



## A new family of Cavilabiata from the Lower Cretaceous Yixian Formation, China (Odonata: Anisoptera)

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### Abstract

A new genus *Nodalula* **gen. nov.** and species *Nodalula dalinghensis* **gen. et sp. nov.** is described on the basis of a nearly complete specimen from the Lower Cretaceous of North-east China. Its special pattern of wing venation differs from those of the known Mesozoic Cavilabiata genera and allows us to include it in the new family Nodalulidae within the Neobrachystigmata.

**Key word:** Odonata, Anisoptera, Cavilabiata, fam. nov., Early Cretaceous, Jehol biota, China

### Introduction

The morphological disparity of the Cavilabiata (formerly Cordulegastroidea + Libelluloidea) was very important during the Late Jurassic/Early Cretaceous, even greater than nowadays, with about 10 extinct families, representing numerous stages of the wing venation evolution of this clade. Nearly all these Mesozoic forms became extinct before the Late Cretaceous, probably during the Cenomanian-Turonian, probably in relation with the important changes in the lake water quality correlated to the rise and diversification of the Angiosperms (Fleck and Nel, 2003). The present discovery of a new taxon representing a new family, somewhat 'intermediate' between the Hemeroscopidae and the more modern Neobrachystigmata (a clade to which belong the recent families Corduliidae and Libellulidae, among others) is of great interest for our knowledge on the evolution of the whole group and its past diversity.

The wing venation terminology follows Bechly *et al.* (2001).

### Systematic palaeontology

**Order Odonata Fabricius, 1793**

**Suborder Anisoptera Selys, 1854**

**Clade Cavilabiata Bechly, 1996**

**Family Nodalulidae fam. nov.**

**Type genus. *Nodalula* gen. nov.**

**Diagnosis:** Female ovipositor reduced; ‘cordulegastrid’ gap present; relatively short pterostigmata covering less than three complete cells; in the hind wing the basal CuA before its branching strongly prolonged and very straight; CuAa with four branches; terminal branch of CuAa apparently secondarily branched on CuA; area between MP and CuA slightly basally widened; RP3/4 and MA strictly parallel up to the hind margin; area between RP2 and IR2 distally distinctly widened, with more than one cell row in distal half; well-defined Rspl and Mspl, with one row of cells above them; a distinct pterostigmal brace; lestine oblique cross-vein shifted basally one cell distal of subnodus; hind wing anal cell rhombus-like, seven-celled; arculus not distinctly angled but more or less straight, with posterior part (cross-vein) distinctly shorter than anterior part; hind wing MP distinctly curved towards the hind margin and thus somewhat shortened, ending basal of level of nodus; hypertriangles not much longer than discoidal triangles in both pairs of wings; anterior margin of hypertriangle straight; fore wing Ax1 shifted basal of level of distal angle of discoidal triangle; fore wing discoidal triangle elongate; discoidal cells crossed; in both pairs of wings Ax1 and Ax2 with two secondary antenodal cross-veins between them.

***Nodalula* gen. nov.**

**Type species:** *Nodalula dalinghensis* sp. nov.

**Etymology:** Derived from latin ‘noda’ (knot) and ‘alula’ (wing).

**Diagnosis:** As for the family.

**Distribution and age:** North China; Lower Cretaceous.

***Nodalula dalinghensis* sp. nov.**

Figs. 1–3

**Material:** A nearly complete adult dragonfly with the four wings and the trunk (except the head) preserved with brown colour, without counterpart. The wings are strongly distorted, especially in their anterior parts. Cat. No. 123517.

**Etymology:** Derived from Dalinghe, a name of a river in this area.

**Locality and horizon:** Yixian Formation, Barremian, Early Cretaceous, Dalinghou, in the Jianshangou of Beipiao City, Liaoning Province (Sha, 2007).

**Description:** A nearly complete body of an adult female with the thorax, abdomen, the six legs and four wings in connection, but with most part of head missing; whole body 62.2 mm long.

Thorax 13.6 mm long, 8.0 mm wide; prothorax small, 1.6 mm long, 8 mm wide, with its anterior margin bend forward, narrower than posterior margin; synthorax large, 12 mm long, 8.0 mm wide.

Coxa of fore leg large and stout; femur strong, with one row of regular spines along inner margin; tibia as long as femur, furnished with strong spines; mid leg larger and stouter than fore leg, with stout femur, tibia incompletely preserved, femur and tibia with spines along their inner margins; hind leg the largest, femur large, tibia incomplete, both furnished with spines.

