



Widespread Grylloblattid Insects After the End-Permian Mass Extinction

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The end-Permian mass extinction (EPME) led to a severe terrestrial ecosystem collapse. However, the ecological response of insects to the EPME remains poorly understood. Here, we report a new species assigned to *Chauliodites*, *Chauliodites tongchuanensis* sp. nov. (Grylloblattida: Chaulioditidae), from the Middle Triassic Tongchuan Formation of Shaanxi, northwestern China, and redescribe *Chauliodites fuyuanensis* (Lin, 1978) from the Lower Triassic Kayitou Formation of Yunnan and *Chauliodites nanshenghuensis* (Lin, 1978) comb. nov. from the Middle Triassic of Guizhou, southwestern China. Our results show that *Chauliodites* widely distributed after the EPME is probably related to the rise of isoetalean-dominated low-productivity terrestrial ecosystems.

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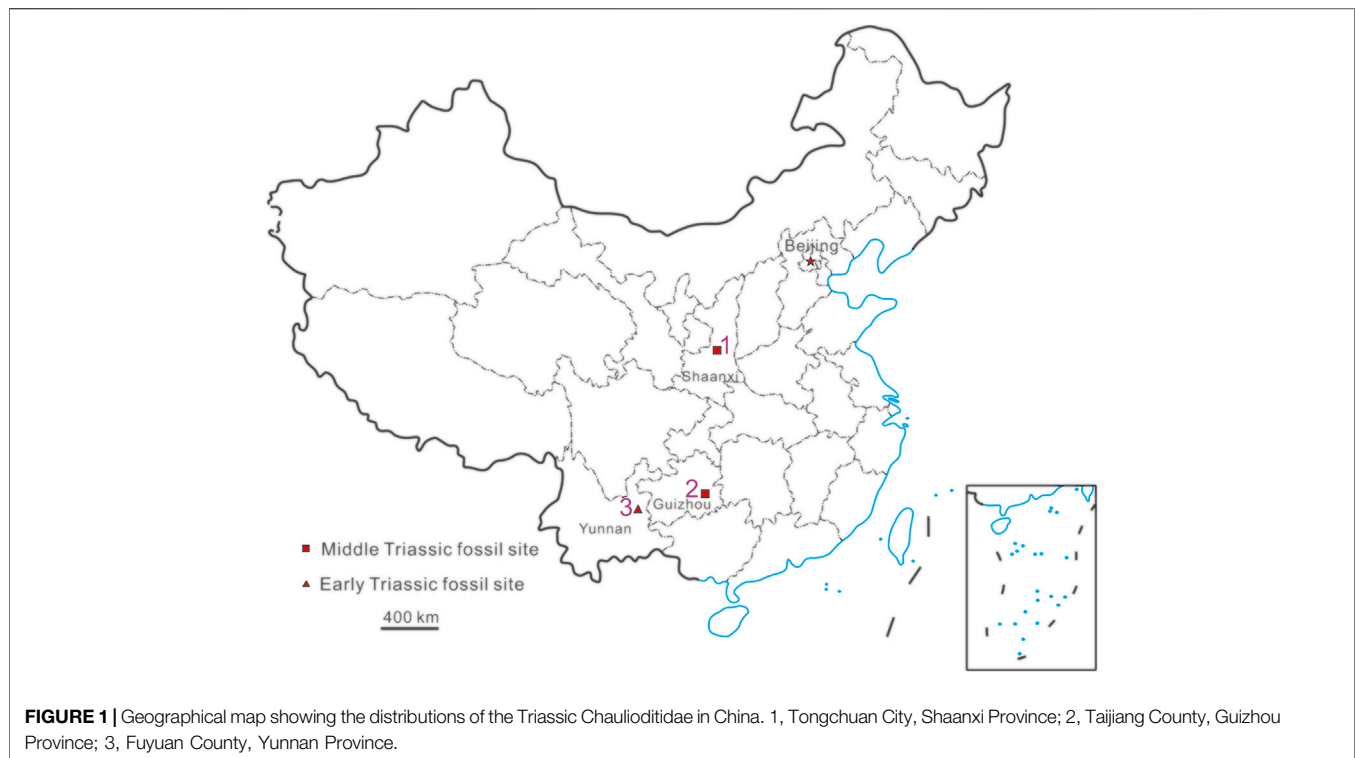
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INTRODUCTION

