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# *Telmaeshna paradoxica* gen. et sp. nov., a new fossil dragonfly (Insecta: Odonata: Anisoptera) from the Yixian Formation, Liaoning, China

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## Abstract

*Telmaeshna paradoxica* **gen. et sp. nov.**, is described from the Upper Jurassic to Lower Cretaceous Yixian Formation, near Chaomidian Village, Beipiao City, Liaoning Province, China. It is included in the Anisoptera: Aeshnoptera: Aeshnomorpha: Panaeshnida, on the basis of the following characters: strongly elongated pterostigma; well-defined anal loop and Rspl; undulated RP2, RP3/4 and MA; divided hypertriangle and discoidal triangle; and prolonged gaff. It cannot be assigned to any described extant or extinct family of Panaeshnida, but we refrain from erecting a new family to accommodate it until more features (forewing, body characters) are known. Consequently, this new genus is provisionally retained as family uncertain. Its phylogenetic relationships within Anisoptera are discussed.

**Key words:** Insecta, Odonata, Anisoptera, Aeshnoptera, fossil, Upper Jurassic, Lower Cretaceous, China

## Introduction

At present, about nine families, 28 genera and 55 species of Mesozoic Aeshnoptera have been described (Bechly *et al.* 2001; Huang *et al.* 2003; Zhang *et al.* 2006). Liupanshaniidae, Progobiaeshnidae, Rudiaeschnidae, *Parapetala* (family position uncertain) and *Sopholibellula* were originally discovered in China.

The Yixian Formation consists of grey tuff, siltstone and mudstone which have yielded insects, conchostracans, plants, primitive birds and feathered theropods. The age of the biota has been discussed by Wang *et al.* (2005) who summarized different theories about the age of the Yixian Formation based on abundant fossil data as compared the Yixian biota with the Solnhofen biota of Germany, the Purbeck biota in England, Late Jurassic Teri-type and Ryoseki-type floras in Japan, the Middle Jurassic Yorkshire flora, and the Great Estuarine conchostracan fauna in the UK. Wang *et al.* (2005) believe the Yixian Stage to be Late Tithonian to Berriasian, thus we regard the lower part of Yixian Formation as transition from Upper Jurassic to Lower Cretaceous.

Nineteen species of Odonata have been described from this formation up to now: *Sinaeschnidia heishankowense* Hong; *Archaeogomphus labius* Lin; *Pseudosamarura largina* Lin; *Dissurus liaoyuanensis* Hong; *Sinogomphus taoshanensis* Hong; *Hebeiaeschnidia fengningensis* Hong; *Chrysogomphus beipiaoensis* Ren; *Sinaeschnidia cancellosa* Ren; *Liogomphus yixianensis* Ren & Guo; *Mesocordulia boreala* Ren & Guo; *Rudiaeschna limnobia* Ren & Guo; *Dracontaeschnidium orientale* Zhang & Zhang; *Sinojagoria imperfecta* Bechly, Nel & Martínez-Delclòs; *Stylaeschnidium rarum* Zhang & Zhang; *Bellabrunetia catherinae* Fleck & Nel; *Abrohemeroscopus mengi* Ren, Liu & Chen; *Parapetala liaoningensis* Huang, Nel & Lin; *Sopholibellula eleganti* Zhang, Ren & Zhou; *Sopholibellula amoena* Zhang, Ren & Zhou. (Lin 1976; Hong 1982, 1984; Ren

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1994, 2002; Ren & Guo, 1996; Zhang 1999; Bechly *et al.* 2001; Zhang & Zhang 2001; Fleck & Nel 2002; Huang *et al.* 2003; Ren *et al.* 1995, 1996, 2003; Zhang *et al.* 2006).

Wing venation nomenclature follows Bechly (2001). Anx, Asnx, Pnx and Psnx = antenodal, antesubnodal, postnodal, and postsubnodal crossveins respectively. The higher classification of fossil and extant Odonata is based on the phylogenetic system of Bechly (1996, 2007). The classification of the Aeshnoptera is based on the work of Bechly *et al.* (2001). Visual observations and drawings were made with a LEICA MZ12.5 stereomicroscope and Adobe Illustrator 11.0 software. The Odonata fossils studied here, collected by Dong Ren from a small section of the Yixian Formation of Liaoning Province, are housed in the Key Lab of Insect Evolution & Environmental Changes, the College of Life Sciences, Capital Normal University, Beijing, China (CNU; Dong Ren, Curator).

