New discoveries of Neogene hawker dragonflies (Insecta, Odonata, Aeshnidae) from Shandong province in China

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KEY WORDS
Insecta,
Odonata,
Aeshnidae,
Middle Miocene,
Shanwang Formation,
China,
new species.

ABSTRACT
Epiaeschna matutina (Zhang, 1989) is re-described and species diagnosis is amended. Two new species, *Aeshna shanwangensis* n. sp. and *Aeshna forficatum* n. sp., are described from the Middle Miocene deposit of Shanwang Formation, Shandong Province, East China. Comparison with other related fossil and recent species is provided.

MOTS CLÉS
Insecta,
Odonata,
Aeshnidae,
Miocène moyen,
Formation Shanwang,
Chine,
espèces nouvelles.

RÉSUMÉ
Nouvelles découvertes de libellules (Insecta, Odonata, Aeshnidae) du Néogène de la province du Shandong, Chine.
Epiaeschna matutina (Zhang, 1989) est redécrite et sa diagnose est amendée. Deux nouvelles espèces, *Aeshna shanwangensis* n. sp. et *Aeshna forficatum* n. sp., sont décrites du Miocène moyen de la formation Shanwang, province du Shandong, dans l'est de la Chine. Ces fossiles sont comparés avec les espèces fossiles et récentes.

INTRODUCTION

Northeastern China continues to surprise the world by its great mid Mesozoic fossil findings, especially from the western Liaoning Province. As a continuum of the palaeoentomological records, the Cenozoic Shanwang Formation plays an important role in the reconstruction of evolutionary history and palaeobiogeography of the insects. Aeshnopteran dragonflies from Chinese Cenozoic are rare, in contrast to the mid Mesozoic abundant records and high diversity (Li *et al.* 2011). The family Aeshnidae, with more than 400 extant species in about 50 genera, has a worldwide distribution (Garrison *et al.* 2006: 25-64); but the aeshnid Cenozoic record is mostly documented from Europe, Siberia and North America (Timon-David 1946; Nel 1986, 1987; Martínez-Delclòs & Nel 1991; Nel *et al.* 1994, 2005; Prokop & Nel 2000, 2002; etc.). Recently, we found six new well-preserved aeshnid specimens from the Shanwang Formation. Morphology and taxonomy of these new findings are presented in this paper, helping better knowledge on evolutionary history of Aeshnidae.

MATERIAL AND METHODS

The Shanwang Basin, in which the Shanwang Formation was deposited, lies in eastern part of Linqu County, central Shandong Province, 36°32'00"-36°34'30"N, 118°40'22'-118°44'00"E (Fig. 1) (Sun *et al.* 2002). Shanwang Basin contains an exceptionally well-preserved Middle Miocene fossil biota, in its diatomaceous shale lacustrine deposit, with more than 500 fossil species discovered, including fungi, diatoms, higher plants, insects, ostracodes, fishes, amphibians, reptiles, birds, and mammals (Yang & Yang 1994). Its age is currently considered as early middle Miocene (Li *et al.* 2010).

We follow the wing venation nomenclature and terminology for aeshnopteran dragonflies as proposed by Bechly *et al.* (2001), after that of Nel *et al.* (1993). The new material is stored in the Capital Normal University, Beijing (CNU-ODO).

SYSTEMATICS

Family AESHNIDAE Leach, 1815

Genus *Epiaeschna* Hagen, 1875

TYPE SPECIES. — *Aeshna heros* Fabricius, 1798 (recent).

OTHER SPECIES. — *Epiaeschna pseudoheros* Nel & Petrulevičius, 2010 (late Oligocene, France), *Epiaeschna stauropolitana* Martynov, 1927 (middle Miocene, Crimea), *Epiaeschna magnifica* (Martynov, 1929) (late Oligocene, Kazakhstan), *Epiaeschna gossi* (Campion, 1916) (middle-late Eocene, UK), *Epiaeschna matutina* (Zhang, 1989) (middle Miocene, China).

Epiaeschna matutina (Zhang, 1989)
(Figs 2-9)

MATERIAL. — Four well preserved specimens: No. CNU-ODO-SS2011007 (print of thorax with nearly complete left wings and overlapped right wings), No. CNU-ODO-SS2011008 (print of a nearly complete right forewing plus two hindwings with apices missing), No. CNU-ODO-SS2011009 (print and counterprint, thorax with attached partly overlapped right wings and left wing bases), and No. CNU-ODO-SS2011010 (print of a complete hindwing). All specimens deposited at the College of Life Science, Capital Normal University, Beijing, China.

AGE AND OUTCROP. — Shanwang Formation, Middle Miocene. Shanwang Village, Linqu County, Shandong Province, China.

EMENDED DIAGNOSIS. — Wings uniformly sandy beige coloured; anal membranule strongly reduced; forewing arculus angled, sectors of arculus arising near its lower end, result in a prolonged anterior part; anal loop relatively enlarged (generally divided into about twelve cells, but nine cells in No. CNU-ODO-SS2011009); male anal triangle three-celled; forewing primary antenodal bracket Ax1 and Ax2 are oblique (Ax1 more oblique than Ax2), while hindwing has its Ax1 and Ax2 nearly perpendicular.

REMARK

The type specimen of this species is based on a thorax with fragments of legs and abdomen plus four wings with median portions partly destroyed. Several characters were unknown for this species.

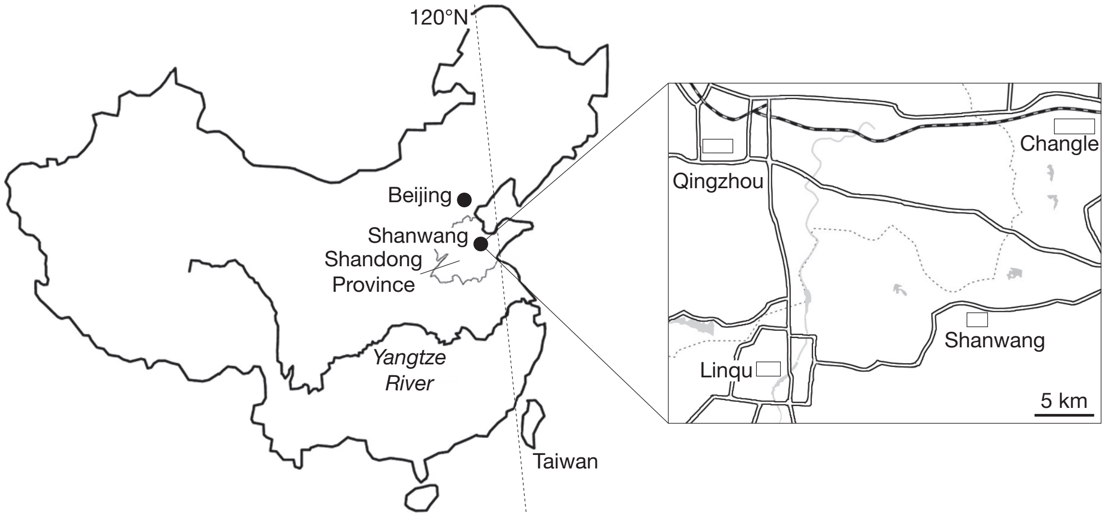

FIG. 1. — Location of the Shanwang Formation, modified from Sun *et al*. (2002). Dotted lines represent the limits of counties and grey zones represent the outcrops.