The end-Permian mass extinction (EPME: approximately 252 million years ago) witnessed the most severe biodiversity crisis during Earth history (Shen et al., 2011). How terrestrial ecosystems were affected during the EPME is still highly controversial (Benton and Newell, 2014; Gastaldo, 2019). In the terrestrial realm, insects were the earliest and most successful flying animals, which could spread and disperse globally in a relatively short time. Their often small size, powered flight, and metamorphic development could have helped insects to survive extreme events such as the EPME (Condamine et al., 2016; Montagna et al., 2019). Nearly all Permian insect families decreased from the Middle to Late Permian, and approximately one-third of families became extinct at the Permian/Triassic (P/T) boundary, while overall insect diversity was probably stabilized because of the emergence of new families (Ponomarenko, 2016). However, the ecological response of insects to the EPME remains poorly understood due to the rather low number of species described (Labandeira and Sepkoski, 1993; Béthoux et al., 2005; Benton and Newell, 2014; Schachat and Labandeira, 2020; Zhao et al., 2021).

Grylloblattida (Paraplecoptera) is comparatively abundant during the Permian, with three families continuing into the Mesozoic (Ponomarenko, 2016). Among them, the family Chaulioditidae (composing subfamilies Chaulioditinae and Kargalellinae) ranges from the Middle Permian to Middle Triassic and is represented near the Permo-Triassic boundary (Bashkuev et al., 2012; Aristov et al., 2013). These grylloblattidans were stonefly-like extinct insects, but most of their nymphs apparently lived on land (Ponomarenko, 2006) and probably played an important role in Early Triassic terrestrial ecosystems (Ponomarenko, 2016) with biostratigraphical potential (Aristov, 2008). *Chauliodites*, the type genus of Chaulioditidae, is the most widespread genus in this family and is also among the most important insectan index fossils during the Late Permian and Early Triassic (Aristov, 2008; Shcherbakov, 2008; Bashkuev et al., 2012).



Therefore, we investigated the fossil record of *Chauliodites* to help provide new insights into how insects were affected by the EPME.

Here, we report one new species assigned to *Chauliodites* from the Middle Triassic Tongchuan Formation of northwestern China and redescribe *Chauliodites fuyuanensis* (Lin, 1978) from the Early Triassic Kayitou Formation and *Chauliodites nanshenghuensis* comb. nov. from the Middle Triassic of southwestern China.

MATERIALS AND METHODS

The Triassic grylloblattidan specimens (registration numbers NIGP51619, NIGP51620, and NIGP162048) were collected from the Middle Triassic Tongchuan Formation in Tongchuan City, Shaanxi Province, NW China (Zheng et al., 2018); the Lower Triassic Kayitou Formation in Fuyuan County, Yunnan Province, SW China (Lin, 1978; Liu and Yao, 2002); and unnamed Middle Triassic strata at Nanshenghu in Guizhou Province, SW China (Lin, 1978), respectively (Figure 1). All specimens are housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), and were observed and photographed using a stereomicroscope system (ZEISS Stereo Discovery V16). Line drawings and interpretations were prepared using CorelDRAW 2019. The terminology of the tegminal venation is based on Kukalová (1964) and Storozhenko (1998): Sc, subcosta; RA, radius anterior; RP, radius posterior; MA, median anterior; MP, median posterior; CuA, cubitus anterior; CuP, cubitus posterior. However, M5,

which is considered as strengthened crossvein, is not adopted here (Cui et al., 2021).

SYSTEMATIC PALEONTOLOGY

Family Chaulioditidae Handlirsch, 1906.

Type genus. *Chauliodites* Heer, 1865.

Diagnosis (revised from Aristov, 2004). Tegmen oval; costal area wider than postcostal area, crossed by simple branches of Sc; M bifurcated beyond RP base; CuA1 simple and curved, area between CuA and CuP basally narrow.

Composition. *Chauliodites* Heer, 1865; *Paratomia* Aristov, 2003; and *Yontala* Aristov, 2005.

Genus *Chauliodites* Heer, 1865.

Type species. *Chauliodites picteti* Heer, 1865.

