Geinitz (1884), Handlirsch (1906–1908, 1939)
Pliensbachian (J1)	Kyzyl-Kiya ²⁵ , Kyrgyzstan	<i>Procercopina asiatica</i> (Martynov, 1937) <i>Anthoscytina reducta</i> (Becker-Migdisova, 1949)	Becker-Migdisova (1949), Martynov (1937)
Badaowan Fm., Hettangian– Sinemurian (J1)	Tuzigou ²⁶ , Karamay; Nan'anji ²⁷ , Shawan, China	<i>Procercopina delicata</i> Zhang et al., 2003 and <i>P shawanensis</i> (Zhang et al., 2003)	Zhang et al. (2003)
Dzhil Fm., Hettangian (J1)	Issyk-Kul ²⁸ , Kyrgyzstan	<i>Procercopina longipennis</i> (Becker-Migdisova, 1962)	Becker-Migdisova (1962)

Superscript numbers indicate localities labeled in Figure 1.

Abbreviations: Fm., formation; J1, Lower Jurassic; J2, Middle Jurassic; J3, Upper Jurassic; K1, Lower Cretaceous; K2, Upper Cretaceous.

TABLE 2 Definition of morphological characters and states

No.	Morphological characters and states
Tegmen	
1	Width of tegmen: 0, slender, with length about 3 times or more as long as width; 1, shortened, at most twice as long as wide
2	Level of sclerosis: 0, sclerotized all over; 1, costal area and clavus sclerotized, but other parts membranous
3	Peripheral membrane: 0, absent or not prominent; 1, very wide
4	Anterior margin at ScP terminal position: 0, smooth; 1, concave
5	Pc + CP: 0, thick and long, distinctly exceeding basal cell; 1, weak and short, or even completely fused with costal margin at wing base
6	Independent basal part of ScP: 0, short, not fused with stem R; 1, extremely long, almost as long as 1/3 of wing length, fused with stem R
7	R bifurcating into RA and RP: 0, near basal 1/3 of wing length; 1, near or beyond middle of tegmen
8	Number of terminal branches of RP: 0, single (occasionally two); 1, multibranching (four)
9	RP: 0, ending at apical margin; 1, terminal part fused with crossvein
10	MP: 0, multibranching (commonly with five or more terminal branches); 1, three-branched; 2, two-branched; 3, unbranched
11	MP ₁₊₂ : 0, branched; 1, unbranched
12	MP ₃₊₄ : 0, branched; 1, unbranched
13	Branching position of MP: 0, before or at the same level of claval tip; 1, beyond claval tip
14	CuA: 0, two-branched; 1, multibranching; 2, single-branched
15	CuA ₂ : 0, long, slightly shorter than CuA ₁ ; 1, shortened, just about half as long as CuA ₁
16	RP, terminal branches MP, and CuA ₁ beyond crossveins <i>ir</i> , <i>rp-mp</i> , <i>imp</i> , <i>mp-cua</i> when those crossveins single in number: 0, strongly curved and/or not subparallel to each other; 1, almost straight and subparallel
17	A ₁ : 0, originating at claval margin far away from wing base, not fused with Pcu. 1, originating near wing base and fused with Pcu terminally
18	Crossveins when just one in number: 0, far away from wing tip; 1, migrated to wing apical margin
19	Crossvein <i>ir</i> : 0, simple, just one in number (occasionally two); 1, four; 2, five
20	Crossvein <i>rp-mp</i> : 0, four; 1, simple, just one in number (occasionally two); 2, five; 3, eight
21	Crossvein <i>imp</i> : 0, present; 1, absent
22	Crossvein <i>mp-cua</i> connecting MP: 0, at MP ₃₊₄ ; 1, at stem MP
23	Crossvein <i>mp-cua</i> connecting CuA: 0, at branch CuA ₁ far away from bifurcation of CuA; 1, almost at the bifurcation of CuA
24	Crossvein <i>cua-cup</i> : 0, connecting MP + CuA; 1, connecting R + MP + CuA at its branching position
Hind wing	
25	Peripheral membrane: 0, absent; 1, narrow and outer margin smooth; 2, very wide and outer margin sinuous
26	Stem R: 0, short, bifurcating near wing base; 1, long, bifurcating near or even considerably beyond wing mid-length
27	RP: 0, independent; 1, terminal part fused with RA
28	MP: 0, multibranching (five); 1, bifurcation; 2, single-branched
29	Bifurcating position of MP: 0, almost at the same level of bifurcating position of CuA; 1, distinctly beyond bifurcating position of CuA
30	MP ₃₊₄ : 0, independent; 1, fused with MP ₁₊₂ terminally
31	Crossveins <i>rp-mp</i> and <i>mp-cua</i> : 0, present; 1, absent
32	Crossvein <i>mp-cua</i> : 0, connecting MP ₃₊₄ ; 1, connecting stem MP

proposed, assuming that CuA gets fused with MP + R stem at wing base and connected with CuP by a specialized crossvein *cua-cup*, which is remarkably different from the traditional interpretations. In Chen et al. (2018), the first longitudinal vein in clavus is treated as Pcu rather than A₁ and the independent median vein is treated as MP instead of M.

2.3 | Character choice

Most Mesozoic cercopoids were described just based on wings, and few body structures bearing phylogenetic significance have been reported. Therefore, we herein only employ wing traits in our cladistic analyses.

The morphological matrix comprises 32 characters: Characters 1–24 are based on tegmen, and characters 25–32 are based on hind wing (Table 2). Of them, 26 characters were coded as binary and 6 as multistate. Multistate characters were treated as non-additive. All the characters are unordered and of equal weight. Missing and inapplicable data are coded with “?” and “–,” respectively. The data matrix is in Table 3.

2.4 | Taxon sampling

The vast majority of fossil procercopid species were erected on the basis of isolated tegmen or hind wing. To reduce the impact of missing

TABLE 3 Morphological character state matrix of 32 characters included in the phylogenetic study

Taxon/ character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
<i>Vietocycla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Stictocercopis</i>	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0	
<i>Cercopion</i>	0	0	0	0	?	1	1	0	0	3	-	-	-	1	1	-	0	-	1	3	-	-	0	0	0	1	?	0	2	-	1	-	
<i>Aphrophora</i>	0	0	0	0	1	1	1	0	0	3	-	-	-	0	1	1	0	1	0	1	-	-	0	0	2	1	0	2	-	-	0	-	
<i>Clastoptera</i>	1	0	1	0	1	1	1	0	1	3	-	-	-	2	1	1	0	1	0	1	-	-	0	0	2	1	1	2	-	-	0	-	
<i>Procerpopsis</i>	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	-	0	-	2	2	0	0	0	0	0	1	1	0	1	0	0	1	
<i>Procerpocina</i>	0	0	0	0	1	0	0	0	0	{12}	1	{01}	0	0	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?	?	
<i>Anthoscytina</i>	0	0	0	0	1	0	0	0	0	{12}	1	{01}	1	0	1	1	0	1	0	1	1	0	0	0	1	1	0	1	1	0	0	1	
<i>Titanocercopis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	1	0	1	1	0	0	1	
<i>Jurocercopis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	?	1	0	1	1	0	0	1	
<i>Cretocercopis</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	-	0	1	0	1	0	1	1	1	0	1	1	0	1	
<i>Stellularis</i>	0	0	0	0	1	0	0	0	0	{23}	1	1	1	0	1	1	1	0	1	0	1	1	0	0	0	1	1	0	2	-	-	0	-
<i>Sinocercopis</i>	0	0	0	0	1	0	0	0	0	{23}	{01}	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0	2	-	-	0	-

Note: The “?” and “-” denote that the state is unknown or inapplicable, respectively. { } indicates two states present for the character of the taxon.

data, the phylogenetic reconstruction is inferred at genus level instead of species level. All eight valid procerpocid genera are included as in-groups. Hylcelloidea is considered to be the ancestral group to all the five modern superfamilies of Cicadomorpha (Szwedo, 2018; Wang et al., 2012), but just a few genera, for example, *Vietocycla* Shcherbakov, 1988, contain information on both tegmen and hind wing, and so *Vietocycla* is chosen as the ultimate out-group herein. *Stictocercopis* Fu and Huang, 2018 is chosen as another out-group because the genus is one of primitive forms of the Sinoalidae (Chen et al., 2017, 2018; Chen, Wang, Zheng, Jarzembowski, et al., 2019). The Mesozoic monogeneric family Cercopionidae is represented by its nominal genus *Cercopion* Hamilton, 1990. Modern Cercopoidea is likely divided into two lineages according to molecular and morphological data: (Aphrophoridae + Epipygidae + Cercopidae) + (Clastopteridae + Machaerotidae) (Paladini et al., 2018). We herein choose *Aphrophora* Germar, 1821 and *Clastoptera* Germar, 1839 as the representatives of modern Cercopoidea.

2.5 | Phylogenetic analyses

Bayesian inference analysis (BI) in MRBAYES 3.1.2 (Ronquist & Huelsenbeck, 2003) and maximum parsimony analysis (MP) in PAUP* (Swofford, 2003) were performed. For BI analysis, the Mk model with only variable characters (also called Mkv model) and default settings for priors were chosen. This model, as a likelihood phylogenetic approach for discrete morphological characters, assumes all states have the same frequency and all transitions between different states occur at the same rate (Allman, Holder, & Rhodes, 2009; Lewis, 2001). Bayesian Markov chain Monte Carlo chains were run for 10 million generations. Twenty-five percent trees were discarded as burn-in to ensure that the analysis had stabilized. The Bayesian posterior probabilities (PP) of the tree nodes were calculated. For MP analysis, heuristic searches were executed for 1,000 replicates with TBR branch swapping. Non-parametric bootstrap analysis (BS) with 1,000 replicates was performed to assess nodal reliabilities.

