A new genus and species of aeshnopteran dragonfly from the Lower Cretaceous of China

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Abstract

Parapetala liaoningensis gen. et sp. nov. is described from the Lower Cretaceous of China. It has a very basal position in the clade Aeshnoptera (Odonata. Petalura, Spec. 2 (1996) 402), basal or close to the Upper Jurassic family Mesuropetalidae. This discovery confirms the high diversity of this group of dragonflies during the Late Jurassic–Early Cretaceous, suggesting rapid evolution of this clade in the Early or Middle Jurassic.

Keywords: Insecta; Odonata; Aeshnoptera; New genus; Phylogeny; Early Cretaceous; China

1. Introduction

With the recent discoveries of representatives of the fossil families Liupanshaniidae Bechly et al., 2001, Progobiaeschnidae Bechly et al., 2001, Rudiaeschnidae Bechly et al., 2001, and Gomphaeschnidae Tillyard and Fraser, 1940, the continental Mesozoic of China is proving to be one of the most important regions for investigations of the past diversity of the Aeshnoptera (Ren & Guo, 1996; Bechly et al., 2001; Li & Ren, 2002; Lin et al., 2002). The present discovery of a new aeshnopteran dragonfly in the Lower Cretaceous of Liaoning Province confirms the high diversity of this group in China during the Mesozoic.

We follow the wing venation nomenclature of Riek (1976) and Riek & Kukalová-Peck (1984), as amended by Nel et al. (1993), Bechly (1996), and Bechly et al. (2001). The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996). The classification of the Aeshnoptera is based on the work of Bechly et al. (2001). The phylogenetic analysis of the extant Aeshnidae of von Ellenrieder (2002) cannot be used here because our fossil occupies a position basal to the Austropetalida.

2. Systematic palaeontology

Clade: Aeshnoptera Bechly, 1996
Family uncertain
Genus Parapetala gen. nov.

2.1. Derivation of name

After its strong affinities with the fossil genus Mesuropetala Handlirsch, 1906.

2.2. Type species

Parapetala liaoningensis sp. nov.

2.3. Diagnosis

Eyes distinctly separated; wing veins RP1 and RP2 long, parallel, basal of pterostigma; veins Rspl and Mspl absent in both fore- and hindwings; anal loop small, three-celled, closed, and not elongate; discoidal triangles unicellular, that of forewing being distinctly broader than that of hindwing; arculus close to Ax1; pterostigmal braces well defined, aligned with basal sides of
pterostigmata; RP2 and IR2 not convergent close to posterior wing margin; RP3/4 and MA undulate and parallel from base to apex; trigonal planates present in both forewing and hindwing, more developed in hindwing.

2.4. Remarks

Ren (1994), text-fig, pl. 1) described and figured the fossil genus *Chrysogomphus* and species *C. beipiaoensis* from the Upper Jurassic of Liaoning Province, and placed these in the family Liassogomphidae. Fleck et al. (in press) indicated *Chrysogomphus* does not belong in the Liassogomphidae but is more likely to be an Aeshnoptera. It is very similar to *Parapetala* gen. nov., the main differences being as follows: the forewing discoidal triangle is divided by a cross-vein; the hind wing anal loop is posteriorly opened; there are three rows of cells in the forewing postdiscoidal area just distal of the triangle (only two in *Parapetala*); in the forewing, there are two rows of cells between RP1 and RP2 for a longer distance than in *Parapetala*. Nevertheless, *Chrysogomphus* is probably also in a very basal position in the aeshnopteran lineage.

2.5. Derivation of name

After Liaoning Province where the fossil was collected.

2.6. Holotype

Specimen 133694, deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, China.

2.7. Type locality and stratigraphic horizon

Western Liaoning Province, China, Lower Cretaceous, Yixian Formation?

2.8. Diagnosis

As for genus.
2.9. Description

The four wings are nearly complete, with only the apices missing, in connexion to the poorly preserved thorax. Two legs and the head are present but the abdomen is missing and was reconstructed.

Head 6.2 mm long, 9.8 mm wide; eyes 3.1 mm wide, well separated, 3.2 mm apart. Prothoracic claw with a small lateral tooth.