## Systematic palaeontology

### Order Odonata Fabricius, 1793

### Suborder Anisoptera Selys in Selys & Hagen, 1854

### Clade Aeshnoptera Bechly, 1996

### Aeshnomorpha Bechly *et al.*, 2001

### Panaeshnida Bechly *et al.*, 2001

### Family uncertain

### Genus *Telmaeshna* gen. nov.

**Etymology.** The generic name is a combination of the Greek prefix *telm-* (meaning "swamp") and *Aeshna* (a genus within family Aeshnidae). The gender is feminine.

**Type species:** *Telmaeshna paradoxica* **sp. nov.**

**Diagnosis:** All known characters from a hind wing. No Anx present between Ax0 and Ax1; Ax1 and Ax2 relatively close together with only one intermediary antenodal crossvein; two oblique veins ('O') present; Pterostigma very long and strong; Pseudo-IR1 not well defined (zigzag, very short and originating distinctly distal of the pterostigma); base of RP2 not aligned with subnodus; area between RP1 and RP2 broad with three rows of cells up to pterostigma; Mspl absent; median space free of crossveins; hind wing hypertriangle and discoidal triangle divided into five or more cells respectively, subdiscoidal triangle three-celled; approximately pentagonal anal loop large and nine-celled, with prolonged gaff; hind wing distinctly broad and rather round in shape.

### *Telmaeshna paradoxica* gen. et sp. nov.

Figs. 1–3

**Etymology.** From Greek '*paradoxicus*' = special.

**Holotype.** Specimen No. CNU-OD-LB2004001-1, part, No. CNU-OD-LB2004001-2, counterpart, gender undetermined, fossilized with an ephemeropteran larva.

**Type locality and stratigraphic horizon.** The Late Jurassic to Early Cretaceous, Yixian Formation, near Chaomidian Village, Beipiao City, Liaoning Province, China.

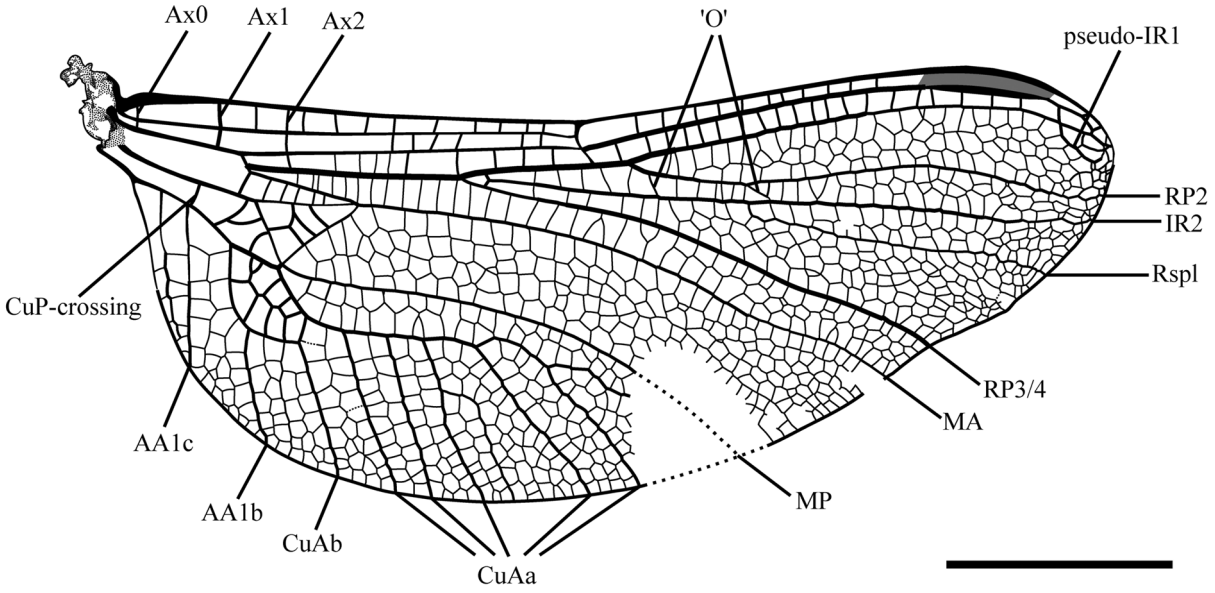


**FIGURE 1.** *Telmaeshna paradoxica* **gen. et sp. nov.**, holotype CNU-OD-LB2004001-1, line drawing of hindwing (scale bar represents 10 mm)

**Diagnosis:** As for genus.

**Description.** A well-preserved hyaline hind wing (part and counterpart), with an oval brown 5.8 by 5.1 mm spot at middle of posterior wing margin due to an artifact of preservation. Gender undetermined.

