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Sinaspidoneura magnifica nov. gen., nov. sp., first Chinese Caloneurodea (Insecta: Archaeorthoptera)

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ABSTRACT

We describe the first Chinese Caloneurodea, *Sinaspidoneura magnifica* nov. gen., nov. sp. from the middle Permian Yinping Formation, in the small family Aspidoneuridae, previously known from two genera and species, one from the latest Carboniferous of France and another from the late early Permian of North America. This discovery shows that this order was more widespread during the Middle Permian than previously supposed, under a great variety of palaeoclimates. This clade is still unknown in the Late Permian, and possibly became extinct because of the crisis of biodiversity that happened at the end of the Middle Permian.

Keywords: Aspidoneuridae; paleobiogeography; Laurussia; Southern China; nov. gen., nov. sp.; Middle Permian extinction.

1. Introduction

The small extinct order Caloneurodea Martynov, 1938 is currently only known between the late Carboniferous and the end of the middle Permian, in Western Europe, North America, and Russian Federation. With 22 described genera, it is one of the smallest order of Paleozoic insect orders. Its position was uncertain till Béthoux et al. (2004) discovered that their pattern of wing venation was that of the superorder Archaeorthoptera Béthoux and Nel, 2002, the total group of the recent Orthoptera Olivier, 1789 and some other extinct clades such as the Titanoptera Sharov, 1968. The Caloneurodea are well-characterized by a series of characters of the forewing venation, the most obvious being the veins 'MP+CuA+CuPa α and CuPa β close, parallel and straight'. Very little is known about their body structures, young stages and biology. They could adapt to the important climatic changes and environments that happened between the Carboniferous and the middle Permian. They were widespread in the Laurussia but still unknown elsewhere during the Middle Permian.

For China, Hong and Wang (1976: 82-83, pl. 51, fig. 5-5a) described *Sinogramma reticularis* in the caloneurodean Pleisigrammatidae Carpenter, 1943 from the Lower Cretaceous Guyang Formation (Inner Mongolia). It is in fact the cubito-anal area of a Dictyoptera Leach, 1818. Hong (1984: 147-148, fig. 22, pl. 63, fig. 3) described another early Cretaceous taxon (from Hebei) he attributed to the Caloneurodea, in the family Mesogrammatidae Hong, 1984, for the genus and species *Mesogramma divaricata* Hong, 1984, these names being later replaced by Hebeigrammidae, and *Hebeigramma divaricata* (Hong, 2003). This fossil has not the main synapomorphy of the Caloneurodea, viz. veins 'MP+CuA+CuPa α and CuPa β close, parallel and straight'. After the original photograph of the holotype, the general shape of venation rather fits with a Phasmatodea Jacobson and Bianchi, 1902, but a revision of the type material would be necessary to precise its affinities.

Here we report the first discovery of a Chinese Caloneurodea from the middle Permian Yinping Formation near the Houdong Village, Chaohu City, Anhui Province, Southern China,

corresponding at that time to a group of islands in the eastern margin of the paleo-Thetys, under a climate very different from those of the northern part of the Permian Pangea.

2. Material and methods

The fossil was preserved in the black shale of the Yinping Formation at the Paomaling Section near the Houdong Village, Chaohu City, Anhui Province, Southern China (detail map see Szweo and Huang, 2019, fig. 2). Its age was assigned within the late part of Capitanian, Middle Permian (Zhang et al., 2018), or considered around the boundary of middle-late Permian (Yao et al., 2015). Our fossil was collected from the lower part of the formation that would be more convincing of the latest part of the middle Permian age.

The fossil wing was prepared using a sharp knife. Photographs were taken using a digital camera attached to a Zeiss Discovery V16 microscope. Line drawings were drafted with Adobe Illustrator CC 2018 graphic software.