The original description and figure of Zhang (1989: 32-33, fig. 14) are relatively poor. Thanks to the present discovery, we can complete the diagnosis and description.

REDESCRIPTION

Wings uniformly sandy beige coloured; pterostigma dark brown.

Forewing (mainly based on specimen No. CNU-ODO-SS2011008, left forewing). Wing 55.5 mm long, 12.4 mm wide at level of nodus; distance from wing base to Ax1 3.7 mm, to Ax2 9.7 mm, to arculus 5.8 mm, to nodus 27.3 mm; distance from nodus to base of pterostigma 17.0 mm, to level of bifurcation of IR2 12.4 mm; pterostigma 5.5 mm long and 0.8 mm wide, covering five cells; pterostigma brace oblique, well aligned with basal side of pterostigma; Ax1and Ax2 oblique (Ax1 more oblique), with six secondary antenodal crossveins and four or five antesubnodal crossveins between them; 19 secondary antenodal crossveins not aligned with 18 antesubnodal crossveins distal of Ax2; 21 postnodal crossveins not aligned with 18 postsubnodal crossveins; arculus angled, sectors of arculus arising near its lower end, resulting in a prolonged anterior part; IR1 originating from RP1 nearly at level of basal fourth of pterostigma, with three to four rows of cells between it and RP1; RP1 and RP2 strictly parallel to level of pterostigma, with one row of cells in between; RP2 evenly curved toward posterior wing margin at level of pterostigma; anterior branch of IR2 more or less parallel with RP2 with only one row (rarely two rows) of cells between them, area between them distally constricted; IR2 symmetrically forked, 4.2 mm basal of level of basal side of pterostigma, five to seven rows of cells in area between forks of IR2; Rspl nearly straight, area between Rspl and posterior branch of IR2 with three rows of cells in its widest part, constricted and with only one row of cells distally; RP3/4 and MA parallel, with one row of cells in between, but two rows of cells distally; one oblique vein "O" slightly distal of base of RP2; Mspl slightly curved, area between Mspl and MA with three rows of cells in widest part, but distally constricted and with two rows of cells; MP smoothly curved; CuA with five posterior branches; area between MP and CuA with only one row of cells; median space free; submedian space crossed by six crossveins, including strong CuP; PsA not stronger than other crossveins in submedian space, so no well defined subdiscoidal triangle; hyper-

Fig. 2. — *Epiaeschna matutina* (Zhang, 1989), photograph of specimen CNU-ODO-SS2011007. Scale bar: 20 mm.

triangle very elongated, 9.0 mm long, seven-celled; discoidal triangle elongated, 6.7 mm long and 1.9 mm wide (basal side 2.3 mm and costal side 7.4 mm long), nine-celled; convex trigonal planate in postdiscoidal area basally straight during four cells and distally zigzagged; anal area with two to three rows of cells.

Hindwing (mainly based on specimen No. CNU-ODO-SS2011007 left hindwing). Wing 55.6 mm long, width at level of nodus 17.2 mm; distance from wing base to Ax1 4.1 mm, to Ax2 9.3 mm, to arculus 5.9 mm, to nodus 23.2 mm; distance from nodus to base of pterostigma 19.1 mm, to wing apex 32.4 mm, to level of fork of IR2 14.0 mm; ptero-

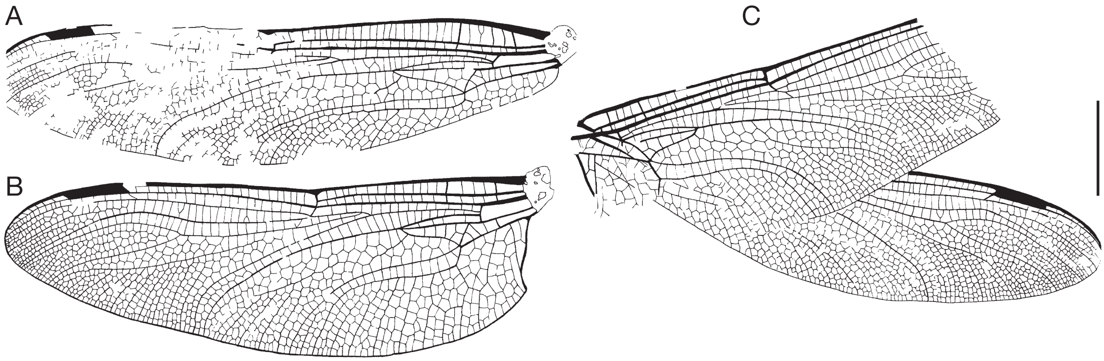

FIG. 3. — *Epiaeschna matutina* (Zhang, 1989), line drawing of specimen CNU-ODO-SS2011007: **A**, left forewing; **B**, left hindwing; **C**, right forewing and hindwing. Scale bar: 10 mm.