Fore wing 40 mm long, 8 mm wide, approximately four times as long as wide; distance from base to nodus 17 mm, nodus to pterostigma 12.3 mm, pterostigma to wing apex 3.5 mm, base to arculus 3.4 mm; hind wing broader than fore wing, 38.6 mm long, 11.6 mm wide, approximately four times as long as wide; distance from base to nodus 14.5 mm, nodus to pterostigma 15.2 mm, pterostigma to wing apex 3.5 mm, base to arculus 5.5 mm; pterostigma 3.1 mm long, 1 mm wide, approximately 3 times as long as wide, covering three cross-veins, pterostigmal brace strong and distinctly oblique; no cross-vein in distal antesubnodal area (‘cordulegastrid’ gap); ScP with a strong curve at nodus; nodal cross-vein aligned with ScP at nodus, perpendicular

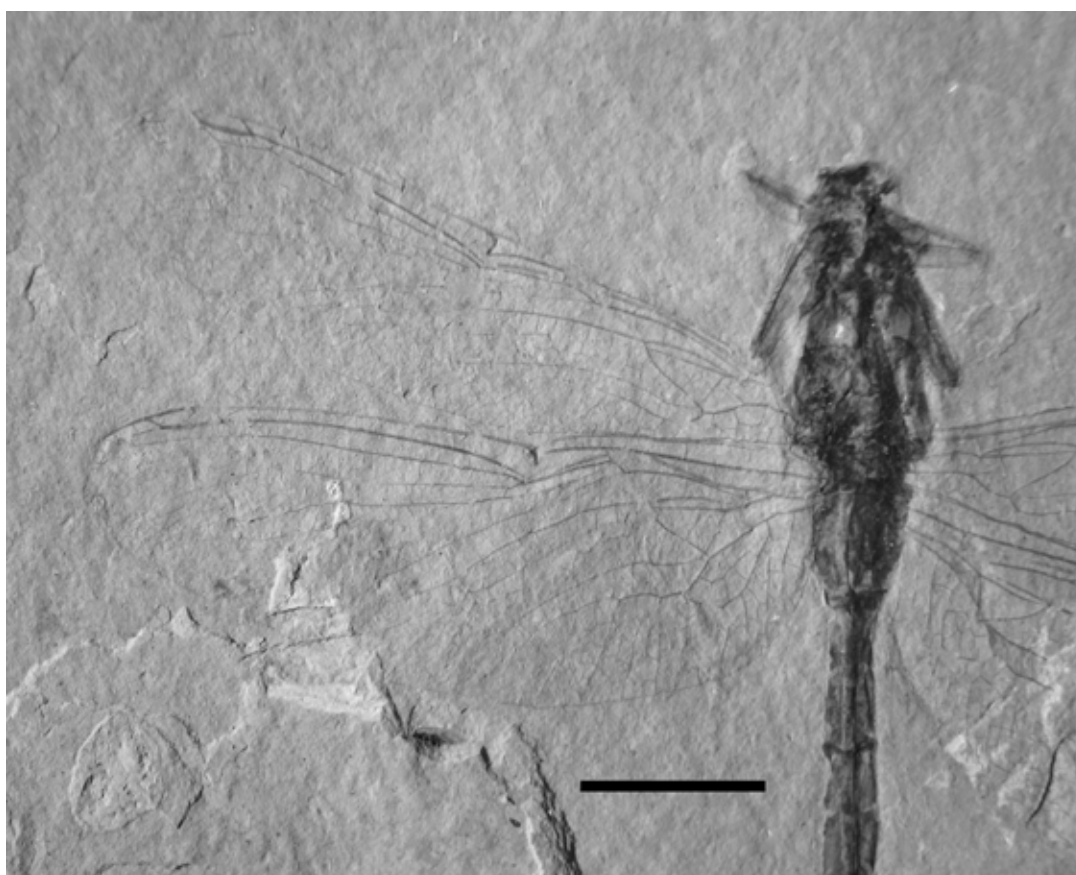


**FIGURE 1.** *Nodalula dalinghensis* **gen. et sp. nov.**, holotype Cat. No. 123517 (female), photograph of dorsal view (scale bar represents 10 mm).