We follow the wing venation terminology of Béthoux and Nel (2002) and the classification of the Caloneurodea of Béthoux et al. (2004). Abbreviations of wing venation: ScP subcostal posterior; RA radius anterior; RP radius posterior; MA media anterior; MP media posterior; CuA cubitus anterior; CuP cubitus posterior, AA anal anterior.

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3. Systematic paleontology

Superorder Archaeorthoptera Béthoux and Nel, 2002

Subclade Panorthoptera Crampton, 1928 (sensu Béthoux and Nel 2002)

Order Caloneurodea Martynov, 1938

Family Aspidoneuridae Carpenter, 1961

Type genus. *Aspidoneura* Carpenter, 1943. Other genera. *Homaloptila* Handlirsch, 1919, *Sinaspidoneura* gen. nov.

Genus *Sinaspidoneura* nov.

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Derivation of the name: Named after ‘Sina’, Latin name for China, and *Aspidoneura*. Gender feminine.

Type species: *Sinaspidoneura magnifica* nov. sp., here designed and by monotypy.

Diagnosis: Forewing ScP extending to wing apex; anterior branch of MA strongly sigmoidal; three branches of RP; base of RP very close to that of M+CuA, just distal to base of MA; vein AA2 absent or strongly reduced; wing basally petiolate with a reduced anal area.

Sinaspidoneura magnifica nov. gen., nov. sp.

Figs 1, 2, 3

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Derivation of the name: Named after the wonderful state of preservation of the holotype.

Holotype: NIGP173204 (a complete wing, with part and counterpart, perfectly preserved); **paratype NIGP173730**, stored at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Type horizon and locality: Late Capitanian, middle Permian; Yinping Formation, Houdong Village, Chaohu City, Anhui Province, Southern China.

Diagnosis: As for the genus.

Description: (**Based on holotype specimen**) preserved part of wing 19.5 mm long, wing ca. 20.0 mm long, 4.1 mm wide; ScP reaching anterior wing margin at wing apex; RA and RP diverging ca. 3.8 mm distal of wing base; RA simple; first posterior branch from RP 8.6 mm

distal of its origin; RP with two posterior branches, all simple; MA emerging from M+CuA+CuPa α slightly basal of origin of RP; MA branched 4.9 mm distal of its origin; anterior branch of MA simple and strongly sigmoidal; MP+CuA+CuPa α simple, strongly convex and straight; CuPa β and CuPb simple, straight, and concave; AA1 simple, straight, ending at level of base of M+CuA; AA2 not visible, possibly absent or very short at wing base; area between AA1 and posterior wing margin with one row of cells; crossveins all simple and straight; wing basally petiolated.

Paratype with same venation (Fig. 3).

4. Discussion

Sinaspidoneura nov. gen. falls in the Caloneurodea because of the following characters (Béthoux et al., 2004): in forewing, MA with only two branches; MP+CuA+CuPa α simple; fusion of CuPa α with M+CuA; MP+CuA+CuPa α (convex) and CuPa β (concave) close, parallel and straight (main synapomorphy); MP running fused with CuA+CuPa α at length. It has also the following additional characters, present in a majority of Caloneurodea: RP posteriorly pectinate when branched; anterior branch of MA strongly sigmoidal; marked convexity of crossveins; absence of anterior branches of RA.

Béthoux et al. (2004) gave a list of the species of the Caloneurodea, to which it is necessary to add the following taxa: *Ligogramma wichita* Beckemeyer, 2009 (early Permian, Oklahoma, USA); *Lusitaneura covensis* Loureiro et al., 2010 (latest Carboniferous, Portugal); *Isadistica issada* Rasnitsyn et Aristov, 2013 (Isady, Vologda, Russia; Severodvinian); *Aviogramma gracilis* Prokop et al., 2014 (Avion, France Early Late Carboniferous); *Gallogramma galadrieli* Garrouste et al., 2018 and *Paleuthygramma* cf. *acuta* Carpenter, 1943 (Lodève, France, middle Permian).