The strict consensus tree inferred from maximum parsimony trees was used in character mapping, executed in the morphological analysis software program WinClada ver. 1.00.08 (Nixon, 2002).

3 | RESULTS

3.1 | Systematic paleontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cercopoidea Leach, 1815

3.1.1 | Family Procerpocidae Handlirsch, 1906

Included genera

Procerpopsis Handlirsch, 1906; *Procerpocina* Martynov, 1937; *Anthoscytina* Hong, 1983; *Titanocercopis* Chen, Zhang and Wang,

2015; *Juroceropsis* Wang and Zhang, 2009; *Cretocercopsis* Ren, 1995; *Stellularis* Chen, Yao, et al., 2015; *Sinocercopsis* Hong, 1982.

Diagnosis

Tegmen sclerotized and punctate all over, with peripheral membrane not prominent, independent basal part of ScP short, fused to stem R + MP + CuA basad of tip of basal cell, stem R bifurcating into RA and RP near basal 1/3 of wing length, *imp* commonly present, *mp-cua* connecting CuA₁ far away from bifurcation of CuA, *cua-cup* connecting MP + CuA; hind wing with peripheral membrane narrow and smooth, stem R long, bifurcating near the middle of wing, MP reduced, commonly with single or two terminal branches, bifurcating position of MP distinctly beyond that of CuA when MP two-branched, crossvein *mp-cua* connecting stem MP.

Occurrence

Lower Jurassic of Kyrgyzstan, NW China, and Germany; Middle to Upper Jurassic of NE China; Upper Jurassic of Siberia; and Lower Cretaceous of Siberia, Mongolia, and NE China.

Remarks

Compared to its ancestral group Hylcelloidea and early cercopoid Sinoalidae, Procercopidae possesses the tegmen with few derived features, but the hind wing showing some autapomorphies, such as bifurcating position of MP distinctly beyond that of CuA and crossvein *mp-cua* connecting stem MP instead of MP₃₊₄. All the eight genera of Procercopidae were erected mainly based on tegminal characters. At genus and species levels, the hind wing can be venationally divided into three types: (a) early procercopids of Jurassic share the hind wing with almost same topology with MP bearing two free terminal branches, except for *Procercopis debilis* and *P wunnenbergi* with additional crossveins and *P abscissa* with Pcu multibranched; (b) Cretaceous *Cretocercopsis* possesses the hind wing with MP₃₊₄ fused with MP₁₊₂ apically; and (c) Cretaceous *Stellularis* and *Sinocercopsis* bear the hind wing with single MP as seen in Cercopionidae and modern Cercopoidea.

3.1.2 | Genus *Procercopis* Handlirsch, 1906

Included species

Type species: *P alutacea* Handlirsch, 1906 (tegmen), by subsequent designation of Becker-Migdisova (1962). Other species: *P jurassica* (Geinitz, 1884) (hing wing); *P liasina* Handlirsch, 1906 (hind wing); *P coriacea* Handlirsch, 1939 (tegmen); *P similis* Handlirsch, 1939 (hing wing); *P abscissa* Bode, 1953 (hing wing); *P completa* Bode, 1953 (hing wing); *P debilis* Bode, 1953 (hing wing); *P lacerata* Bode, 1953 (hing wing); and *P wunnenbergi* Bode, 1953 (hing wing).

Occurrence

Lower Jurassic of Germany.

Remarks

Procercopis is remarkably different from its confamilials in having tegmen with crossveins *ir* and *rp-mp* numerous, totally five in

number. Its hind wing shows considerably variable: *P liasina*, *P similis*, *P jurassica*, and *P completa* possess hind wing with topology almost the same as in other Jurassic procercopids, but *P debilis* and *P wunnenbergi* have hind wing with numerous crossveins, and *P abscissa* with numerous terminal branches of CuA. These totaling variations are probably genus-level morphological features. However, considering that the type species of *Procercopis* was erected based on an isolated tegmen and its congeners on isolated tegmina or hind wings, it is hard to re-determine their taxonomic placement precisely based on available materials and so we herein tentatively retain them in the genus *Procercopis*.

3.1.3 | Genus *Procercopina* Martynov, 1937

Included species

Type species: *P asiatica* Martynov, 1937 (tegmen), by original designation. Other species: *P longipennis* (Becker-Migdisova, 1962), comb. n. (tegmen); *P frenzeli* Ansorge, 1996 (tegmen); *P delicata* Zhang, Wang, and Zhang, 2003 (tegmen); and *P shawanensis* (Zhang et al., 2003), comb. n. (tegmen).

Occurrence

Lower Jurassic of Kyrgyzstan, northwestern China, and Germany.

Remarks

Procercopina is similar to *Procercopis* in possessing a slender tegmen with MP₁₊₂ single, but differs from the latter with crossveins *ir* and *rp-mp* not numerous. *P longipennis* was originally attributed to *Procercopis* due to its two *rp-mp* crossveins. Nevertheless, this character is apparently different from that in *Procercopis* spp. with five *ir* and *rp-mp* crossveins, and is likely an individual mutation as seen in other procercopids, such as *Anthoscytina longa* and *A hongii* (Chen, Wang, et al., 2015; Shcherbakov, 1988). *P shawanensis*, described on the basis of an incomplete tegmen with only one *rp-mp* crossvein present, was originally attributed to *Procercopis* due to its similarity to *P longipennis*. In fact, these two species are similar to the type species of *Procercopina*, and so are transferred to this genus. "*Procercopina*" *thailandica* was erected by Heggemann, Kohring, and Schlutert (1990) based on a nearly complete tegmen from the Middle Jurassic of Thailand. The tegmen, however, is extremely small (2.6 mm as preserved), partly sclerotized and punctate, with CuA₁ fused with M₃₊₄, completely differing from all other procercopids. We exclude the taxon from the Procercopidae and tentatively transfer it to Hylcellidae following Ansorge (1996), but its precise systematic position requires a further study.

3.1.4 | Genus *Anthoscytina* Hong, 1983

Included species

Type species: *A longa* Hong, 1983 (tegmen), by original designation. Other species: *A reducta* (Becker-Migdisova, 1949) (tegmen); *A liugouensis* (Hong, 1983) (whole-bodied); *A daica* Shcherbakov, 1988 (whole-bodied); *A parallelica* Ren, 1995 (tegmen); *A perpetua* Li, Shih

and Ren 2013 (whole-bodied); *A hongi* Chen, Wang and Zhang, 2015 (tegmen); *A brevineura* Chen, Wang and Zhang, 2015 (whole-bodied); and *A elegans* Chen, Wang and Zhang, 2015 (whole-bodied).

Occurrence

Lower Jurassic of Kyrgyzstan, Middle to Upper Jurassic of north-eastern China, and Upper Jurassic of Chita, Russia.

Remarks

Anthoscytina can be compared to Cretaceous *Stellularis* and *Sinocercopis* in their tegmen being similar in shape and reduced venation, suggesting that these three genera are closely related; however, this Jurassic genus is distinctly different from the latter two in bearing a hind wing retained with two-branched MP.

3.1.5 | Genus *Titanocercopis* Chen, Zhang and Wang, 2015

Included species

Type species: *T borealis* Chen, Zhang and Wang, 2015 (whole-bodied), by original designation.

Occurrence

Uppermost Middle to lowermost Upper Jurassic of northeastern China.

Remarks

Titanocercopis was established based on several insect fossils with complete body structures and is the hitherto largest proceropid, with total body length about 30 mm and tegmen length about 25 mm (Chen, Zhang, et al., 2015). The genus retains some primitive morphological traits on tegmen as seen in primary cercopoid Sinoalidae and most Hylcelloidea, such as Pc + CP long and thick, MP multibranched with MP₁₊₂ two-branched, but its hind wing is typical as of all other Jurassic proceropid genera.

3.1.6 | Genus *Jurocercopis* Wang and Zhang, 2009

Included species

Type species *J grandis* Wang and Zhang, 2009 (whole-bodied), by original designation.

Occurrence

Uppermost Middle to lowermost Upper Jurassic of northeastern China.

Remarks

Jurocercopis is similar to *Titanocercopis* with a giant body and multi-branched RA and MP on tegmen, but differs the latter in having a relatively smaller size (tegmen about 20 mm long) and a tegmen with crossvein *imp* absent.

3.1.7 | Genus *Cretocercopis* Ren 1995

Included species

Type species: *C yii* Ren, 1995 (whole-bodied), by original designation.

Occurrence

Barremian–Aptian, Lower Cretaceous of Beijing, China.

Remarks

Cretocercopis is similar to the Jurassic genera *Jurocercopis* and *Titanocercopis* in having a tegmen with RA and MP multibranched, but the genus possesses a series of derived features remarkably different from all the other proceropids, for example, in having a tegmen with anterior margin at ScP terminal obviously concave, RP multibranched, crossvein *mp-cua* connecting stem MP instead of MP₃₊₄, and having a hind wing with MP₃₊₄ fused with MP₁₊₂ apically.

