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The oldest ‘Megapodagrionidae’ (Odonata, Zygoptera) discovered in the Lower Cretaceous Yixian Formation, China

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ABSTRACT

Cretapodagrion sibelleae gen. et sp. nov., oldest representative and first Mesozoic ‘Megapodagrionidae’, is described on the basis of a complete wing from the Lower Cretaceous of Yixian Formation (ca. 124.6 Ma) in China. It shows some similarities with the three extant genera of the ‘Megapodagrioninae’ and the enigmatic genus *Mesopodagrion*.

Keywords:

Insecta

Odonata

‘Megapodagrionidae’

first appearance date

gen. et sp. nov.

China

1. Introduction

The damselfly family ‘Megapodagrionidae’ is rather frequent and diverse in the Cenozoic, with ca. 20 species, ranging between the Paleocene and the Pliocene, exclusively from the Palaearctic and Nearctic regions (Azar and Nel, 2008; Zessin, 2011). This ‘family’ is nowadays restricted to warm, mainly intertropical, biotas. Nearly all the known fossil taxa are based on wing compressions in lacustrine sediments, while body fragments are rarely preserved. Dijkstra et al. (2014) demonstrated that the ‘Megapodagrionidae’ is a polyphyletic group. The ‘megapodagrionid’ Argiolestinae Fraser, 1957 is currently considered as a separate family Argiolestidae, but also without ‘unequivocally unique character available for adults’ (Kalkman and Theischinger, 2013). The ‘megapodagrionid’ Philosininae Ris, 1917 was also considered in its own family Philosinidae by Dijkstra et al. (2014) who restricted the Megapodagrionidae to the sole extant genera *Allopodagrion* Förster, 1910, *Megapodagrion* Selys, 1885, and *Teinopodagrion* De Marmels, 2001. There is no clear synapomorphy about wing venation that would characterize these families. Thus it is difficult to attribute the fossil ‘megapodagrionids’ to the families proposed by Dijkstra et al. (2014).

The distribution of the extant ‘Megapodagrionidae’ in all the intertropical areas suggests a great antiquity for these damselflies. Nevertheless they remain unknown in the Cretaceous, despite the recent progresses in our knowledge on the damselflies of this period (Zheng et al., 2016a-c, 2017a,b; Huang et al., 2017; etc.). Here we describe the first Cretaceous fossil attributable to the ‘Megapodagrionidae’, probably closely related to the Megapodagrionidae sensu stricto.

2. Material and methods

Only one specimen with part and counterpart collected during 2015 at Sihetun locality (41°37’ North, 120°50’ East), Beipiao City, Liaoning Province (Fig. 1). It is an isolated wing preserved in grayish finely laminated tuffaceous shale of a volcanic paleolake under warm climate (Jiang et al., 2012). It co-occurred with abundant *Eosestheria*. The Sihetun locality has yielded very rich animal fossils such as dinosaurs, birds, mammals, insects, conchostracans, ostracods, crustaceans, and bivalves. Isotopic dating indicates that the fossil rich layer is 124.6 Ma in age (Swisher III et al., 1999, 2001).

We follow the wing venation nomenclature of Nel et al. (1993) and Bechly (1996), modified from that of Riek and Kukalová-Peck (1984). Abbrevations for vein names are: AA analis anterior; Ax1 and Ax2 primary antenodal crossveins; IRx intercalary radial vein; MA median anterior; MP median posterior; N nodus; Pt pterostigma; RPx branches of radius posterior; CuA cubitus anterior; CuP cubitus posterior.

The ZooBank number for the genus *Cretapodagrion* is urn:lsid:zoobank.org:act:C3139CE3-13C6-4811-B006-7823AE86EDDB, and that for *Cretapodagrion sibelleae* is urn:lsid:zoobank.org:act:ED94AF25-0584-4F13-AC3E-52DC9062B0FA.

3. Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Zygoptera Selys, 1854

Family Megapodagrionidae Calvert, 1913 (sensu lato)

Genus ***Cretapodagrion*** gen. nov.

Type species: *Cretapodagrion sibelleae* sp. nov.

Etymology. Named after the Cretaceous period and Podagrion.