Revised diagnosis. RA usually with several branches fewer than Sc; RP with more than two branches, area between RA and RP wide in mid-tegmen; RA and RP initially divided in apical mid-tegmen; MA and MP usually with two–six branches in total. CuA first fork basal of R dividing.

Age and occurrence. Middle and Late Permian of Russian Federation; Early Triassic of China, Mongolia, and Russia; Middle Triassic of China, France, Germany, Poland, and Russia.

Species included. Twenty-six species: *Chauliodites afonini* Aristov, 2008, *C. anisicus* Grauvogel-Stamm et Marchal-Papier, 2011, *C. antiquus* (Aristov, 2003) Aristov, 2004 (Ansorge and Brauckmann, 2008), *C. babyi* Aristov, 2020a, *C. (T.) cancellata* (Aristov, 2003) Aristov, 2004, *C. circumornatus* Aristov et al., 2013 (Aristov et al., 2013a), *C. costalis* (Martynov, 1936) Aristov,

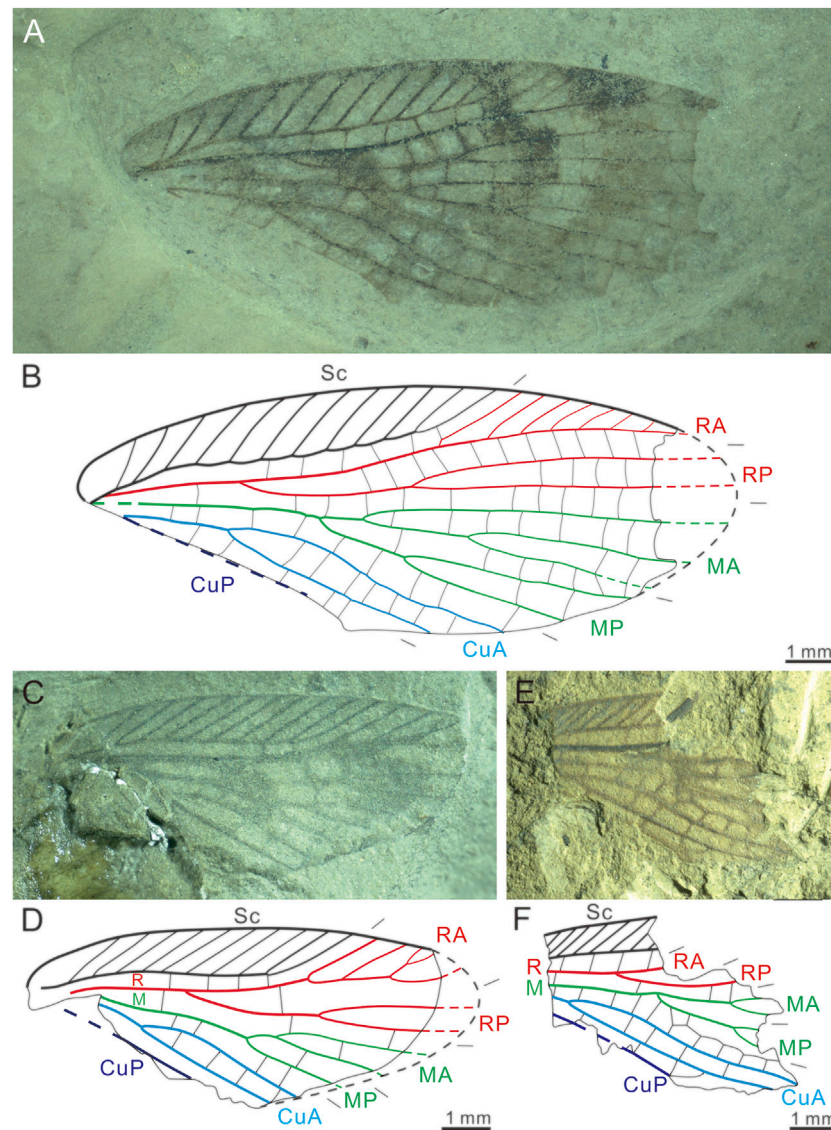


FIGURE 2 | (A) Reversed photograph of *Chaulioidites tongchuanensis* sp. nov. Holotype, NIGP162048a; **(B)** venational interpretation of **(A)**; **(C)** reversed photograph of *Chaulioidites nanshenghuensis* (Lin, 1978) comb. nov., Holotype, NIGP51620; **(D)** venational interpretation of **(C)**; **(E)** photograph of *Chaulioidites fuyuanensis* (Lin, 1978) Aristov, 2004, holotype, NIGP51619; **(F)** venational interpretation of **(E)**.

