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Short communication

Female sinoalid froghoppers in mid-cretaceous Kachin amber with description of a new genus and species (Hemiptera, Cicadomorpha)

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ABSTRACT

Although the extinct hemipteran Sinoalidae is well documented in the mid-Cretaceous Kachin amber of northern Myanmar, its adults with female organs preserved remain unknown. We herein report three female sinoalids: two specimens trapped in one amber piece are attributed to *Fangyuania xiai*, and the third representing the new genus and species *Mesolongicapitis peii* gen. et sp. nov. The individuals of *F. xiai* show a considerable variation in length/width ratio of both the crown and the tegmen as well as tegminal cell patterns, but they are assigned to the same species since a similar intra-specific variation has been well documented in Mesozoic Cercopoidea. *Mesolongicapitis peii* gen. et sp. nov. is remarkably different from all known sinoalids by displaying a series of novel morphological traits, e.g., specialized compound eyes, and the tegmen with an extremely long MP+CuA stalk and an extremely short RA_1. Its crown with distinct epicranial suture and anterior arms, and its frons with a median ocellus are similar to those of the Middle to Late Jurassic sinoalids from northeastern China, resembling the basal model of Clypeata. In addition, the three froghoppers reported herein bear a long and ensiform ovipositor just like their Jurassic relatives, indicating a morphological and probable corresponding behavioral stasis.

1. Introduction

The Mesozoic froghopper family Sinoalidae is known from the latest Middle to earliest Late Jurassic Yanliao Biota of northeastern China and mid-Cretaceous Kachin amber of northern Myanmar (Wang et al., 2012; Fu and Huang, 2018; Chen et al., 2017, 2018, 2019b, c, d). This extinct family, as one of the Mesozoic groups of Cercopoidea, is considered as the sister lineage of Procercopidae, which is the ancestral group of all modern froghopper families (Wang et al., 2012; Chen et al., 2015a, b, 2017, 2019c). Sinoalids are abundant and highly diverse in the Middle to Late Jurassic Yanliao Biota, and finds from mid-Cretaceous Kachin amber further expand their duration and geographic distribution and also provide a chance to explore the diversity of this extinct family (Chen et al., 2018, 2019b, d).

To date, three fossil froghoppers contained in Kachin amber pieces have been described and ascribed to three genera and species: *Fangyuania xiai* Chen, Szwedo and Wang, 2018 (Chen et al., 2018) erected based on one male adult, *Jiaotouia minuta* Chen and Wang, 2019 (Chen et al., 2019d) and *Ornatiala amoena* Chen and Wang, 2019 (Chen et al., 2019b) on one incomplete fossil with pygofer missing. Therefore, sinoalid specimens with female organs have never been recorded from Kachin amber up to now. Here we report three female sinoalid adults in Kachin amber, two of which are ascribed to *F. xiai* and one to a new genus and species, *Mesolongicapitis peii* gen. et sp. nov. is erected, providing more novel information on the morphology and evolution of Sinoalidae as well as early Clypeata.

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2. Material and methods

The three froghopper specimens described herein are contained in two transparent yellowish amber pieces from the Hukawng Valley, Kachin State of northern Myanmar (see locality in Fig. 1 of Chen et al., 2019e). Two new specimens of *Fangyuania xiai* (BA19002 and BA19003) trapped in one amber piece are deposited in the Lingpoge Amber Museum in Shanghai, China, and the holotype of *Mesolongicapitis peii* gen. et sp. nov. (NIGP171033) is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

The age of Kachin amber was indicated to be the earliest Cenomanian (98.79 ± 0.62 Ma) based on U-Pb dating of volcanoclastic zircon crystals (Shi et al., 2012), and this view has been widely supported by biostratigraphical evidences in this century (e.g., Cruickshank and Ko, 2003; Grimaldi et al., 2005; Ross et al., 2010), although its precise age may be older (close to the boundary between the Albian and Cenomanian or even the Late Albian) (Mao et al., 2018). Amber affords exceptional three-dimensional preservation of extinct organisms (Chen et al., 2016), and the mid-Cretaceous Kachin amber, with more than one thousand species reported (Ross, 2018, 2019), is now recognized as a significant window to the late Mesozoic world (Cruickshank and Ko, 2003; Poinar et al., 2008; Kania et al., 2015).

The VHX 5000 digital microscope platform was used to examine, photograph and measure the three fossil specimens. Image-editing software CorelDraw 12.0 and Adobe Photoshop CS3 were used to prepare the line drawings of tegmina of sinoalid taxa described from Kachin amber. Venational terminologies used herein follow Nel et al. (2012) and Bourgoinet al. (2015), with slight modification, and the nomenclature of body structures mainly follows Evans (1966) and Moulds (2005).

All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:AFAF9F7B-F734-4B6E-81D2-EC3C15B5F5BF.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Cicadomorpha Evans, 1946
Superfamily Cercopoidea Leach, 1815
Family Sinoalidae Wang et al., 2012 in Wang et al. (2012)

Genus ***Fangyuania*** Chen et al. (2018) in Chen et al. (2018)
Type species: *Fangyuania xiai* Chen et al. (2018) in Chen et al. (2018)

Diagnostic characters. Crown broad and produced anteriorly, length/width ratio nearly 0.7 to 0.8, with anterior margin smoothly angled and coronal margin before compound eyes distinctly convex. Three ocelli arranged in isosceles triangle with wide base. Postclypeus longitudinally concave in middle. Pronotum shortened, with length/width ratio nearly 0.3. Tegmen with length/width ratio nearly 2.8 to 3.3; apical margin somewhat truncate; basal cell relatively broad; costal area broad, extremely long, reaching wing apex; Independent bScP with basal part thick, then migrating to R+MP+CuA and disappearing, not fusing with the latter; a short stem MP+CuA present, connected to CuP by crossvein *cua-cup* just at its bifurcation to MP and CuA. Hind wing with extremely narrow and wrinkled appendix present at apex; posterior margin lobate with anal portion strongly rippled.
Remarks. The holotype of the type and only included species of *Fangyuania* is not well preserved and so some morphological characters are missing; and so, the amended diagnosis of this genus is provided on the basis of new material.