to C and RA; subnodus not well-preserved; in fore wing about 14 secondary antenodal and antesubnodal cross-veins, not aligned; in hind wing about 12 secondary antenodal and antesubnodal cross-veins, not aligned; Ax1 well basal and Ax2 distal of discoidal triangle, with two secondary cross-veins between them; base of RP2 aligned with subnodus; RP2 and IR2 with a double curve; RP3/4 and MA also undulate but less distinctly than RP2; Rspl well-defined and parallel to IR2, with one row of cells between it and IR2; IR1 short, with its base below middle of pterostigma; arculus straight, perpendicular to RA, with its costal part distinctly longer than its ventral part; RP and MA well-separated in the arculus; discoidal triangle in fore and hind wings transverse, of similar shape, although the fore wing one is slightly narrower than that of hind wing, both divided in two cells by a cross-vein, distal side MAb slightly curved; anterior margin (MA) of hypertriangle more or less straight; hypertriangle elongate and narrow, free of cross-veins; subtriangles of fore and hind wings unicellular, but well-defined by PsA vein, that of fore wing being broader than that of hind wing, with its posterior margin more rounded; postdiscoidal area of fore wing with two rows of cells just distal of triangle, three in hind wing; Mspl well defined and parallel to MA, with one row of cells between them; hind wing MP somewhat shortened and distinctly curved towards hind margin, reaching this margin nearly opposite nodus; hind wing area between MP and CuAa not very broad, with only one row of transverse cells near

discoidal triangle; CuAa curved, with only four posterior branches; basal part of CuA straight but rather long, 1.6 mm long; anal loop complete rather transverse, rhombus-like, divided into seven cells; anal area rather broad, with five rows of cells between anal loop and posterior wing margin; hind wing base of anal margin rounded (female).

Abdomen 48.6 mm long, 4.6 mm wide; first abdominal segment well developed and large, obconic in form, its anterior margin about 1.5 time as wide as its posterior margin; second abdominal segment longer, but narrower than first, about three times as long as wide; third segment similar to second, about 2.3 times as long as wide; fourth and fifth similar, slightly broader than third; but slight shorter than the 3<sup>rd</sup>; sixth similar to fourth in width, but shorter, about two times as long as wide; seventh shorter than sixth, longer than wide; eighth shorter than seventh, as long as wide; a median longitudinal carina on second to eighth terga; a pattern of light coloration on second to sixth segments, consisting in two longitudinal stripes and two outer apical spots; two superior anal appendages normally developed; median appendage shorter than superior anal appendages; no visible ovipositor.



**FIGURE 2.** *Nodalula dalinghensis* **gen. et sp. nov.**, holotype Cat. No. 123517, Enlarged view showing the left fore and hind wings venation (scale bar represents 10 mm).

**Discussion:** The attribution of *Nodalula* **gen. nov.** to the Cavilabiata Bechly, 1996 is supported by the following characters: distal part of antesubnodal area free of cross-veins ('cordulegastrid gap'); gaff (= basal CuA before its branching) of the hind wing distinctly prolonged. The third venational character, viz. the RP3/4 and MA slightly undulating in both pairs of wings, is impossible to determine because of the important deformations of these wings.

Affinities with the Cordulegastrida Bechly, 1996 can be excluded because *Nodalula* has not the 'female ovipositor strongly elongated into a gently tapered spade', and the venational synapomorphies of this clade, viz. wings with a basal furcation of IR2 basal of the lestine oblique vein; pterostigmal brace vein reduced; dis-