2004, *C. durus* (Aristov, 2003) Aristov, 2004 (Ansorge and Brauckmann, 2008), *C. eskovi* Aristov, 2011, *C. esperstedtensis* van Eldijk et al., 2017, *C. fuyuanensis* (Lin, 1978) Aristov, 2004 (Ansorge and Brauckmann, 2008), *C. geniatus* Aristov et al., 2013 (Aristov et al., 2013a), *C. gomankovi* Aristov, 2008, *C. incanus* Aristov, 2015, *C. issadensis* Aristov, 2009, *C. kitshmengensis* Aristov, 2013, *C. monglicus* Aristov, 2005, *C. nedubrovensis* Aristov, 2013, *C. niedzwiedzki* Aristov et al., 2013, *C. picteti* Heer, 1865, *C. ponomarenkoi* Aristov, 2008, *C. ramosa* (Aristov, 2003) Aristov, 2004, *C. sakmaris* Aristov, 2020b, *C. sennikovi* (Aristov, 2003) Aristov, 2004, and two new species [*C. nanshenghuensis* (Lin, 1978) comb. nov. and *C. tongchuanensis* sp. nov.] proposed here.

***Chaulioidites tongchuanensis* sp. nov. (Figures 2A,B).**

2018 *Chaulioidites*: Zheng et al., p. 3, Fig 3H.

Etymology. The specific epithet comes from the name of the city of Tongchuan in the fossil-bearing area.

Holotype. NIGP162048a, b; a forewing without clavus and apex; part and counterpart.

Type locality. Hejiafang Village, Tongchuan City, Shaanxi Province, northwestern China.

Age and horizon. Ladinian, late Middle Triassic; top bed of the lower Tongchuan Formation.

Diagnostic characters. Costal/postcostal width ratio more than 2:1; no crossveins connecting branches of Sc in costal area; initial division of RP basal of RA dividing; branches of RA developed; M with five branches in total; dark-colored stripes present.