Fangyuania xiai Chen et al. (2018)
Figs. 1A, 2–5

Material. Holotype: BA16003, a complete male adult insect in an amber piece. Other material: BA19002 and BA19003, two complete female adults in the same amber piece.
Description. BA19002. Total body with wings in repose 7.74 mm long.

Head with compound eyes narrower than pronotum; anterior margin smoothly angled. Crown broad and produced

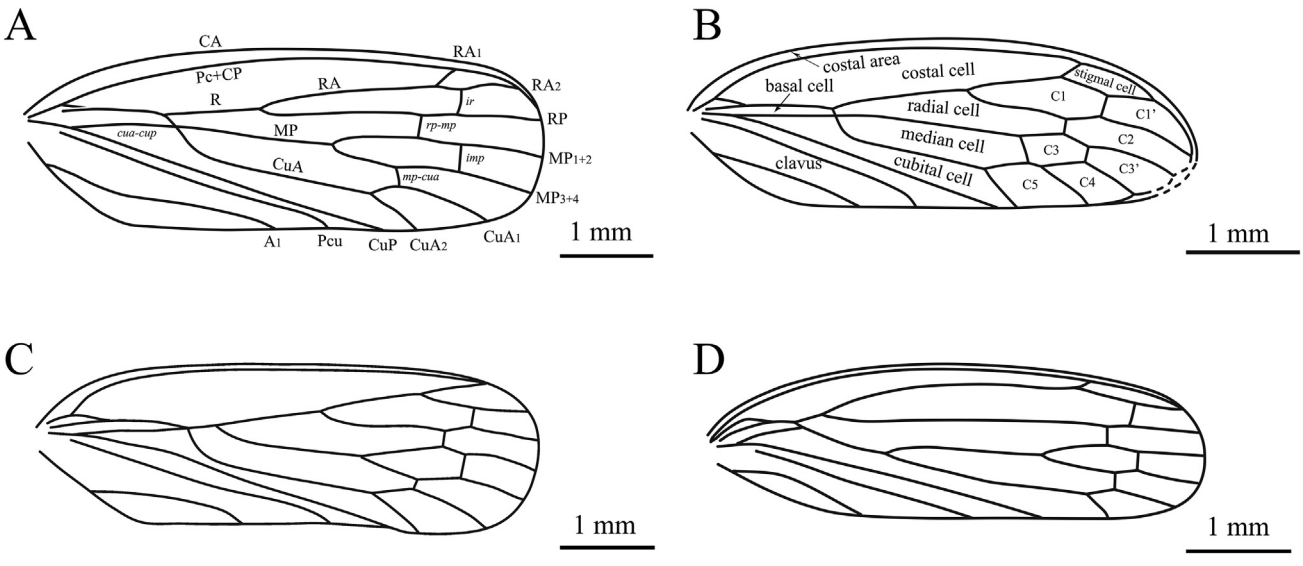

Fig. 1. Line drawings of tegmina of Sinoalidae recorded in mid-Cretaceous Kachin amber. (A), holotype of *Fangyuania xiai* Chen, Szwedo and Wang (2018), with venational terminology labelled; (B), holotype of *Jiaotouia minuta* Chen and Wang, 2019, with costal area, costal cell, clavus and terminology of wing cells labelled; (C), holotype of *Ornatiala amoena* Chen, Wang and Zhang, 2019; (D), holotype of *Mesolongicapitis peii* Chen, Zhang and Wang, gen. et sp. nov. Scale bars = 0.5 mm.

anteriorly, with length 1.28 mm, width with compound eyes 1.55 mm, length/width ratio about 0.83; coronal margin before compound eyes distinctly convex; disc densely covered with tiny granules. Compound eyes touching anterior margin of pronotum, large, almost oval in dorsal view, not bulging, 0.55 mm long, 0.28 mm wide in dorsal view. Three ocelli between eyes on crown, arranged in isosceles triangle with wide base. Antennal pit not distinct; antenna 0.84 mm long, with scape shorter than pedicel, flagellum long and aristiform, with basal segments thicker than apical ones. Postclypeus vey large and broad, somewhat depressed, longitudinally concave in middle. Anteclypeus oval, much smaller than postclypeus. Rostrum with labium stout and short, and stylet fascicle much longer than labium.

Pronotum shortened, 0.64 mm long, 2.11 mm wide, with length/width ratio about 0.3, and widest at its lateral angles, densely

