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Palaeozoic insects from China with discussion on their ages

YE-HAO WANG, MING-LI WAN, HUA ZHANG, CHEN-YANG CAI & DI-YING HUANG*
State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Paleoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China
wangyh@nigpas.ac.cn; https://orcid.org/0000-0002-4638-974X
hzhang@nigpas.ac.cn; https://orcid.org/0000-0002-5871-8264
mlwan@nigpas.ac.cn; https://orcid.org/0000-0001-6287-3294
cycai@nigpas.ac.cn; https://orcid.org/0000-0002-9283-8323
dyhuang@nigpas.ac.cn; https://orcid.org/0000-0002-5637-4867
**Corresponding author*

Abstract

The late Palaeozoic is the key period for understanding the origin and early evolution of insects, but Palaeozoic insects from China are poorly explored. Up to now, a total of 53 Carboniferous species, 27 Permian species and 1 Carboniferous–Permian species (12 orders or 2 superorders) have been described. Recently, with the development of biostratigraphy and isotope chronology, new insights into the stratigraphy of China and its timescale have been greatly improved. In this study, we discuss the ages of published Palaeozoic insects from China and summarize 23 Carboniferous species, 57 Permian species and 2 Carboniferous–Permian species.

Keywords: Late Palaeozoic, insect fossils, Carboniferous, Permian

Introduction

Misof *et al*. (2014) dated the origin of insects to the Early Ordovician (~479 Ma), insect flight to the Early Devonian (~406 Ma) and major extant lineages to the Mississippian (~345 Ma) based on phylotranscriptomic evidence. The earliest known convincing pterygote insects appeared in the Upper Mississippian, *i.e*., *Delitzschala bitterfeldensis* from the upper Serpukhovian of Bitterfeld/Delitzsch area, Germany (Brauckmann *et al*., 1996). Several early small-sized fossils from the the Moscovian (France and Germany) and Gzhelian (France) were reported, suggesting that some forms of Recent insects (Eumetabola) have emerged at that time (Nel *et al*., 2014). The Pennsylvanian, a significant epoch for the radiation of insects, witnessed the radiation of early insects that occurred worldwide (*e.g*., Brauckmann *et al*., 2003).

Palaeoentomological studies of Palaeozoic insects in China was initiated by Lin (1978), who described two species from the Upper Permian Xuanwei Formation, Guizhou Province. Other Palaeozoic insects were later described by some Chinese palaeoentomologists (*e.g*., Hong, 1980, 1983; Lin, 1982; Peng *et al*., 2005; Chen *et al*., 2021). The well-known Qilianshan Entomofauna established by Hong (1998) yielded the majority of Carboniferous insects of China (*e.g*., Peng *et al*., 2005; Zhang *et al*., 2006, 2013; Béthoux *et al*., 2011, 2012a, b; Gu *et al*., 2011, 2014a, 2017; Su *et al*., 2012; Li *et al*., 2013a, b; Wei *et al*., 2013; Pecharová *et al*., 2015; Du *et al*., 2017; Chen *et al*., 2021). Most described Permian insects from China (Fig. 1) have been reported from the upper Guadalupian Yinping Formation, Anhui Province (Lin, 1982; Lin *et al*., 2010; Ponomarenko *et al*., 2014; Szwedo & Huang, 2019; Fu & Huang, 2020; Huang *et al*., 2007, 2020a, b, 2022).

Despite the remarkable progress made on the Palaeozoic stratigraphy in China, the ages of the fossiliferous deposits are often mis-interpreted by most palaeoentomologists. For example, the insects from Taiyuan and Shanxi formations were assigned to the late Carboniferous (Hong, 1980, 1983, 1985a, b), but the formations should belong to, the late Pennsylvanian—early Cisuralian and early Cisuralian respectively (Shen B. *et al*., 2021, 2022). Gu *et al*. (2014b) summarized the Palaeozoic insects of China, but the ages simply followed the original publications. Nevertheless, with the recent development of biostratigraphy and isotope chronology, the stratigraphy and timescale of the Palaeozoic of China have been refined based on multiple lines of evidence. Therefore, it is necessary to re-consider the ages of Palaeozoic insects of China. In this study, we present a list of Palaeozoic insects of China with revised ages (Fig. 2).

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Material and methods

We presented new photographs of some published Palaeozoic insects by using a digital camera attached to a Zeiss Discovery V16 microscope (Fig. 1). Photographs were refined and composed in Adobe Photoshop 2020. The illustrations were made by using Adobe Photoshop 2020. The newly photographed fossils are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.