3.1.8 | Genus *Stellularis* Chen, Yao and Ren, 2015

Included species

Type species: *S longirostris* Chen, Yao and Ren, 2015 (whole-bodied), by original designation. Other species: *S senjituensis* (Hong, 1984), comb. n. (whole-bodied); *S apthosa* (Ren et al., 1998) (whole-bodied); *S bineuris* Chen and Wang, sp. n. (whole-bodied); and *S minutus* Chen and Wang, sp. n. (whole-bodied).

Emended diagnosis

Tegmen mottled, darkly stained at apical cell between two terminal branches of CuA, with RA and RP unbranched, MP single or two-branched, CuA₁ apparently longer than CuA₂ and commonly geniculate at its connection with crossvein *mp-cua*, A₁ short, ending at claval margin and not fused with Pcu; crossveins *ir* and *rp-mp* almost at same level, obvious apicad of *mp-cua*; hind wing with peripheral membrane present and outer margin smooth, RA, RP, and MP unbranched, crossvein *mp-cua* connecting to stem CuA.

Occurrence

Lower Cretaceous of northeastern China.

Remarks

Stellularis along with its type species (*S longirostris*) was established based on several fossil insects with body and wing information preserved from the Lower Cretaceous Yixian Formation, NE China (Chen, Yao, et al., 2015). In Chen, Yao, et al. (2015), *Luanpingia senjituensis* was attributed to Sinoalidae because the species and the type species of *Luanpingia* (*L longa*, belonging to Sinoalidae; Wang et al., 2012) are “very similar in size and structure of forewing, and are from same deposits.” In fact, *L senjituensis* is remarkably different from the type species in vein M branching near apex of tegmen, as stated in Wang et al. (2012). More importantly, the two species are not from the same deposits: *L longa* is from the Middle Jurassic Jiulongshan Formation of Zhouyingzi,



FIGURE 2 *Stellaris bineuris* sp. n. (a) HBJ-MC001a; (b) HBJ-MC001b; (c) NND08005; and (d) HBJ-MC007. Scale bars = 5 mm

Luanping, China, while *L senjituensis* is from the Yixian Formation of Shidongzi, Fengning, China (Hong, 1984). *L senjituensis* should be attributed to *Stellaris* based on the following tegminal characters: darkly stained at apical cell between two terminal branches of CuA, CuA₁ apparently longer than CuA₂, and A₁ not fused with Pcu. *Anthoscytina aphthosa* is also transferred to *Stellaris* as proposed in Chen, Wang, et al. (2015), resulting in *S aphthosa* (Ren et al., 1998). In *S aphthosa*, the terminal branches of MP on tegmen are not very stable, even for the left and right tegmina of the same individual, varying from one (commonly) to two in number (Ren et al., 1998, figure 11).

3.1.9 | *Stellaris bineuris* Chen and Wang, sp. n. (Figures 2 and 3)

Material

Holotype: HBJ-MC001a, b (part and counterpart), whole-bodied adult in laterodorsal aspect with gender unknown, wings slightly outspread; paratypes: HBJ-MC007, NND08005, whole-bodied

adults in laterodorsal aspect with gender unknown, wings slightly outspread (Figures 2 and 3).

Locality and horizon

Huangbanjigou (HBJ-CM001a, b, HBJ-CM007) of Beipiao, Liaoning and Yangshuwanzi (NND08005) of Chifeng, Inner Mongolia, China; Lower Cretaceous Yixian Formation.

Etymology

The specific epithet is derived from the Latin prefix “bi-” (meaning two) and “neurus” (meaning vein), which refers to stem M with two terminal branches.

Diagnosis

Tegmen with length about 12–14 mm, width about 5 mm; apical cells five in number, apical cell between terminal branches of CuA very broad, somewhat quadrangular; stem MP + CuA about half as long as stem R; MP two-branched; CuA₁ much longer than CuA₂ and geniculate at connection with crossvein *mp-cua*.

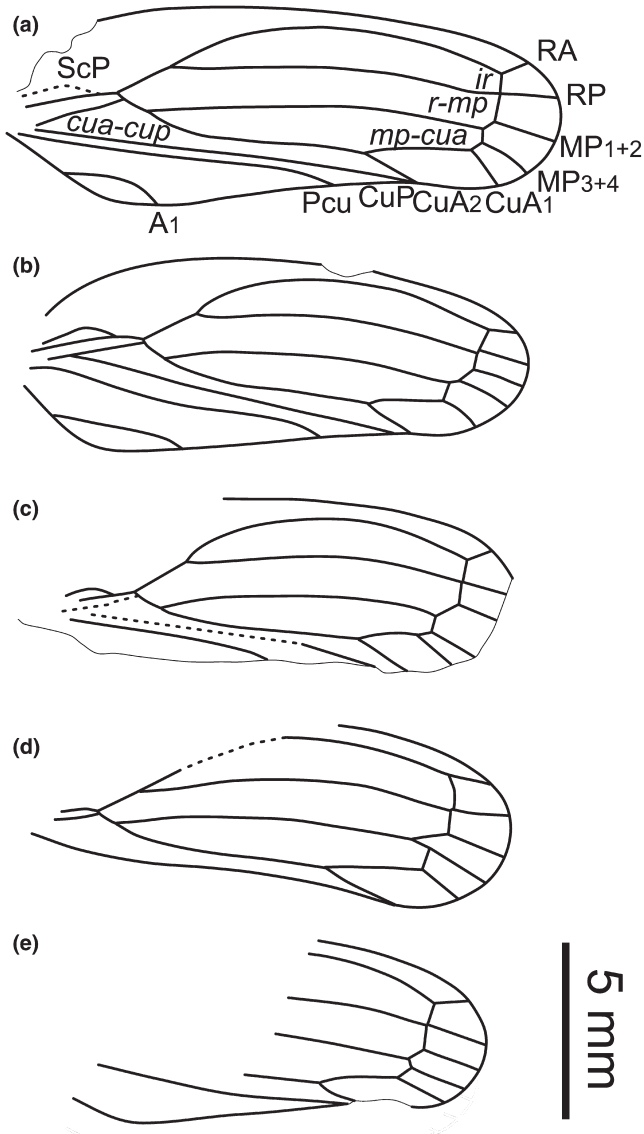


FIGURE 3 Line drawings of tegmina of *Stellularis bineuris* sp. n. (a) left tegmen of HBJ-MC001; (b) left tegmen of NND08005; (c) right tegmen of NND08005; (d) left tegmen of HBJ-MC007; and (e) right tegmen of HBJ-MC007. All to scale bar

Description

HBJ-MC001. Body structures not preserved well, and right tegmen slightly destroyed with venation clear; left tegmen and hind wings not preserved well. Postclypeus with distinct transverse grooves. Fore femur and tibia with a distinct ridge. Tegmen mottled, darkly stained at apical cell between two terminal branches of CuA, about 14.1 mm long, 5.0 mm wide, with length/width ratio 2.82. Costal area and clavus long and broad. Apical cells five in number, apical cell between terminal branches of CuA very broad, somewhat quadrangular. R + MP + CuA forking at basal 0.2 wing length. R bifurcating into RA and RP at basal 0.3 wing length; RA and RP unbranched. Crossvein *cua-cup* connecting MP + CuA close to bifurcation of R + MP + CuA. Stem MP + CuA about half as long as stem R, oblique, bifurcating into MP and CuA at basal 0.25 wing length.

MP two-branched, bifurcating at basal 0.86 wing length; MP₁₊₂ and MP₃₊₄ geniculate at connection with crossveins *rp-mp* and *mp-cua*, respectively. Crossveins *ir* and *rp-mp* almost at the same level. Stem CuA smoothly curved at base, bifurcating at basal 0.64 wing length; CuA₁ much longer than CuA₂ and geniculate at connection with crossvein *mp-cua*. Crossvein *mp-cua* basad of crossveins *ir* and *rp-mp*. CuP long and straight. Pcu close to CuP. A1 short, ending at claval margin and not fused with Pcu.

NND08005. Body structures deformed and obscure, both tegmina with venation clear, venation of hind wings partly preserved. Tegmen mottled, darkly stained at apical cell between two terminal branches of CuA, about 12.8 mm long, 4.8 mm wide, with length/width ratio 2.67. Venation of tegmina in general as in holotype (HBJ-MC001), except for left tegmen with crossvein *mp-cua* connecting stem MP instead of MP₃₊₄.

HBJ-MC007. Body structures obscure, right tegmen with costal area destroyed, left tegmen largely destroyed, venation of hind wings poorly preserved. Tegmen mottled, darkly stained at apical cell between two terminal branches of CuA, about 12.5 mm long. Venation of tegmina in general as in holotype (HBJ-MC001), except for left tegmen with MP₃₊₄ not geniculate at connection with crossvein *mp-cua*.

Remarks

Stellularis bineuris sp. n. can be distinguished from congeneric *S longirostris* and *S apthosa* in having a tegmen with stem MP + CuA about half as long as R and MP two-branched. The new species resembles *S senjituensis*, in bearing a tegmen with MP two-branched, but distinctly differs from the later in apical cell between terminal branches of CuA being very broad, somewhat quadrangular, CuA₁ geniculate at connection with crossvein *mp-cua*.