Hind wing distinctly broad and rather round in shape; length 45.1 mm; max width 17.1 mm; width at nodus 16.5 mm; distance from base to arculus 6.3 mm, from base to nodus 21.5 mm (47.7% of wing length), from nodus to pterostigma 15.3 mm, from pterostigma to the apex 2.5 mm; pterostigma very long and strong (5.8 by 0.9 mm, 12.8 % of wing length), covering four and two-third cells and braced by a weakly oblique crossvein that is nearly aligned with its basal side; costal margin and RA thickened along pterostigma; 11 Pnx between nodus and pterostigma, these not aligned with corresponding 15 Psnx; 10 secondary Anx between costal margin and ScP, not strictly aligned with six secondary Anx between ScP and RA; primary Anx Ax1 and Ax2 aligned and stronger than secondary Anx, but Ax2 less distinct, not so strong as Ax1; Ax1 1.3 mm basal to arculus and Ax2 3.0 mm distal to Ax1; one secondary antenodal crossvein of first row situated midway between two primary Anx; corresponding Anx in the second row not preserved; basal brace (Ax0) thickened; no Anx present between Ax0 and Ax1; 10 Asnx visible basal to subnodus, thus no "cordulegastrid gap" (*sensu* Bechly, 1996) present; RP and MA distinctly separated at angulate arculus; five bridge-crossveins (Bqs) visible; midfork 4.3 mm basal to nodus; base of RP2 not aligned with subnodus, but a cell distal to subnodus; oblique veins 'O' two and eight cells distal to subnodus respectively, with distal accessory oblique vein more strongly oblique than true basal one; pseudo-IR1 not well defined (very short, 2.4 mm, and originating distinctly distal to pterostigma); Rspl of three cell rows, straight, well-defined; RP2 and IR2 are more or less parallel with only a single row of cells in between up to level of halfway between nodus and pterostigma, but more distally with up to three rows of cells between these veins; IR2 straight, slightly arched distally; RP2 slightly curved at level of pterostigma; RP1 and RP2 slightly divergent basally with two or three rows of cells in between, but near pterostigma, these veins becoming more divergent with 4–6 rows of cells in between; RP3/4 and MA parallel and gently undulate with a single row of cells in between to level of first oblique vein, but distally with two rows of cells in between to level of second oblique vein, and divergent near wing margin with three or four cells in between; Mspl absent, but two inconspicuous single secondary veins originating at

MA at distal postdiscoidal area; postdiscoidal area with four rows of cells distal of discoidal triangle and over ten rows of small cells along posterior wing margin; MP and MA largely parallel; two rows of cells between MP and CuAa; CuAa with five well-defined posterior branches with a smaller branch originating from the third posterior branch; CuA reaching posterior wing margin at level with nodus; about ten rows of cells between CuAa and posterior wing margin; CuAb well-defined; median space free; submedian space apparently traversed only by Cup-crossing; hypertriangle with five crossveins; discoidal triangle longitudinally elongated, five-celled; oblique PsA between AA and MP+CuA weakly defined, slightly angled, appearing as an oblique cubito-anal crossvein rather than a secondary anterior branch of AA; subdiscoidal triangle divided into three cells by two cambered veins; large approximately pentagonal anal loop composed of nine cells, the basal side and the side between AA1b and CuAb smoothly connected and forming an arc, posteriorly closed; gaff prolonged; AA1b and AA1c distinct; anal margin rounded; a distinct concavity at wing margin at the end of RP3/4; cells between the apex and the concavity along margin small and irregular.