Sinaspidoneura nov. gen. differs from all the described Caloneuroidea, except *Aspidoneura flexa* Carpenter, 1943 and *Homaloptila similis* (Meunier, 1911), in the conjunction of the following characters: ‘ScP extending to wing apex’ and ‘anterior branch of MA strongly sigmoidal’ (Zalessky, 1933; Carpenter, 1943, 1970; Béthoux et al., 2004). Some taxa, viz. *Caloneurella carbonaria* Carpenter, 1934 and *Isadistica issada*, have a long ScP nearly reaching wing apex, but they differ from *Sinaspidoneura* nov. gen. in the presence of four branches of RP or more, and the anterior branch of MA parallel to the posterior branch, with a narrower area between the two than in *Sinaspidoneura* nov. gen. (Carpenter, 1934; Rasnitsyn and Aristov, 2013). *Plesiogramma medialis* Carpenter, 1943 has also a very long ScP, but a simple MA and four branches of RP. *Synomaloptila longipennis* Martynov, 1938 has a long ScP, but four branches of RP and an anterior branch of MA strongly curved but not sigmoidal (Martynov, 1938).

Sinaspidoneura nov. gen. differs from *Aspidoneura flexa* in the less sigmoidal anterior branch of MA, the presence of three branches of RP, instead of two, and the base of RP very close to that of M+CuA, just distal to base of MA (Béthoux et al., 2004, fig. 15). *Homaloptila similis* has four branches of RP, but also a more pronounced sigmoid in the anterior branch of MA and the base of RP well distad of the base of MA (Béthoux et al., 2004, fig. 16). *Aspidoneura* and *Homaloptila* were classified together in the same family Aspidoneuridae with the following diagnosis: ‘Sc extending to about the apex of the wing ; CuA and CuP very close together and nearly parallel; MP forked broadly and unevenly, the anterior branch (MP1+2) arching strongly away from MP3+4 ; 3 anal veins’ (Carpenter, 1961, p. 151), that is, with the current terminology: ScP extending to wing apex; MP+CuA+CuPa α and CuPa β very close together and nearly parallel (a character present in nearly all the Caloneuroidea); anterior branch of MA strongly away from its posterior branch; three veins CuPb, AA1 and AA2 present.

Sinaspidoneura nov. gen. has all these characters except the presence of a vein AA2. More precisely, if AA2 is present, it should be a very short vein in the basally petiolate wing.

The strongly sigmoidal anterior branch of MA is a potential synapomorphy supporting the family Aspidoneuridae. The polarization of the character ‘ScP extending to wing apex’ is more uncertain. Thus we propose to place *Sinaspidoneura* nov. gen. in this family.

5. Conclusion

Homaloptila is known from the latest Carboniferous of Commentry in France, while *Aspidoneura* is known from the early Permian of Elmo (Wellington Formation, Oklahoma, USA). These two outcrops correspond to very different palaeoenvironments, viz. an equatorial hot and humid swamp-forest for Commentry while Elmo is supposed to have been ‘a humid spot in a regional environment of more or less pronounced and long-continued aridity’ (Carpenter, 1930, p. 72). Tasch (1964) interpreted the layers of Elmo with insects as limnic deposits; Zeller (1968: 50) indicated that the ‘Wellington is predominantly shale with minor amounts of limestone and dolomite, siltstone, and gypsum and anhydrite’, with ‘marine and brackish- and fresh-water deposits’; Hall et al (2005) suggested a ‘deposition in a marginal-marine environment’; and Beckemeyer (2000, p. 3) considered that the region was a ‘coastal plain at the edge of an inland sea’. Thus the Aspidoneuridae could adapt to a more contrasted climate and environment between the Latest Carboniferous and the early Permian.