The new species shows a considerable venational variation in connecting position of crossveins and shape of terminal branches of median vein on tegmen. However, these tegmina are very similar in size and shape, and the variation is commonly intra-individual (Chen, Zhang, et al., 2015). Therefore, it is reasonable to assign these specimens to the same species.

3.1.10 | *Stellularis minutus* Chen and Wang, sp. n. (Figure 4)

Material

Holotype: HBJ-MC011, whole-bodied female adult in lateral view with overlapping wings on top of the body; paratypes: HBJ-MC010, NND08010, NND08015, all whole-bodied adult females in lateral aspect with overlapping wings on top of the body; NND08014, whole-bodied male (?) adult in lateral view with overlapping wings on top of the body (Figure 4).

Locality and horizon

Huangbanjigou (HBJ-MC010, HBJ-MC011, NND08014, NND08015) and Jianshangou (NND08010) of Beipiao, Liaoning, China; Lower Cretaceous Yixian Formation.

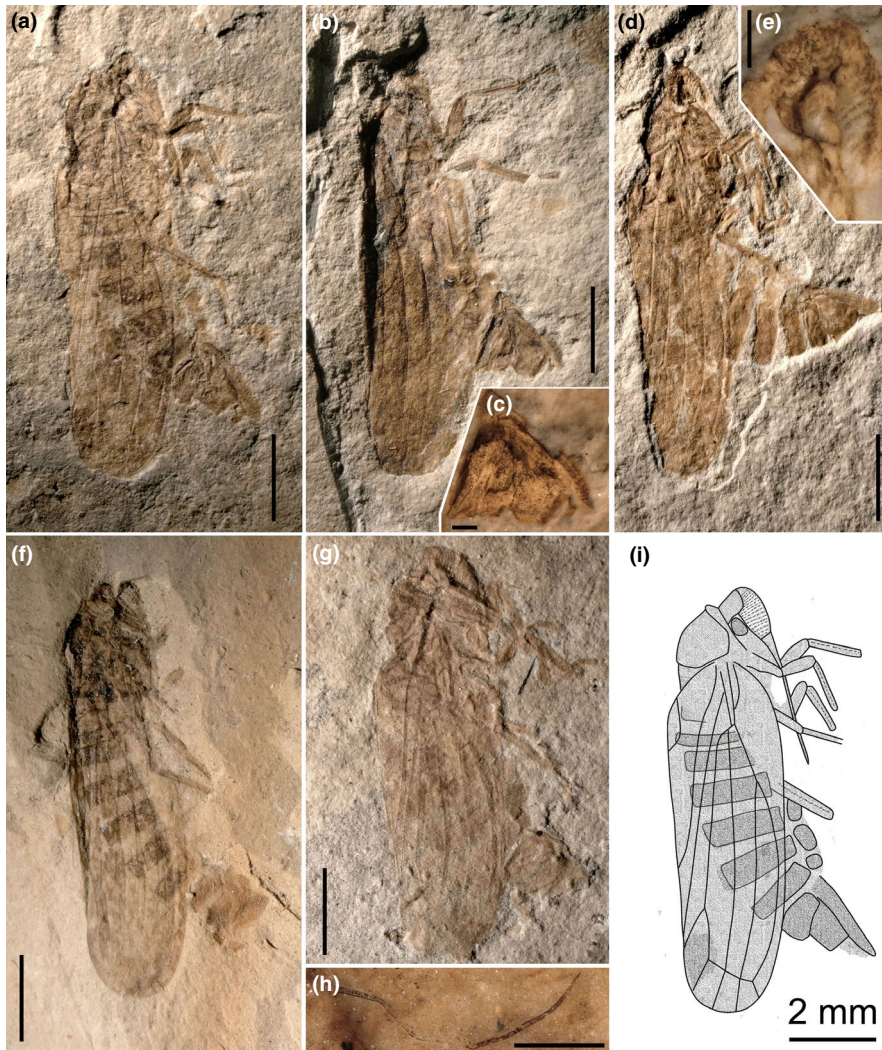


FIGURE 4 *Stellaris minutus* sp. n. (a) HBJ-MC011; (b) HBJ-MC010; (c) details of pygofer of HBJ-MC010, under alcohol; (d) NND08010; (e) details of head of NND08010, under alcohol; (f) NND08014; (g) NND08015; (h) details of antenna of NND08015, under alcohol; and (i) illustration of HBJ-MC011. Scale bars for A, B, D, F, G = 2 mm, C, E, H = 0.5 mm

Etymology

Specific epithet refers to the small size of the new species.

Diagnosis

Size small; tegmen with length <10 mm, width about 3 mm; stem MP + CuA distinctly shorter than stem R; MP unbranched; Crossveins *ir*, *rp-mp*, *mp-cua* almost at the same level.

Description

HBJ-MC011. Well-preserved, but legs partly destroyed. Body about 12.8 mm long including tegmen in repose. Postclypeus with distinct transverse grooves. Compound eyes large. Fore femur strong, about 2/3 as long as fore tibia. Fore, middle, and hind tibiae with distinct ridge. Ovipositor well-developed, slightly extending beyond anal tube. Tegmen mottled, darkly stained at apical cell between two terminal branches of CuA, about 9.5 mm long, 3.0 mm wide, with length/width ratio 3.17. ScP strong, fused with R + MP + CuA. R + MP + CuA forking at basal 0.18 wing length. Stem R long and nearly straight, branching into RA and RP at basal 0.34 wing length; RA smoothly curved and then geniculate at connection with crossvein *ir*; RP almost straight. Crossvein *cua-cup*

connecting MP + CuA close to bifurcation of R + MP + CuA. Stem MP + CuA extremely short, about 1/7 as long as stem R. MP almost straight, subparallel to RP. CuA strongly curved in basal part, then almost straight, bifurcating at basal 0.69 wing length; CuA₁ geniculate at crossvein *mp-cua*, about twice as long as CuA₁. Crossveins *ir*, *rp-mp*, *mp-cua* almost at the same level. CuP straight. Pcu slightly sinuous. A₁ short, strongly curved and ending at claval margin. Hind wing invisible.

HBJ-MC010. Slightly deformed, with legs partly preserved. Body about 12.3 mm long including tegmen in repose. Tegmen about 8.9 mm long. Body structures and venation of tegmina in general as in holotype (HBJ-MC011). Ovipositor densely covered with transverse ridges.

NND08010. Well-preserved, but legs partly destroyed. Body about 12.1 mm long including tegmen in repose. Tegmen about 8.8 mm long, 2.8 mm wide, with length/width ratio 3.14. Body structures and venation of tegmina in general as in holotype (HBJ-MC011). Antenna filiform.

NND08014. Slightly deformed, with legs partly preserved. Body about 11.5 mm long including tegmen in repose. Tegmen about 9.2 mm long. Body structures and venation of tegmina in

