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Original article

First fossil Calopterygoidea (Odonata: Zygoptera) from Southeastern Asia: A new genus and species from the Paleogene of China☆

Premier Calopterygoidea fossile de l'Asie du Sud-Est : un nouveau genre et espèce du Paléogène de Chine

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Abstract

Sinocalopteryx shangyongensis nov. gen., nov. sp., the first fossil calopterygoid from eastern Asia, is described from the earliest Eocene of Southwest China. Although the new genus has the principle synapomorphies of Calopterygoidea, it possesses a unique structure (possible reversal) in the pattern of vein RP1/2.
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Keywords: Odonata; Calopterygoidea; nov. gen.; nov. sp.; Eocene; Phylogeny; Dating

Résumé

Sinocalopteryx shangyongensis nov. gen., nov. sp. de l'Eocène basal du Sud-Ouest de la Chine est le premier Calopterygoidea fossile de l'Asie du Sud-Est. Bien que le nouveau genre ait les principales synapomorphies des Calopterygoidea, il montre une structure unique (possible réversion) dans le patron de la nervure RP1/2.
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Mots clés : Odonata ; Calopterygoidea ; nov. gen. ; nov. sp. ; Eocène ; Phylogénie ; Datation

1. Introduction

Fossil Calopterygoidea are rather infrequent and all are Cenozoic in age (Nel and Paicheler, 1993; Nel and Brisac, 1994; Rust, 1999; Nel and Petrulevičius, 2010). The oldest records are from Eocene Baltic amber (Bechly and Wichard, 2009; Fleck et al., 2009), of possible age ranging between 38–47 Ma (Ritzkowski, 1997; Perkovsky et al., 2007). The lack of Mesozoic Calopterygidae is rather surprising as the zygopteran sister group may be as old as the Triassic and fossil lestoid and coenagrionoid Zygoptera are recorded from the Lower Cretaceous (Bechly, 1996). Dumont et al. (2005, 2007) recently recovered phylogenetic hypotheses of intrafamilial relationships, which allowed to precise the potential dates of separation between the different calopterygoid clades. Calopterygoidea have relatively large wings and strong bodies, hence their English common name as "broad-winged damselflies", which should be preserved more

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easily as fossils than the small and very delicate Hemiphlebiidae. Nevertheless, the latter are known from the Lower Cretaceous (Bechly, 2007; Lak et al., 2009). Modern broad-winged damselflies are common river and stream dwellers, which does not constitute very good environments for fossilisation and could explain their relative rarity in the fossil record. The present discovery of two new calopterygoids from the early Eocene of China partly fills this gap.

Both fossils were collected during 1977 from a locality near the Shangyong Village, Mengla County, Yunnan Province, Southwest China. This place is very close to the border with Laos. The geological setting of this area is poorly known. The original label noted that the specimens came from Mengyejing Formation, associated with fossil conchostracans, ostracods, spores, and pollens (see Nanjing Institute of Geology and Palaeontology et al., 1975). A rather diverse entomofauna co-occurred with our new odonate. Fossil insects are frequent in the yellowish mudstone and represented by mostly isolated fragments such as beetle elytra. The true Mengyejing Formation is an early Late Cretaceous stratum. However, the 'Mengyejing Formation' near Shangyong Village may belong to an undefined stratum. Analyses of spore-pollen assemblages suggest a Lower Tertiary age but this does not exclude the possibility of a Late Cretaceous age (Nanjing Institute of Geology and Palaeontology et al., 1975). An early Eocene age (Ypresian) is more convincing on the basis of the study of the conchostracan *Paraleptestheria menglaensis* (Chen and Shen, 1980; Shen et al., 2006).

In the description below we follow the wing venation nomenclature of Riek and Kukalová-Peck (1984), amended by Nel et al. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters followed in the present work, are based on the phylogenetic system proposed by Bechly (1996), because they are based on morphological characters available in our fossils, although Dumont et al. (2005, 2007) proposed new hypotheses for the phylogenetic classification of the Calopterygoidea based on molecular analyses.

We use the following standard abbreviations: anal vein (AA), anal posterior (AP), Ax0 Ax1 Ax2 primary antenodal crossveins, distal branch of cubitus anterior (CuAa), proximal branch of cubitus anterior (CuAb), intercalary radial veins (IRi), distal branch of median anterior (MA), median posterior (MP), nodus (N), oblique vein (O), pterostigma (Pt), radius anterior (RA), radius posterior (RP).

2. Systematic paleontology

Order ODONATA Fabricius, 1793.

Family CALOPTERYGIDAE Selys, 1850 (*sensu* Bechly, 1996).

Genus ***Sinocalopteryx*** gen. nov.