The Yinping Formation at Chaohu area, from where *Sinaspidoneura* nov. gen. comes, was a group of islands in the paleo-Thetys ocean, separated from the Pangea (and Laurussia) during the Middle Permian (Campi, 2012; Zhang et al., 2019, fig. 1). It was at the level of equator and probably under a much more humid and equally warm than the paleo-regions where the other Permian taxa of the Caloneurodea were found (Chumakov and Zharkov, 2002; Wang and Pfefferkorn, 2013). The very broad distribution of these insects during the Permian

suggests that they could adapt to very different climates and biotas. Apparently the Caloneurodea are unrecorded in the late Permian. The younger ones are late Capitanian. Maybe they became extinct during the middle Permian crisis of diversity, maybe in relation to the ‘major changeover in plant taxa’ that happened at the end of the Guadalupian (Rampino and Shen, 2020).

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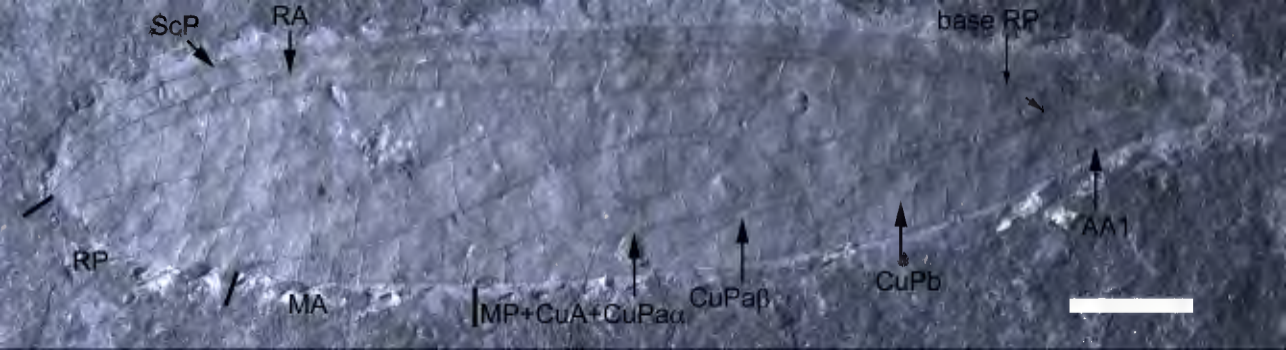
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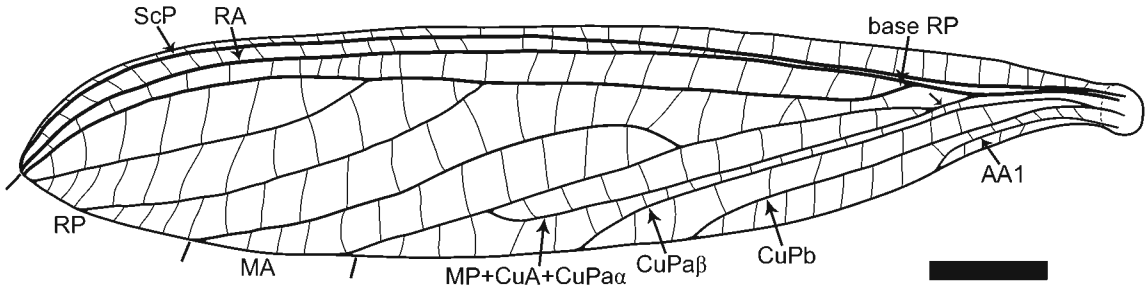
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Fig. 1. *Sinaspidoneura magnifica* gen. et sp. nov., holotype NIGP173204, photographs of forewing. **A.** Part (NIGP173204a). **B.** Enlargement of A showing details of wing base. **C.** Enlargement of A showing details of wing apex. **D.** Counterpart (NIGP173204b). Scale bars: 2 mm (A,D), 1 mm (B,C).

Fig. 2. *Sinaspidoneura magnifica* gen. et sp. nov., line drawing, small black arrow: base of MA. Scale bar: 2 mm.

Fig. 3. *Sinaspidoneura magnifica* gen. et sp. nov., paratype NIGP173730, photographs of forewing. **A.** Part. **B.** Counterpart. Scale bars: 1 mm.





A**B**