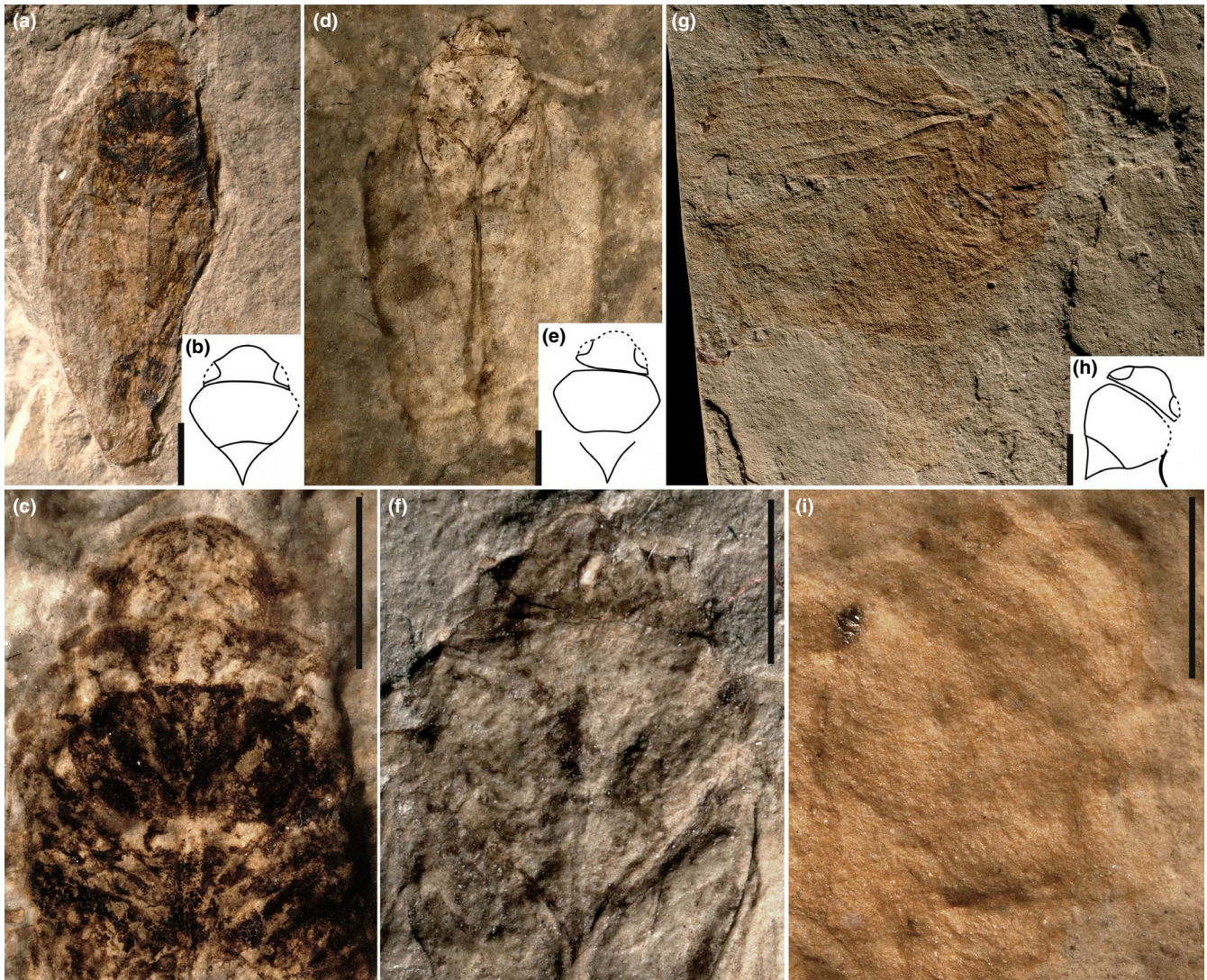


FIGURE 5 *Stellularis* sp. (a) HBJ-MC008; (b) line drawing of HBJ-MC008; (c) enlarged head and thorax of HBJ-MC008, under alcohol; (d) NND08013, under alcohol; (e) line drawing of NND08013; (f) enlarged head and thorax of NND08013; (g) NND05141; (h) line drawing of NND05141; and (i) enlarged head and thorax of NND05141, under alcohol. Scale bars = 2 mm

general as in holotype (HBJ-MC011). Anal tube elongate, genital obscure.

NND08015. Well-preserved, but legs partly destroyed. Body about 10.8 mm long including tegmen in repose. Tegmen about 8.9 mm long, 3.2 mm wide, with length/width ratio 2.78. Body structures and venation of tegmina in general as in holotype (HBJ-MC011). Antenna with scape not preserved; pedicel partly preserved, thick; flagellum long and filiform.

Remarks

Stellularis minutus sp. n. can be distinguished from its congeners in having a smaller size and a tegmen with crossveins *ir*, *rp-mp*, and *mp-cua* almost at the same level. All the specimens assigned to this species have a lateral aspect preservation, indicating that the new species might have a body somewhat more inflated than other *Stellularis* species preserved in dorsoventral view or laterodorsal

view. Moreover, *Stellularis minutus* sp. n. distinctly differs from *S. bineurus* sp. n. and *S. senjituensis* in having a tegmen with MP unbranched. The new species resembles *S. longirostris* and *S. aphthosa*, in having a tegmen with MP commonly unbranched, but is different from the latter two species in having a shorter ovipositor, just exceeding the anal tube.

3.1.11 | *Stellularis* sp. (Figure 5)

Material

HBJ-MC008, slightly deformed adult in dorsoventral aspect with sex unknown, wings on top of the body; NND08013, whole-bodied adult in dorsoventral aspect with sex unknown, wings on top of the body; NND05141a, b (part and counterpart), adult in dorsoventral aspect with gender unknown, right tegmen and hind wing on top of the body and left tegmen and hind wing outspread (Figure 5).

Locality and horizon

Huangbanjigou (HBJ-MC008) and Sihetun (NND08013) of Beipiao, Liaoning, Liutiaogou (NND05141a, b) of Chifeng, Inner Mongolia, China; Lower Cretaceous Yixian Formation.

Description

HBJ-MC008. Body about 14.6 mm long including tegmen in repose. Right wings destroyed and deformed. Head with length/width ratio about 0.43, widest along its posterior margin. Postclypeus swollen, with oblique grooves and a distinct median groove. Compound eyes large, not distinctly bulging. Pronotum expanded, longer and wider than head, with length/width ratio about 0.54; median carina present; anterior margin slightly convex; posterolateral margins about twice as long as anterolateral margins; posterior margin distinctly short than anterior margin, slightly concave. Mesonotum about 0.75 times as long in midline as pronotum; median carina distinct. Tegmen mottled, darkly stained at apical cell between two terminal branches of CuA. Wing venations of tegmen and hind wing not clear.

NND08013. Body about 16.5 mm long including tegmen in repose. Head slightly deformed, with anterior margin destroyed. Compound eyes large. Pronotum expanded with length/width ratio about 0.55; median carina present; anterior margin slightly convex; posterolateral margins about twice as long as anterolateral margins; posterior margin distinctly short than anterior margin, slightly concave. Mesonotum with median carina distinct. Tegmen with length/width ratio about 2.98, darkly stained at apical cell between two terminal branches of CuA; R + MP + CuA branching into R and MP + CuA at basal 0.23 wing length; stem R bifurcating into RA and RP at basal 0.32 wing length; RA and RP unbranched; stem MP + CuA long, connecting crossvein *cua-cup* just at its bifurcation; MP unbranched; A₁ straight, nearly subparallel to Pcu, and ending at claval margin. Hind wing obscure.

NND05141. Wing tips and abdomen not preserved or obscure. Head with length/width ratio about 0.38, widest at its posterior margin. Compound eyes large, elongate, and not distinctly bulging. Pronotum expanded, longer and wider than head; median carina present; anterior margin slightly convex; posterolateral margins about twice as long as anterolateral margins; posterior margin distinctly short than anterior margin, slightly concave. Mesonotum about 0.67 times as long in midline as pronotum. Tegmen with costal area and clavus long and broad; ScP prominent, fused with R + MP + CuA; stem R about 1.5 times as long as stem MP + CuA; Pcu slightly sinuous. A₁ nearly subparallel to Pcu, ending at claval margin. Hind wing with stem R long; RA, RP and M unbranched; CuA two-branched.

Remarks

The three specimens can be attributed to the genus *Stellularis* based on the following morphological characters: tegmen mottled, darkly stained at apical cell between two terminal branches of CuA, with A₁ ending at claval margin, and hind wing with MP unbranched. Nevertheless, due to poor preservation of wing venations, it is impossible to get more specific characters to compare these specimens

with known congeneric species in detail. Therefore, they are maintained in open nomenclature in *Stellularis* herein. Both head and thorax offer some crucial information for high-level classification of modern Cercopoidea. The three whole-bodied specimens, preserved with relatively clear head and thoracic structures, provide new insights into the morphological evolution of Mesozoic cercopoids (see Discussion).

3.1.12 | Genus *Sinocercopis* Hong, 1982*Included species*

Type species: *S liaoyuanensis* Hong, 1982 (whole-bodied), by original designation. Other species: *S lushangfenensis* (Hong, 1984), comb. n. (tegmen); *S pustulosis* (Ren, 1995), comb. n. (whole-bodied); *S trinervis* (Ren, 1995), comb. n. (tegmen); *S macula* (Hu et al., 2014), comb. n. (tegmen).

Emended diagnosis

Tegmen mottled, with RA and RP unbranched, M with single or two terminal branches, CuA₁ apparently longer than CuA₂ and slightly curved or smooth at its connection with crossvein *mp-cua*, A₁ long, not ending at wing margin, migrated to Pcu apically, and even fused with the latter; crossvein *ir* at same level or apical of *rp-mp*, and obviously apical of *mp-cua*; hind wing with peripheral membrane present and outer margin smooth, RA, RP, and MP unbranched, crossvein *mp-cua* connecting to stem CuA or CuA₁.

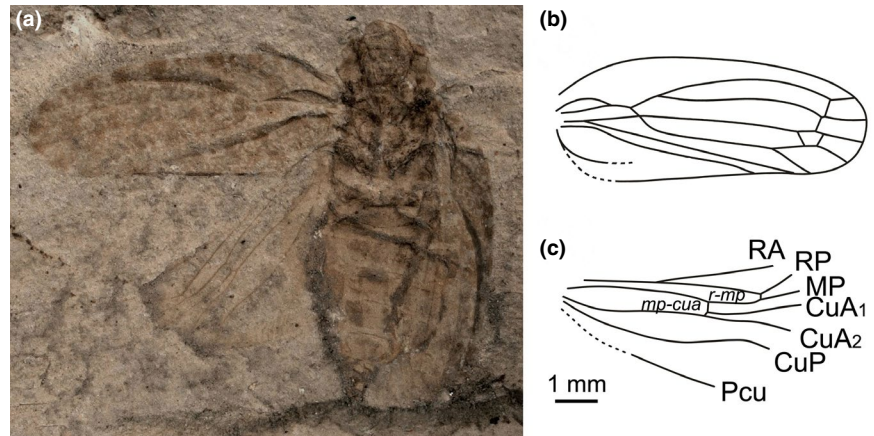
Occurrence

Lower Cretaceous of northeastern China.