Results

The Tupo Formation

Sze & Lee (1945) established Tupo Coal Series, and asserted the age of this strata belonged to the late Carboniferous based on plant fossils, and the series is correlated to the Benxi Formation of North China. The lithology of the Tupo Formation is represented by grayish sandstones alternated with dark siltstones, shales and mudstones, occasionally intercalated with marls, bioclastic carbonate lenses, as well as the thin coal seams (Bureau of Geology and Mineral Resources of Ningxia Hui Autonomous Region, 1996). The deposits of this formation yielded very rich terrestrial animal fossils in the alternated beds of terrestrial and marine sediment along a coastal area, and the insects often occurred in the black shales (Lu *et al*., 2002; Peng *et al*., 2005). The Qilianshan entomofauna was discovered from the Tupo Formation and assigned to Namurian C that is the late Bashkirian (Brauckmann *et al*., 1994; Hong, 1998; Wang *et al*., 2019). Peng *et al*. (2005) described the first insect fossils, and attributed them to the Bashkirian (Namurian B–C in the original text). A detailed geological study of the Tupo Formation near the Xiaheyan Village was provided by Zhang *et al*. (2013), who suggested the fossiliferous layers belong to the upper part of the Tupo Formation. Besides, some authors considered the synonyms of the Tupo formation, *i.e*., Yanghugou Formation, Hongtuwa Formation, Zhongwei Formation (Zhang *et al*., 2013; Wang *et al*. 2019; Li *et al*., 2021). Li *et al*. (2021) suggested that the Yanghugou Formation in North Qishanshan region belongs mainly to the early Bashkirian–Gzhelian, Pennsylvanian. We suggest that the insect-bearing beds of the Tupo Formation are correlated to the Benxi Formation.

The Benxi Formation

The Benxi Formation was established in Benxi City, Liaoning Province (Bureau of Geology and Mineral Resources of Henan Province, 1997). This formation is composed of alternating sandstones and mudstones representing marine-continental deposits with the widely distributed bauxitic rock layer at the bottom (Zhao *et al*., 2021). Fossil insects from the Benxi Formation were poorly known from the Kaiping Basin, Tangshan City, Hebei Province (Mathieu, 1939). In recent years, we have collected hundreds of insects from the Benxi Formation, Kaiping Basin. Some blattids were reported from Benxi group in Weibei Coal Mine, Shaanxi Province, but without illustrations and descriptions (Feng & Shang, 1980). Huang *et al*. (2022) reported some dictyopteran tegmina from the black shales of the upper part of Benxi Formation at Western Hills, Beijing. According to the conchostracan study, the Benxi Formation in Taiyuan City (Shanxi Province) and Kaiping Basin (Hebei Province) was suggested as the middle-late Moscovian to early Kasimovian and more likely the early Kasimovian in age (Liao *et al*., 2019, 2020). Wang *et al*. (2019) assigned the age of Benxi Formation of Taiyuan City to the late Moscovian–early Kasimovian. Shen B. *et al*. (2022) suggested this formation in Beijing, Hancheng City of Shaanxi Province and Baode County, Gaoping City and Taiyuan City of Shanxi Province belonged to the Moscovian–early Gzhelian.

The Taiyuan Formation

The Taiyuan Formation was derived from the Shanxi System, which is the lower part of the coal-bearing strata of the Late Palaeozoic in North China. The lithology of this formation is characterized by alternated marine-continental shales interbedded with several cyclothems composed of sandstones, coals and limestones (Bureau of Geology and Mineral Resources of Shanxi Province, 1997). Fossil insects from the Taiyuan Formation are relatively rare. Hong (1983) reported *Hsuopterites rotundus* from Caocun, Chengcheng County, Shaanxi Province and assigned it to the early Late Carboniferous. Huang *et al*. (2018) discovered *Phyloblatta beijingensis* in Seshufen Village, Mentougou District, Beijing and suggested its age close to the Carboniferous-Permian boundary. The Taiyuan Formation crossing the boundary of Carboniferous and Permian corresponding to the Kasimovian of Pennsylvanian–Asselian of Cisuralian was suggested by recent studies (Wang *et al*., 2019; Shen S. *et al*., 2019; Li *et al*., 2021; Shen B. *et al*., 2021). Shen B. *et al*. (2022) attributed the Taiyuan Formation in Baode County, Gaoping City and Taiyuan City, Shanxi Province to the late Gzhelian–early Asselian, late Pennsylvanian–early Cisuralian.

The Shanxi Formation

The Shanxi Formation is widely distributed in North China. This formation is composed of multiple cyclothems formed by terrestrial sandstones, shales and coals interbedded with several abnormal marine strata containing *Lingula*