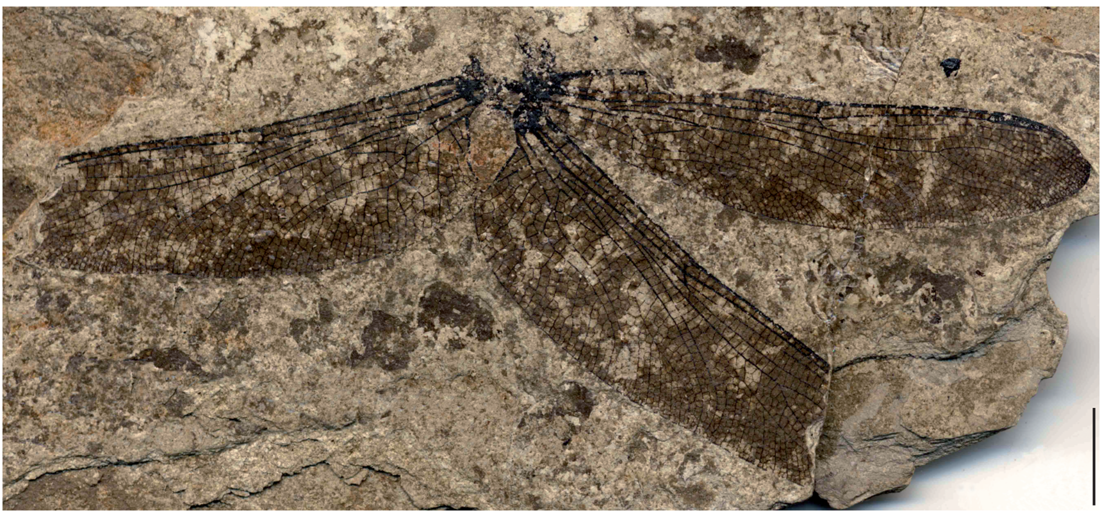

FIG. 4. — *Epiaeschna matutina* (Zhang, 1989), photograph of specimen CNU-ODO-SS2011008. Scale bar: 10 mm.

stigma 6.2 mm long and 0.8 mm wide, covering five cells; pterostigma brace oblique, well aligned with basal side of pterostigma; Ax1 and Ax2 straight and nearly perpendicular to ScP, with three secondary antenodal and antesubnodal crossveins between them; 14 secondary antenodal crossveins not aligned with 13 antesubnodal crossveins distal of Ax2; 22 postnodal crossveins not aligned with 18 postsubnodal crossveins; arculus angled, sectors of arculus arising near its middle; base of IR1 at level of basal side of pterostigma, with two to three rows of cells between it and RP1; RP1 and RP2 strictly parallel to level of pterostigma, with one row of cells in between; RP2 and anterior branch of IR2 parallel with only one row of cells between them, area between them distally constricted; RP2 smoothly bent toward posterior wing margin at level of basal side of pterostigma; IR2 is symmetrically forked, 5.1 mm basal of basal side of pterostigma, four rows of cells in area between forks of IR2; Rspl nearly straight, area between Rspl and posterior branch of IR2 with three rows of cells in widest part, but distally constricted and with only one row of cells; RP3/4 and MA parallel, with one row of cells in between,

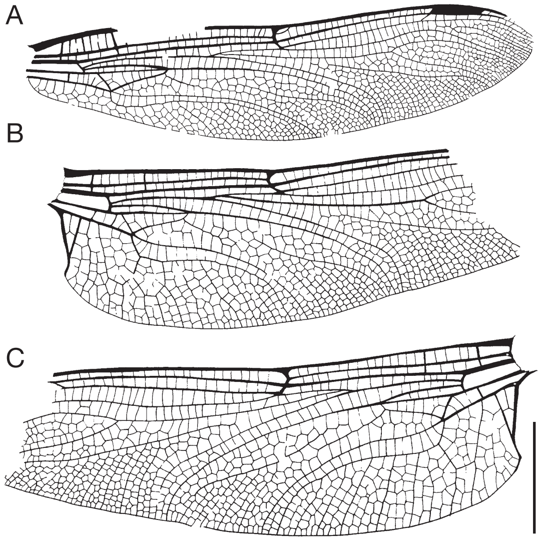

Fig. 5. — *Epiaeschna matutina* (Zhang, 1989), line drawing of specimen CNU-ODO-SS2011008: **A**, right forewing; **B**, right hindwing; **C**, left hindwing. Scale bar: 10 mm.

but two rows of cells distally; one oblique vein "O" slightly distal of base of RP2; Mspl slightly curved, area between Mspl and MA with three rows of cells in widest part, but distally constricted and with two rows of cells; MP shortened, ending on posterior wing margin at level of nodus; CuAa with five posterior branches; area between MP and CuAa with only one row of cells basally, but expanded with three or four rows of cells distally; median space free; submedian space crossed by four crossveins, including CuP; CuP-crossing strong; PsA not stronger than other crossveins in submedian space, so no well defined subdiscoidal triangle; hypertriangle elongated 8.3 mm long, but apparently shorter than in forewing, five-celled; discoidal triangle elongated, 6.6 mm long and 2.2 mm wide (basal side 2.5 mm and costal side 7.1 mm long), six-celled; convex trigonal planate in postdiscoidal area basally straight during three cells and distally zigzagged; anal loop large, pentagonal, transversely elongated, twelve-celled; gaff rather long and straight, 1.9 mm long; basal side of anal loop straight and long, about 5.5 mm long; anal triangle well defined, narrow and three-celled with its basal side slightly curved; membranule strongly reduced; anal angle well defined.

Comparison with other *Epiaeschna* species

Nel & Petrulevičius (2010) synonymized *Mediaeschna* Zhang, 1989 (type species *M. matutina* Zhang, 1989) with *Epiaeschna* Hagen, 1873. These new fossils are very similar to the holotype of *Epiaeschna matutina* (Zhang, 1989). They confirm the generic identity of *Mediaeschna* with *Epiaeschna*. Moreover, all come from the same locality. Significant differences are as follows: 1) our new fossils are smaller, i.e. wing length of about 55-59 mm vs 64 mm in holotype of *E. matutina*; 2) area between MP and CuA has only one row of cells up to level of nodus and is distally expanded in both pairs of wings vs basally two rows of cells and distally constricted in holotype of *E. matutina*. We provisionally consider that these differences are related to intraspecific variations and are not sufficient to support a species separation. But this causes a difficulty in the separation of *E. matutina* from some other species of *Epiaeschna*.

Epiaeschna stauropolitana Martynov, 1927 and *E. magnifica* (Martynov, 1929) have pterostigmata covering much more cells than in other *Epiaeschna* species, including *E. matutina*. Nel *et al.* (2010) proposed the following characters to distinguish *E. matutina* from the other species in *Epiaeschna*: "*Epiaeschna matutina* differs from *E. heros* in its pterostigma covering 6-7 cells, with a more oblique brace, discoidal triangle with 7-8 cells, instead of 4-6 in *E. heros*." The number of cells covered by the pterostigma no longer stands because the new specimens of *E. matutina* have only five cells covered by pterostigma. Nevertheless, the number of cells in discoidal triangle is still valid.

Nel & Petrulevičius (2010) added: "*E. matutina* apparently differs from *E. gossi* (Campion, 1916) in the less numerous postnodal cross-veins but a new description of the forewings of the two species would be necessary to precise the differences between them". The new material confirms that *E. gossi* has much more postnodal crossveins in forewing (31-33) than *E. matutina* (21). Another difference is Ax1 and Ax2 not distinctly oblique in forewing of *E. gossi*, unlike in *E. matutina* (see Jarzembowski 1996: pl. 2, fig. 1).