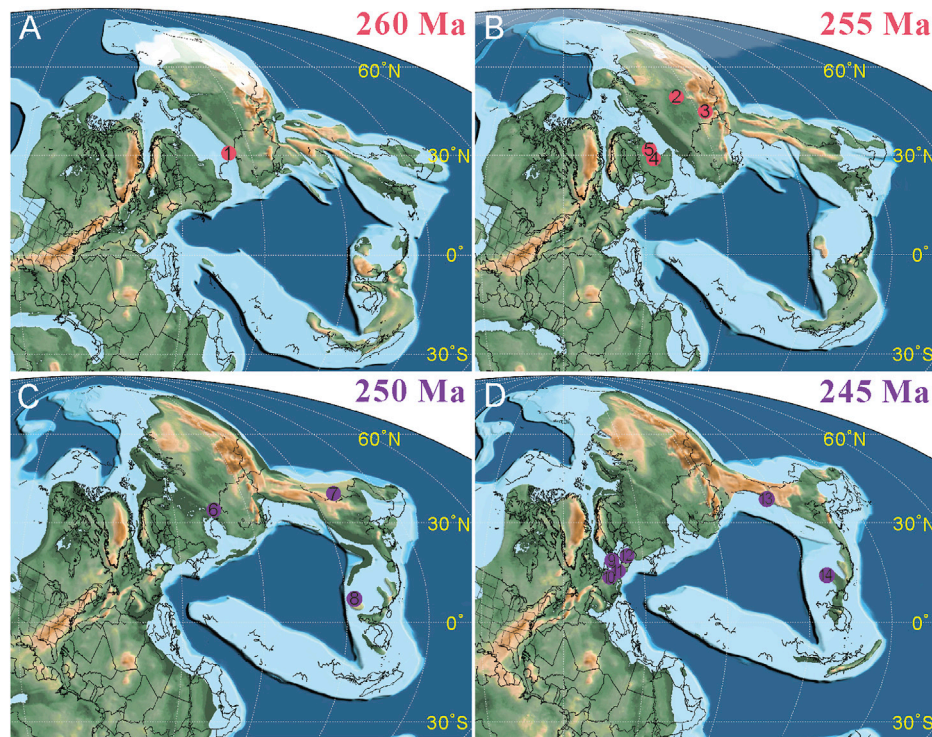


FIGURE 3 | Paleogeographic distribution of *Chauliodites* during the Middle Permian to Middle Triassic: **(A)** (1) Orenburg, Russia; **(B)** (2) Krasnoyarsk, Russia; (3) Kemerovo, Russia; (4) Vladimir, Russia; (5) Vologda, Russia; **(C)** (6) Orenburg, Russia; (7) Nomgon Sum, Mongolia; (8) Yunnan, China; **(D)** (9) Lower Saxony, Germany; (10) Vosges, France; (11) Bavaria, Lower Franconia and Thuringia of Germany; (12) Mniów, Poland; (13) Shaanxi, China; (14) Guizhou, China. Paleogeographic maps modified from Scotese (2021).

Description: Tegmen preserved length 12.2 mm, maximum width 4.7 mm, slightly convex in middle of anterior margin; maximum width of costal margin three times greater than subcostal area width. Twelve simple anterior branches of vein Sc present and seven of RA, nearly parallel and crossed to anterior margin. RA coalesced with Sc at tegminal base with six crossveins connecting Sc and RA in mid-forewing; RA long and curved without forks; stem R divided in basal quarter of tegminal length; RP curved posteriorly, two-forked apical of mid-tegminal length. M straight, possibly coalesced with Sc, divided into MA and MP at two-fifths of tegminal length; MA forked into MA1 and MA2 near mid-tegminal length; MA2 two-divided at apical third of tegminal length; MP two-divided at level of RP forking. CuA straight, nearly parallel to basal part of M, forked into CuA1 and CuA2 near RP base; two branches of CuA present, simple and extended towards posterior margin, CuA1 more curved than CuA2. CuP straight and thin. Crossveins short, simple, and developed between branches of main veins and veinlets. Ornament: three transverse dark-colored stripes of irregular shape across tegmen.

Chauliodites nanshenghuensis (Lin, 1978) comb. nov. (Figures 2C,D).

1978 *Tomia nanshenhuensis* Lin, p. 316; pl. 1; Fig 5.

1997 *Shurabia nanshenhuensis* (Lin, 1978): Storozhenko, pp. 1, 15.

2003 *Nivopteria nanshenhuensis* (Lin, 1978): Aristov, pp. 31, 33, 37, 38.

Holotype. NIGP51620; a forewing with clavus and apical part missing; only partly preserved. Housed at NIGPAS.

Type locality. Nanshenghu Village, Taijiang County, Guizhou Province, southwestern China.

Age and horizon. Middle Triassic.

Diagnostic characters. Costal/postcostal width ratio more than 3:1, no crossveins connected by veinlets in costal area; initial division of RA basal of RP; branches of RA well developed; area between RA and RP widened; M with three branches; CuA two-branched, CuA1 S-shaped; dark-colored stripes present on tegmen.

Description: Tegmen without apical and claval part, length 8.4 mm, 2.6 mm in maximum width. Oval in shape with anterior margin slightly convex; maximum width of costal area about 3.6 times greater than subcostal width. Sc with 10 simple, straight anterior branches without crossveins, R long and curved, parallel to Sc, and connected with Sc by four crossveins, divided into RA and RP at about two-thirds of tegminal length from base; stems RA and RP simple and curved, RA divided four times and forming at least five terminals. RP two-forked at about 0.63 of tegminal length. Area between RA and RP becomes wider distinctly near mid-tegmen. Basal part of M missing, slightly curved, and initially divided into MA and MP at about 0.45 of tegminal length; MA short, two-forked at 0.54 of tegminal length; MP simple. Base of CuA not preserved, nearly straight, forking into simple CuA1 and CuA2 about 0.25 of tegminal length; CuA1 more curved than CuA2. CuP straight, partly preserved.