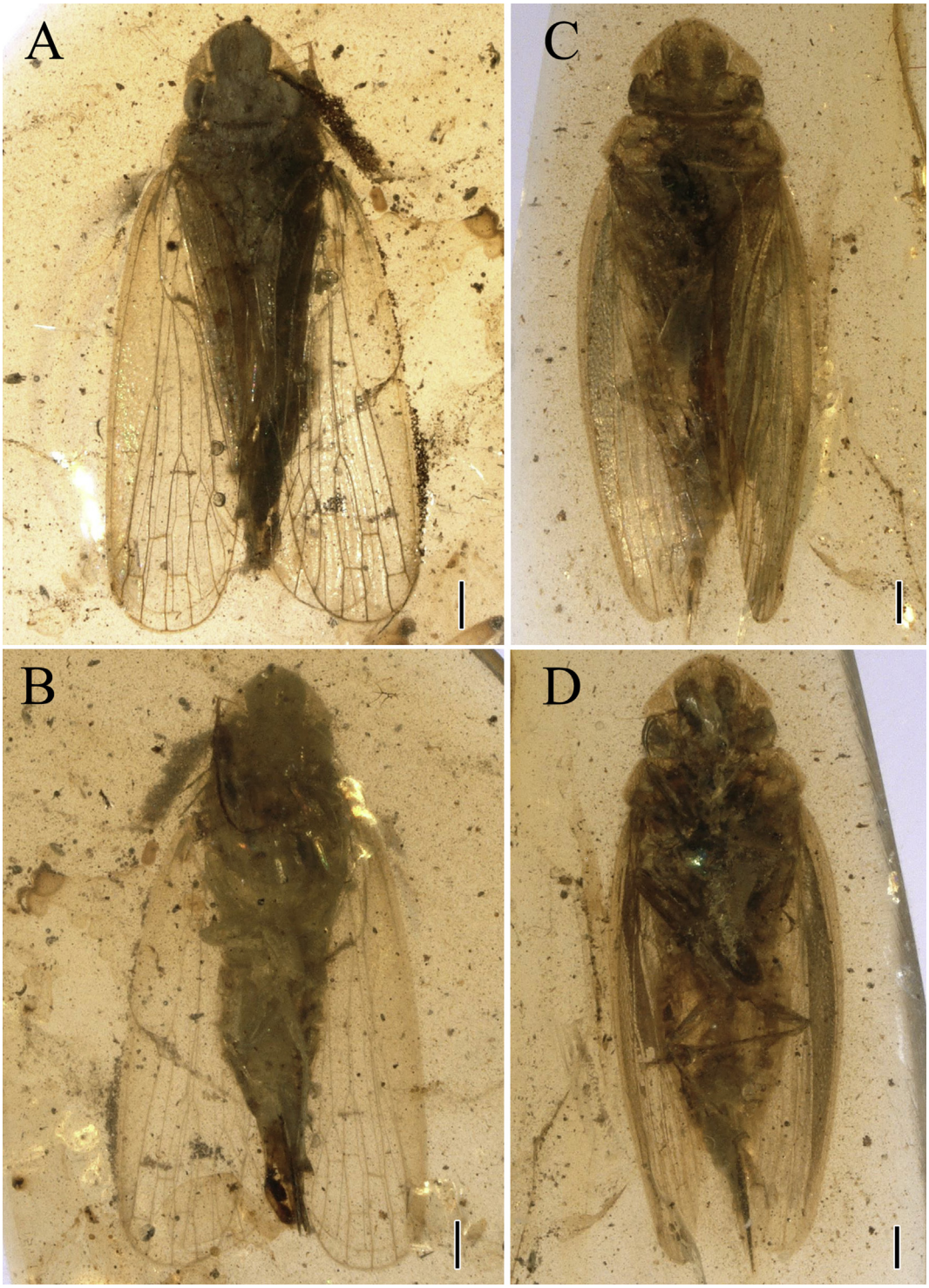

Fig. 2. Photographs of *Fangyuania xiai* Chen, Szwedo and Wang (2018). (A), dorsal view of BA19002; (B), ventral view of BA19002; (C), dorsal view of BA19003; (D), ventral view of BA19003. Scale bars = 0.5 mm.

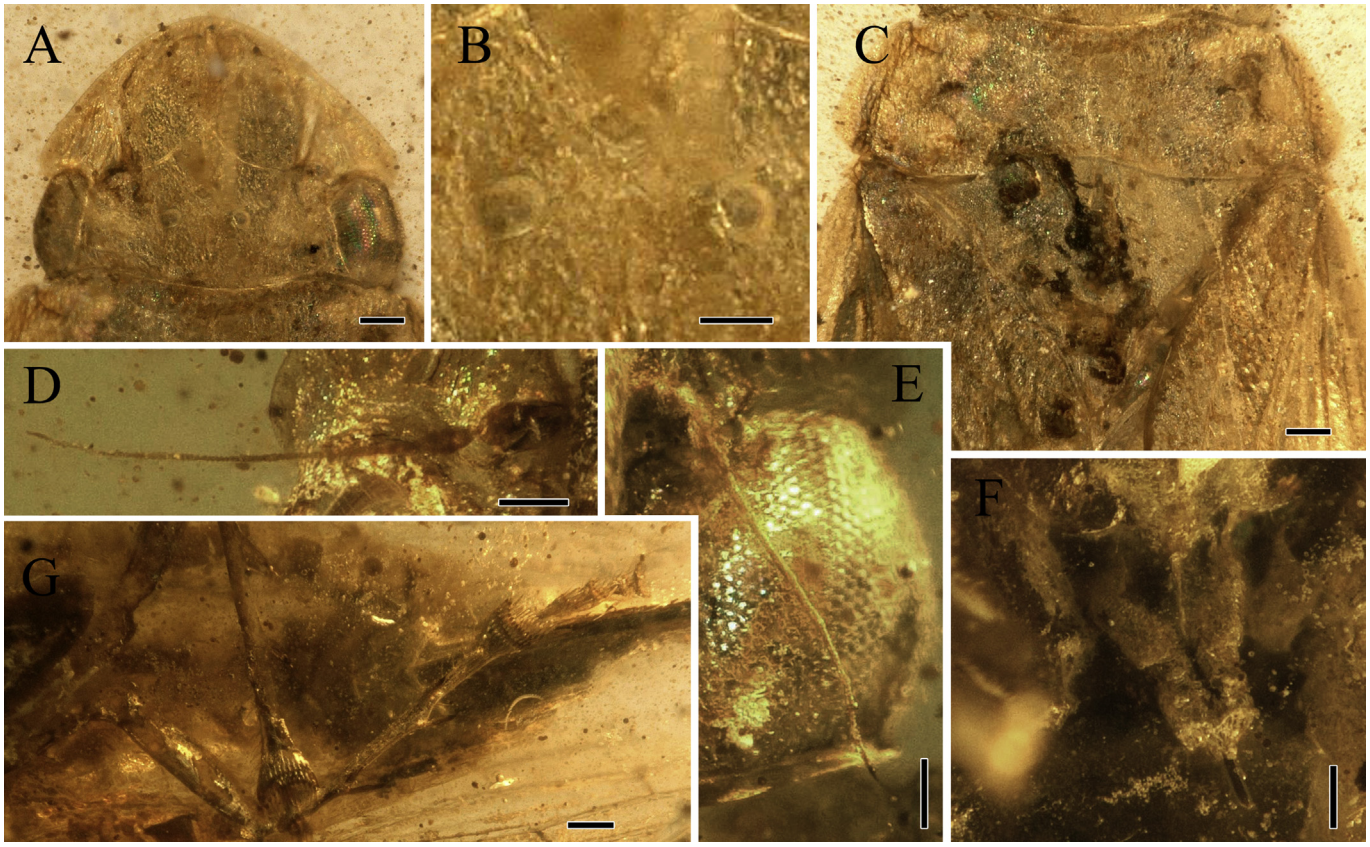

Fig. 3. Details of *Fangyuania xiai* Chen, Szwedo and Wang (2018) (BA19003). (A), crown; (B), ocelli; C, pronotum and mesonotum; (D), right antenna; (E), left antenna; F, rostrum; (G), right metathoracic leg. Scale bars = 0.2 mm (A, C, G), 0.1 mm (B, E-F).