Diagnosis. Wing characters only: basal side of pterostigma and pterostigmal brace not oblique; postnodal area relatively short, with only 12 postnodal crossveins; a zigzagged long secondary longitudinal vein between IR1 and RP1; distal side of discoidal cell strongly oblique; CuP basad of base of AA; MP+Cu apparently basally fused with anal vein (or at least strongly approximate; base of RP3/4 well basad of subnodus; base of IR2 below subnodus.

Cretapodagrion sibelleae sp. nov.

Fig. 2

Material: Holotype NIGP166620, stored at Nanjing Institute of Geology and Palaeontology, China.

Etymology. Named after Sibelle Azar, geologist and wife of ~~one of~~ Dany Azar, who has collected this specimen.

Locality and occurrence. Sihetun, Beipiao City, West Liaoning Province, NE China; Yixian Formation, Barremian-Aptian, Lower Cretaceous.

Diagnosis. As for the genus, wing hyaline, ca. 30 mm long.

Description. A complete wing, axillary sclerite and ScA visible; wing apparently hyaline, with pterostigma pale brown; wing 30.1 mm long, 5.8 mm wide, distance from base to arculus 6.5 mm, from arculus to nodus 5.9 mm, from nodus to pterostigma 12.7 mm, from pterostigma to wing apex 3.9 mm; from base to Ax1 4.3 mm, between Ax1 and Ax2 2.1 mm; pterostigma elongate and broad, 2.7 mm long, 0.9 mm wide, covering three cells; pterostigmal brace aligned with basal side of pterostigma, but very weakly oblique; distal side of pterostigma slightly more oblique than basal side, but anterior margin not distinctly longer than posterior one; no secondary antenodal crossvein; Ax2 aligned with arculus; 12 postnodal crossveins, nearly all aligned with the corresponding postsubnodals; one crossvein in antesubnodal space; subnodus and nodal brace weakly oblique; base of RP3/4 nearly midway between arculus and

subnodus, at 2.5 mm from subnodus; base of IR2 below subnodus; base of RP2 four cells, 3.4 mm distal of subnodus; base of IR1 three cells, 2.4 mm distal of that of RP2; a zigzagged secondary longitudinal vein between IR1 and RP1, beginning four cells distal of base of IR1; a tendency to form pseudo-transverse veins in distal part of areas between IR2, RP3/4, MA and MP, caused by an alignment of row of cells; 1-2 rows of cells between IR1 and RP2, RP2 and IR2, IR2 and RP3/4, and RP3/4 and MA; distal end of MA zigzagged; a tendency to form only one row of cells in postdiscoidal area, also in area between MP and CuA, and below CuA; discoidal cell elongate and narrow, with basal side 0.3 mm long, anterior side 1.2 mm long, posterior side 1.9 mm long, and distal side 0.8 mm long, distal side strongly oblique, not parallel to basal side; petiole very long; MP+Cu apparently fused to anal vein for a long distance in petiole, separating just basal of Ax1; CuP emerging from MP+Cu just basal of base of AA; CuA very long, ending on posterior wing margin only at a level five cells basal of pterostigma.

4. Discussion

Cretapodagrion gen. nov. can be attributed to the Coenagrionomorpha Bechly, 1996 on the basis of the following characters (Bechly, 1996, 2016): pterostigma shortened, compared to those of the clade Calopterygida Bechly, 1996 (in the ground plan, the pterostigma being reduced in many Calopterygidae); postnodal and postsubnodal crossveins aligned; lestine oblique vein absent; tendency towards the formation of pseudo-transverse veins in distal part of wing, caused by an alignment of rows of crossveins. Within the Coenagrionomorpha, the Hypolestidae Tillyard & Fraser, 1938 are excluded because of the positions of the bases of RP3/4 and IR2, and shape of distal parts of main veins, not distinctly curved apically. The Coenagrioniformia Bechly, 1996 are also excluded because *Cretapodagrion* has intercalary longitudinal veins between main veins, a relatively long

pterostigma, postnodal and postsubnodal crossveins not aligned with the crossveins immediately below them.

Cretapodagrion shows some similarities with the extant 'Megapodagrionidae' sensu stricto sensu Dijkstra et al. (2014), viz. a relatively long and broad pterostigma, a basal side of pterostigma and a pterostigmal brace not oblique, RP1 not making an angle, presence of intercalary longitudinal veins between main veins, base of IR2 aligned with subnodus while that of RP3/4 is distinctly basal with an elongate cell between them, long discoidal cell with distal side very oblique, distal part of MA long and zigzagged, very long CuA and MP (Bechly, 1996). *Cretapodagrion* differs from these extant genera in the CuP basal of base of AA, and the presence of a long intercalary longitudinal vein between IR1 and RP1 (Münz, 1919; Garrison et al., 2010).