TABLE 1 | Floristic compositions of *Chauliodites* species bearing strata.

Species	Formation (Age)	Floral	References
<i>C. babyi</i> Aristov, 2020a	Maltsevo Fm. (P3)	<i>Lepidopteris</i>	Karasev (2015)
<i>C. cancellata</i> (Aristov, 2003) Aristov, 2004			
<i>C. costalis</i> (Martynov, 1936) Aristov, 2004			
<i>C. ramosa</i> (Aristov, 2003) Aristov, 2004			
<i>C. circumornatus</i> Aristov, 2013	Poldarsa Fm. (P3)	Conifer shoots	Karasev et al. (2019)
<i>C. geniatus</i> Aristov, 2013			
<i>C. issadensis</i> Aristov, 2009			
<i>C. ponomarenkoi</i> Aristov, 2008			
<i>C. durus</i> (Aristov, 2003) Aristov, 2004	Bugarikta Fm. (P3)	Ferns, peltasperms, and conifers	Shcherbakov et al. (2021)
<i>C. eskovi</i> Aristov, 2011	Agitkan Fm. (P3)	<i>Todites</i> , <i>Acrostichides</i> , <i>Pecopteris</i> , <i>Rhipidopsis</i> , <i>Lepidopteris</i>	Sadovnikov, (2008)
<i>C. kitshmengensis</i> Aristov, 2013	Vokhma Fm. (P3)	<i>Tatarina</i>	Aristov, (2013)
<i>C. nedubrovensis</i> Aristov, 2013			
<i>C. fuyuanensis</i> (Lin, 1978) Aristov, 2004	Kayitou Fm. (T1)	<i>Gigantopteris</i>	Feng et al. (2020)
<i>C. sakmaris</i> Aristov, 2020b	Petropavlovka Fm. (T1)	<i>Densoisporites</i> , <i>Pleuromeia</i>	Shcherbakov et al. (2020)
<i>C. anisicus</i> Aristov, 2011	Grès à Voltzia Fm. (T2)	<i>Lycopsids</i>	Gall and Grauvogel-Stamm, (2005)
<i>C. esperstedtensis</i> van Eldijk et al., 2017	Vossenveld Fm. (T2)	<i>Triadispora</i>	Hemgreen et al. (2005)
<i>C. niedzwiedzki</i> Aristov, 2013	Samsonów Fm. (T2)	<i>Punctatisporites</i> , <i>Cyclotriletes</i> , <i>Cyclovrertriletes</i> <i>Densoisporites</i>	Żyła et al. (2013)
<i>C. picteti</i> Heer, 1865	Solling Fm. (T2)	<i>Pleuromeia</i>	Kustatscher et al. (2014)
<i>C. tongchuanensis</i> sp. nov.	Tongchuan Fm. (T2)	<i>Annalepis</i> - <i>Tongchuanophyllum</i> assemblage	Zhou and Zhou, (1983)
<i>C. incanus</i> Aristov, 2015	Amanak Fm. (P2)	Unknown	—
<i>C. sennikovi</i> Aristov, 2003 Aristov, 2004	Rybinsk Fm. (P3)	Unknown	—
<i>C. antiqua</i> (Aristov, 2003) Aristov, 2004	Salarevo Fm. (P3)	Unknown	—
<i>C. mongolicus</i> Aristov, 2005	Yamaan-Us Fm. (T1)	Unknown	—
<i>C. nanshenghuensis</i> (Lin, 1978) comb. nov.	Unnamed	Unknown	—
<i>C. afonini</i> Aristov, 2008			
<i>C. gomankovi</i> Aristov, 2008			

Crossveins short, simple, and vertically linking main veins and veinlets. Two dark-colored patches on middle and medial areas of tegmen.

Remarks: *Nivopteria* Lin, 1978 is a doubtful genus due to incomplete venational information about the type specimen (Aristov, 2003). Re-examination of the *Nivopteria nanshenghuensis* Lin, 1978 revealed that this species should be assigned to *Chauliodites* Heer, 1865 from characters including costal area wide with developed veinlets on Sc; RP and CuA both two-branched; MP first forked apical of R forking; initial forking of CuA basad of R dividing, and thus suggest that *Nivopteria* Lin, 1978 is a synonym of *Chauliodites* Heer, 1865.