Forwing about 51.3 mm long, 11.6 mm wide (at level of nodus); distance between base and arculus, 5.3 mm; between arculus and nodus, 22.3 mm; between nodus and pterostigma, 14.3 mm; between nodus and wing apex, c. 22.7 mm. Pterostigma long; pterostigmal brace well defined, oblique, aligned with basal side of pterostigma. Primary antenodal cross-veins well defined; Ax1 4.4 mm from wing base, slightly basal of arculus; distance between Ax1 and Ax2, 6.2 mm; Ax2 slightly

Fig. 2. Parapetala liaoningensis, holotype, photograph of bases of wings, head and thorax; scale bar represents 10 mm.
basal of distal angle of discoidal triangle; no secondary antenodal cross-veins basal of Ax1; three secondary antenodal cross-veins between Ax1 and Ax2; 12 secondary antenodal cross-veins of first row between C and ScP, distal of Ax2, not aligned with corresponding antenodal cross-veins of second row between ScP and RA, the most distal antenodal cross-vein being incomplete. Seven postnodal cross-veins of first row between C and RA, not aligned with postnodal cross-veins of second row between RA and RP1. No 'cordulegastrid' gap and no 'libellulid' gap. Sectors of arculus basally well separated; median space free of cross-vein; submedian space only crossed by CuP, 1.3 mm basal of arculus; vein PsA well defined, strong and oblique, clearly separating submedian and subdiscoidal spaces; subdiscoidal space unicellular. Hypertriangles and discoidal triangles free of cross-veins except for a very small one in left discoidal triangle; hypertrianlge long and narrow, 5.8 mm long, 0.4 mm wide; discoidal triangle broad and not very elongate, 3.1 mm long, 2.2 mm wide; with basal side, 2.2 mm long; costal side, 3.3 mm long; distal side MAb, 3.5 mm long. MAb with a slight but distinct angle and a zigzagged convex vein (trigonal planate) emerging from it in postdiscoidal area. Anal area, 2.4 mm wide; with two rows of rather broad cells; CuA and MP separating at posterior angle of discoidal triangle; cubito-anal area long but rather narrow, 2.7 mm wide and with 4–5 rows of cells between CuA and posterior wing margin. CuA reaching posterior wing margin just basal of nodus level, with five short posterior branches; CuA and MP slightly curved and parallel at length; apex of MP just distal of nodus level. Postdiscoidal area with 2–3 rows of cells distal of discoidal triangle, 3.1 mm wide, but distally distinctly broadened, 9.3 mm wide along posterior wing margin; a rudimentary and short vein Mspl. Numerous cross-veins between RP and MA, basal of RP3/4; base of RP3/4 distinctly closer to nodus than to arculus, 16.0 mm from arculus and 6.3 mm from nodus; base of IR2 very close to that of RP3/4. Six cross-veins in area between RA and RP between level of discoidal triangle and base of RP3/4. 4–5 Bqs cross-veins between base of IR2 and oblique cross-vein ‘O’. MA and RP3/4 slightly but distinctly undulating distal of nodus, with a short secondary longitudinal vein between them close to posterior wing margin. Base of RP2 aligned with subnodus; one oblique cross-vein ‘O’ three cells, 2.7 mm distal of base of RP2; IR2 and RP2 slightly curved and parallel along length, with 2–3 rows of cells between them only near posterior wing margin. RP1 and RP2 long, parallel, with area between them narrow basal of pterostigmal brace level. IR1 zigzagged and poorly defined; base of IR1 two cells basal of pterostigmal brace. No Rspl.