Lastly, Nel & Petrulevičius (2010) indicated that *E. pseudoheros* Nel & Petrulevičius, 2010 "differs from *E. matutina* in its pterostigma covering less number of cells (six in *E. matutina*), and hindwing discoidal cells divided into less cells". The first difference no

FIG. 6. — *Epiaeschna matutina* (Zhang, 1989), photograph of specimen CNU-ODO-SS2011009, part. Scale bar: 10 mm.

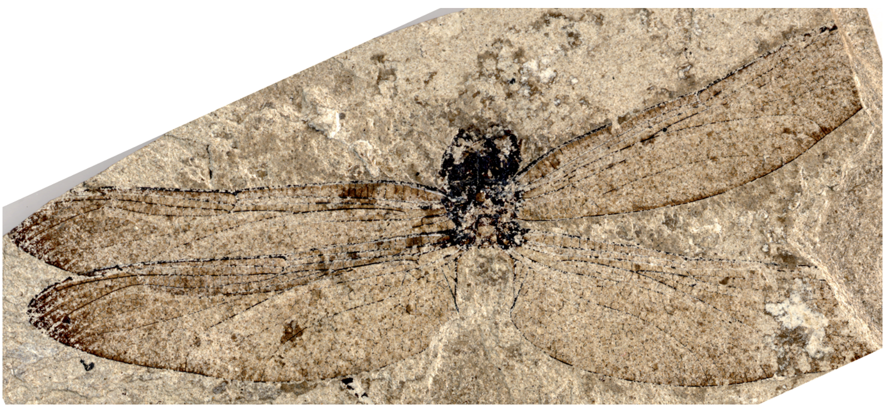

FIG. 7. — *Epiaeschna matutina* (Zhang, 1989), photograph of specimen CNU-ODO-SS2011009, counterpart. Scale bar: 20 mm.

longer stands, but the second one is confirmed by the present study. The trigonal planate is also longer in *E. matutina* than in *E. pseudoheros*.

One further aspect that could be important for the species diagnosis is the wings uniformly sandy beige coloured in *E. matutina* (present in both the holotype and our new fossils). This character remains only of partial use because the exact wing coloration is unknown for several other species of *Epiaeschna* (*E. pseudoheros* or *E. stauropolitana*). It seems to be rather dark in distal half but more hyaline in basal half of forewing of *E. gossi*.

Genus *Aeshna* Fabricius, 1775

TYPE SPECIES. — *Libellua grandis* Linnaeus, 1758 (recent).

Aeshna shanwangensis Li, Nel & Ren, n. sp.
(Figs 10; 11)

TYPE MATERIAL. — Holotype no. CNU-ODO-SS2011011 (one well preserved specimen, with both pairs of wings nearly complete combining with partly preserved thorax,

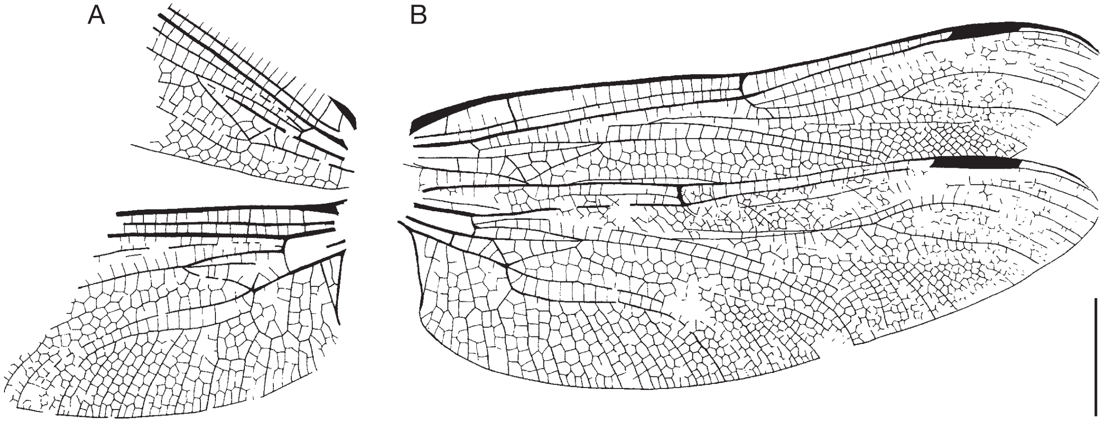

FIG. 8. — *Epiaeschna matutina* (Zhang, 1989), line drawing of specimen CNU-ODO-SS2011009: **A**, parts of left fore- and hindwing; **B**, right fore- and hindwing. Scale bar: 10 mm.

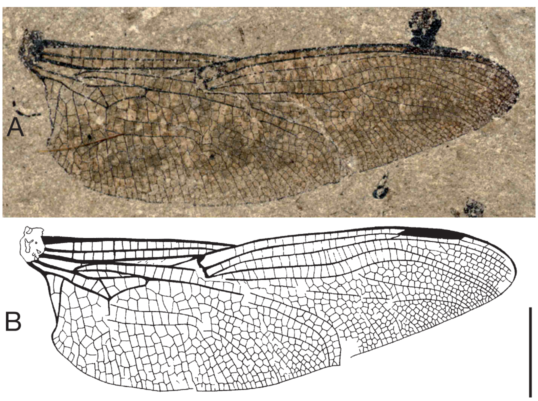

FIG. 9. — *Epiaeschna matutina* (Zhang, 1989): **A**, photograph; and **B**, line drawing of specimen CNU-ODO-SS2011010. Scale bar: 10 mm.

veins and pterostigma dark brown, wings hyaline), deposited at the College of Life Science, Capital Normal University, Beijing, China.

AGE AND OUTCROP. — Shanwang Formation, Middle Miocene. Shanwang Village, Linqu County, Shandong Province, China.

DIAGNOSIS. — Wing characters only. Anal triangle three-celled and with basal side curved; transversely elongated anal loop with 12 or more cells; fork of IR2 well basal of pterostigma, with four rows of cells between its two branches in widest part; Rspl and Mspl with strong concave bend, with four to five rows of cells in areas between Rspl and IR2 as well as Mspl and MA at widest parts; space between MP and CuA at basal third in hindwing twice as wide as at distal third; hindwing membranule as long as one-third to half of anal wing margin.

ETYMOLOGY. — Named after Shanwang Village where the fossil was discovered.