covered with tiny granules; anterior margin concave medially with two lateral convexities; anterolateral angles obtuse; anterolateral margins straight; lateral angles acute; posterolateral margins slightly shorter than anterolateral margins, smoothly curved; posterolateral angles obtuse; posterior margin concave, slightly shorter than anterior margin. Mesonotum broad, much longer than pronotum, 1.31 mm long, 1.62 mm wide, with length/width ratio about 0.83; disc covered with tiny granules. Prothoracic legs with femur strong, nearly as long as tibia; tibia slenderer than femur; tarsus with apical tarsomere distinctly longer than basi- and mid-tarsomere; two tarsal claws well-developed. Mesothoracic legs with femur long, slenderer than fore femur; tibia nearly as long as femur; tarsus with apical tarsomere distinctly shorter than basi- and midtarsomere; two tarsal claws well-developed. Metathoracic legs with femur slender; tibia extremely long, about twice as long as femur, densely covered with setae; lateral spines arranged in two rows (one and two in number for each row); apical teeth arranged in two rows, with apical row with sub-apical long setae; tarsus with basi- and midtarsomere with one row of apical teeth, basitarsomere slightly longer than mid- and apical tarsomere; two tarsal claws distinct.

Abdomen flat, narrower than head and thorax, widest near middle. A long and almost transparent apical process present on anal tube, covered with long and slender hairs. Ovipositor very long and ensiform, 2.10 mm long, 0.27 of body length, exceeding apical process of anal tube.

Tegmen 5.70 mm long, 1.72 mm wide, with length/width ratio about 3.30. Costal cell, clavus and stigmal cell more punctate and sclerotized than other parts. Wing apex with extremely narrow and wrinkled appendix. Costal margin smoothly arched; apical margin somewhat truncate; post-claval margin almost straight; clavus margin strongly arched. Costal cell distinctly longer but narrower than clavus, reaching 0.84 and 0.72 of wing length, respectively. Basal cell relatively broad, about 0.26 of wing length. Cell C3 nearly twice as long as C3'. Costal area broad, extremely long, reaching wing apex. Independent bScP with basal part thick, then migrating to R+MP+CuA and disappeared, not fusing with the latter. R+MP+CuA slightly curved, bifurcating into R and MP+CuA at basal 0.25 of wing length. R almost straight, bifurcating into RA and RP at basal 0.47 of wing length. RA long, smoothly curved at base, then nearly straight, bifurcating into RA_1 and RA_2 at basal 0.80 of wing length. RA_1 much shorter than RA_2, about 1/3 as long as the latter. RP long, connected to RA_2 by crossvein *ir*, and to MP_{1+2} by crossvein *rp-mp*. Stem MP+CuA short, connected to CuP by crossvein *cua-cup* just at its bifurcation into MP and CuA. MP long, nearly straight, bifurcating into MP_{1+2} and MP_{3+4} at basal 0.63 of wing length. MP_{1+2} and MP_{3+4} subequal in the same length, connected by crossvein *imp*. CuA smoothly arched at base, then becoming nearly straight, bifurcating into CuA_1 and CuA_2 at basal 0.68 of wing length, just basad of claval apex. CuP long and nearly straight. Pcu shorter than CuP, slightly curved. A_1 long, slightly curved.

Hind wing membranous, with membrane densely covered with tiny tubercles. Extremely narrow and wrinkled appendix present at wing apex. Posterior margin lobate with anal portion strongly rippled. Stem R much short, forking into RA and RP basad of wing indentation. RA_1 extremely short, ending just apicad of wing-coupling lobe; RA_2 long, nearly straight. RP un-branched and long, connected to MP by crossvein *rp-mp*. MP long and unbranched, connected to CuA_1 by crossvein *mp-cua*. CuA forking into CuA_1 and CuA_2 apicad of bifurcation of RA; CuA_1 slightly longer than CuA_2. CuP long and slightly curved.