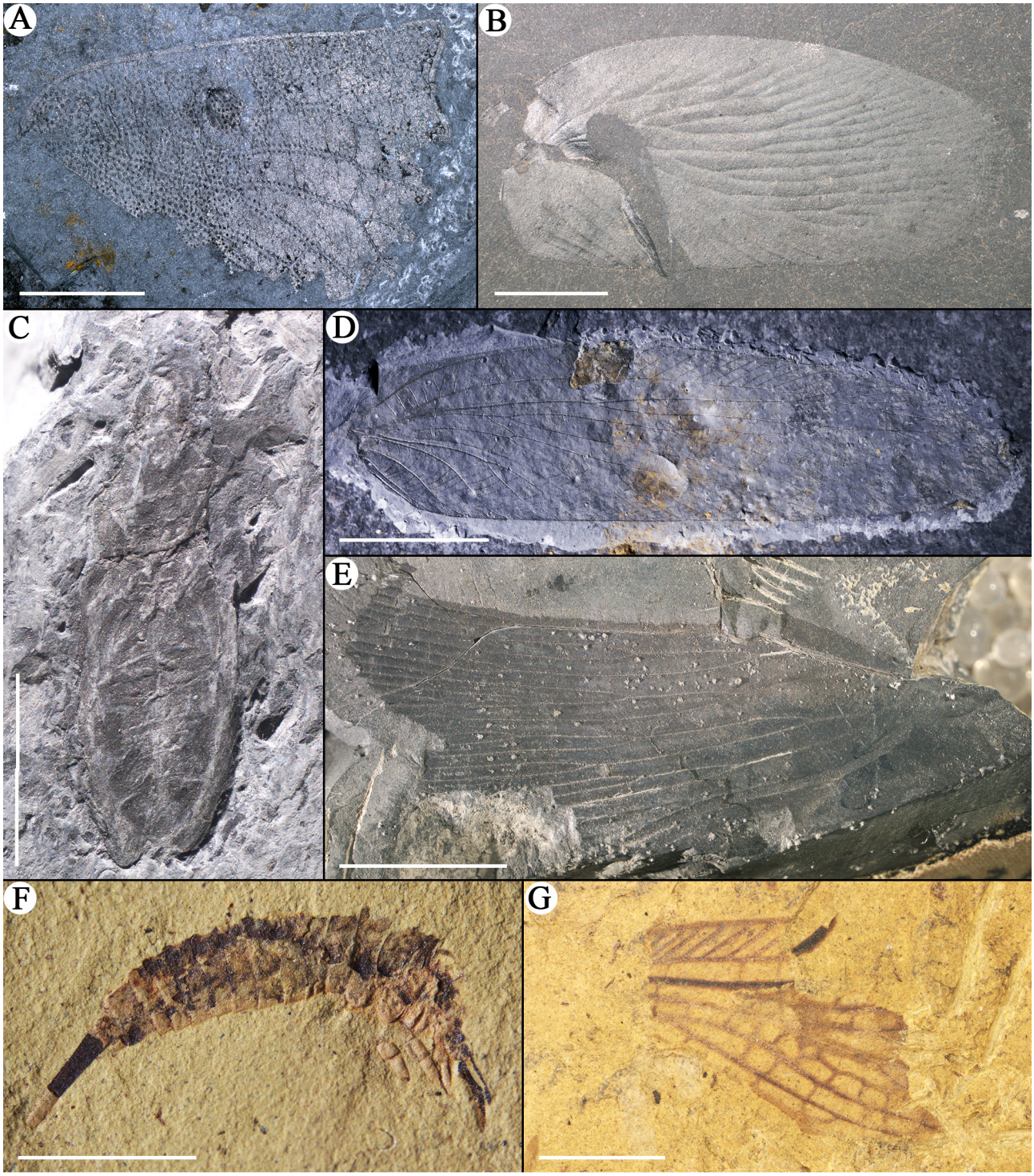

FIGURE 1. New photographs of some published Permian insects in China. **A**, *Sinomorphoptila incompleta* from the Yinping Formation in Yinping, Latest Guadalupian, NIGP173214. **B**, *Aissoblatta brachyna* from the Upper Shihhotse Formation, Cisuralian, NIGP81333. **C**, *Dikerocoleus divisus* from Yinping Formation in Yinping, Latest Guadalupian, NIGP70704. **D**, *Legendreia magnifica* from Yinping Formation in Yinping, Latest Guadalupian, NIGP171019. **E**, *Furcascytina radia* from the Longtan Formation in Benniu Town, Early Lopingian, NIGP52140. **F**, *Dasyleptus sinensis* from the Kayitou Formation in Yinchanggou Coal Mine, Latest Lopingian, NIGP168217. **G**, *Tomia fuyuanensis* from the Kayitou Formation in Qingyun Village, Latest Lopingian, NIGP51619.

and *Bivalvia* (Bureau of Geology and Mineral Resources of Shanxi Province, 1997). Some insects have been described from the Shanxi Formation at Gancaoshan and Renmazhuang, Xiangning County, Linfen City and Xishan, Taiyuan City, Shanxi Province. (Hong, 1980, 1985a, b). The age of the Shanxi Formation is argued for a long time, *i.e.*, cross Carboniferous-Permian boundary, early Permian or late Carboniferous (Tianjin Institute of