Nevertheless, due to the relative confusion in the current 'megapodagrionid' classification, we compare *Cretapodagrion* to all the other 'megapodagrionid' genera. One possible difference between *Cretapodagrion* and all the extant and other fossil 'Megapodagrionidae' is the apparent basal fusion of MP+Cu with the anal vein in the petiole, but in some extant taxa, MP+Cu is so close to the anal vein that they could appear fused, so it is also possible in the fossil (Garrison et al., 2010).

All the extant Neotropical 'Megapodagrionidae' have no intercalary longitudinal vein between IR1 and RP1, unlike *Cretapodagrion* (Garrison et al., 2010).

Also within the extant Argiolestidae, *Amanipodagrion* Pinhey, 1962 has the distal side of discoidal cell not oblique (Pinhey, 1962). The genera *Celebargiolestes* Kennedy, 1925, *Allolestes* Kennedy, 1925, *Austroargiolestes* Kennedy, 1925, *Caledargiolestes* Kennedy, 1925; *Archaeopodagrion* Kennedy, 1939, *Burmargiolestes* Kennedy, 1925, *Bornargiolestes* Kimmins, 1936 (both among the closest relatives of Thaumatoneuridae, after Dijkstra et al., 2014), *Dimeragrion* Calvert, 1913 (not related to Argiolestidae after Dijkstra et al., 2014),

Heteragrion Selys, 1862, *Podopteryx* Selys, 1871, and *Argiolestes* Selys, 1862 have the base of RP3/4 below subnodus (Münz, 1919; Kennedy, 1925, 1939; Kalkman and Theischinger, 2013; Dow, 2014). *Agnophilogenia* Kennedy, 1941, *Caledopteryx* Kennedy, 1925, *Dimeragrion* Calvert, 1913, *Heteragrion* Selys, 1862, *Nesolestes* Selys, 1891, *Trineuragrion* Ris, 1915, *Paraphlebia* Selys in Hagen, 1861, *Neurolestes* Selys, 1882, *Mesagrion* Selys, 1885, *Heteropodagrion* Selys, 1885, *Neuragrion* Karsch, 1891, *Protolestes* Förster, 1899 (not related to Argiolestidae after Dijkstra et al., 2014), *Rhinagrion* Calvert, 1913, *Philogenia* Selys, 1862, *Wahnesia* Förster, 1900, *Sciotropis* Rácenis, 1959, and *Agriomorpha* May, 1933 have a very long postnodal area, with a basal side of pterostigma very oblique (Förster, 1900; May, 1933; Kennedy, 1941; Winstanley and Davies, 1982; Garrison et al., 2010). *Podolestes* Selys, 1862 have a distal side of discoidal cell not oblique (Fraser, 1926). *Calilestes* Fraser, 1926 has a different pattern of branches of CuA (Fraser, 1926). *Miniargiolestes* Theischinger, 1998 and *Griseargiolestes* Theischinger, 1998 has the base of AA opposite or well distal of arculus (Theischinger, 1998).

Tatocnemis Kirby, 1889 (treated under the name *Nesocnemis* Selys, 1891, in Münz, 1919) has veins RP3/4 and IR2 arising distal of the subnodus and very oblique basal side of pterostigma.

Within the Philosinidae, *Cretapodagrion* differs from *Philosina* Ris, 1917 in the relative positions of subnodus and bases of RP2 and IR2. *Rhinagrion* Calvert, 1913 has a very long postnodal area, with a basal side of pterostigma very oblique.

Mesopodagrion McLachlan, 1896, a taxon of uncertain position (Dijkstra et al., 2014), greatly resembles *Cretapodagrion*, but it differs from *Cretapodagrion* in the rather more oblique pterostigmal brace, absence of the intercalary longitudinal vein between IR1 and RP1, and longer postnodal area with much more postnodal crossveins (Yu and Bu, 2009).