Hind wing 51.3 mm long, 16.0 mm in maximum width, 15.1 mm wide at level of nodus; distance between base and arculus, 6.7 mm; between arculus and nodus, 16.5 mm; between nodus and pterostigma, 16.5 mm; between nodus and wing apex, c. 27.6 mm. Pterostigma, c. 5.8 mm long, 0.45 mm wide, covering five cells. Pterostigmal brace well defined, oblique, aligned with basal side of pterostigma; primary antenodal cross-veins well defined. Ax1 6.2 mm from wing base, slightly basal of arculus; distance between Ax1 and Ax2, 5.8 mm; Ax2 slightly basal of distal angle of discoidal triangle; no secondary antenodal cross-veins basal of Ax1; 2–3 secondary antenodal cross-veins between Ax1 and Ax2; eight secondary antenodal cross-veins of first row between C and ScP, distal of Ax2, not aligned with corresponding antenodal cross-veins of second row between ScP and RA, the most distal antenodal cross-vein being incomplete. 8–9 postnodal cross-veins of first row between C and RA, not aligned with postnodal
cross-veins of second row between RA and RP1. No ‘cordulegastrid’ gap and no ‘libellulid’ gap. Sectors of arculus basally well separated. Median space free of cross-vein; submedian space only crossed by CuP; 1.3 mm basal of arculus; vein PsA well defined, strong and oblique, clearly separating submedian and subdiscoidal spaces; subdiscoidal space unicellular. Hypertriangles and discoidal triangles free of cross-veins; hypertriangle long and narrow, 5.3 mm long, 0.9 mm wide; discoidal triangle distinctly more elongate and narrower than that of forewing, 3.6 mm long, 1.8 mm wide; with basal side 1.8 mm long; costal side, 3.6 mm long; distal side MAb, 4.2 mm long. MAb with a strong angle and a well-defined and weakly zigzagged trigonal planate emerging from it in postdiscoidal area. Anal area broad, 9.1 mm wide, with 11 rows of cells between AA and posterior wing margin and four parallel posterior branches of AA. CuA and MP separating at posterior angle of discoidal triangle, cubito-anal area long but broad, 7.1 mm wide and with eight rows of cells between CuA and posterior wing margin; CuA reaching posterior wing margin opposite nodus level, with six long, parallel, posterior branches. A rather well-defined, three-celled, anal loop. CuA and MP slightly curved and parallel along length; apex of MP just distal of nodus level. Postdiscoidal area with two rows of cells distal of discoidal triangle, 3.5 mm wide but distally distinctly broadened, 9.8 mm wide along posterior wing margin. No clear vein Mspl. Numerous cross-veins between RP and MA, basal of RP3/4. Base of RP3/4 distinctly closer to nodus than to arculus, 10.7 mm from arculus and 5.8 mm from nodus; base of IR2 very close to that of RP3/4; eight cross-veins in area between RA and RP. 3–4 Bqs cross-veins between base of IR2 and oblique cross-vein ‘O’. MA and RP3/4 slightly but distinctly undulate distal of nodus, with a short secondary longitudinal vein between them close to posterior wing margin. Base of RP2 aligned with subnodus; one oblique cross-vein ‘O’ two cells, 1.8 mm distal of base of RP2; IR2 and RP2 slightly curved and long parallel, with 2–3 rows of cells between them only near posterior wing margin. RP1 and RP2 parallel at length, with area between them narrow basal of pterostigmal brace level. IR1 zigzagged and poorly defined, base of IR1 two cells basal of pterostigmal brace. No Rspl.

2.10. Discussion

Parapetala gen. nov. is similar in some respects to the Petalurida: Protolindeniidae Handlirsch, 1906, especially in the absence of RSpl and Mspl and in having discoidal triangles that are narrow and elongate in the hindwing and broad and sub-transverse in the forewing, and a small anal loop. Nevertheless, it differs from Protolindenia Deichmüller, 1886 in the following characters: its pterostigmal brace is well aligned with the basal side of the pterostigma instead of being basally recessed or absent; and its veins RP1 and RP2 are not widely diverging 6–9 cells basal of pterostigma (only two rows of cells between RP1 and RP2 just basal of pterostigmata in Parapetala) (Nel et al., 1998, 2001).

According to the phylogenetic analysis of Bechly et al. (2001), Parapetala has two of the main venational synapomorphies of the Aeshnoptera, viz. veins RP1 and RP2 basally parallel up to the pterostigma level, with one row of cells in the area between these veins, between the base of RP2 and 2–3 cells basal of the pterostigma, and RP3/4 and MA distinctly undulate in their distal parts. It does not have the third synapomorphy of this clade, i.e., the presence of at least a weakly defined (zigzagged) Rspl. In the Mesuropetalidae Bechly, 1996, Rspl is reduced to a strongly zigzagged ‘pseudo-Rspl’, with one row of broad cells between it and IR2, but this ‘pseudo-Rspl’ is also absent in Parapetala. In the Austropetaliida Bechly et al., 2001 (Archipetalidiae Lohmann, 1996 and Austropetaliidiae Carle and Loutou, 1994), Rspl is more or less zigzagged, but present and better defined in the hindwing than in the forewing. Furthermore, Parapetala does not have the main venational autapomorphies of this last clade, i.e., the pterostigmal brace is not aligned with the basal side of the pterostigma; IR1 is very long; and the basal true oblique vein is reduced or absent. Thus, it cannot be considered as an Austropetaliida. Other clades of Aeshnoptera (Liupanshanidae Bechly et al., 2001 and more derived Panaeshnida Bechly et al., 2001) have better defined Rspl veins than Austropetaliida and Mesuropetalidae.