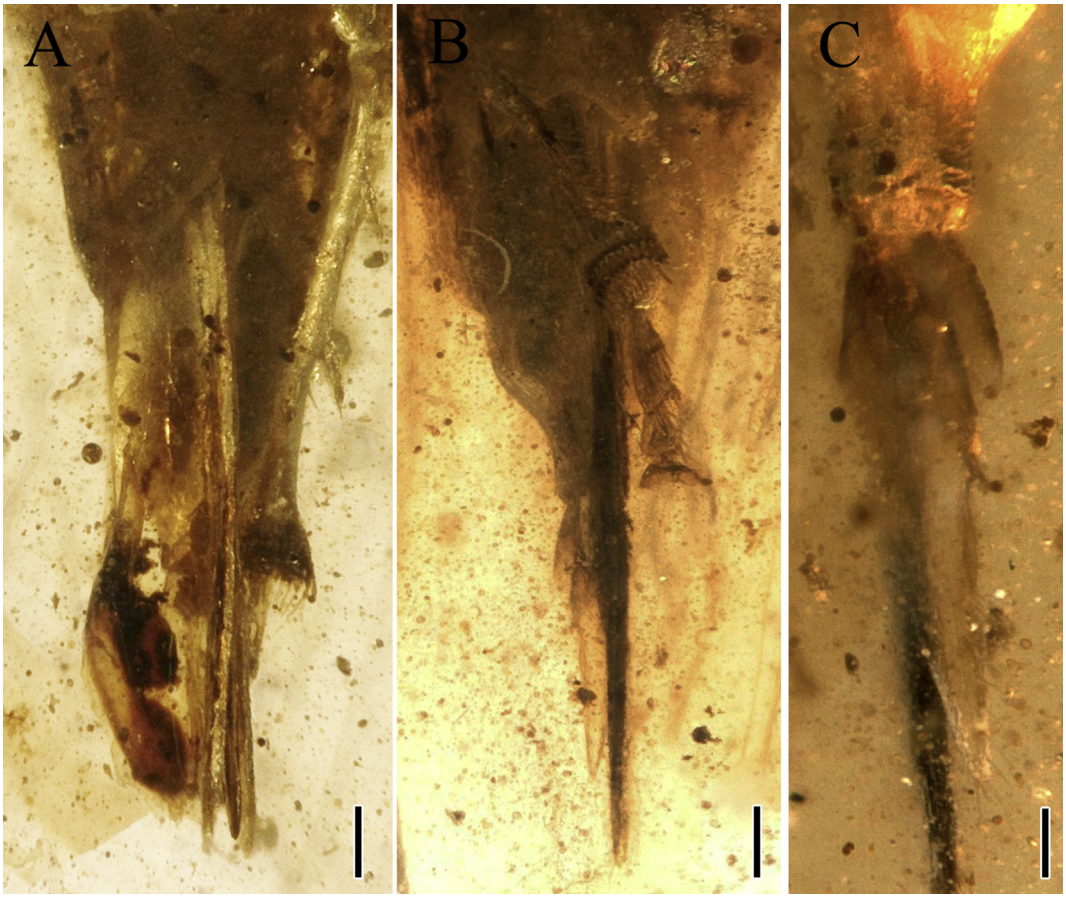

Fig. 4. Female pygofers of *Fangyuania xiai* Chen, Szwedo and Wang (2018). (A), BA19002 (ventral view); (B), BA19003 (ventral view); (C), anal tube of BA19003 (dorsal view). Scale bars = 0.2 mm (A, B), 0.1 mm (C).

BA19003. Total body with wings in repose 7.78 mm long, 2.87 mm wide. Head wider than that of BA19002, with length/width ratio 0.67; ovipositor slightly longer than that of BA19002, 2.25 mm long, 0.29 of body length; tegmen broader than that of BA19002, with length/width ratio 3.21. Other body and wing characters in general as in BA19002.

Genus ***Mesolongicapitis*** Chen, Zhang and Wang, gen. nov.
(urn:lsid:zoobank.org:act:D0D96DEA-C22C-4F15-A6B6-F74F9A38093A)
Type species: *Mesolongicapitis peii* Chen, Zhang and Wang, gen. et sp. nov.

Etymology. The generic name is formed by the combination of 'Mesozoic', the latin 'longus' (long) and 'capitis' (head), indicating its long head.
Diagnosis. Crown strongly produced anteriorly, length/width ratio about 1.26, with anterior margin with an acute angle in the middle. Compound eyes produced posteriorly, distinctly exceeding coronal posterior margin, touching anterolateral margins of pronotum. Pronotum relatively long, with length/width ratio 0.44; anterolateral angles almost rectangular; anterolateral margins with anterior 1/4 strongly concave, remaining parts nearly straight. Tegmen with length/width ratio 3.3; stem R extremely short, bifurcating into RA and RP at about basal 1/4 of wing length; RA_1 thick and extremely short; stem MP+CuA very long, connected to CuP by crossvein *cua-cup*, just beyond its separation from R+MP+CuA, but far away from its bifurcation; CuA bifurcating almost at the same level of costal apex, and distinctly apicad of claval apex.

Remarks. *Mesolongicapitis* gen. nov. bears a series of autapomorphies as mentioned in Diagnosis, well separating it from all known sinoalid taxa. The new genus is somewhat similar to the recently erected genus *Ornatiala* from Kachin amber (Chen et al., 2019b) in sharing the strongly anteriorly produced crown, but remarkably differs from the latter in possessing a much shorter pronotum, a distinct the mesoscutal sulcus and scutellum, and tegmina with stigmal cell longer and extremely narrow, stalk R+MP absent, R extremely short, and RA and RP much longer.

Mesolongicapitis peii Chen, Zhang and Wang, gen. et sp. nov.
(urn:lsid:zoobank.org:pub:AFAF9F7B-F734-4B6E-81D2-EC3C15B5F5BF)
Figs. 1D, 6 ,7

Material. Holotype: NIGP171033, a female adult insect in an amber piece with face and pro- and mesothoracic legs largely missing.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; mid-Cretaceous.
Etymology. The specific epithet is in honor of Mr. Yong Pei, who assisted in collecting Burmese amber.
Diagnosis. As for genus as it is the only so far included species.
Description. Total body with wings in repose 6.78 mm long, 2.98 mm wide.

Head with compound eyes slightly narrower than pronotum; anterior margin with acute angle in the middle. Crown broad and strongly produced anteriorly, with length 1.39 mm, width with compound eyes 1.10 mm, length/width ratio about 1.26; coronal margin before compound eyes slightly convex; disc densely

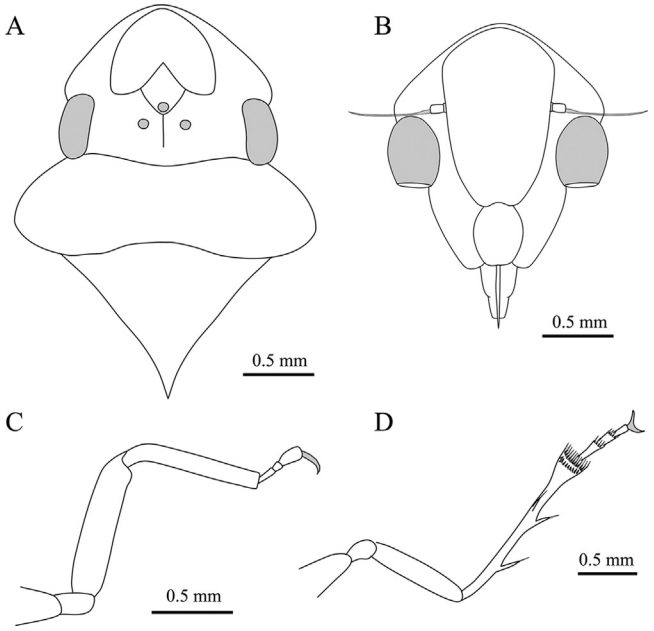

Fig. 5. Line drawings of *Fangyuania xiai* Chen, Szwedo and Wang (2018) (BA19003). (A), crown, pronotum, mesonotum; (B), face in dorsal view; (C), prothoracic leg; (D), metathoracic leg. All to scale bars.