DESCRIPTION

Forewing 47.8 mm long, width at level of nodus 11.9 mm; distance from wing base to Ax1 3.8 mm, to Ax2 8.8 mm, to arculus 6.1 mm, to nodus 20.7 mm; distance from nodus to base of pterostigma 13.1 mm, to level of fork of IR2 15.3 mm; pterostigma 4.1 mm long and 0.6 mm wide, covering four cells; pterostigma brace oblique, well aligned with basal side of pterostigma; Ax1 very oblique, with five antenodal crossveins between it and Ax2; Ax2 straight; fourteen postnodal crossveins not aligned with sixteen postsubnodal crossveins; arculus angled, sectors of arculus arising near its middle; IR1 short, originating from level of mid pterostigma, with three rows of cells between it and RP1; RP1 and RP2 strictly parallel to level of mid pterostigma, with one row of cells in between; RP2 evenly curved toward posterior wing margin at level of distal half of pterostigma; two rows of cells between RP1 and RP2 beneath pterostigma; RP2 and anterior branch of IR2 more or less parallel with only one row of cells between them, then distally constricted; IR2 symmetrically forked 2.3 mm basal of basal side of pterostigma, four rows of cells in area between forks of IR2; Rspl strongly curved, area between Rspl and posterior branch of IR2 with four to five rows of cells in widest part, but distally constricted and with only one row of cells; RP3/4 and MA more or less parallel, with one row of cells in between basally, but two rows of cells after "aeshnid bulla"; MA with a concave bend at level of "aeshnid bulla" (i.e. a characteristic oblique brace between RP3/4 and MA) very pronounced; one oblique vein "O" slightly distal of base of RP2; Mspl strongly curved and a concave bend at distal portion, area between Mspl and MA with four rows of cells in widest part, but distally constricted and with only one row of cells; MP shortened, ending on posterior wing margin nearly at level of nodus; CuA with five weak branches; basal part of area between MP and CuA with only one row of cells; median space free; submedian space crossed by six crossveins, including CuP; PsA not stronger than other crossveins in submedian space, no well defined subdiscoidal triangle; hypertriangle elongated, 7.3 mm long, five-celled; discoidal triangle elongated, 5.0 mm long and 2.2 mm wide (basal side 2.5 mm and costal side 5.8 mm long), six-celled in left forewing but five-celled in right forewing; trigonal planate present but not very distinct; anal area with two rows of cells, with first row of cells larger than second row.

Hindwing 47.2 mm long, width at level of nodus 14.8 mm; distance from wing base to Ax1 4.1 mm, to Ax2 9.2 mm, to arculus 5.5 mm, to nodus 18.3 mm; distance from nodus to base of pterostigma 18.0 mm, to wing apex 28.3 mm, to level of fork of IR2 14.6 mm; pterostigma 4.4 mm long and 0.7 mm wide, covering three cells; pterostigma brace oblique, well aligned with basal side of pterostigma; Ax1 and Ax2 not oblique, with five or four antenodal crossveins between them; eight secondary antenodal crossveins not aligned with seven antesubnodal crossveins, distal of Ax2; 15 postnodal crossveins not aligned with 20 postsubnodal crossveins; arculus angled, sectors of arculus arising near its middle; IR1 short, originating below basal half of pterostigma, with two-three rows of cells between it and RP1; RP1 and RP2 strictly parallel to level of mid pterostigma, with one row of cells in between; RP2 and anterior branch of IR2 more or less parallel with only one row of cells between them, then distally constricted; RP2 bend toward posterior wing margin at level of distal half of pterostigma; two rows of cell between RP1 and RP2 beneath pterostigma; IR2 symmetrically forked, 2.7 mm basal of basal side of pterostigma, four rows of cells in area between forks of IR2; Rspl strongly curved, area between Rspl and posterior branch of IR2 with four-five rows of cells in its widest part, but distally constricted and with only one row of cells; RP3/4 and MA more or less parallel, with one row of cells in between basally, but two rows of cells after "aeshnid bulla" and three rows of cells in widest part; one oblique vein "O" slightly distal of base of RP2; Mspl strongly curved, area between Mspl and MA with four-five rows of cells in widest part, but distally constricted and with two rows of cells; MP shortened, ending on posterior wing margin at level of nodus; CuA with five weak branches; area between MP and CuA with two rows of cells in basal half, and basal part twice as wide as distal part; MP and CuA converging towards wing margin; median space free; submedian space crossed by five crossveins, including CuP; CuP-crossing strong, aligned with AA2b; PsA not stronger than other crossveins in submedian space, no well defined subdiscoidal triangle; hypertriangle elongated (5.8 mm long) but apparently shorter than in forewing, five-celled; discoidal triangle elongated, 4.0 mm long and 2.3 mm wide (basal side 2.5 mm and costal side 4.3 mm long), but apparently shorter than in forewing, five-celled; trigonal planate short, immediately bend toward MP; anal loop pentagonal, transversely elongated, 12-celled in right hindwing and 13-celled in left hindwing; gaff prolonged and straight, 2.9 mm long; basal side of anal loop straight and long, about 5.7 mm long; anal triangle well defined (male specimen), very narrow, three-celled and with basal side curved; membranule well defined but short, about as long as 1/2-1/3 of anal wing margin.

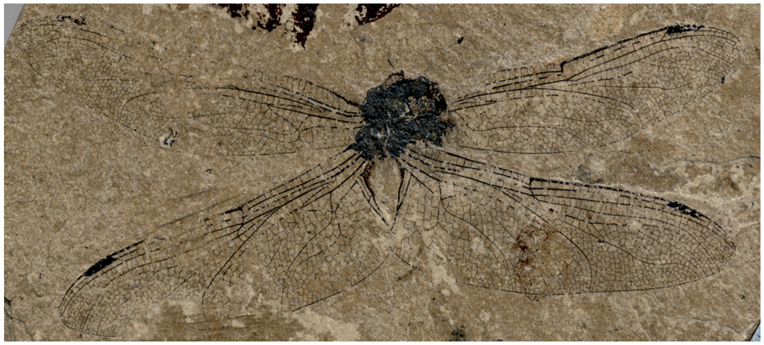

FIG. 10. — *Aeshna shanwangensis* n. sp., photograph of specimen CNU-ODO-SS2011011. Scale bar: 10 mm.

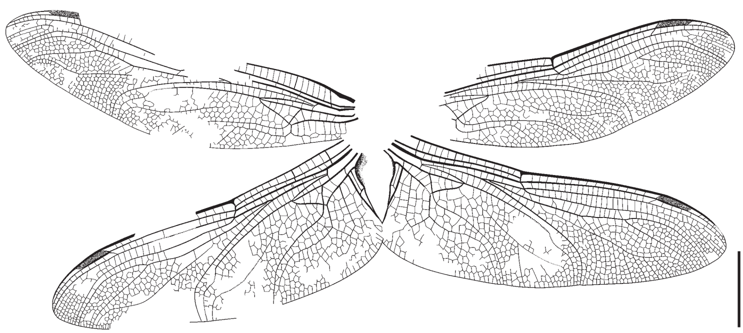

FIG. 11. — *Aeshna shanwangensis* n. sp., line drawing of specimen CNU-ODO-SS2011011. Scale bar: 10 mm.