Cretapodagrion is clearly different from all the fossil taxa currently attributed to the 'Megapodagrionidae': *Eopodagrion* Cockerell, 1921 (Lowermost Oligocene of Florissant, U.S.A.) has a short pterostigma covering no more than two cells (Cockerell, 1921). *Thanetophilosina* Nel et al., 1997 (Paleocene, Menat, France) has much more postnodal crossveins, CuP distal of base of AA, and a broader discoidal cell (Nel et al., 1997). *Melanagrion* Cockerell, 1907 (Lowermost Oligocene of Florissant, U.S.A.) has two rows of cells in the cubito-anal area and in area between C and RA distad of pterostigma (Cockerell, 1907). *Miopodagrion* Kennedy, 1925 (Lowermost Oligocene of Florissant, U.S.A.) has two rows of cells between C and RA distad of pterostigma (Kennedy, 1925). *Vulcagrion* Nel & Paicheler, 1994 (Miocene-Pliocene of central France has veins IR2 and RP3/4 fused basally distad of subnodus (Nel et al., 1996). *Eckfeldia* Petrulevičius et al., 2008 and *Furagrion* Petrulevičius et al., 2008 (Paleocene – Eocene of Denmark) have a distinctly oblique basal side of pterostigma and a very long postnodal space (Petrulevičius et al., 2008). *Morsagrion* Zessin, 2011 (Paleocene – Eocene of Denmark) has a less oblique basal side of pterostigma, but a postnodal space longer than in *Cretapodagrion* and no intercalary longitudinal vein between RP1 and IR1 (Zessin, 2011). *Hanklitia* Zessin, 2011 (Paleocene – Eocene of Denmark, based on the basal third of a wing) differs from *Cretapodagrion* in the more distal position of CuP, distal of base of AA (Zessin, 2011). *Cerdanyagrion* Nel et al., 1996 (Upper Miocene, Spain) shares with *Cretapodagrion* the presence of a long intercalary longitudinal vein between RP1 and IR1 but it has a distinctly oblique basal side of pterostigma (Nel et al., 1996). *Oligoargiolestes* Kennedy, 1925 (Latest Eocene of UK) differs from *Cretapodagrion* in the absence of an intercalary longitudinal vein between RP1 and IR1 and the oblique basal side of pterostigma (Nel and Fleck, 2014). *Lithagrion* Scudder, 1890 (Early Oligocene, USA; Early Miocene, Kazakhstan) shares with *Cretapodagrion* similar pterostigma and a relatively broad area between IR1 and RP1, but it has a postnodal area longer than in *Cretapodagrion*

and no intercalary longitudinal vein between RP1 and IR1 (Scudder, 1890; Martynov, 1929). *Electropodagrion* Azar and Nel, 2008 (Eocene Baltic amber) shares with *Cretapodagrion* a relatively short postnodal area, but it differs from *Cretapodagrion* in the absence of an intercalary longitudinal vein between RP1 and IR1 (Azar and Nel, 2008).

5. Concluding remarks

Cretapodagrion shows similarities with the three extant genera of Megapodagrionidae sensu stricto but also with *Mesopodagrion*. Thus we provisionally attribute this new genus and species to the 'Megapodagrionidae' sensu lato because, after the study of Dijkstra et al. (2014), the venation seems to be not sufficient to define the phylogenetic relationships within the 'Megapodagrionidae' sensu lato. Further discoveries of new specimens showing the body structures and especially the genitalia, will help to solve the position of *Cretapodagrion*. Nevertheless the discovery in the Lower Cretaceous of China of a taxon attributable to the 'Megapodagrionidae' strongly suggests the antiquity of these damselflies, formerly only known in the Cenozoic.