Remarks

Sinocercopis, with its type species erected from the Lower Cretaceous Yixian Formation of Liaoyuan, Jilin, NE China, is distinctly different from all known Cercopoidea in having a tegmen with A₁ fused with Pcu, forming a Y-shaped vein in clavus as in Fulgoromorpha and early Cicadomorpha. *Sunoscytinopteris*, reported from the Lower Cretaceous Lushangfen Formation of Beijing, China, and originally placed in Scytinopteridae (Prosorrhyncha) (Hong, 1984), actually shares a similar tegminal shape and venation with *Sinocercopis*. Ren (1995) described several fossil insects with tegmina similar to those of *Sunoscytinopteris* from the same horizon (Lushangfen Formation) and a nearby locality (Chongwenshuiku, Beijing; Figure 1), established one new genus *Cathaycixius* with two new species, and attributed this genus to the modern fulgoroid family Cixiidae based on the simplified longitudinal veins and Y-shaped vein formed by Pcu and A₁ on tegmen. Chen, Yao, et al. (2015) argued that *Cathaycixius* shared some tegminal characters with *Anthoscytina* and should be synonymized with the latter. Nevertheless, their long A₁ and Y-shaped vein on tegmen and unbranched MP on hind wing indicate that these insects are absolutely not the Cretaceous representatives of the Jurassic genus *Anthoscytina*. We herein treat *Sunoscytinopteris* and *Cathaycixius* as junior homonyms of *Sinocercopis*, proposing *S lushangfenensis* (Hong, 1984), comb. n., *S pustulosis* (Ren, 1995), comb. n.,

FIGURE 6 *Sinocercopis* cf. *macula* (Hu et al., 2014). (a) NND08016; (b) line drawing of tegmen of NND08016; and (c) line drawing of hind wing of NND08016. All to scale bar



and *S trinervis* (Ren, 1995), comb. n. In addition, *Anthoscytina macula*, reported from the Yixian Formation of Huangbanjigou, Beipiao, NE China (Hu et al., 2014), should be transferred to *Sinocercopis* based on its mottled tegmen with special Y-shaped vein and hind wing with single MP.

3.1.13 | *Sinocercopis* cf. *macula* (Hu, Yao and Ren, 2014), comb. n. (Figure 6)

Material

NND08016, whole-bodied adult in dorsoventral aspect with gender unknown, left tegmen and hind wing on top of the body and right tegmen and hind wing outspread (Figure 6).

Locality and horizon

Huangbanjigou of Beipiao, Liaoning, China; Lower Cretaceous Yixian Formation.

Description

Body excluding tegmen about 9.2 mm long. Body structures not well preserved. Postclypeus well-developed, swollen. Hind tibiae long and thick; tarsi with basi- and mid-tarsomere with similar length, greatly inflated apically, slightly shorter than apical tarsomere; tarsal claws well-developed.

Tegmen mottled, with length about 8.0 mm, width about 2.8 mm (left one). Costal area and clavus long and broad; costal margin smoothly curved. ScP prominent, fused with R + MP + CuA. R + MP + CuA branching into R and MP + CuA at basal 0.23 wing length. Stem R about twice as long as stem MP + CuA, bifurcating into RA and RP at basal 0.33 wing length; RA and RP unbranched. Crossvein *ir* slightly apicad of crossvein *rp-mp*. Crossvein *cua-cup* long, connecting MP + CuA just at its bifurcation. MP unbranched. Crossveins *mp-cua* two in number. CuA curved at base, forking into CuA₁ and CuA₂ at basal 0.39 wing length; CuA₁ distinctly longer than CuA₂. CuP long and straight. Pcu close to CuP, slightly sinuous. A₁ long, strongly curved at base, migrated to Pcu, but obscure apically.

Hind wing with RA and RP unbranched; RP strongly curved at connection with crossvein *rp-mp*. MP unbranched, slightly sinuous.

Crossvein *mp-cua* connecting CuA₁. CuA with two terminal branches; CuA₁ nearly as long as CuA₂. CuP sinuous.

Remarks

Sinocercopis macula was erected by Hu et al. (2014) on the basis of one whole-bodied specimen from the Yixian Formation of Huangbanjigou, Beipiao, NE China. The new specimen described above, from the same horizon and locality, is similar to the holotype in body size, most morphological characters and even taphonomic posture (dorsoventral aspect with one tegmen and hind wing on top of the body and the other tegmen and hind wing outspread), and so is tentatively referred to this species. However, the new fossil differs from the holotype in having a tegmen with stem MP + CuA longer, two *mp-cua* crossvein, and having a hind wing with crossvein *mp-cua* connecting CuA₁ instead of CuA. Number of crossveins on tegmen is likely easy to mutate (see Remarks of *Procercopina*) and should be considered as individual variation for the new specimen; for the other two characters, however, more fossil materials are required to determine whether they are species-level diagnostic characteristics or just individual variations.

3.2 | Phylogenetic assessments

Bayesian inference analysis converged before 10 million generations, and the average standard deviation of split frequencies was well below 0.01 at the end, and so stationarity was considered to be reached. The 50% majority-rule consensus tree from Bayesian analysis is shown in Figure 7a (left), with posterior probabilities (PP) labeled near tree nodes. Maximum parsimony analysis yielded 40 most parsimonious trees, with the following characteristics: tree length = 41, consistency index (CI) = 0.951, and retention index (RI) = 0.955. The 50% majority-rule consensus tree is shown in Figure 7a (right), with bootstrap support values (BS) labeled near tree nodes. The topologies of the two 50% consensus trees are same at nodes with high support values; however in spite of low support (BS: <30%), MP tree recovered more dichotomic nodes, but these relationships were not resolved in BI tree (polytomies). The strict consensus tree of 40 most parsimonious trees showed identical

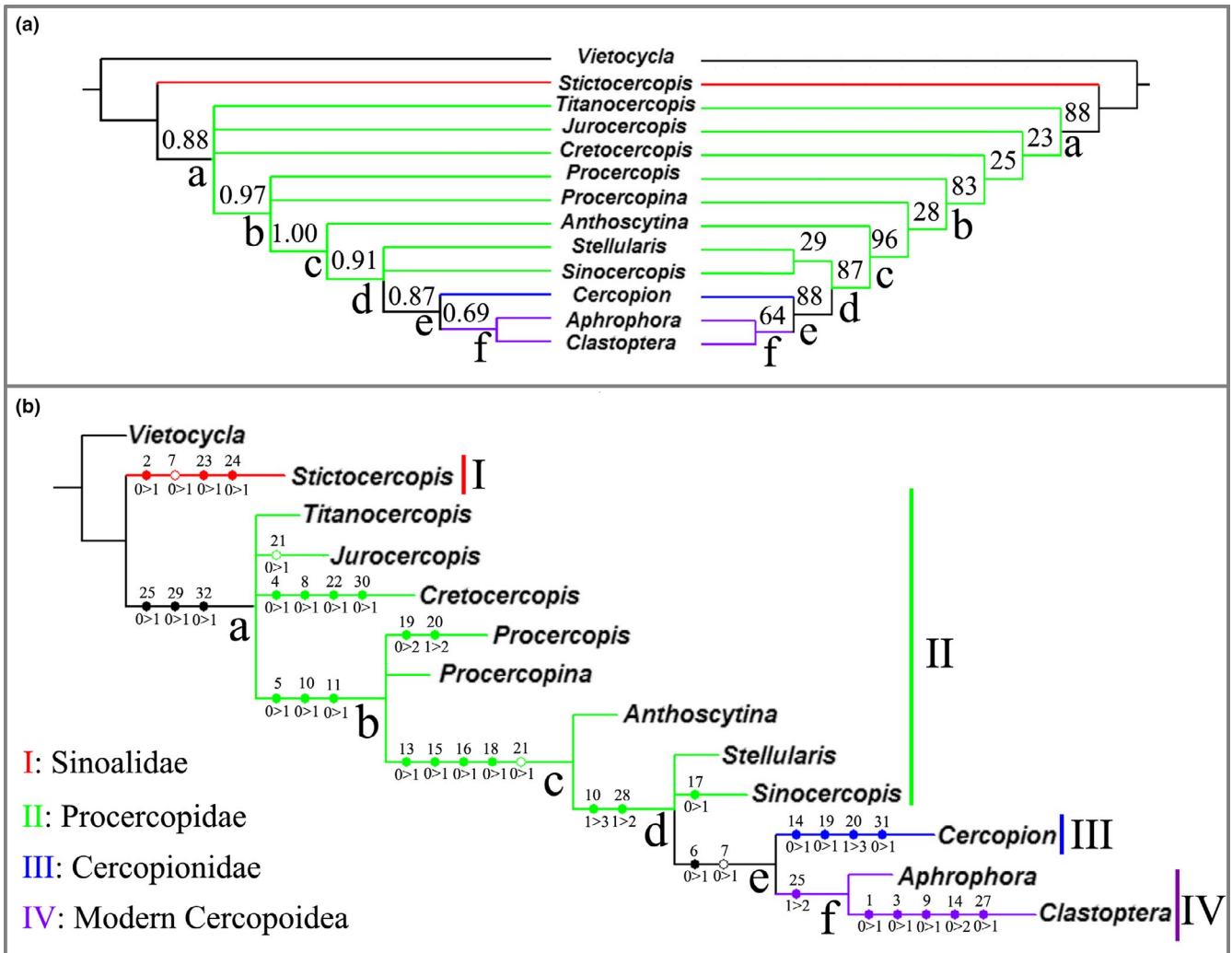


FIGURE 7 Phylogenetic trees of Procercopidae based on 32 morphological characters of tegmen and hind wing. (a) 50% majority-rule consensus trees inferred from Bayesian inference analysis (left) with numbers above the nodes indicating posterior probabilities and maximum parsimony analysis (right) with numbers above the nodes indicating bootstrap support values; (b) character mapping on the strict consensus tree of 40 maximum parsimony trees with numbers above branches indicating character numbers, and below branches indicating character state changes. Nodes labeled with alphabets (a to f) refer to specific clades discussed in the text

topology as the 50% majority-rule consensus tree inferred from Bayesian analysis, and character mapping was executed on this tree as shown in Figure 7b.

