The largest known odonate in China: *Hsiufua chaoi* Zhang et Wang, gen. et sp. nov. from the Middle Jurassic of Inner Mongolia

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A new genus and species, *Hsiufua chaoi* Zhang et Wang, is established based on a forewing from the Middle Jurassic Haifanggou Formation in Inner Mongolia, China and attributed to Campteropteroidea, Isophlebioidea, Odonata. It is the largest odonate known in China and the fourth in the world in terms of forewing length. The maximum size (based on forewing length) of Odonata is smaller in the Permian than in the Mesozoic which is probably due to competition for prey between Odonata and Protodonata in the Permian. The reason that the maximum size of Jurassic odonates is larger than that of their extant relatives is most probably less competition and lower predation pressure from contemporary aerial vertebrates.

***Hsiufua chaoi* Zhang et Wang, new genus and species, largest odonate, Middle Jurassic, China**

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Insects constitute the largest and most diverse group of organisms and over one million species have been described in the Class Insecta. They are the only invertebrates that can fly and the earliest animals to rule the air. They occurred much earlier and have a longer geological record than flying vertebrates. Winged insects had appeared at least by the end of the Early Carboniferous (320–300 Ma) [1], and probably as early as in the Early Devonian (about 400 Ma) [2]. Among vertebrates, pterosaurs are the earliest fliers and are known from the Middle Triassic (mid-Norian, about 210 Ma) [3]; birds appeared in the Late Jurassic (about 150 Ma) [4] or later [5], and bats first occur in the Early Eocene (52.5 Ma) [6].

Most extant insects have a body length of 5–15 mm and a wingspan of 15–45 mm. In general, only a minority of insects are comparatively large. The stick insect *Phobaeticus chani* Bragg from Borneo is the world's longest extant insect with a maximum body length of 357 mm [7]; the owl

moth *Thysania agrippina* (Cramer) from Central and South America is the world's broadest extant insect with a wingspan of up to 360 mm [8]. The Atlas Moth, *Attacus atlas* (Linnaeus), is the largest extant insect in China with a wingspan of up to 240 mm [9].

The superorder Odonatoptera includes the orders Geroptera, Protodonata and Odonata [10]. The Geroptera lived in the early Late Carboniferous (Namurian), the Protodonata in the Late Carboniferous–Permian, and the Odonata from the Permian to the present [10] now comprising three suborders: Anisoptera (dragonflies), Zygoptera (damselflies) and Anisozygoptera (damsel-dragonflies). The so-called Palaeozoic “giant dragonflies” are not true dragonflies but members of the Protodonata: Meganeuridae. The Early Permian meganeurid *Meganeuropsis permiana* Carpenter from the USA has a wingspan of up to 710 mm and is by far the largest known insect in the world [10]; the late Carboniferous meganeurid *Shenzhousia qilianshanensis* Zhang et al. [11] is the largest insect found in China with a wingspan of 400–500 mm.

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1 Material and methods

The specimen NIGP156221, part and counterpart, is a damsel-dragonfly forewing collected from the Middle Jurassic Haifanggou Formation of Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China. The part is a nearly complete forewing with the middle fractured and damaged, the apical 1/3rd damaged near the posterior margin and the wing apex missing. The counterpart is incomplete with only the wing apex preserved. The photograph of the whole specimen was taken using a Canon 5D camera. The specimen was examined dry and under alcohol, using a Nikon SMZ1000 stereomicroscope and drawings were made with the aid of a camera lucida. The photographs were prepared using a digital camera (DXM1200) connected to the above stereomicroscope, and the line drawings were finalised using photographs and image-editing software (CorelDRAW 9.0 and Adobe Photoshop CS). The specimen is housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of Riek [12] and Riek and Kukalová-Peck [13], as amended by Nel et al. [14] and Bechly [15]. We use the following standard abbreviations: AA, anal anterior; AP, anal posterior; Arc, arcus; Ax0 Ax1 Ax2, primary antenodal cross-veins; CuAa, distal branch of cubitus anterior; CuAb, proximal branch of cubitus anterior; IR1, IR2, intercalary radial veins; MAa, distal branch of median anterior; MAb, posterior branch of median anterior; MP, median posterior; N, nodus; "O", oblique vein; Pt, pterostigma; RA, radius anterior; RP, radius posterior; Su.C, subdiscoidal cell; D.C., discoidal cell. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly [15].