Type species: *Sinocalopteryx shangyongensis* nov. gen., nov. sp.

Etymology: The new generic name is a combination of Sinica, Latin name for China, and *Calopteryx*, type genus of the family. The name is feminine.

Diagnosis: Wing broad with numerous rows of cells between main longitudinal veins; RP1/2 straight after its base; two rows of cells in broad antesubnodal area between RA and RP1/2; pterostigma absent; pterostigmal brace absent; secondary antenodal crossveins very numerous but not developed as brackets similar to the two primary antenodal crossveins; numerous rows of cells between MP and CuA and between CuA and hind margin, discoidal cell very elongate and narrow, and traversed by numerous crossveins; arculus shifted proximally near Ax1; median and submedian spaces traversed by numerous crossveins (reversed in several genera of Calopteryginae), with numerous antenodal crossveins; discoidal cell not strongly curved, but elongate and narrow, and traversed by numerous crossveins; distal discoidal vein MAb and subdiscoidal vein with reversed obliquity; CuA not secondarily forked into two strong branches CuAa and CuAb.

Sinocalopteryx shangyongensis nov. gen., nov. sp.
Figs. 1–4.

Etymology: Named after the Shangyong Village.

Material: Holotype NIGP 151367 (Figs. 1 et 2), paratype NIGP 151368 (Figs. 3 et 4).

Type locality and horizon: Shangyong Village, Mengla County, Yunnan Province, Southwestern China; ?early Eocene, 'Mengyejing Formation' near Shangyong.

Repository of types: Part and counterpart housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Diagnosis: As for the genus.

Description: Specimen NIGP 151368: distal two third of a probable hind wing, with extreme base missing, dark brown with a broad darker basal area and two transverse costal white zones, preserved part 40 mm long; probable wing length ca. 45 mm, width 18.1 mm; distance from base to arculus and from arculus to nodus unknown, from nodus to wing apex 25.7 mm; pterostigma absent; pterostigmal brace absent; subdiscoidal cell, discoidal cell, median and submedian areas not preserved; primary antenodal crossveins Ax1 and Ax2 not preserved; numerous secondary crossveins of first row and of the second row between Ax2 and nodus; kink of ScP at nodus abrupt and Z-like; subnodus aligned with nodal crossvein Cr, both strongly

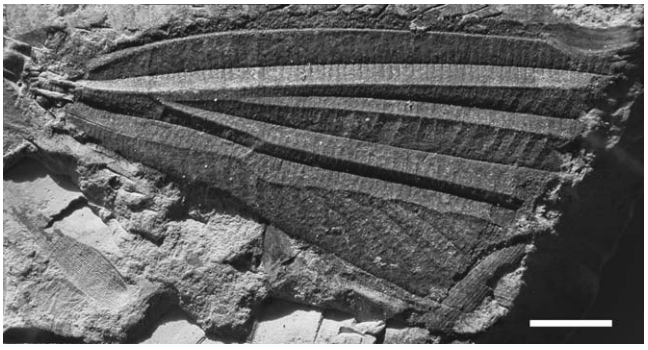

Fig. 1. *Sinocalopteryx shangyongensis* nov. gen., nov. sp., holotype NIGP 151367, photograph of wing. Scale bar: 3 mm.
Sinocalopteryx shangyongensis nov. gen., nov. sp., holotype NIGP 151367, photographie de l'aile. L'échelle représente 3 mm.

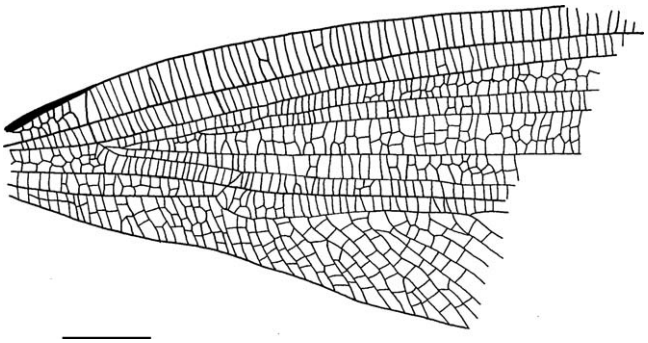

Fig. 2. *Sinocalopteryx shangyongensis* nov. gen., nov. sp., holotype NIGP 151367, drawing of wing. Scale bar: 3 mm.
Sinocalopteryx shangyongensis nov. gen., nov. sp., holotype NIGP 151367, dessin de l'aile. L'échelle représente 3 mm.