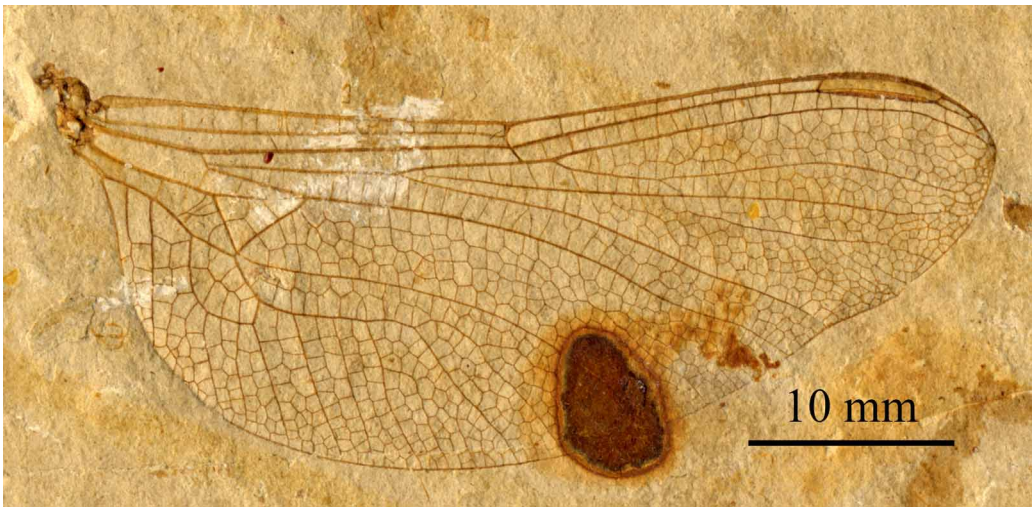


**FIGURE 2.** *Telmaeshna paradoxica* **gen. et sp. nov.**, photograph of holotype CNU-OD-LB2004001-1, part (scale bar represents 10 mm)

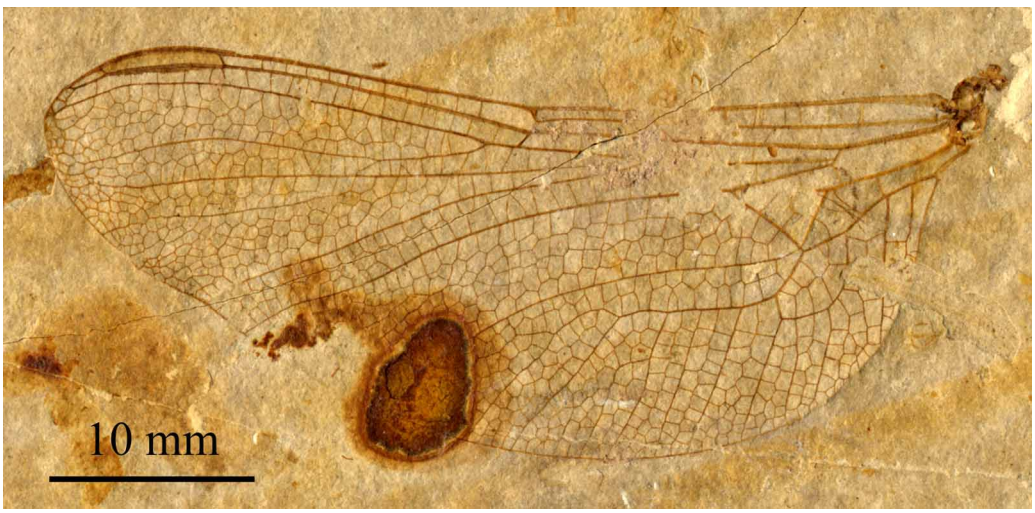


**FIGURE 3.** *Telmaeshna paradoxica* **gen. et sp. nov.**, photograph of holotype CNU-OD-LB2004001-2, counterpart (scale bar represents 10 mm)

**Discussion**

This new fossil genus is diagnosed by agreement with principal characters diagnostic with Anisoptera (viz. well-defined anal loop; distinct membranule of the hind wing; pterostigma strongly elongated) and Aeshnoptera (viz. undulated RP3/4 and MA; the presence of Rspl) and Aeshnomorpha (viz. hypertriangles divided by at least one crossvein; slightly undulate RP2; well defined Rspl; prolonged gaff) and Panaeshnida (viz. well-defined Rspl; hypertriangles divided by several parallel crossveins; discoidal triangles divided into more than two cells). The last diagnosis of Aeshnoptera proposed by Bechly *et al.* (2001, p.19) is "RP1 and RP2 basally parallel up to the pterostigma, thus, the area between these two veins is basally distinctly narrowed with only one row of cells between them in the groundplan." This character is reversed in *Aeschnopsis tischlingeri* Bechly, Nel & Martínez-Delclòs, 2001 and *A. jurassica* Bechly, Nel & Martínez-Delclòs, 2001, Archipetaliidae, *Gobiaeshna occulta* Pritykina, 1977, Valdaeshninae, Rudiaeschnidae, and some fossil Gomphaeschninae, e.g. *Alloaeschna* and *Progomphaeschnaoides, Plesigomphaeschnaoides*, and *Gomphaeschnaoides*) (Bechly 1996), and also seems to be reversed in *Telmaeshna*. Another character of Panaeshnida proposed by Bechly (2001, p.66) is "submedian space divided by one or more accessory cubito-anal crossveins between CuP-crossing and PsA." This was not adopted because it is subject to numerous convergences and reversals within Panaeshnida, especially based on the hind wing.