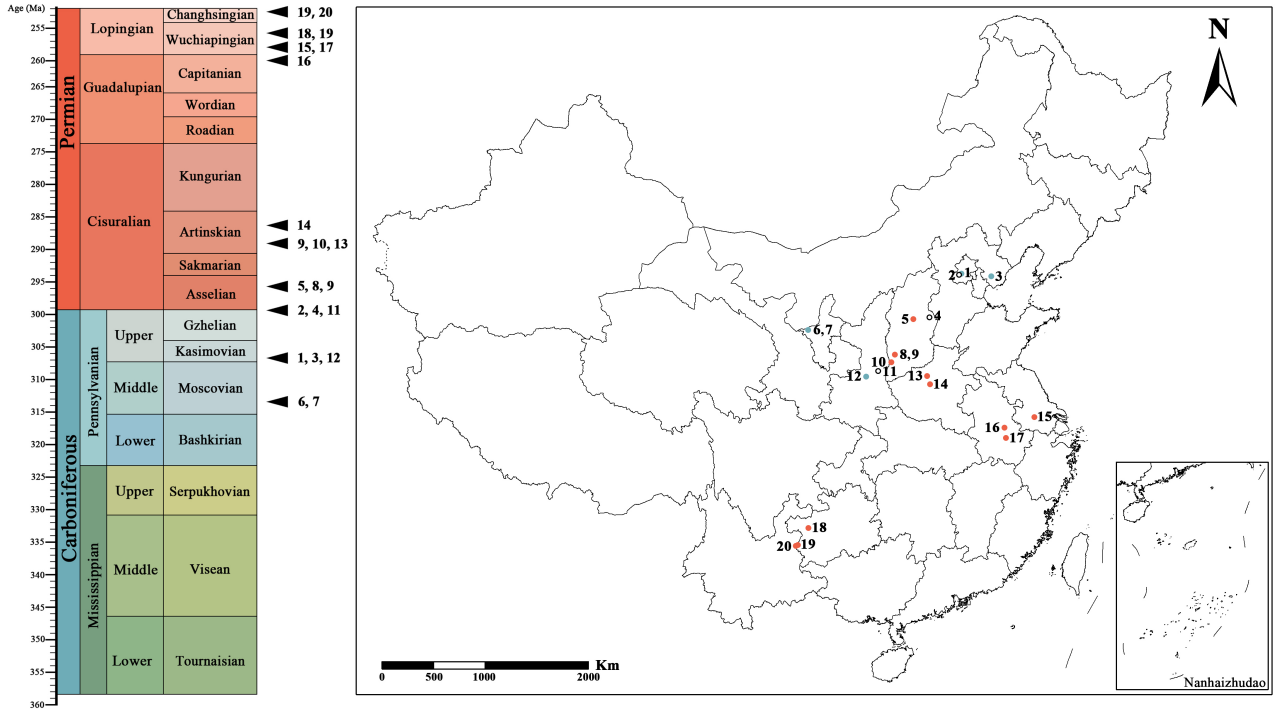

FIGURE 2. The distribution of the Palaeozoic fossil localities in China and the Chronostratigraphic chart with the projection of the localities. 1, Longquanwu Community; 2, Seshufen Village; 3, Kaiping Basin; 4, Yangquan City; 5, Xishan; 6, Xiaheyan Village; 7, Shangheyan Village; 8, Gancaoshan; 9, Renmazhuang Village; 10, Modigou; 11, Cao Village; 12, Weibei Coal Mine; 13, Dayugou Coal Mine; 14, Fangshan; 15, Benniu Town; 16, Yinping; 17, Tongling City; 18, Mazongling; 19, Qingyun Village; 20, Yinchanggou Coal Mine. Without the Wulasu Valley projected on the map because of its uncertain location. The orange dots on the map meaning the localities assigned to the Permian, blue dots meaning Carboniferous, hollow circles meaning Permian–Carboniferous.

Geology and Mineral Resources, 1985). The insect fossils were suggested as late Carboniferous in age (Hong, 1980, 1985a, b). Here we adopt the recent studies by Shen B. *et al*. (2021, 2022), who assigned the Shanxi Formation in Baode County, Gaoping City and Taiyuan City, Shanxi Province to the Asselian, Early Cisuralian.

The Lower Shihhotse Formation

The Lower Shihhotse and the Upper Shihhotse formations are derived from the Shihhotse System in Dongshan Mountain, Shanxi Province (Bureau of Geology and Mineral Resources of Shanxi Province, 1997). The lithology of the Lower Shihhotse Formation is characterized by a set of light-grey gravelly-coarse sandstones, grey-white medium-coarse sandstones and grey-green lithic quartz sandstones dominated by intracontinental deposition (Chen L. *et al*., 2001; Chen R. *et al*., 2022). Hitherto, four insect species have been described from the Lower Shihhotse Formation. Hong (1983) reported *Sunopterites hejinensis* in Modigou, Hejin City, Shanxi Province, but its exact systematic position remains uncertain (Gu *et al*., 2014b). Hong (1985b) described another two species, *Pinegia*? *meidigouensis* and *Anthohymen hejinensis* from the Renmazhuang Village, Xiangning County, Linfen City and Modigou, Hejing City, Shanxi Province. Lin and Liang (1988) reported *Phyloblatta parviradia* from the north of the Dayugou Coal Mine, Gongyi City, Henan Province. All published insects from the Lower Shihhotse Formation have been considered as the early Permian in age (Hong, 1983, 1985b; Lin & Liang, 1988). Shen S. *et al*. (2019) attributed the Lower Shihhotse Formation to the late Sakmarian–Roadian, the early Cisuralian–early Guadalupian. Shen B. *et al*. (2021, 2022) suggested that the range of the Lower Shihhotse Formation was very short, and assigned the Lower Shihhotse Formation in Baode County, Gaoping City and Taiyuan City, Shanxi Province to the late Asselian, early Cisuralian and the formation in Yuzhou City and Yongcheng City, Henan Province to early Sakmarian, Cisuralian.