covered with tiny granules; a large concavity located at anterior 1/2 of crown, and divided into two areas by distinct middle carina, fused with sunk frons in middle of posterior margin; epicranial suture with its two anterior arms distinct. Compound eyes produced posteriorly, distinctly exceeding coronal posterior margin, touching anterolateral margins of pronotum, 0.52 mm long, 0.17 mm wide in dorsal view. Three ocelli close to each other, with lateral two in vertex, aside epicranial suture, and median ocellus sunk in frons, surrounded by anterior arms of epicranial suture. Antenna 0.76 mm long, with scape thicker but apparently shorter than pedicel, flagellum long and aristiform. Face largely destroyed; postclypeus, anteclypeus and rostrum not preserved.

Pronotum relatively long, 0.61 mm long, 1.40 mm wide, with length/width ratio about 0.44, and widest at its lateral angles, covered with distinct granules; anterior margin slightly concave medially; anterolateral angles almost rectangular; anterolateral margins with anterior 1/4 strongly concave, remaining part nearly straight; lateral angles acute; posterolateral margins much shorter than anterolateral margins, about 1/2 as long as latter, smoothly curved; posterolateral angles obtuse; posterior margin acutely concave in the middle, almost as long as anterior margin. Mesonotum broad, much longer than pronotum, 1.11 mm long, 0.97 mm wide, with length/width ratio about 1.22; disc covered with granules in middle area; lateral margin acutely concave at mesoscutal sulcus; scutellum about 1/3rd as long as whole mesonotum. Pro- and mesothoracic legs not preserved. Metathoracic legs poorly preserved; femur slender, much shorter than tibia; tibia long, just two lateral spines preserved in one row; apical teeth obscure, but

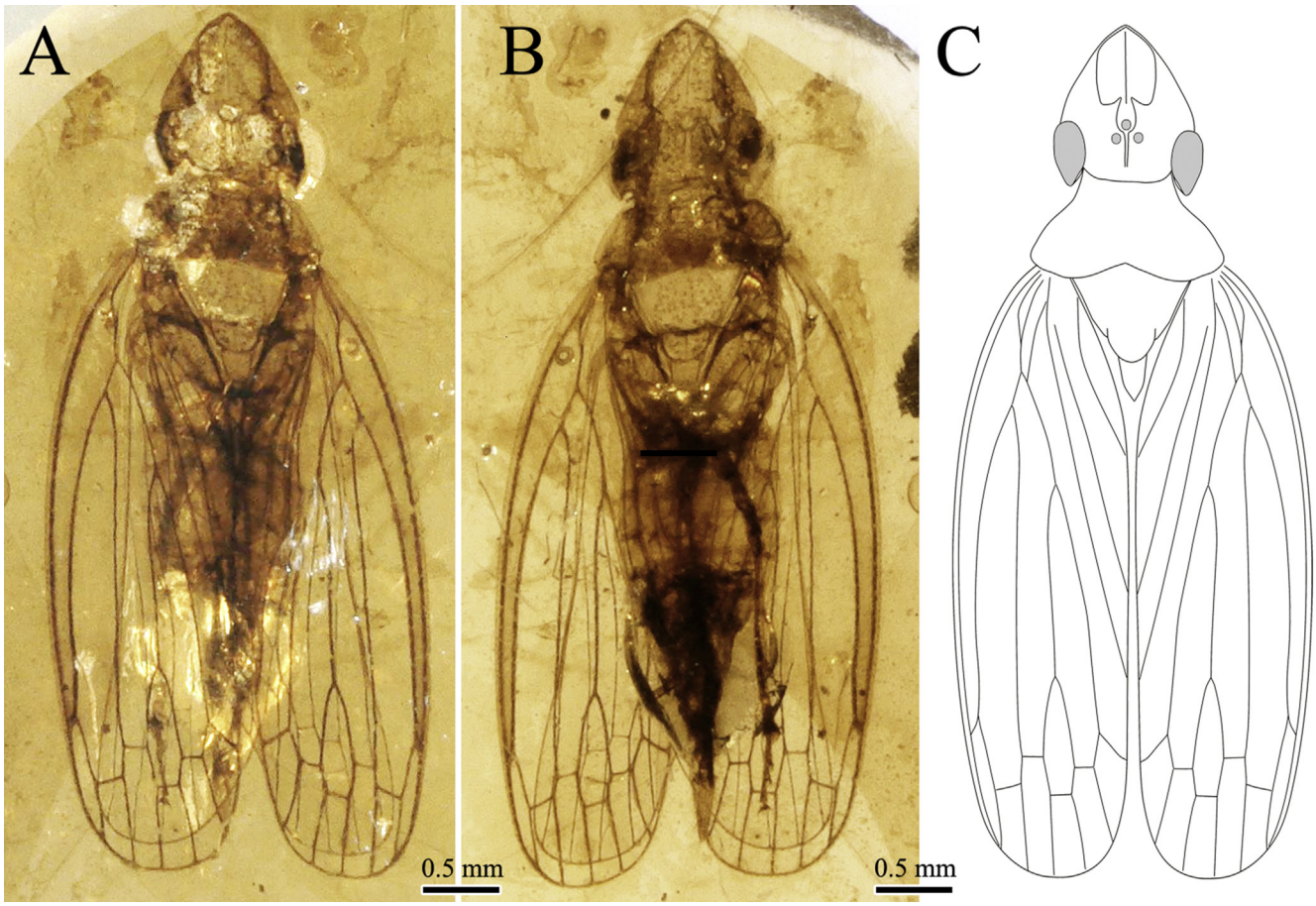

Fig. 6. Holotype of *Mesolongicapitis peii* Chen, Zhang and Wang, gen. et sp. nov., NIGP171033. (A), photograph in dorsal view; (B), photograph in ventral view; (C) line drawings in dorsal view. All to scale bars.