oblique and aligned with basal part of ScP; bases of RP3/4 and IR2 distinctly closer to arculus than to nodus; probably no basal curving of RP1/2; numerous crossveins in antesubnodal area; postdiscoidal area with only one row of cells between discoidal cell and nodus level, but greatly widened distally, and with at least one long secondary longitudinal vein; area between MP and CuA progressively broadened and with four long secondary longitudinal veins; cubito-anal area considerably broad, 7.8 mm wide in its broadest part, and with five-six long concave and five long convex secondary longitudinal veins; area between MA and RP3/4 progressively but greatly broadened; area between RP3/4 and IR2 progressively broadened, with at least one long secondary longitudinal vein; base of RP2 distinctly basal of subnodus; base of IR1 close to that of RP2; IR1, RP2, IR2, and RP3/4 curved; numerous postnodal crossveins and postsubnodal crossveins, both in two rows; four longitudinal secondary veins between RP1 and IR1.

Specimen NIGP 151367: basal third of a probable forewing, dark brown, preserved part of wing 21.8 mm long, 10.7 mm wide; distance from base to arculus 2.6 mm, from arculus to nodus ca. 19 mm; wing petiole absent, anal area broad, with four rows of cells; median and submedian areas with numerous cells; discoidal cell elongate and narrow, 5 mm wide, divided into 20 cells; subdiscoidal cell also crossed by numerous veins; numerous antefurcal crossveins between basal parts of RP and MA; arculus shifted basally near Ax1; primary antenodal crossveins Ax1 and Ax2 distinctly stronger than secondaries;

Fig. 3. *Sinocalopteryx shangyongensis* nov. gen., nov. sp., paratype NIGP 151368, photograph of wing. Scale bar: 3 mm.
Sinocalopteryx shangyongensis nov. gen., nov. sp., paratype NIGP 151368, photographie de l'aile. L'échelle représente 3 mm.

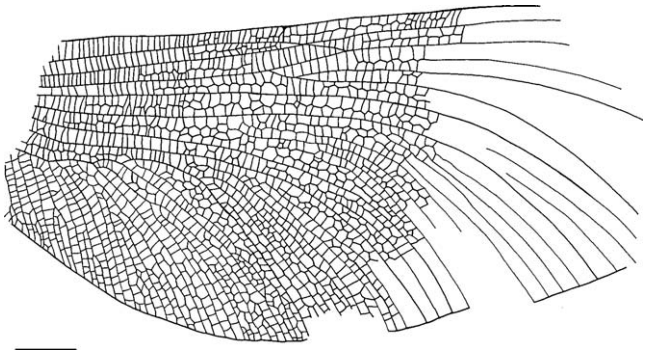

Fig. 4. *Sinocalopteryx shangyongensis* nov. gen., nov. sp., paratype NIGP 151368, drawing of median part of wing. Scale bar: 3 mm.
Sinocalopteryx shangyongensis nov. gen., nov. sp., paratype NIGP 151368, dessin de l'aile. L'échelle représente 3 mm.

numerous secondaries of first and second rows; nodus not preserved; base of RP3/4 close to arculus, base of IR2 3.3 mm distally; no basal curving of RP1/2; numerous crossveins and even two rows of cells in a broad antesubnodal area between RA and RP1/2; postdiscoidal area with only one row of cells between discoidal cell and nodus level; area between MP and CuA rather broad at base, narrower distally; CuA not secondarily forked into two strong branches CuAa and CuAb; cubito-anal area considerably broad, 3.5 mm wide in its broadest part, and with numerous long concave and long convex secondary longitudinal veins; anal area 1.3 mm wide; areas between MA and RP3/4 and between RP3/4 and IR2 progressively broadened; base of RP2 not preserved.

Discussion: Both fossils, although only partly preserved, can be accurately attributed to the same species because they have the same wing coloration, compatible sizes, and general pattern of venation, especially in the shape of vein RP1/2 and the numerous cells and crossveins. Specimen NIGP 151368 is likely a hindwing fragment owing to its considerably broad cubito-anal area and presence of two rows of cells in those areas between ScP and RA and between RP1/2 and IR2 basal to the nodus, while NIGP 151367 (possible forewing fragment) lacks these features. The broad dark patch at the base of the hindwing that disappears near the tip of the wing is reminiscent of the modern *Calopteryx virgo*. *Sinocalopteryx* nov. gen. falls in the Calopterygomorpha Bechly (1996) rather than in the Amphipterygida Bechly (1996) because of the following characters: antenodal area with numerous antenodal crossveins that are close together; kink of ScP at nodus abrupt and Z-like; tendency towards a basal curving of RP1/2 which seems to arise on RP with a secondary insertion; strong tendency towards an elongation of discoidal cell and its subdivision by crossveins.