The Upper Shihhotse Formation

The Upper Shihhotse Formation consists mainly of thick sandy mudstones with thin layer of fine-grained sandstones representing sediments from deltaic to alluvial plain depositional facies (Ma *et al*., 2021). Only one insect, *Aissoblatta brachyna*, was reported from the Upper Shihhotse Formation in Fangshan, Yuzhou City, Henan Province (Lin & Han, 1985), who attributed this

stratum to late Permian. Shen B. *et al*. (2021) attributed the Upper Shihhotse formation in Yuzhou City to the early Sakmarian–early Kungurian, Cisuralian.

The Yinping Formation

The Yinping Formation was established in 1987 (Regional Geology of Anhui Province, 1987) and distributed mainly in South Anhui Province (Lin *et al*., 2010). The lithology of this formation is mainly represented by the gray and dark gray siltstones and black shales deposited under palaeoenvironment varying from coastal marine to lagoon, and insect fossils were excavated from the black shales. Lin (1982) first reported two insects, *Yinpingia caesia* and *Dikerocoleus divisus* from Houdong Village, Chaohu City, Anhui Province. These species were attributed to the Gufeng and the Longtan formations, respectively (Lin, 1982). Lin *et al*. (2010) and Ponomarenko *et al*. (2014) stated that the *Y. caesia* and *D. divisus* were collected from the Yinping Formation. To date, a total of 14 species have been described from the Yinping Formation (Lin, 1982; Lin *et al*., 2010; Huang *et al*., 2007, 2020a, b; Ponomarenko *et al*., 2014; Szwedo & Huang, 2019; Fu & Huang, 2020a, b; Huang *et al*., 2022). The age of the Yinping Formation was attributed to the last part of the Capitanian (Zhang *et al*., 2019), or considered as crossing the Guadalupian-Lopingian boundary (Yao *et al*., 2015). Shen B. *et al*. (2021) assigned the Yinping Formation in Nanjing City, Jiangsu Province to the late Capitanian–early Wuchiapingian. Fossil insects were collected from the lower part of the Yinping Formation (*e.g*., Lin *et al*., 2010; Huang *et al*., 2020a), so that the fossiliferous strata should be assigned to latest Capitanian, Guadalupian.

The Longtan Formation

The Longtan Formation was derived from the Longtan Coal Series in Longtan Town, Nanjing City, Jiangsu Province (Bureau of Geology and Mineral Resources of Guizhou Province, 1997). The lithology of this formation consists of black carbon shales, silty mudstones, sandstones, siltstones, marlites, and coals, which indicate marine-continental sediments. Hitherto, only two hemipteran insects, *Furcascytina radia* and *Scopiprosbole caespis,* have been discovered from the Longtan Formation in Benniu Town, Wujin District, Changzhou City, Jiangsu Province and an unknown locality of Tongling City, Anhui Province, respectively (Lin, 1982). The Longtan Formation was dated to the Wuchiapingian, early Lopingian (Shen *et al*., 2019), and the Wuchiapingian for the Longtan Formation in Nanjing City, Jiangsu Province (Shen B. *et al*., 2021).

The Xuanwei Formation

The Xuanwei Formation originated from the Xuanwei Coal Series in Xuanwei City, Yunnan Province (Bureau of Geology and Mineral Resources of Guizhou Province, 1997). This formation is mainly composed of grey fine-grained sandstones, siltstones, silty mudstones, mudstones and coal seams, among which bearing coal seams is the major difference from the overlaying Kayitou Formation (Dai *et al*., 2008). The palaeoenvironment is represented by the terrestrial facies of floodplains, swamps, rivers and deltas (Bureau of Geology and Mineral Resources of Guizhou Province, 1997). Insects from the Xuanwei Formation were extremely sparse, with only two blattids, *Cubitoblatta concina* and *Cubitoblatta fidelis*, described by Lin (1978) from the Qingyun Village, Fuyuan County, Qujing City, Yunnan Province and Mazongling, Nayong County, Bijie City, Guizhou Province, respectively. Regarding the validity of the Kayitou Formation, some assigned the Kayitou Formation to the upper part of the Xuanwei Formation and suggested that the Xuanwei Formation belongs to the Late Permian to the Early Triassic (*e.g*., Bureau of Geology and Mineral Resources of Yunnan Province, 1996). Shen B. *et al*. (2021) attributed the Xuanwei Formation in Xuanwei City to the early Wuchiapingian–late Changhsingian, Lopingian.

The Kayitou Formation

The Kayitou Formation was derived from the Kayitou sand-shale layers named by Zhuquan Wang and Qingchang Bi when they investigated the Yangchang Coal Mine in 1940 (Wang, 2001). The lower part of this formation is yellow-green, gray-green, and brownish yellow combination of siltstones, conglomerates, clay and shales, and the lithology is similar with the Xuanwei Formation, but does not contain coal seams at the base, which is used to define this formation (Wang, 2001). The upper part of this formation is yellow-green, gray-green, brownish yellow siltstones, clay and shales combination interspersed with purple-red rock, and the proportion of purple-red rock increases from bottom to top (Wang, 2001). To date, insects unearthed from the Kayitou Formation are rare. Lin (1978) described the first species, *Chauliodites fuyuanensis*, at the Qingyuan Village, Fuyuan County, Qujing City, Yunnan Province, which was considered as the Early Triassic. Liu *et al*. (2021) reported the second insect, a bristletail named *Dasyleptus sinensis*, from the green-greyish layer of the upper part of the Kayitou Formation in the adjacent locality of *C. fuyuanensis*, Yinchanggou Coal Mine, and indicated the species belonged to the Latest Permian. The Kayitou sand-shale layers were originally attributed to the late Permian or Triassic (Wang, 2001). Some considered the Kayitou Formation as the lower part of the Feixianguan or Yelang formations as the lowest Triassic, or the upper part of Xuanwei Formation as the uppermost Permian or lowest Triassic (Bureau of Geology and Mineral Resources of Yunnan Province, 1990, 1996; Bureau of Geology and

TABLE 1. A list of Palaeozoic insects in China with revised age.