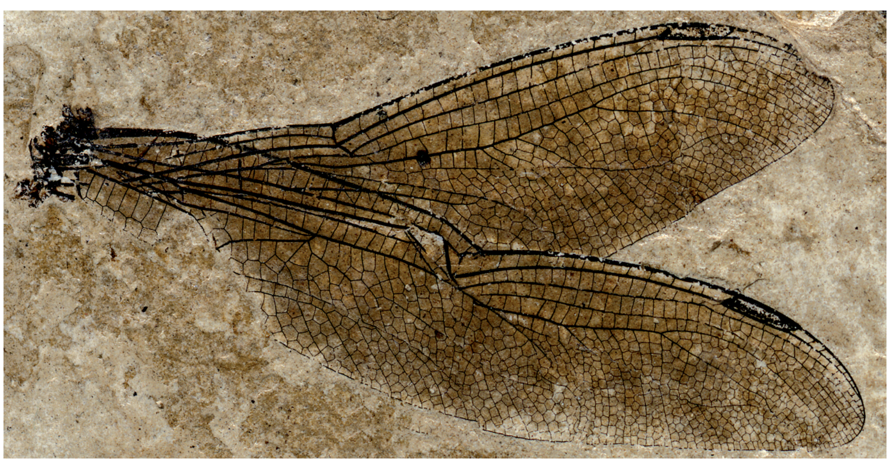

FIG. 12. — *Aeshna forficatum* n. sp., photograph of specimen CNU-ODO-SS2011012. Scale bar: 10 mm.

Aeshna forficatum Li, Nel & Ren, n. sp. (Figs 12; 13)

Type material. — Holotype No. CNU-ODO-SS2011012 (a pleated forewing and a partly preserved hindwing partly overlapped, both coloured with sandy beige, pterostigma black or puce, venation black), deposited at the College of Life Science, Capital Normal University, Beijing, China.

Age and outcrop. — Shanwang Formation, Middle Miocene, Shanwang Village, Linqu County, Shandong Province, China.

Diagnosis. — Wing characters only. Wings uniformly sandy beige coloured; slightly curved pterostigmal brace very oblique and long; Ax1 and Ax2 both oblique in forewing; arculus angled, sectors of arculus arising from its upper end; fork of IR2 well basal of pterostigma, with four rows of cells between its two branches; discoidal triangle rather elongated, with costal side about 2.8 times as long as basal side; Rspl and Mspl with strong concave bend, with four to five rows of cells in areas between Rspl and IR2 as well as Mspl and MA in widest parts.

Etymology. — Name after the Latin word "*forficatus*" to reflect the shape of the partly overlapped wings.

Description

Forewing 55.5 mm long, width unknown; distance from wing base to Ax1 4.2 mm, to Ax2 10.8 mm, to arculus 6.7 mm, to nodus 26.7 mm; distance from nodus to base of pterostigma 22.6 mm, to level of fork of IR2 17.0 mm; pterostigma 4.3 mm long and 0.7 mm wide, covering four cells; pterostigma brace very oblique and long, slightly curved, well aligned with the basal of pterostigma; Ax1 and Ax2 oblique, with five antenodal crossveins between them; 17 secondary preserved antenodal crossveins not aligned with antesubnodal crossveins, distal of Ax2; 15 postnodal crossveins not aligned with 17 postsubnodal crossveins; arculus angled, sectors of arculus arising from its upper end; IR1 short, originating from level of distal half of pterostigma; RP1 and RP2 strictly parallel to level of mid pterostigma, with one row of cells in between; RP2 smoothly bend toward posterior wing margin at level of mid pterostigma; two rows of cells between RP1 and RP2 beneath pterostigma; RP2 and anterior branch of IR2 more or less parallel with only one row of cells between them, then distally constricted; IR2 symmetrically forked, 5.0 mm basal of basal side of pterostigma, four rows of cells in area between forks of IR2; Rspl strongly curved, area between Rspl and posterior branch of IR2 with four-five rows of cells in its widest part, but distally constricted and with only one row of cells; RP3/4 and MA more or less parallel, with one row of cells in between basally, but two rows of cells after "aeshnid bulla", and three rows of cells at level of "aeshnid bulla"; at "aeshnid bulla" a well defined characteristic oblique brace between RP3/4 and MA; one oblique vein "O" slightly distal of base of RP2; Mspl strongly curved, area between Mspl and MA with four rows of cells in widest part, but distally constricted; strong secondary intercalary veins between Rspl and IR2 and between Mspl and MA; numerous secondary intercalary veins originating from Rspl and Mspl; basal area between MP and CuA with only one row of cells; median space free; submedian space crossed by several crossveins but number unknown; hypertriangle narrow and long, 9.0 mm long, five-celled; six-celled discoidal triangle rather elongated, about 7.3 mm long and 2.3 mm wide (basal side about 2.8 mm and costal side about 7.8 mm long); anal area with two rows of cells, with cells of first row distinctly larger than those of second row.

Hindwing preserved wing length 52.0 mm, 14.3 mm wide at the distal third; pattern of venation very similar to that of forewing in distal half of wing, except for the broader wing; unfortunately the cubito-anal area is not preserved so it is impossible to determine the structure of anal loop and anal triangle and to determine the sex of the specimen.

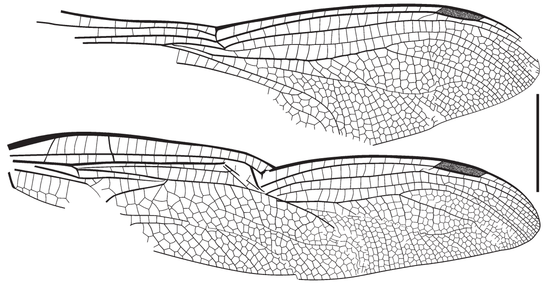

Fig. 13. — *Aeshna forficatum* n. sp., line drawing of specimen CNU-ODO-SS2011012: **A**, hindwing; **B**, forewing. Scale bar: 10 mm.