2 Systematic palaeontology

Superorder Odonatoptera Martynov, 1932

Order Odonata Fabricius, 1793

Superfamily Isophlebioidea Handlirsch, 1906

Family Campteroptophlebiidae Handlirsch, 1920

Genus *Hsiufua* Zhang et Wang, gen. nov.

Type species: *Hsiufua chaoi* Zhang et Wang, gen. et sp. nov.

Etymology: The generic name is dedicated to the late and famous Chinese entomologist, Professor Chao Hsiu-fu.

Diagnosis: Forewing characters only. Forewing extremely narrow and elongate. Gaff (basal part of CuA) straight and very long; proximal part of area between MP and CuA about three times as wide as that between MA and MP; Ax1 basal of arcus, far from wing base and nearly perpendicular to ScP; Ax2 subparallel to Ax1, and slightly closer to wing base than to nodus; a secondary longitudinal vein in anal area parallel to AA and posterior wing margin; a long single cell covering basal part of area between MP and CuA, just distal of gaff; area between IR2 and RP3/4 clearly broadened in its mid part and greatly constricted near wing margin; CuAa short; pterostigma narrow and elongate, brown, far from wing apex, with a long, central unpigmented area; no cells below pterostigma; IR2 not originating from RP3/4; oblique vein "O" very oblique and strong, only four cells distal of base of RP2.

***Hsiufua chaoi* Zhang et Wang, gen. et sp. nov.** (Figures 1 and 2)

Etymology: The specific name is dedicated to the late and famous Chinese entomologist, Professor Chao Hsiu-fu.

Material: A nearly complete forewing (holotype), part and counterpart, as noted above.

Locality and horizon: Daohugou village, Wuhua Township,

Figure 1 Photographs of forewing of *Hsiufua chaoi* Zhang et Wang, gen. et sp. nov. (a) Photograph of the whole specimen 156221a (dry); (b) photograph of specimen 156221b (under alcohol); (c) photograph of specimen 156221a, apical area (under alcohol); (d) photograph of specimen 156221a, pterostigmal area (under alcohol); (e) photograph of specimen 156221a, basal area (under alcohol).

Ningcheng County, Chifeng City, Inner Mongolia, China; Middle Jurassic Haifanggou Formation.

Description: Forewing hyaline, 107.6 mm long, 14.3 mm wide. Distance between wing base and arculus 13.8 mm, between arculus and nodus 37.1 mm; distance between pterostigmal base and nodus 28.9 mm, between pterostigmal apex and wing apex 20.7 mm; distance between Ax1 and wing base 12.9 mm, between Ax1 and Ax2 10.1 mm, between Ax2 and nodus 28.3 mm; Ax1 1.2 mm basal of arculus, and nearly perpendicular to ScP; Ax2 slightly oblique towards wing apex; pterostigma 6.7 mm long, about 1.1 mm wide, brown with central unpigmented area about half as long as pterostigma; neither pterostigmal brace nor cells below it present; veins C and RA not widened along pterostigma; median and submedian spaces free of cross-veins; discoidal space basally open; subdiscoidal cell free of cross-veins, narrow, elongate and nearly trapezoidal, 4.2 mm long, and 0.8 mm wide in mid part; a long single cell covering whole area between MP and CuA, just distal of gaff; AA distally strongly bent towards posterior wing margin at CuP, more or less parallel to CuA, then distally fused with a secondary longitudinal vein into a strong vein parallel to posterior wing margin and distally ending in CuA; anal area (not preserved basally) with 3 rows of cells basally and 2 rows of large cells distally; gaff 5.2 mm long; basal cell between MP and CuA 5.6 mm long, 0.8 mm wide; basal part of area between MP and CuA 2.7 times as broad as that between MA and MP; CuAa parallel to posterior wing margin, then progressively weakening and fused with posterior wing margin, 16.7 mm long, with one row of cells below CuA; CuAb very short and directed towards posterior wing margin; area between CuA and MP with 3 rows of large cells basally; area between MP and posterior wing margin with 6 rows of cells at same level as end of CuAa; MP nearly straight, ending in posterior wing margin far distal of