Vietocykla (Hylcelloidea) was chosen as ultimate out-group and *Stictocercopsis* (Sinoalidae) occupied the most basal position as the sister clade to all other Cercopoidea. The Procercopidae, Cercopionidae, and modern Cercopoidea (representing by *Aphrophora* and *Clastoptera*) constituted a monophyletic clade (Clade a) with significant support (PP: 0.88; BS: 88%) and three synapomorphies (25:0 > 1, 29:0 > 1, 32:0 > 1). *Titanocercopsis*, *Jurocercopsis*, and *Cretocercopsis* occupied the basal position of Clade a, and their relationships to each other were not resolved (support values very low or polychotomy). Within well-supported Clade b (0.97; 83%; 5:0 > 1, 10:0 > 1, 11:0 > 1), *Procercopsis* and *Procercopina* occupied the basal position with the relationship to each other not resolved, and *Anthoscytina*, Cretaceous *Sinocercopsis*, *Stellaris*, Cercopionidae, and modern Cercopoidea constituted a monophyletic clade (Clade c)

with high support (1.00; 96%; 13:0 > 1, 15:0 > 1, 16:0 > 1, 18:0 > 1, 21:0 > 1). Within Clade c, *Anthoscytina* occupied the basal position, with sister relationship to the three Cretaceous taxa and modern Cercopoidea (Clade d). *Sinocercopsis* and *Stellaris* occupied the basal position of well-supported Clade d (0.91; 87%; 10:1 > 3, 28:1 > 2) with the relationship to each other not resolved. Cercopionidae and modern Cercopoidea were recovered as a monophyletic group (Clade e) with significant support (0.87; 88%; 6:0 > 1; 7:0 > 1). Modern Cercopoidea constituted a monophyletic lineage (Clade f) with moderate support (0.69; 64%; 25:1 > 2).

4 | DISCUSSION

Up to now, thirty-seven species attributed to eight genera within Procercopidae have been reported from the Jurassic and Cretaceous of Eurasia (Table 1; Figures 1 and 8), and some undescribed specimens

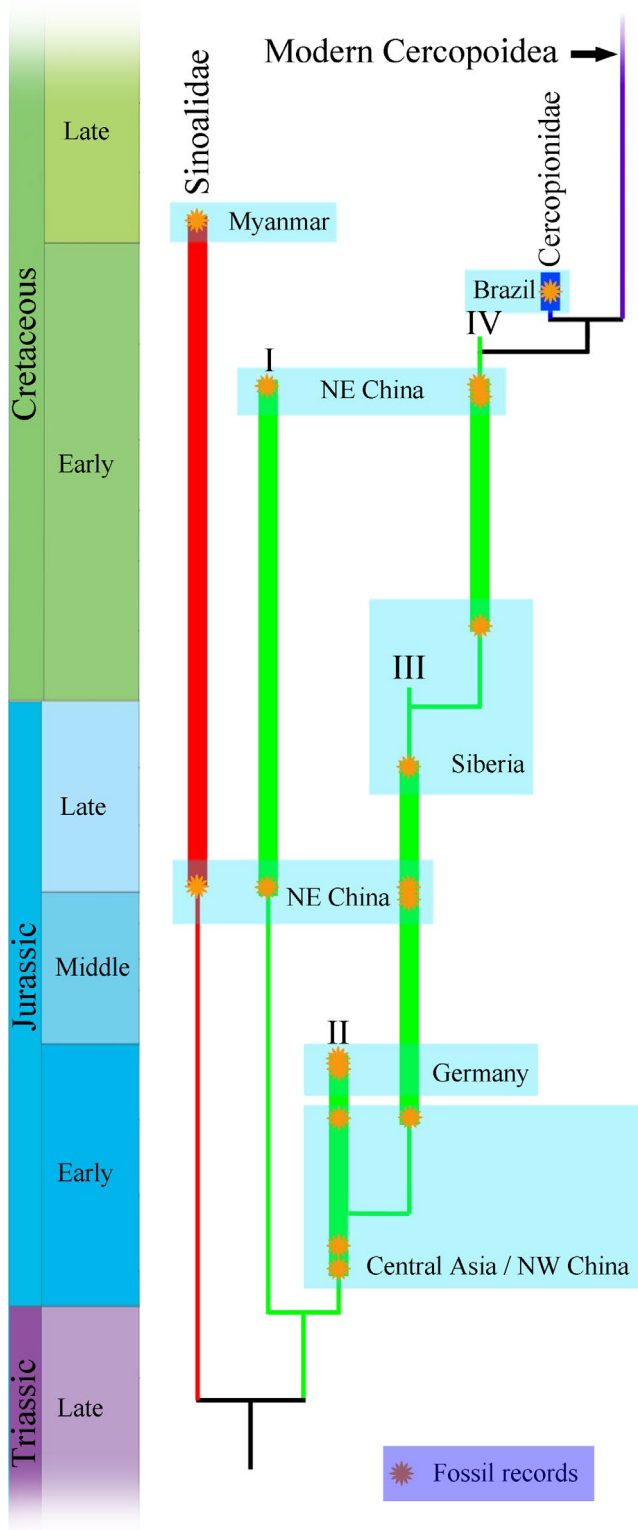


FIGURE 8 Simplified scheme of chronology and evolutionary history of Mesozoic Cercopoidea, with fossil records indicated on. The four presumptive lineages of Procercopidae are as follows: I, *Titanocercopsis* + *Jurocercopsis* + *Cretocercopsis*; II, *Procercopis* + *Procercopina*; III, *Anthoscytina*; and IV, *Stellularis* + *Sinocercopsis*

assigned to this family were also recorded from the Upper Jurassic to Lower Cretaceous of Siberia and Mongolia (Shcherbakov, 1988). McLoughlin, Martin, and Beattie (2015) reported an insect fossil from the Upper Jurassic of Talbragar Fossil Bed, Australia, and assigned it to Procercopidae. The specimen, however, is poorly preserved with few diagnostic characters recognized, and so its precise systematic position requires more fossil materials with clear morphological features. Thus, definite Procercopidae was only recorded in the Mesozoic of Eurasia to date. Considering the general paucity of fossil insects in the Southern Hemisphere and the geological history of insects based mostly on discoveries in the Northern Hemisphere (Beattie & Avery, 2012; Schluter, 2003), the fossil record of Procercopidae exclusively in Eurasia is likely related to the taphonomic and collecting bias.

Chengdecercopsis Hong, 1983, reported from the Middle Jurassic Jiulongshan Formation of NE China, is widely accepted as a representative of Procercopidae (Chen, Zhang, et al., 2015; Hamilton, 1992; Hong, 1983; Wang et al., 2012). However, *Chengdecercopsis* bears a tegmen with costal area more sclerotized and punctate, ScP + R, MP, and CuA dividing almost at the same point, crossvein *cua-cup* connecting CuA almost at the branching position of ScP + R + MP + CuA, and crossvein *mp-cua* connecting CuA at its bifurcation, resembling the sinoalid *Stictocercopsis* Fu and Huang, 2018 but differing from all known procercopids. Therefore, the genus should be transferred from the family Procercopidae to the Sinoalidae.

Anomoscytina, established from the Lower Cretaceous of NE China on the basis of an incomplete adult insect fossil without tegmen preserved and originally placed in Procercopidae (Ren et al., 1998), was excluded from the family by Wang et al. (2012) and was still retained in Procercopidae in Chen, Yao, et al. (2015). Although two-branched MP with crossvein *mp-cua* connecting to MP₃₊₄ instead of stem MP on hind wing resembles that of Sinoalidae, the hind tibia with seven spines arranged in a row distinguishes the genus from all Mesozoic cercopoid groups. The genus apparently does not belong to Procercopidae, and its precise systematic position is pending, needing a further study based on additional fossils with tegminal information.

The Cretaceous Procercopidae are known to be relatively abundant and highly diverse, and be only recorded in northeast Asia (Siberia, Mongolia, and NE China), with all taxa formally erected from NE China. Although procercopid fossils are common in the Lower Cretaceous of Siberia and Mongolia, only a damaged hind wing from the Cretaceous Daya Formation of Siberia has been reported and illustrated, and was attributed to *Sinocercopsis* based mainly on unbranched MP of hind wing (Shcherbakov, 1988). Nevertheless, the procercopid hind wing lacks diagnostic traits at genus and species levels and late Procercopidae in the Cretaceous, such as *Stellularis* and *Sinocercopsis*, shares a hind wing with almost the same topology. Therefore, the specimen should be considered as genus *incertae sedis* in Procercopidae.