DISCUSSION

Specimen No. CNU-ODO-SS2011011 has all the autapomorphies of the family Aeshnidae as defined by Bechly (1996, 2007), i.e. 1) "aeshnid bulla" in distal part of MA in both pairs of wings; 2) enlarged anal loop; 3) subdiscoidal triangle of both wings crossed by one crossvein; 4) Rspl and Mspl distinctly curved with more than one row of cells between them and IR2 or MA, and area in between divided by oblique intercalary veins; 5) more than two rows of cells in basal part of postdiscoidal area between level of distal angle of discoidal triangle and level of midfork; and 6) hypertriangle traversed by at least three crossveins in forewings and more than three in hindwings.

Specimen No. CNU-ODO-SS2011012 has also the characters 1, 3, 4, 5 and 6, supporting an attribution to Aeshnidae.

After the study of Ellenreider (2002), specimen No. CNU-ODO-SS2011011 fits into the clade "Aeshnini" for the following synapomorphies: more than one cubito-anal crossvein; IR2 fork present; RP2 evenly curved; MA and RP3/4 not parallel, MA with a concave bend before wing margin; Mspl with a concave bend at distal portion; Rspl not parallel to IR2, with a concave bend; space between MP and CuA at basal third in hindwing twice as wide as at distal third, MP and CuA converging towards wing margin; hindwing membranule length as long as one-third to half of anal wing margin. Its attribution to a precise genus in this clade is much more delicate to establish because missing body characters are used as synapomorphies of different subgroups. The RP2 without marked convex bend at proximal end of pterostigma, male anal angle of hindwing angulated, fusion of AA & AP with AA2b parallel before anal angle are plesiomorphic character states that would exclude affinities with the group (*Anaciaeschna* Selys, 1878 – *A. isosceles* – *Andaeschna* De Marmels, 1994 – *Anax* Leach, 1815 – *Hemianax* Selys, 1883), plus the fossil genus *Merlax* Prokop & Nel, 2000, although we do not have apomorphies to support an attribution to one of the other genera of Aeshnini, i.e. *Castoraeschna* Calvert, 1952, *Coryphaeschna* Williamson, 1903, *Remartinia* Navás, 1911, *Oreaeschna* Lieftinck, 1937, and *Aeshna* Fabricius, 1775.

Nevertheless, specimen No. CNU-ODO-SS2011011 differs from *Castoraeschna, Oreaeschna, Coryphaeschna*, and *Remartinia* in the broad area between the branches of IR2, forking of IR2 well basal of pterostigma, plus the shape of anal triangle with a subdivision into three cells by a long transverse vein, absent in the two latter genera (Lieftinck 1937; Carvalho 1992). Therefore, an attribution to the genus *Aeshna* is the most probable and coherent with the available characters.

Specimen No. CNU-ODO-SS2011012 has also several apomorphies of the clade "Aeshnini", even if some listed above are not known for this fossil (those of the hindwing cubito-anal area). The remaining characters are: IR2 fork present; RP2 evenly curved; MA and RP3/4 not parallel, MA with a concave bend before wing margin; Mspl with a concave bend at distal portion; Rspl not parallel to IR2, with a concave bend. The same difficulties as for specimen No. CNU-ODO-SS2011011 are encountered for a more precise generic attribution. Nevertheless, RP2 without marked convex bend at proximal end of pterostigma is a plesiomorphic state that would exclude affinities with the group (*Anaciaeschna* – *A. isosceles* – *Andaeshna* – *Anax* – *Hemianax*). Also, the broad area between the branches of IR2, and forking of IR2 well basal of pterostigma support an attribution to *Aeshna* to the exclusion of the genera *Castoraeschna*, *Oreaeschna*, *Coryphaeschna*, and *Remartinia*.

These two new fossils differ in the following characters: *Aeshna forficatum* n. sp. has coloured wings, while these are hyaline in *A. shanwangensis* n. sp.; *A. forficatum* n. sp. has much larger wings (55.5 mm long instead of 47.8 mm in *A. shanwangensis* n. sp.); *A. forficatum* n. sp. has its hypertriangle and discoidal triangle further prolonged; *A. forficatum* n. sp. has three rows of cells between MA and PR3/4 at level of the "aeshnid bulla"; the pterostigma brace of *A. forficatum* n. sp. is longer and more oblique than that of *A. shanwangensis* n. sp. Therefore, they certainly belong to different *Aeshna* species.

It is nearly impossible to compare these fossils to the recent species within the genus *Aeshna*, for the lack of information on body structures. Nevertheless, we compare them to the known fossil species.

Zhang (1989: 34-36, pl. 4, fig. 4, text-fig. 18) described *Aeshna ignivora* from the same outcrop on the basis of a thorax with head, legs, and basal halves of the four wings attached. It differs from the two new fossils in a distinctly narrower postdiscoidal area in forewing, with two rows of cells between MA and MP just distal of discoidal triangle, instead of four in our fossils. Several important characters important for an accurate generic attribution are not preserved in the holotype of *A. ignivora* (shape of fork of IR2, bend of RP2, Rspl, etc.); so its attribution to the genus *Aeshna* is uncertain.

The Miocene *Aeshna stavropolensis* Nel *et al.*, 2005 has hindwing much larger (62 to 63 mm long) than these two fossils (Nel *et al.* 2005). The Oligocene *A. oligocenica* Nel, Martínez-Delclòs, Escuillié & Brisac, 1994 has the fork of IR2 opposite basal side of pterostigma, instead of being much more basal as in our fossils (Nel *et al.* 1994). The Miocene *A. vosendorfensis* Papp & Mandl, 1951 has a forewing 55 mm long but with a pterostigma covering only three cells and three rows of cells between Mspl and MA (Papp & Mandl 1951; Bachmayer 1960; Nel *et al.* 1994). The three Miocene species *A. messiniana* Gentilini & Peters, 1993, *A. ghiandonii* Gentilini & Peters, 1993, and *A. multicellulata* Gentilini & Peters, 1993 differ from our fossils in the fork of IR2 just basal or opposite basal side of pterostigma (Gentilini & Peters 1993). The Early Oligocene *A. solida* Scudder, 1890 and the Miocene *A. turoliana* Riou & Nel, 1995 have also this fork just basal of pterostigma plus three rows of cells between MA and Mspl (Scudder 1890; Riou & Nel 1995). The Miocene *A. cerdanica* Nel *et al.*, 1994 and *A. andancensis* Nel *et al.*, 1994 have wings distinctly smaller than our two fossils (*c.*40 mm long). The Oligocene *A. ollivieri* Nel, 1986 has a rudimentary fork of IR2 (Nel 1986). The other Oligocene *A. paleocyanea* Nel, 1987 is a poorly known taxon, maybe even not related to *Aeshna* (Nel 1987; Nel *et al.* 1994). Other fossils that were attributed to the genus *Aeshna* are too poorly preserved to be compared to these fossils (Nel *et al.* 1994).