Chauliodites fuyuanensis (Lin, 1978) Aristov, 2004 (Figures 2E,F).

1978 *Tomia fuyuanensis* Lin, p. 316; pl. 1; Figs. 4-6.

1997 *Shurabia fuyuanensis* (Lin, 1978): Storozhenko, pp. 1, 14.

2004 *Chauliodites fuyuanensis* (Lin, 1978): Aristov, S147

2008 *Chauliodites fuyuanensis* (Lin, 1978): Ansorge and Brauckmann, p. 255.

Holotype. NIGP51619; a forewing with mid-wing preserved; part and counterpart.

Type locality. Qingyun Village, Fuyuan County, Yunnan Province, southwestern China.

Age and horizon. Olenekian, Early Triassic; Kayitou Formation.

Diagnostic characters. Costal/postcostal width ratio less than 2:1, no crossveins connected by veinlets in costal area; secondary

crossveins present between MP2 and CuA1; M with four branches at least; CuA two-branched, CuA1 S-shaped; dark-colored stripes present.

Description: Middle part of tegmen preserved, 5.2 mm in maximum length, 3.3 mm in maximum width. Eight anterior branches of Sc present, nearly straight and parallel to each other. Costal/postcostal width ratio 1.4:1. R simple, slightly curved posteriorly, connected with Sc by four crossveins; RP simple, more curved than R; M divided into MA and MP apically at level of R forking. MA and MP both two-branched, forking nearly at the same level, secondary crossveins between MP and CuA developed. CuA forked basal of R dividing, CuA1 and CuA2 curved and parallel. CuP simple and straight.

DISCUSSION

The stratigraphical range of *Chauliodites* varies within Laurasia from the Middle Permian (Guadalupian) to Middle Triassic (Figure 3). In the Middle Permian, there are only two species reported from one fossil site in Russia (Figure 3A); in the Late Permian (Lopingian), *Chauliodites* bloomed with 15 species reported from four sites in Russia (Figure 3B); only three from sites around the Neo-Tethys during the Early Triassic (Figure 3C), and during the Middle Triassic, six species are known from six sites in total (Figure 3D). This genus disappeared from the fossil record by the late Middle

Triassic. The extinction of this taxon may result from the turnover of flora or competition from new types of insects (e.g., holometabolan), and further research is still needed to confirm the hypothesis.

Plant/insect interaction in terrestrial ecosystems is also a consideration, especially in the light of the EPME. The dominant flora in the latest Permian to Early Triassic turnover changed dramatically from gymnosperm to isoetalean lycophyte communities (mainly genera *Annalepis*, *Pleuromeria*, and *Tomiostrabus*) according to the palynological and megafloral record (Grauvogel-Stamm and Ash, 2005; Hermann et al., 2012; Feng et al., 2020; Liu et al., 2020; Looy et al., 2021). The Permo-Triassic transitional Kayitou Formation is widely exposed in southwestern China and, when yielding *Chauliodites fuyuanensis*, is dominated by isoetaleans (*Annalepis*) in the *Gigantopteris* floral (Yu et al., 2008; Chen et al., 2011; Feng et al., 2020). Rainforest on land is considered to have been replaced by herbaceous vegetation in the tropics, but the response of land plants to the Permo-Triassic crisis is variable due to latitudinal gradient (Feng et al., 2020). However, *Chauliodites*, spread across the floras of Angara, Euramerica, and Cathaysia, was little affected by latitude. The occurrence of isoetaleans is up to 12.5% in the megaflora and 24.0% in the microflora in the Olenekian (Early Triassic) (Looy et al., 2021). Floristic compositions of the *Chauliodites* bearing strata are listed (Table 1). Our study suggests that *Chauliodites* possibly become abundant with the rise of an isoetalean (lycophyte)-dominated

flora, considered environmentally and climatically tolerant plants in the low-productivity terrestrial ecosystems after the end-Permian terrestrial crisis (Feng et al., 2020).

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

Designing the project: BW. Preparing the fossil material and performing morphological analyses: QZ and BW. Preparing photographs and figures: QZ. Analyzing the data: QZ, BW, and EJ. Writing the manuscript: QZ, BW, and EJ.

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