nodus, and 67.8 mm from wing base (at 63% of wing length); MA slightly arched and subparallel to MP; one row of cells in post-discoidal area, greatly constricted near wing margin; base of RP3/4 14.0 mm distal of arculus and 23.0 mm basal of nodus; vein CP bent towards ScP, not preserved near nodus; subnodus very oblique; PR2 aligned with subnodus; oblique vein "O" ill-preserved, 4 cells and 6.0 mm distal of base of RP2; RP2 slightly arched in mid part; area between RP2 and IR2 with one row of cells from their bases to level of pterostigma, distally widened with 10–12 rows of cells (as estimated) near posterior wing margin; IR1 subparallel to RP1, nearly straight basally; base of IR1 8.4 mm distal of base of RP2; area between MA and RP3/4 very narrow basally with only one row of cells, greatly widened distally but badly preserved near wing margin with 13 rows of cells observed (over 20 rows of cells estimated); IR2 without origin on RP3/4; area between RP3/4 and IR2 gradually widened towards its middle, but basally and distally constricted, with 2 rows of cells in mid part, and only one row basally and distally; area between IR1 and RP2 progressively widened distally, with 2 secondary longitudinal veins, and 6 rows of cells distally (but not preserved near wing margin); area between IR1 and RP1 slightly widened distally (not preserved near wing margin), with a weak secondary longitudinal vein, and 7 rows of cells observed distally.

Comparison and remarks: The genus undoubtedly belongs to Campteroptlebiidae based on the following characteristics in the forewing: the discoidal cell is basally open, vein MAb is not far from the arculus, and no secondary antenodal cross-veins are present between C and ScP [16,17]. The Campteroptlebiidae is the largest damselfly family living in Eurasia in the Late Triassic–Cretaceous and includes 49 species in 30 genera [17–19]. So far, 11 species in 7 genera have been discovered in the Middle Haifanggou

Figure 2 Line drawing (a) and reconstruction (b) of forewing of *Hsiufua chaoi* Zhang et Wang, gen. et sp. nov.

Formation of Daohugou in Inner Mongolia [18,20–25] and they are: *Amnifleckia guttata* Zhang, Ren and Cheng, 2006, *Amnifleckia splendida* Huang et al., 2006, *Bellabrunetia catherinae* Fleck et Nel, 2002, *Ctenogampsophlebia reni* Petrulavicius, Huang et Nel, 2011, *Parabrunetia celinea* Huang et al., 2006, *Qibinlina sinica* Huang et Nel 2009, *Sinokaratawia daohugouica* Zhang, Ren et Pang, 2008, *Sinokaratawia gloriosa* Zhang, Ren et Pang, 2008, *Sinokaratawia magica* Zhang, Ren et Pang, 2008, *Sinokaratawia prokopi* Nel, Huang et Lin, 2007, and *Zygokaratawia reni* Nel, Huang et Lin, 2008. These insects are well preserved due to the special taphonomic conditions there [26].

The new genus has a very narrow and elongate forewing which is at least 20% longer than that of other campterothlebiid genera and possesses a much higher length/width ratio (up to 7.5 in the new genus and less than 6.3 in the other genera). The unpigmented area in the pterostigma is sharply and evenly separated from the brown pterostigma (Figure 1(d)), indicating that the centrally unpigmented area is a diagnostic character of the new genus and its presence is not the result of poor preservation of the pterostigma. The above features easily differentiate the new genus from all other campterothlebiid genera. The forewing of the new genus is very similar to that of *Bellabrunetia* Fleck et Nel from the same locality and horizon (originally given as the Yixian Formation in Liaoning Province, China by mistake) but differs in that the former is much longer than the latter (the former is as wide as but 20% longer than the latter); has a nearly straight antenodal cross-vein Ax2 about midway between the wing base and nodus (the latter has a distinctly oblique Ax2 at a basal 1/3rd position between the wing base and nodus); has the basal part of the area between MP and CuA about 3 times as broad as that between MA and MP (the latter twice); and has 4 cells between oblique vein “O” and base of RP2 (the latter has only 2).