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REFERENCES

Bachmayer F. 1960. — Insektenreste aus den Congerienschichten (Pannon) von Brunn-Vösendorf (Südl. von Wien), Niederösterreich. *Sitzungberichte der Oesterreiche Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* (1) 169: 11-16.

Bechly G. 1996. — Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, Böblingen, Special Volume 2, 402 p.

Bechly G. 2007. — *Phylogenetic Systematics of Euanisoptera/Aeshnoptera*. Download: http://www.bernstein.naturkundemuseum-bw.de/odonata/anisopt1.htm#aeshnidae

Bechly G., Nel A., Martínez-Delclòs X., Jarzembowski E. A., Coram R., Martill D., Fleck G., Escuillié F., Wisshak M. M. & Maisch M. 2001. — A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). *Neue Paläontologische Abhandlungen* 4: 219 p.

Carvalho A. L. 1992. — Revalidation of the genus *Remartinia* Navas, 1911, with the description of a new species and a key to the genera of Neotropical Aeshnidae (Anisoptera). *Odonatologica* 21: 289-298.

Ellenrieder N. von 2002. — A phylogenetic analysis of the extant Aeshnidae (Odonata: Anisoptera). *Systematic Entomology* 27: 437-467.

Garrison R. W., Ellenrieder N. von & Louton J. A. 2006. — *Dragonfly of the New World: an Illustrated and Annotated Key to the Anisoptera*. The John Hopkins University Press, Baltimore, 368 p.

Gentilini G. & Peters G. 1993. — The Upper Miocene aeshnids of Monte Castellaro, Central Italy, and their relationships to extant species (Odonata: Aeshnidae). *Odonatologica* 22: 147-178.

Jarzembowski E. A. 1996. — Fossil insects from the Bournemouth Group (Eocene: Late Ypresian, Lutetian). *Tertiary Research* 16: 203-211.

LIEFTINCK M. A. 1937. — The dragonflies (Odonata) of New Guinea and neighbouring islands. *Nova Guinea* (N.S.) 1: 1-82.

LI Y.-M., FERGUSON D. K., WANG Y.-F. & LI C.-S. 2010. — Paleoenvironmental inferences from diatom assemblages of the middle Miocene Shanwang Formation, Shandong, China. *Journal of Paleolimnology* 43: 799-814.

LI Y.-M., NEL A., REN D. & PANG H. 2011. — A new genus and species of hawker dragonfly of uncertain affinities from the Middle Jurassic of China (Odonata: Aeshnoptera). *Zootaxa* 2927: 57-62.

MARTÍNEZ-DELCLÒS X. & NEL A. 1991. — Découverte de trois insectes fossiles dans l'Oligocène du bassin de l'Ebre (Espagne) (Odonata, Lestidae, Aeshnidae). *Bulletin du Muséum national d'Histoire naturelle* 4e série, section C, 13: 157-165.

NEL A. 1986. — Sur la présence du genre *Aeschna* Fabricius, 1775 dans les calcaires stampiens de Céreste (Odonata, Aeshnidae). *L'Entomologiste* 42: 195-198.

NEL A. 1987. — Sur une espèce nouvelle d'Aeschnidae du Stampien supérieur du Bois d'Asson (Manosque, Alpes-de-Haute-Provence). *L'Entomologiste* 43: 321-323.

NEL A., MARTÍNEZ-DELCLÒS X., PAICHELER J. C. & HENROTAY M. 1993. — Les « Anisozygoptera » fossiles. Phylogénie et classification (Odonata). *Martinia*, Numéro Hors-Série 3: 1-311.

NEL A., MARTÍNEZ-DELCLÒS X., ESCUILLIÉ F. & BRISAC P. 1994. — Les Aeshnidae fossiles : état actuel des connaissances (Odonata, Anisoptera). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 194: 143-186.

NEL A., PETRULEVIČIUS J. F. & JARZEMBOWSKI E. A. 2005. — New fossil Odonata from the European Cenozoic (Insecta: Odonata: Thaumatoneuridae, Aeshnidae, ?Idionychidae, Libellulidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 235: 343-380.

NEL A. & PETRULEVIČIUS J. F. 2010. — Afrotropical and Nearctic genera of Odonata in the French Oligocene: biogeographic and paleoclimatic implications (Insecta: Calopterygidae and Aeshnidae). *Annales de la Société entomologique de France*, (n.s.) 46: 228-236.

PAPP A. & MANDL K. 1951. Insekten aus den Congerienschichten des Wiener Beckens. *Sitzungberichte der Oesterreichische Akademie Wissenschaftchen, Mathematisch-Naturwissenschaftliche Klasse* (1) 160: 295-302.

PROKOP J. & NEL A. 2000. — *Merlax bohemicus* gen. n., sp. n., a new fossil dragonfly from the Lower Miocene of northern Bohemia (Odonata: Aeshnidae). *European Journal of Entomology* 97: 427-431.

PROKOP J. & NEL A. 2002. — New Tertiary dragonflies from Lower Oligocene of the České středohoři Mts and Lower Miocene of the Most Basin in the Czech Republic (Odonata: Anisoptera). *Acta Societatis Zoologicae Bohemicae* 66: 141-150.

RIOU B. & NEL A. 1995. — Nouveaux Odonates fossiles du Miocène supérieur de l'Ardèche. (Odonata: Sieblosiidae, Lestidae, Libellulidae, Corduliidae, Aeshnidae). *Travaux de l'École Pratique des Hautes Études, Biologie et Évolution des Insectes* Paris 7/8: 125-144.

SCUDDER S. H. 1890. — The fossil insects of North America (with notes on some European species). 2. The Tertiary insects. *Report of the United States Geological Survey of the Territories* 13: 1-734.

SUN Q.-G., COLLINSON M. E., LI C.-S., WANG Y.-F. & BEERLING D. J. 2002. — Quantitative reconstruction of palaeoclimate from the Middle Miocene Shanwang flora, eastern China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 180: 315-329.

TIMON-DAVID J. 1946. — Insectes fossiles de l'Oligocène inférieur des Camoins. 3. Description d'une nouvelle espèce d'Odonate. *Bulletin de la Société entomologique de France* 51: 94-96.

YANG H. & YANG S. 1994. — The Shanwang fossil biota in Eastern China: a Miocene konservat-lagerstatte, in lacustrine deposits. *Lethaia* 27: 345-354.

ZHANG J.-F. 1989. — [*Fossil Insects from Shanwang, Shandong, China.*] Shandong Science and Technology Publishing House, Jinan, 459 p. (in Chinese with abstract in English).

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