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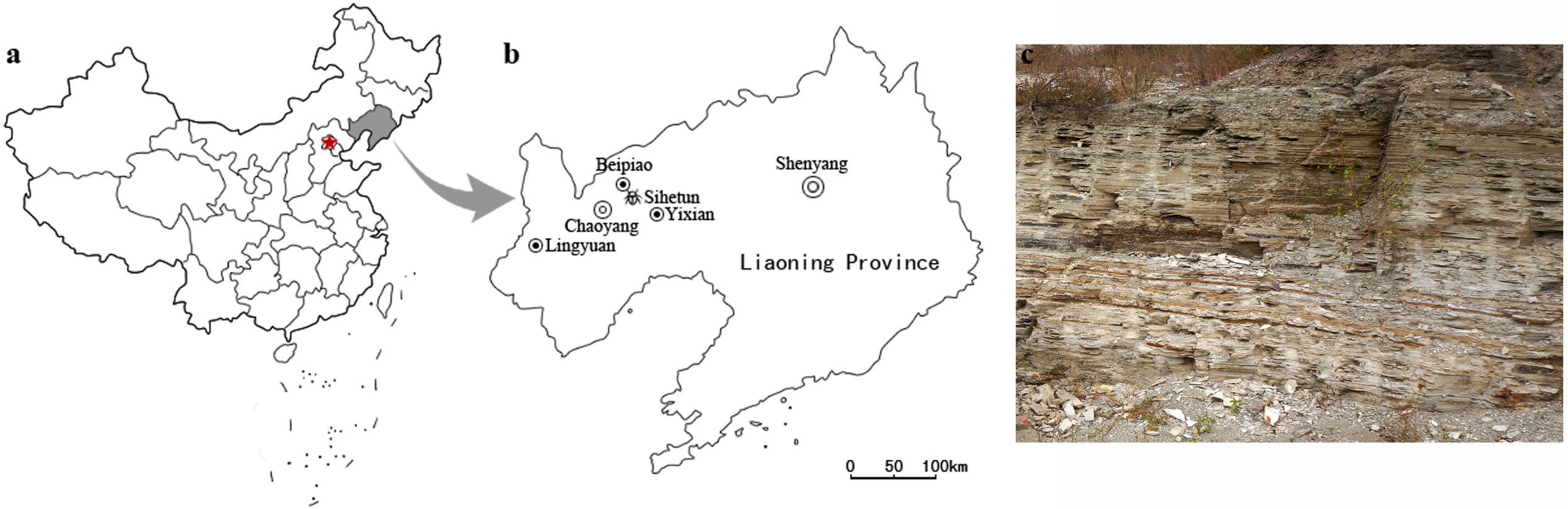
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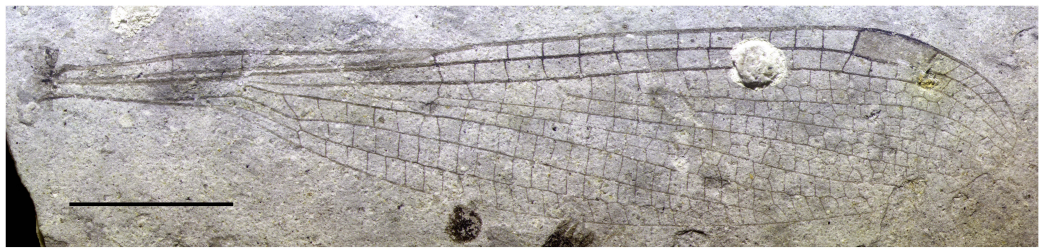
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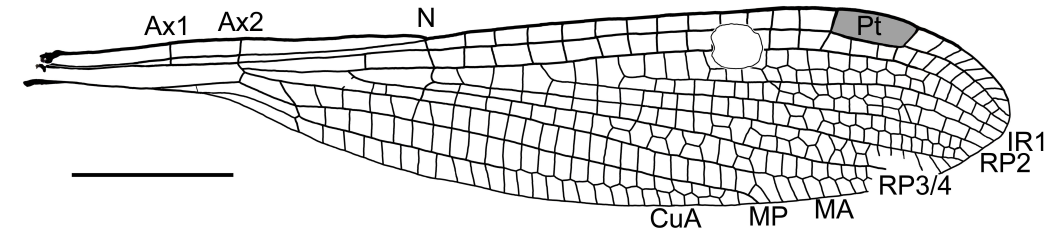
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Fig. 1. A, Chinese map with location of Liaoning Province; B, Map of Liaoning Province with location of Sihetun fossil locality (indicated by a bug); C, Shales of Yixian Formation where the material was collected.

Fig. 2. *Cretapodagrion sibelleae* gen. et sp. nov., holotype. a, photograph; b, drawing. Scale bars = 5 mm.


a
b
c
Beipiao
Sihetun
Yixian
Chaoyang
Lingyuan
Shenyang
Liaoning Province
0 50 100km




Ax1
Ax2
N
Pt
IR1
RP2
RP3/4
MA
MP
CuA