Species	Formation	Locality	Original age	Refined age	Reference
Acariformes					
Carbolohmannia maimaiphilus	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian, Late Carboniferous	Pennsylvanian	Robin *et al*., 2016
Archaeognatha					
Dasyleptus sinensis	Kayitou Formation	Yinchanggou Coal Mine, Fuyuan County, Xuanwei City, Yunnan Province	latest Permian	latest Lopingian	Liu *et al*., 2021
Archaeorthoptera					
Chenxiella liuae	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian B-C, Late Carboniferous	Pennsylvanian	Liu *et al*., 2009
Ctenoptilus frequens	Yanghugou Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Latest Bashkirian (Latest Duckmantian) to Middle Moscovian (Bolsovian), Early Pennsylvanian	Pennsylvanian	Chen *et al*., 2021
Heterologus duyiwuer	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian, Late Carboniferous	Pennsylvanian	Béthoux *et al*., 2012a
Legendreia magnifica	Yinping Formation	Houdong Village, Chaohu District, Hefei City, Anhui Province	late Middle Permian	latest Guadulapian	Huang *et al*., 2020b
Longzhua loculata	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian, Pennsylvanian	Pennsylvanian	Gu *et al*., 2011
Miamia maimai	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Early Pennsylvanian	Pennsylvanian	Béthoux *et al*., 2012b
Pinegia? *meidigouensis*	Lower Shihhotse Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Permian	Cisuralian	Hong, 1985b
Protomiamia yangi	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian, Early Pennsylvanian	Pennsylvanian	Du *et al*., 2017
Sinaspidoneura magnifica	Yinping Formation	Houdong Village, Chaohu City, Anhui Province	late Capitanian, Middle Permian	latest Guadulapian	Huang *et al*., 2020a
Sinoedisgraasdadchia carbonica	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Sinoedischia granulata	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Sinogerarus pectinatus	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian B-C?, Late Carboniferous	Pennsylvanian	Gu *et al*., 2017
Sinopteron huangheense	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian B-C, Late Carboniferous	Pennsylvanian	Prokop & Ren, 2007
Xixia huban	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian, Late Carboniferous	Pennsylvanian	Gu *et al*., 2014
Yinpingia caesia	Yinping Formation	Houdong Village, Chaohu City, Anhui Province	Early Permian	latest Guadalupian	Lin, 1982; Lin *et al*., 2010
Dictyoptera					
Aissoblatta brachyna	Upper Shihhotse Formation	Fangshan, Yuzhou City, Henan Province	Late Permian	Cisuralian	Lin & Han, 1985
Angusticubitus caochunensis	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Atimoblatta carbonica	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Cubitoblatta concina	Xuanwei Formation	Qingyun Village, Fuyuan County, Yunnan Province	Late Permian	Lopingian	Lin, 1978
Cubitoblatta fidelis	Xuanwei Formation	Mazongling, Nayong County, Guizhou Province	Late Permian	Lopingian	Lin, 1978

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TABLE 1. (Continued**)**

Species	Formation	Locality	Original age	Refined age	Reference
Dictyna chengchengensis	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Dictyoptera spp.	Benxi Formation	Longquanwu Community, Mentougou District, Western Beijing	Pennsylvanian	Middle-late Pennsylvanian	Huang *et al.*, 2022
Gangamoblatta lohoensis	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Hsuopterites rotundus	Taiyuan Formation	Cao Village, Chengcheng County, Shaanxi Province	early Late Carboniferous	Late Pennsylvanian–early Cisuralian	Hong, 1983
Ignaroblatta panda	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Kinklidoblatta youhei	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian B-C, early Bashkirian, Early Pennsylvanian	Pennsylvanian	Wei *et al*., 2013
Liroblatta internata	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Lohoblatta longa	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Metaxyblatta gancaoshanensis	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	late Carboniferous	early Cisuralian	Hong, 1980
Miaroblatta eurys	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Miaroblatta reticulata	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Miaroblatta sp.	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Olethroblatta sp.	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Palaeocicadopsis chinensis	-	Wulasu Valley, Inner Mongolia	Permian		Tan, 1980
Paucineura hsui	Shanxi Formation	Gancaoshan and Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1980; Hong, 1985b
Phyloblatta beijingensis	Taiyuan Formation	Seshufen Village, Wangping Town, Mentougou District, Beijing	Carboniferous–Permian	Late Pennsylvanian–Early Cisuralian	Huang *et al*., 2018
Phyloblatta cf. *picturata*	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Phyloblatta elliptica	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Phyloblatta extensa	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Phyloblatta lobata	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Phyloblatta parviradia	Lower Shihhotse Formation	North of Dayugou Coal Mine, Gongyi City, Henan Province	Early Permian	Cisuralian	Lin & Liang, 1988
Phyloblatta rara	Shanxi Formation	Xishan, Taiyuan City, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985a
Phyloblatta rigida	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Phyloblatta scabrata	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b