coidal triangles of similar elongate shape in both pairs of wings, correlated with a secondarily less distinct pseudo-anal vein PsA and subdiscoidal triangle. On the contrary, it has the venational synapomorphies of the Brachystigmata Bechly, 1996, i.e. relatively short pterostigmata that cover only 1–3 complete cells; in the hind wing the gaff (= basal CuA before its branching) is strongly prolonged and very straight (in the ground plan); area between MP and CuA basally widened; terminal branch of CuAa seems to be secondarily branched on CuA; RP3/4 and MA strictly parallel up to the hind margin; area between RP2 and IR2 distally distinctly widened, with more than one cell row in the distal half. Within this clade, the comparison with the Mesozoic Nannogomphidae Bechly, 1996 is not easy because there is no strong synapomorphy for this family. Affinities with *Nannogomphus* Handlirsch, 1906 are excluded because the latter is characterized by the synapomorphy ‘CuAa without posterior branches’ (Bechly *et al.*, 1996). Affinities with *Prohemeroscopus* Bechly *et al.*, 1998 (originally in Hemeroscopidae, but latter transferred into the Nannogomphidae) are more delicate to discuss. Nevertheless, *Nodalula* can be attributed to the Eubrachystigmata Bechly, 1996, sister group of the Nannogomphidae, on the basis of the apomorphy ‘hind wing CuAa more distinctly curved towards the hind margin, and thus further shortened with less than five posterior branches’. Within this group, *Nodalula* differs from *Hemeroscopus* Pritykina, 1977 (Hemeroscopidae Pritykina, 1977) in its crossed discoidal cells, presence of well-defined Rspl and Mspl, presence of a distinct pterostigmal brace; shorter pterostigma, lestine oblique cross-vein shifted basally one cell distal of the subnodus, and narrower and smaller hind wing anal cell. The monophyly of the Neobrachystigmata Bechly, 1996, sister group of the Hemeroscopidae, is supported by the following synapomorphies: ‘arculus not distinctly angled but more or less straight, with posterior part (cross-vein) of arculus distinctly shorter than anterior part’. This character seems to be present in *Nodalula* although it is not obvious because the arculus are partly broken; ‘hind wing MP distinctly curved towards the hind margin and thus somewhat shortened, ending basal of the level of the nodus’. Despite the deformation of the costal region of its wings, it seems that *Nodalula* has a significant curvature of the hind wing MP. Within this group, our fossil has not the synapomorphy of the Chlorogomphida Bechly, 1996, viz. ‘hypertriangles much longer than discoidal triangles in both pairs of wings’. *Nodalula* shares with the Paneurypalpidomorpha Bechly, 1996, sister group of the Chlorogomphida, two synapomorphies, i.e. ‘lestine oblique vein only 1–2 cells distad of the subnodus in both pairs of wings’, ‘fore wing ax1 shifted basal of the level of the distal angle of the discoidal triangle’, but not several others, viz. ‘anterior margin of hypertriangle distinctly convex, especially in the hind wings, because of a basally arched MA’, ‘fore wing discoidal triangle more or less transverse instead of elongate’, and ‘in both pairs of wings Ax1 and Ax2 relatively close together with not more than one secondary antenodal cross-vein between them’. The Paneurypalpidomorpha comprises the Mesozoic Juracorduliidae Bechly, 1998 and the Eurypalpidomorpha. *Nodalula* also differs from *Juracordulia* Bechly, 1998 in its less elongate anal loop and CuAa with more branches (plesiomorphies) (Bechly, 1998). It has not the main synapomorphy of the Eurypalpidomorpha Bechly, 1996 (clade comprising the Mesozoic families Valdicorduliidae Bechly, 1996, Araripephlebiidae Bechly, 1998, Eocorduliidae Bechly, 1996, Araripebellulidae Bechly, 1996, and the fossil and modern Eurypalpida Bechly, 1996), viz. ‘in the hind wing the elongated gaff (= basal CuA before its branching) sigmoidally curved, CuAb shifted very far distally, and CuAa with only one or two posterior branches’ (Pritykina, 1986; Nel and Paicheler, 1994; Ren and Guo, 1996; Jarzembowski and Nel, 1996; Bechly, 1998).

In conclusion, *Nodalula* can be considered as a Neobrachystigmata that does not belong to the clade Chlorogomphida and shares some synapomorphies with the Paneurypalpidomorpha, but which is neither a Juracorduliidae nor a Eurypalpidomorpha. It could well be the sister group of the whole clade Paneurypalpidomorpha.

A larval dragonfly from the same strata described by Huang and Nel (2004) has been placed in the clade Cavilabiata. This specimen shows some strong similarities with the ultimate larval instars of *Sona nectes* described from western Mongolia (Pritykina 1986). The ultimate larval instars always display few comparable features to the corresponding adult in Odonata. This ultimate larval instars of the ‘*Sona nectes* type’ larva bear

strongly developed spines rows on legs that resemble those of *Nodalula dalinghensis* **gen. et sp. nov.** However, their correspondence still remains uncertain due to the strong morphological gap between larvae and adults.



**FIGURE 3.** *Nodalula dalinghensis* **gen. et sp. nov.**, holotype Cat. No. 123517, Enlarged view showing the apex of abdomen (scale bar represents 10 mm).

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