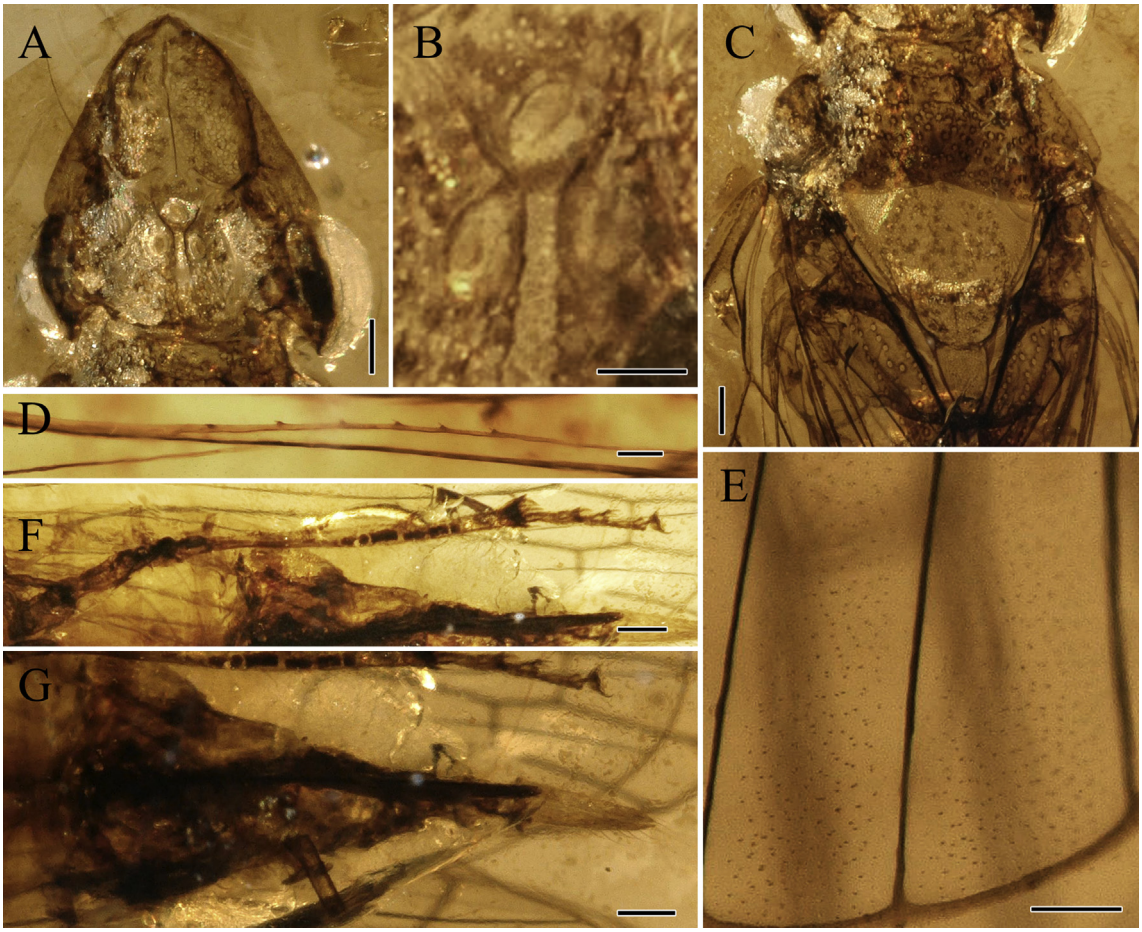

Fig. 7. Details of holotype of *Mesolongicapitis peii* Chen, Zhang and Wang, gen. et sp. nov., NIGP171033. (A), crown; (B), ocelli; (C), pronotum and mesonotum; (D), piliferous tubercles on costal margin of left hind wing; (E), tiny tubercles on left hind wing; (F), right metathoracic leg; (G), pygofer. Scale bars = 0.2 mm (A, C, F, G), 0.1 mm (B, D, E).

subapical long setae visible; tarsus with basitarsomere much longer than mid- and apical tarsomere, basi- and midtarsomere with long apical teeth; two tarsal claws well developed, with tip sharp.

Abdomen flat, almost as wide as head, apparently narrower than thorax, widest near middle. Long and almost transparent apical process present on anal tube, with long and slender hairs. Ovipositor very long and ensiform, 1.69 mm long, 0.25 of body length, exceeding apical process of anal tube.

Tegmen 4.89 mm long, 1.48 mm wide, with length/width ratio about 3.30. Costal cell and clavus more punctate and sclerotized than other parts. Wing apex without distinct appendix. Costal margin smoothly arched; apical margin somewhat truncate; postclaval margin almost straight; clavus margin smoothly arched. Costal cell much narrower but longer than clavus, reaching 0.77 and 0.67 of wing length, respectively. Basal cell relatively broad, 0.19 of wing length. Costal area relatively narrow, extremely long, but just reaching termination of RA_2. Stigmal cell long and very narrow, somewhat lanceolate. Cell C3 slightly longer than cell C3'. bScP not fused with Pc+CP for a long distance. Independent bScP relatively long, migrating to R+MP+CuA and then fusing with the latter slightly beyond middle of basal cell. R+MP+CuA slightly curved, bifurcating into R and MP+CuA at basal 0.18 of wing length. Stem R extremely short, nearly straight, bifurcating into RA and RP at basal 0.23 of wing length. RA extremely long, slightly curved, bifurcating into RA_1 and RA_2 at basal 3/4 of wing length. RA_1 thick and extremely short. RA_2 long and nearly straight. RP longitudinal, extremely long, slightly curved at base, and then becoming nearly straight, connected to RA_2 by crossvein *ir*, and to MP_{1+2} by crossvein *rp-mp*. Stem MP+CuA very long, connected to CuP by crossvein *cua-cup*, just beyond its separation from R+MP+CuA, but far away from its bifurcation. MP slightly curved at base, bifurcating into MP_{1+2} and MP_{3+4} at basal 0.68 of wing length. MP_{1+2} and MP_{3+4} subequal in length, connected by crossvein *imp*. Stem CuA slightly curved, and bifurcating into CuA_1 and CuA_2 at basal 0.68 of wing length, almost at the same level of costal apex, and distinctly apicad of claval apex. CuP long and nearly straight. Pcu shorter than CuP, slightly curved. A_1 relatively short, arched.