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TABLE 1. (Continued**)**

Species	Formation	Locality	Original age	Refined age	Reference
Phyloblatta scabrata	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Phyloblatta sinica	Shanxi Formation	Gancaoshan and Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1980; Hong, 1985b
Phyloblatta variata	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Phyloblatta xiangningensis	Shanxi Formation	Gancaoshan and Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1980; Hong, 1985b
Qilianiblatta namurensis	The upper Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region	Namurian B-C, Early Bashkirian, Early Pennsylvanian, earliest Late Carboniferous	Pennsylvanian	Zhang *et al*., 2013
Sardyoblatta lata	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Sardyoblatta pectinata	Shanxi Formation	Xishan, Taiyuan City, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985a
Sardyoblatta xiashanensis	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Shanxiblatta striata	Shanxi Formation	Gancaoshan and Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1980; Hong, 1985b
Shanxiblatta suni	Shanxi Formation	Gancaoshan and Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1980; Hong, 1985b
Shensiblatta ramulata	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Sibiroblatta lenticulata	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Tomacblatta bifurcullata	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Tomacblatta reticulata	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Xenoblatta longa	Shanxi Formation	Gancaoshan, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Zavjaloblatta sp.	Benxi Group	Weibei Coal Mine, Shaanxi Province	late Middle Carboniferous	Middle-Late Pennsylvanian	Feng & Shang, 1980
Coleoptera					
Archosyne permiana	Yinping Formation	Yinping, Chaohu City, Anhui Province	Late Capitanian, terminal Middle Permian	latest Guadalupian	Ponomarenko *et al*., 2014
Asiocoleopsis hongi	Yinping Formation	Yinping, Chaohu City, Anhui Province	Late Capitanian, terminal Middle Permian	latest Guadalupian	Ponomarenko *et al*., 2014
Chaocoleus limnebius	Yinping Formation	Yinping, Chaohu City, Anhui Province	Late Capitanian, terminal Middle Permian	latest Guadalupian	Ponomarenko *et al*., 2014
Dikerocoleus divisus	Yinping Formation	Houdong Villiage, Chaohu City, Anhui Province	Late Capitanian, terminal Middle Permian	latest Guadalupian	Lin, 1982; Ponomarenko *et al*., 2014
Linicupes yinpinensis	Yinping Formation	Yinping, Chaohu City, Anhui Province	Late Capitanian, terminal Middle Permian	latest Guadalupian	Ponomarenko *et al*., 2014
Taldycupes pingi	Yinping Formation	Yinping, Chaohu City, Anhui Province	Late Capitanian, Terminal Middle Permian	latest Guadalupian	Ponomarenko *et al*., 2014

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TABLE 1. (Continued**)**

Species	Formation	Locality	Original age	Refined age	Reference
Glosselytrodea					
Sinojurina permiana	Yinping Formation	Yinping Mountains, SW Chaohu City, Anhui Province	near the Middle Permian and Late Permian boundary, Middle Permian	latest Guadalupian	Huang *et al*., 2007
Grylloblattida					
Sinonamuropteris ningxiaensis	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian, Late Carboniferous	Pennsylvanian	Peng *et al*., 2005; Cui *et al*., 2011
Hemiptera					
Furcascytina radia	Longtan Formation	Benniu Town, Wujin District, Jiangsu Province	Late Permian	early Lopingian	Lin, 1982
Linglunxiellus chaohuensis	Yinping Formation	Yinping Mountains, Chaohu City Anhui	Capitanian, Latest Middle Permian	latest Guadalupian	Szwedo & Huang, 2019
Rhipiscytina brimis	-	Benniu Town, Wujin District, Jiangsu Province	Late Permian		Lin, 1982
Scopiprosbole caespis	Longtan Formation	Tongling City, Anhui Province	Late Permian	early Lopingian	Lin, 1982
Sinomorphoptila incompleta	Yinping Formation	Houdong Village, Sanbing Township, Chaohu City, Anhui Province	Capitanian, Middle Permian	latest Guadalupian	Fu & Huang, 2020
Mecoptera					
Sinoagetopanorpa permiana	Yinping Formation	Yinping Mountains, SW Chaohu City, Anhui Province	Middle Permian (near the Middle Permian and the Late Permian boundary)	latest Guadalupian	Lin *et al*., 2010
Megasecoptera					
Anhuihymen medianelongata	Yinping Formation	Houdong Village, Chaohu City, Anhui Province	Late Capitanian, Middle Permian	latest Guadalupian	Huang *et al*., 2022
Anthohymen hejinensis	Lower Shihhotse Formation	Modigou, Hejin City, Shanxi Province	Late Permian	Cisuralian	Hong, 1985b
Brodioptera sinensis	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian B-C, Bashkirian, the Early Pennsylvanian, Upper Carboniferous	Pennsylvanian	Pecharová *et al*., 2015
Paleohymen renmazhuangensis	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Paleohymen shanxiensis	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Sinohymen gancaoshanensis	Shanxi Formation	Renmazhuang Village, Xiangning County, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985b
Sunohymen xishanensis	Shanxi Formation	Xishan, Taiyuan City, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985a
Odonatoptera					
Arctotypus? *carbonica*	Shanxi Formation	Xishan, Taiyuan City, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985a
Aseripterella sinensis	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian, Early Pennsylvanian	Pennsylvanian	Li *et al*., 2013a
Erasipterella jini	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian B-C, Late Carboniferous	Pennsylvanian	Su *et al*., 2012; Li *et al*., 2013a
Oligotypus huangheensis	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian B-C, Late Carboniferous	Pennsylvanian	Ren *et al*., 2008; Li *et al*., 2013a