Given the presence of numerous rows of cells between MP and CuA (postsubdiscoidal space distally widened) and between CuA and the hind margin, *Sinocalopteryx* nov. gen. does not fall within the Chlorocyphoidea Cowley, 1937, but shares with the Calopterygiformia Bechly (1996) the presence of numerous basal accessory antenodal crossveins between Ax0 and Ax1. The genus lacks one of the main apomorphies of the Calopterygida Bechly (1996), i.e. RP1/2 strongly curved after its base, arising on RP with a secondary insertion, but it has several other synapomorphies of this clade, i.e. discoidal cell elongate and

narrow, and traversed by numerous crossveins; arculus shifted proximally near Ax1. The Euphaeida Bechly (1996) have shorter discoidal cells than in *Sinocalopteryx* nov. gen. and the Calopterygida. Also, *Sinocalopteryx* nov. gen. does not have the polythorid type of arculus. *Sinocalopteryx* nov. gen. shares with the Calopterygoidea Selys, 1850 the submedian space (cubital cell and subdiscoidal cell) traversed by numerous crossveins, so that the CuP-crossing is unidentifiable; [M and Cu] or MP not kinked or bent at the arculus; but it again lacks another apomorphy of this group: the two rows of antenodal crossveins are developed as brackets similar to the two primary antenodal crossveins. The genus also does not fit in the Heliocharitidae Tillyard and Fraser, 1939 owing to its considerably broad anal and cubito-anal areas and non-petiolate wing. *Sinocalopteryx* nov. gen. also differs from the Caliphaeidae Fraser, 1929 in the considerably broad cubito-anal area. *Sinocalopteryx* nov. gen. has all the synapomorphies of the Calopterygidae Selys, 1850, viz. wings secondarily non-petiolate and more densely reticulate, with numerous antenodal crossveins; median space traversed by numerous crossveins (reversed in several genera of Calopteryginae); discoidal cell elongate and narrow, and traversed by numerous crossveins; distal discoidal vein MAb and subdiscoidal vein with reversed obliquity. Nevertheless, *Sinocalopteryx* nov. gen. lacks the apomorphies of the calopterygid subfamily Hetaerininae Tillyard and Fraser, 1939: arculus obliquely slanted, straight and posterior part of arculus strongly reduced; sectors of arculus diverging from a single point; discoidal cell strongly curved; MP of both pairs of wings with a unique kink shortly distal of the discoidal cell, apparently correlated with a unique curvature of CuA beneath the discoidal cell. While *Sinocalopteryx* nov. gen. shares with the Calopteryginae the numerous cells and secondary veins and crossveins, it lacks CuA secondarily forked into two strong branches CuAa and CuAb. *Sinocalopteryx* nov. gen. has a further character present in many Calopteryginae, viz. the pterostigma and pterostigmal brace completely absent.

Sinocalopteryx nov. gen. shares numerous derived characters of the Calopteryginae but it lacks two of the main characters that support the broader clade Calopterygida (RP1/2 strongly curved after its base, arising on RP with a secondary insertion, and the two rows of antenodal crossveins developed as brackets similar to two primary antenodal crossveins), present in Heliocharitidae (= Dicteriadidae), Caliphaeidae, and Calopterygidae, suggesting either that these characters were convergently acquired by these families or that they are reversed in *Sinocalopteryx* nov. gen. The same difficulty is present if we consider the phylogeny of the Calopterygoidea obtained by the molecular analysis of Dumont et al. (2005) who considered the Dicteriadidae as sister group of the clade Calopterygidae (incl. *Caliphaea*) + Hetaerinidae.

This absence of curvature of RP1/2 in *Sinocalopteryx* nov. gen. is correlated perhaps to the presence of two rows of cells in the broad antesubnodal area between RA and RP1/2. Also the two rows of antenodal crossveins not developed as brackets could be correlated to the great number of these crossveins. Thus, they would correspond most likely to reversal in *Sinocalopteryx* nov. gen.. *Sinocalopteryx* nov. gen. either belongs to the subfamily Calopteryginae, with reversed conditions in the base of RP1/2 and the structure of the antenodal crossveins; or it corresponds to an extinct aberrant taxon that belongs to the crowngroup of the Calopterygoidea. We provisionally include it into the Calopterygidae.

The present discovery of a highly derived calopterygoid from the early Eocene (or Late Cretaceous - Paleocene?) implies an older, at least Late Cretaceous age for the clade, fitting well with the hypothesis of Dumont et al. (2005) who dated the beginning of their radiation around 65 Ma. This fossil is also the oldest representative of the clade, as the previously oldest records were larvae from mid-Eocene Baltic amber (Bechly and Wichard, 2009; Fleck et al., 2009).

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