3 Discussion

The order Odonata includes about 5900 extant species [27], and their body length varies from 30 mm to 90 mm. The extant largest odonate is the damselfly *Megaloprepus caerulatus* (Drury) living in Central and South America with a wingspan of up to 190 mm [28]. In the evolutionary history of the Odonata, however, some species had a distinctly much larger size: the Middle Triassic *Triadotypus guillaumei* Grauvogel et Laurentiaux from France is the largest known with a forewing of 136 mm in length [29] and a wingspan of 280 mm (as estimated); the Middle Jurassic *Hemerobioides giganteus* Westwood from UK has a forewing of 120 mm in length (estimated) [30]; the Late Jurassic *Isophlebia aspasia* Hagen from Germany has a forewing of 110 mm in length [12] and a wingspan of 228 mm (estimated); and the Late Jurassic *Aeschnogomphus kuempeli* Bechly from Germany has a forewing of 106 mm in length and a wingspan of 220

mm [31]. *Hsiufua chaoi* Zhang et Wang described herein has a forewing of 107.6 mm in length and a wingspan of 225 mm (estimated), and is considered to be the world's fourth largest odonate and the largest one known from China.

Distinct changes in body size have occurred in the superorder Odonatoptera during its long evolutionary history. In the Late Carboniferous and Early Permian, some giant species appeared and are exemplified by the Late Carboniferous *Meganeura monyi* Brongniart with a wingspan of up to 650 mm [32] and the Early Permian *Meganeuropsis permiana* Carpenter with a wingspan of up to 710 mm [10]. After these periods, however, no odonatopterans with a wingspan greater than 300 mm are known from the fossil record [12,29–31]. The great change in insect size has been attributed to changes in the level of atmospheric oxygen: on this model, a great increase in the level of atmospheric oxygen in the Late Palaeozoic resulted in the appearance of giant insects and the subsequent decrease resulted in the loss of gigantism in insects [33,34]. It is estimated that atmospheric oxygen partial pressures in the late Palaeozoic were 27–35 kPa greater than the current one at 21 kPa [34–37] (Figure 3). Another hypothesis is that the lack of aerial vertebrate predators allowed these insects to evolve to their maximum size during the Carboniferous and Permian periods, and that the extinction and permanent disappearance of giant flying insects after the Permian is directly correlated with the predatory threat from the swifter and stronger aerial pterosaurs, birds and bats [38]. No comparatively large ground-dwelling insects are known from the late Palaeozoic fossils, perhaps because predators such as large amphibians, early reptiles, and large arachnids prohibited such a dramatic size increase [38]. Recent studies of some extant insects indicate that most insects develop smaller body sizes in hypoxia, whilst some develop and evolve larger sizes in hyperoxia [39,40]. Hence, it is reasonable to consider the hyperoxia in the late Palaeozoic atmosphere to be at least one important reason for the appearance of giant insects, and the subsequent appearance of their competitors and predators (pterosaurs, birds and bats) undoubtedly limited the maximum body size of insects. An analysis of changes in the wing length of the largest odonatopterans through their geological history demonstrates that the level of atmospheric oxygen is only one of the controlling factors limiting maximum body size of insects [41]. A recent study shows [42] that changes in wing length of the largest insects from the Middle Carboniferous to the Late Jurassic are consistent with changes in the level of atmospheric oxygen shown by the GEOCARBSULF model [37]. If the changes in atmospheric oxygen partial pressures in the Phanerozoic are correctly predicted by the GEOCARBSULF model (Figure 3), then the fact that the maximum size (forewing length) of Odonata is smaller in the Permian than in the Mesozoic [41] probably results from earlier competition for food resources between Odonata and Protodonata. On the other hand, atmospheric oxygen partial pressures in the Jurassic

Figure 3 Various patterns of modelled aPO₂ during the Phanerozoic. Solid line (Bergman et al., 2004) [36], dotted line (Berner, 2009) [37], dashed line (Berner and Canfield, 1989) [35].

are thought to be lower than the current one at 21 kPa [37], but the maximum size of Jurassic odonates is greater than that of their extant relatives. It most probably results from less competition and lower predation pressure from aerial vertebrates in the Jurassic, including comparatively low pterosaur diversity and more limited flying ability in early birds which appeared during the Late Jurassic [4] (or later [5]).

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