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TABLE 1. (Continued)

Species	Formation	Locality	Original age	Refined age	Reference
Shenzhousia qilianshanensis	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian C, Late Carboniferous	Pennsylvanian	Zhang *et al*., 2006
Sylphalula laliquei	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian, Early Pennsylvanian	Pennsylvanian	Li *et al*., 2013a
Tupus orientalis	Tupo Formation	Shangheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian B-C, Late Carboniferous	Pennsylvanian	Su *et al*., 2012; Li *et al*., 2013a
Palaeodictyoptera					
Namuroningxia elegans	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian B-C, Late Carboniferous	Pennsylvanian	Prokop & Ren, 2007
Palaeoneura qiligouensis	Shanxi Formation	Xishan, Taiyuan City, Shanxi Province	Late Carboniferous	early Cisuralian	Hong, 1985a
Sinodunbaria jarmilae	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian B-C, Bashkirian, Late Carboniferous	Pennsylvanian	Li *et al*., 2013b
Tytthospilaptera wangae	Tupo Formation	Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region	Namurian, early Late Carboniferous	Pennsylvanian	Liu *et al*., 2015
Paraplecoptera					
Tomia fuyuanensis	Kayitou Formation	Qingyun Village, Fuyuan County, Yunnan Province	Triassic	latest Lopingian	Lin, 1978
Plecoptera					
Gulou carpenteri	Tupo Formation	Xiaheyan Village, Zhongwei City, Ningxia	Pennsylvanian	Pennsylvanian	Béthoux *et al*., 2011
Phyloblatta sp.	Benxi Formation	Kaiping Basin, Tangshan, Hebei Province		Middle-Late Pennsylvanian	Mathieu, 1939
Soomylacris sp.	Benxi Formation	Kaiping Basin, Tangshan, Hebei Province		Middle-Late Pennsylvanian	Mathieu, 1939
Incertae sedis					
An insect wing fragment	Taiyuan Formation	Yangquan City, Shanxi Province	Early Permian	Late Pennsylvanian–early Cisuralian	Wang *et al*., 2019
Sunopterites hejinensis	Lower Shihhotse Formation	Modigou, Hejin City, Shanxi Province	Early Permian	Cisuralian	Hong, 1983
Wulasua maculata	-	Wulasu Valley, Inner Mongolia	Permian		Tan, 1980

Note: "-" indicating no available data from the original paper.

Mineral Resources of Guizhou Province, 1987, 1997; Wang, 2001). Others believed that the Kayitou Formation represented a transitional stratum extending from the Lopingian to the Lower Triassic (Wang, 2001; Zhang *et al*., 2016; Scholze *et al*., 2020). Shen S. *et al*. (2019) and Shen B. *et al*. (2021) assigned the Kayitou Formation as late Changhsingian, Lopingian.

Conclusion

To date, a total of 23 carboniferous species, 57 Permian species and 2 Carboniferous–Permian species, placed in 12 orders and 2 superorders have been described from the Palaeozoic of China in light of our discussion on the ages (Table 1). Currently, discoveries of Carboniferous insects of China are largely confined to the North China Block, and fewer from South China (Fig. 2). The Permian insects are mainly from South China, but they are sporadically reported in North China (Fig. 2).

Compared with the international research of Palaeozoic insects, relatively fewer Palaeozoic insects of China have been studied, mainly including those from the Pennsylvanian Xiaheyan Entomofauna in Ningxia and the Guadalupian Yinping Entomofauna in Chaohu, Anhui Province. However, the Carboniferous and Permian terrestrial strata and marine-nonmarine strata in China are relatively well-developed, so there is a great potential for further exploration of Palaeozoic insects in China.

For example, our research group has recently collected hundreds of insect fossils in the Benxi Formation of the Kaiping Basin in Tangshan, Hebei Province, and the Yinping Formation in Chaohu City, Anhui Province. Continuing to study these fossil insects will further strengthen our understanding of the early evolution of insects. The Carboniferous-Permian icehouse was the longest-lived ice age of the Phanerozoic (Montañez & Poulsen, 2013), and a more accurate understanding of the fossil records of insects during this critical period will help to understand the evolution of the terrestrial ecosystem and palaeoclimate at that time, especially the icehouse-greenhouse transitions.

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