Panaeshnida contains Progobiaeshnidae and Aeshnida. Only one wing venational autapomorphy of Aeshnida proposed by Bechly (2001) is the presence of a Mspl. *Telmaeshna* lacks Mspl. Aeshnida includes nine families (Bechly 1996, 2001): Cymatophlebiidae, Rudiaeschnidae, Paracymatophlebiidae, Eumorbaeschnidae, Gomphaeschnidae, Allopetaliidae, Brachytronidae, Telephlebiidae and Aeshnidae. The first two families (both included in Cymatophlebioidea) have one to three convex oblique and undulated secondary veins anastomosing between IR2 and RP3/4 immediately basal to origin of Rspl (at least in hind wings). The distal second oblique vein 'O' of Paracymatophlebiidae is thought to be secondarily absent. In Eumorbaeschnidae, RP2, RP3/4 and MA are strongly undulate and the hind wing subdiscoidal triangle two-celled. Gomphaeschnidae possess a "cordulegastrid gap" and two-celled discoidal triangle. There are two rows of cells between Rspl and IR, Mspl and MA, as well as PR1and RP2 basal of the pterostigma in Allopetaliidae. The pterostigmal brace vein of Brachytronidae is reduced. Ax2 is recessed to the basal angle of the discoidal triangle in Telephlebiidae. Aeshnidae can be easily recognized by the characteristic bulge in distal part of MA in both pairs of wings ("aeshnid bulla"); two-celled subdiscoidal triangle; distinctly curved Rspl and Mspl; the widened wing space between IR2 and Rspl and MA and Mspl is at least basally divided by oblique intercalary veinlets. All these above mentioned diagnostic characters are not present in *Telmaeshna*.

The family in Bechly's system most resembles *Telmaeshna* is Progobiaeshnidae, its characters include: (1) pseudo-IR1 strongly reduced (short and originating distally to pterostigma); (2) anal loop enlarged and divided into nine cells, correlated with a more pronounced elongation of the gaff; (3) several rows of cells between IR2 and Rspl which are approximately parallel; (4) hind wing subdiscoidal triangle two celled; (5) RP2 and IR2 weakly undulated and strictly parallel with only a single rows of cells in-between; (6) two oblique veins 'O' present; (7) Mspl absent; (8) very long veins MP and CuA (the latter with about seven posterior branches in both wings) distally diverging; (9) absence of any angle or curve in the straight distal side of the discoidal triangle; (10) subdiscoidal triangles divided into two cells in both pairs of wings; (11) three rows of cells in the basal postdiscoidal area of both pairs of wings; (12) no secondary longitudinal vein in the postdisoidal area originating on distal side of discoidal triangle; (13) PsA delimiting a distinct subdiscoidal triangle, but appearing like an oblique cubito-anal crossvein rather than a secondary anterior branch of AA. Bechly proposed the first four as autopomorphies and others as further diagnosis characters of Progobiaeshnidae. Our fossil specimen cannot be assigned to this family because of disagreement with the (4), (5), (8), (10), and (11). Furthermore, it can easily be distinguished from Progobiaeshnidae by base of RP2 not aligned with subnodus, much broader and rounder hind wing, much longer pterostigma and nodus located much closer to mid-wing.

As noted above, a new family seems warranted. For the present, however, we refrain from erecting a new family until more features (forewing, body characters) are known. Consequently, a new genus was erected here to accommodate this specimen, which retained family uncertain provisionally.

## Remarks

In *Telmaeshna*, base of RP2 is distinctly not aligned with subnodus, but a cell distal of the subnodus. This character is anomalous within Anisoptera. The character "base of RP2 not strictly aligned with subnodus" was first noted by Bechly (1996) as one of the three autapomorphies of Stenophlebioptera, which is certainly unrelated to *Telmaeshna*. Fleck *et al.* (2003) claimed that this character is also frequently present in taxa of other groups, such as some Anisoptera: Gomphomacromiidae (*Gomphomacromia*) and Libellulidae (*Nannothemis*), and in many Isophlebioidea. They also gave another example: in *Stenophlebia latreille*i (Germar), RP2 is aligned with the subnodus in the forewing and not aligned in the hind wing. In the phylogenetic system of Odonatoptera proposed by Bechly (1996, 2007), "RP2 strictly aligned with subnodus" is one of the autapomorphies of Pananisoptera (the sister group of Stenophlebioptera), the group in which the Anisoptera is included. We have assigned *Telmaeshna* to Anisoptera and based on all the other characters believe that it belongs to the Aeshnoptera-Aeshnomorpha.

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