Parapetala has the two venational autapomorphies of the Mesuropetaloidae Bechly, 1996 (sensu Bechly et al., 2001), i.e., the arculus is shifted very close to the first primary antenodal Ax1, and RP3/4 and MA are closely parallel up to the wing margin in both pairs of wings. It also shares with the Mesuropetalidae a forewing discoidal triangle that is broader than that of the hindwing. Nevertheless, in Mesuropetalidae, the forewing discoidal triangle is much more transverse than in Parapetala, RP2 and IR2 are more closely parallel, even converging near the posterior wing margin, and the anal loop is longitudinally elongate, unlike that in Parapetala.

Furthermore, Parapetala has well-defined trigonal planates, especially in the hindwings, unlike the Mesuropetalidae, the Austropetaliida and the more basal clades of Panaeshnida (Progobiaeshnidae Bechly et al., 2001, Rudiaeschnidae Bechly et al., 2001, Eumorbaeschnidae Bechly et al., 2001, and Cymatophlebiidae: Cymatophlebiinae). Such trigonal planates are present in the more advanced Neoestheshnia Bechly, 1996, but also in the more basal groups Liupanshanidae and Cymatophlebiidae: Valdaeshnidae. Thus, if this character is a
further difference between *Parapetala* and the Mesuropetalidae, it is not alone sufficient to attribute the former to a more derived lineage, because it is clearly subject to convergencies.

*Parapetala* has well-separated eyes, as in Mesuropetalidae, which is a plesiomorphic condition in Aeshnoptera. In Liupanshaniidae, Liupanshaniida, and Panaeshnida (at least in the basal group Cymatophlebiidae and in the extant Aeshnoptera), the eyes are closer together or more or less meet. This suggests a basal position for *Parapetala*. Nevertheless, this character has to be verified in several fossil families of Panaeshnida (Progobiaeshnidae, Rudiæaeschnidae, Paracymatophlebiidae) in which the head is unknown.

Bechly *et al.* (2001, p. 19) considered that there is an unresolved trichotomy between the genus *Cymatophlebiella* Pritykina, 1968, the Mesuropetaloidea, and the Aeshnomorpha Bechly *et al.*, 2001 (=Austropetaliida+Panaeshnida). *Parapetala* differs from *Cymatophlebiella* in the presence of a small but distinctly closed anal loop and the unicellular discoidal triangle of the hindwing, and in the absence of any Rspl (a short Rspl is present in Paracymatophlebiella) (see Bechly *et al.*, 2001, p. 204).

In conclusion, *Parapetala* is in a very basal position in the Aeshnoptera, basal or close to the Mesuropetaloidea, but it does not belong to either the Mesuropetalidae or the Liupanshaniidae. It probably corresponds to a different, new, family but there is no known autapomorphic character with which to characterize it. Thus, we prefer to consider it as an Aeshnoptera of uncertain familial affinities.

3. Conclusion

The fossil record of Mesozoic Aeshnoptera is not well congruent with the phylogenetic tree of this group, as noted by Bechly *et al.* (2001, text-fig. 2). Representatives of the very basal family Mesuropetalidae are known only from the Upper Jurassic but the more basal genus *Parapetala* is from the Lower Cretaceous. The Rudiaeænaschidae is Early Cretaceous but the more advanced family Eumorbaeschnidae is known from the Upper Jurassic of Germany. This suggests that the fossil record of Mesozoic Aeshnoptera is still very incomplete, even if recent records of the diversity of this group are spectacular, with six new families having been discovered since 1990. The present discovery also indicates increased aeshnopteran diversity during the Late Jurassic–Early Cretaceous. The Mesozoic history of the Aeshnoptera seems to indicate rapid evolution during the Early or Middle Jurassic, followed by the extinction of at least five major clades before the Late Cretaceous. Further discoveries of Aeshnoptera in the Middle Jurassic and in the Albian–Cenomanian will be necessary to test this hypothesis.

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