Hind wing membranous, with membrane densely covered with tiny tubercles. Appendix not distinct. Wing margin almost not concave at termination of longitudinal veins. Apical cell between CuA_1 and CuA_2 long and narrow. Stem R, forking into RA and RP basad of wing indentation, and shorter than two terminal branches. RA_1 extremely short, ending just apicad of wing-coupling lobe; RA_2 long, slightly curved. RP unbranched and long, connected to MP by crossvein *rp-mp*. MP long and unbranched, connected to CuA_1 by crossvein *mp-cua*. CuA forking into CuA_1 and CuA_2 almost at same level as bifurcation of RA; CuA_1 slightly longer than CuA_2.

4. Discussion

Up to now, three genera and species (*Fangyuania xiai*, *Jiaotouia minuta* and *Ornatiala amoena*) have been described based on three specimens from the mid-Cretaceous Kachin amber (Chen et al., 2018, 2019b, d). We herein report two new froghopper fossils

(BA19002 and BA19002) trapped in one amber piece and attribute them to *F. xiai*. The three individuals of *F. xiai* show considerable intraspecific variations: the length/width ratio is 0.78, 0.83 and 0.67 for crown in specimens BA16003, BA19002 and BA19003, respectively (Figs. 2, 3A; Figs. 1, 3A of Chen et al., 2018); 2.78, 3.30 and 3.21 for tegmen in BA16003, BA19002 and BA19003 respectively (Figs. 1A, 2); the tegminal cell C3 is about 2/3 as long as C3' in BA16003 (Fig. 1A), but about twice as long as the latter in BA19002 and BA19003 (Fig. 2). The variability might reflect its biological nature, but also is likely strongly influenced by taphonomic deformation and/or optical distortion of amber. A high intraspecific variation in the tegminal length/width ratio has been recorded in Mesozoic Cercopoidea based on multi-individuals (Chen et al., 2015a, 2019c), and the ratio even ranges from 2.74 to 4.10 in 42 specimens of *Juroala daohugouensis* in Chen et al. (2019c). High variation in venational patterns and corresponding wing cell patterns has also been well recorded in early Cercopoidea (e.g., Ansorge, 1996; Ren, 1995; Chen et al., 2015a, b, 2017, 2019c). Considering that similar variations are well documented in early Cercopoidea, all *Fangyuania* specimens come from the same amber biota, and specimens BA19002 and BA19003 are even trapped in one amber piece, it is reasonable to assign them to the same species.

The third sinoalid specimen described herein, with some remarkably novel morphological characteristics, is ascribed to the new genus and species *Mesolongicapitis peii* gen. et sp. nov. An intriguing feature of this new genus and species is the crown with epicranial suture and its two anterior arms distinct, and the median ocellus sunk in frons and surrounded by anterior arms of epicranial suture (Fig. 6). Early sinoalids from the Middle Jurassic to Late Jurassic Yanliao biota of northeastern China commonly possess distinct suture structures on crown (Wang et al., 2012; Fu and Huang, 2018; Chen et al., 2019c). The crown is not well-preserved in the known *Ornatiala* material (Fig. 2A of Chen et al., 2019b); nevertheless, the epicranial suture with anterior arms is likely preserved in *Fangyuania* and *Jiaotouia* (Fig. 3A; Fig. 4b in Chen et al., 2019d), but are apparently not as thick as those in the holotype of *Mesolongicapitis peii* gen. et sp. nov. The general pattern of head capsule possessed by Sinoalidae, with crown sclerites divided by suture structures and frons with a median ocellus, is conservative, resembling the basal model proposed for Clypeata by Dmitriev (2010) (Chen et al., 2019a).

The hitherto known sinoalids from Kachin amber are one male adult (*F. xiai*) and two adults with the pygofer destroyed (*J. minuta* and *O. amoena*) (Chen et al., 2018, 2019b, d). The present study adds three well-preserved female adults to *F. xiai* and *M. peii* gen. et sp. nov., respectively, providing more information on morphological and ecological diversification of Sinoalidae. The three froghoppers bear a long and ensiform ovipositor, exceeding the apical process of anal tube, just like their Jurassic relatives (Wang et al., 2012; Chen et al., 2017, 2019c). Sinoalids likely used the long and ensiform ovipositor to insert eggs into plant tissues, but the alternative scenario that they lay eggs inside soil should not be completely rejected, since nymphs of basal Clypeata are proposed to be subterranean (Shcherbakov, 1989; Shcherbakov and Popov, 2002; Chen et al., 2019c), and some modern nymphal froghoppers parasitize roots or the plant base near the soil surface (Bartlett, 2018).

5. Conclusions

With the current study, four genera and species attributed to Sinoalidae have been described from the Kachin amber biota (Chen et al., 2018, 2019b, d; this study), suggesting that this hemipteran group remained diverse in the mid-Cretaceous (Chen et al., 2018, 2019b, d). The known sinoalid species were all erected based on a single specimen. Two additional new specimens of *Fangyuania xiai* described herein indicate that this species bears considerable intraspecific variation in morphology. Additionally, the head capsule and female pygofer of our new material provide some novel insights into the evolution and ecology of Sinoalidae as well as early Clypeata.

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