The taxonomy and classification of Cretaceous procercopids from NE China are rather chaotic. *Sinocercopsis* was originally placed

in modern Cercopoidea (Hong, 1982), but successively transferred to Procercopidae (Ren, 1995; Shcherbakov, 1988). *Luanpingia senjituensis*, treated as systematic position *incertae sedis* by Wang et al. (2012) but attributed to Sinoalidae in Chen, Yao, et al. (2015), is considered to belong to *Stellularis* herein. Based on similarities in tegminal shape and venation, *Anthoscytina aphthosa* and *A macula* were transferred to *Stellularis* by Chen, Wang, et al. (2015). Considering its special Y-shaped vein on tegminal clavus, *A macula* should be attributed to *Sinocercopis*. *Cathaycixius* including two species, originally placed in the modern fulgoroid family Cixiidae (Ren, 1995) and later synonymized under *Anthoscytina* by Chen, Yao, et al. (2015), is actually a junior homonym name of *Sinocercopis*. Thus, *Anthoscytina* is only recorded in the Jurassic of Asia (Becker-Migdisova, 1949; Chen, Wang, et al., 2015; Hong, 1983) and might become extinct in the Cretaceous. Besides, *Sunoscytinopterus*, similar to *Cathaycixius* from the same horizon and a nearby locality but originally placed in Scytinopteridae (Hong 1984), should also be synonymized under *Sinocercopis*.

Our cladistic analyses based on wing character states recovered the high-level relationships within the Cercopoidea as follows: Sinoalidae + (Procercopidae + (Cercopionidae + modern cercopoids)) (Figures 7 and 8). Sinoalidae, recently reported in Middle-Late Jurassic deposits in northeastern China and mid-Cretaceous Burmese amber (Chen et al., 2017, 2018, 2019a, 2019b; Chen, Wang, Zhang, et al., 2019; Chen, Wang, Zheng, Jarzembowski, et al., 2019; Chen, Zhang, Wang, Jiang, Jiang, et al., 2019; Fu, Cai, & Huang, 2017; Fu & Huang, 2018, 2019; Wang et al., 2012), shares some plesiomorphic characters with ancient Clypeata and bears some remarkably specialized traits. This family occupies the most basal position as the sister clade to all other Cercopoidea in our phylogenetic reconstruction, indicating that the family likely represents a primitive cercopoid lineage. The hitherto earliest record of Sinoalidae is from the Middle to Late Jurassic of NE China; however, considering that Procercopidae has been well recorded in the Lower Jurassic in Eurasia and *Procercopina* was even reported from the lowermost Jurassic Dzhil Formation of Kyrgyzstan (formerly reported as Triassic) (Table 1; Figure 8), the two main lineages of Cercopoidea (Sinoalidae and Procercopidae) likely originated and radiated in the Late Triassic after their common ancestor split with Cicadoidea (Cryan, 2005; Shcherbakov & Popov, 2002; Wang et al., 2012).

Procercopidae was recovered as a paraphyletic group with Cercopionidae and modern cercopoids nested in it (Figure 7). This lineage (Clade a) is supported by a series of synapomorphic characters on hind wing: peripheral membrane present, bifurcating position of MP migrating to wing tip and crossvein *mp-cua* connecting stem MP. The Middle to Late Jurassic *Tianocercopis* and *Jurocercopis*, and the Cretaceous *Cretoercopis* were recovered as basal representatives within Procercopidae. The relationships among these three genera were not resolved herein, but probably resulted from taxon choosing in phylogenetic reconstruction: MP four-branched on tegmen, a common character for ancient Cicadomorpha including Hylacelloidea (e.g., *Hylacella* Evans, 1956), Cicadoidea (Chen et al., 2016), and Sinoalidae (unpublished data), is likely the ancient

state of Cercopoidea and so multibranching MP (at least five terminal branches) might be a homologous trait for the three procercopid genera, evolving independently and in parallel to out-groups *Vietocyclus* (Hylacelloidea) and *Stictocercopis* (Sinoalidae) in our cladistic analyses. The Early Jurassic *Procercopis* and *Procercopina* bear a tegmen with Pc + CP reduced (weak and short) and MP reduced in number, shared also by the Jurassic *Anthoscytina* and the Cretaceous *Stellularis* and *Sinocercopis*. Terminal branches of MP on tegmen and hind wing of the two Cretaceous procercopid genera became further reduced. Unbranched vein M on tegmen and hind wing are considered as apomorphic characters for extant cercopoids (Chen, Wang, et al., 2015). The morphological features, shared by the Early Cretaceous *Stellularis* and *Sinocercopis*, suggest that these two genera likely represent transitional forms between Procercopidae and recent Cercopoidea.

Cercopionidae was erected based on a whole-bodied adult insect fossil from the Lower Cretaceous Crato Formation of Brazil. Hamilton (1990) proposed that *Mesoassula* Evans, 1956 from the Upper Triassic of Australia and *Sinocercopis* Hong, 1982 from the Lower Cretaceous of NE China might belong to this family, which, however, has been questioned by other authors (e.g., Chen et al., 2018; Ren, 1995; Shcherbakov, 1988; Wang et al., 2012). Therefore, reliable Cercopionidae is exclusively known from the Lower Cretaceous of Brazil up to now. In our phylogenetic trees, the family nested in the Procercopidae and was resolved as the sister group to modern cercopoids. Cercopionidae shares a unique tegminal trait (ScP on tegmen extremely long, fused with R instead of R + M + CuA) with modern cercopoids, but it is also specialized with a series of autapomorphies on both tegmen and hind wing (Figure 7) as well as other body structures, suggesting that this family is likely an offshoot of the ancestral group of modern Cercopoidea. The late Procercopidae (represented by *Stellularis* and *Sinocercopis*) from Yixian Formation of Jehol Biota, NE China, shares some distinct tegminal features with modern cercopoids and the modern Cercopoidea-like Cercopionidae from Crato Formation, Brazil, indicating that Procercopidae likely became extinct and the common ancestor of modern Cercopoidea originated and diversified in the late Early Cretaceous (Table 1; Figure 8). The recent divergence time, estimated using a relaxed clock Bayesian approach based on molecular data, elucidates that main lineages of modern Cercopoidea appeared successively in the Late Cretaceous and Paleocene (Paladini et al., 2018). The major radiation of crown group angiosperms (flowering plants) took place in the late Early Cretaceous and onwards in the Cretaceous Terrestrial Revolution as indicated by the numerous records of fossil flowers and isolated floral organs as well as leaves (Herendeen, Friis, Pedersen, & Crane, 2017; Lloyd et al., 2008). Therefore, the extinction of Procercopidae and origin and early diversification of modern Cercopoidea probably resulted from the rise and explosive radiation of flowering plants in this terrestrial ecological revolution.

In spite of abundance in the Mesozoic of Eurasia, the fossil record of early Cercopoidea is somewhat fragmentary, and these reported fossils are mostly isolated wing impressions (Chen, Wang, et al., 2015; Hu et al., 2014; Wang et al., 2012). Plenty of cercopoid fossils with body structures preserved have been reported from the Middle

to Late Jurassic Yanliao Biota and Early Cretaceous Jehol Biota of NE China since the 1980s (Table 1), providing novel insights into the morphological evolution. Head and thorax offer some crucial information for high-level classification within Cercopoidea. The new materials provided in the present study show that head and thoracic structures are similar for late Procercopidae in the Cretaceous: head distinctly wider than its length, narrower than thorax, with anterior margin (tylus?) slightly protruding in dorsal view, pronotum expanding and hexagonal with posterolateral margin longer than anterolateral margin and posterior margin slightly concave, and mesonotum broad and slightly shorter than pronotum (Chen, Yao, et al., 2015; Hu et al., 2014; Ren et al., 1998; this study). It is intriguing that the Middle to Late Jurassic *Jurocercopsis*, recovered as the basal group of Procercopidae in our phylogenetic reconstruction, bears both head and thorax very similar to those in Cretaceous confamilials (Figure 3f in Wang & Zhang, 2009). Certain wing characteristics were likely gradually developed from ancestral forms as possessed in *Jurocercopsis* and *Procercopina* to derived forms in late Early Cretaceous shared with modern Cercopoidea (Figure 7), even leading to *Sinocercopsis* which was previously assigned to the modern family Cercopidae (Hong, 1982); the reported body structures, however, revealed as long-term morphological stasis with a slow rate of morphological changes, suggest that it is applicable to place these Cretaceous froghoppers in the Procercopidae. Body characteristics probably evolved rapidly in the ancestral group of modern Cercopoidea; the pronotal hind margin, as an example, became distinctly concave and W-shaped. Subsequently, body traits became specialized in different lineages, such as elongate mesonotum in Clastopteridae and Machaerotidae.

5 | CONCLUSIONS

For the evolutionary history of early Cercopoidea and the origin of its modern groups, results provided by molecular, morphological, and fossil data tend to be consistent in recent studies (Paladini et al. 2018; Wang et al. 2012). Nevertheless, the intriguing issue, how stem Cercopoidea evolved step by step into its modern forms in the Mesozoic, remains unclear to now. Certainly, fossil data, directly providing information on trends in the evolution of morphological traits, can offer vivid evidence for this scientific problem. Although Procercopidae, recorded from the Early Jurassic to Early Cretaceous in Eurasia, is widely believed to be the ancestor of modern cercopoids (Chen et al. 2018; Shcherbakov 1992; Wang et al. 2012), the fragmentary fossil record and confusing taxonomic history hamper our understanding of its evolutionary transition into recent froghoppers. Via detailed taxonomic review and phylogenetic inference, we herein sketch a relatively clear outline for the evolutionary trend of Procercopidae as well as the origin of modern cercopoids. However, the fossil record of Cercopoidea is still too fragmentary, and some key issues about the evolution of the Mesozoic froghoppers, especially the rise of the main lineages of modern cercopoids in the Late Cretaceous and Paleogene, need to be solved on the basis of additional fossil materials.

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