

A new species of *Sinonemestrius* (Diptera: Brachycera) from the Weald Clay (Lower Cretaceous, southern England), with a discussion of its affinities and stratigraphical implications¹



*E. A. Jarzembowski and †M. B. Mostovski

*Maidstone Museum & Bentlif Art Gallery, St. Faith's St., Maidstone, Kent ME14 1LH and PRIS, The University, Reading, UK

†Arthropod Laboratory, Palaeontological Institute, 123 Profsoyuznaya St., Moscow 117647, Russia

Revised manuscript accepted 30 June 2000

A distinctive but rare fly, *Sinonemestrius akirai* sp. nov. (family Xyophagidae), is described from the upper Hauterivian of southern England. This extends the range of the genus *Sinonemestrius* outside of China for the first time, and supports a Cretaceous date for the Laiyang Formation. © 2000 Academic Press

KEY WORDS: Diptera; brachycerous flies; Xylophagidae-Sinonemestriini; Wealden; Laiyang Formation; new species.

1. Introduction

The order Diptera (true flies) is well represented in the Lower Cretaceous of southern England. The suborder Brachycera, however, is infrequent (under 10% of Diptera found) and in the main composed of Empididae (dance flies) and Rhagionidae (snipe-flies) (Jarzembowski, 1984; Coram *et al.*, 1995; Mostovski *et al.*, 2000). In addition, Jarzembowski (1987) reported a rare and unusual *Heterostomus*-like brachyceran as present in the Weald Clay. The taxonomy and systematics of this enigmatic form are resolved herein. In addition, the stratigraphy and palaeo-environment of the Wealden species and its equally rare Chinese congener are discussed below.

2. Systematic description

Order: Diptera L., 1758

Suborder: Brachycera Zetterstedt, 1842

Family: Xylophagidae Fallén, 1810 (*s.l.*)

Subfamily: Heterostominae Nagatomi, 1977

Tribe: Sinonemestriini Nagatomi *et al.*, 1998 stat. nov.

Genus *Sinonemestrius* Hong *et al.*, 1990

¹Contribution No. 3 to Rev. P. B. Brodie commemorative series of papers.

Type species. *Sinonemestrius tuanwangensis* Hong *et al.*, 1990; Lower Cretaceous, People's Republic of China.

Diagnosis. Vein R1 short; R2+3 curved, relatively short, terminating near the tip of R1; R4 sigmoidal; R5 nearly straight, aligned with stem of R4+5. Transverse crossvein r-m present. Veins M1, M2 and M3 sinuous; M1, M2 and R5 terminating near the wing apex. Anal cell open.

Remarks

Systematics. The genus was originally referred to the extant family Nemestrinidae (Hong & Wang, 1990). It certainly resembles species of the extinct nemestrinid subfamily Archinemestriinae and even some extant nemestrinids in that veins R4, R5, M1 and M2 terminate near the wing apex. Nevertheless, the short R1, relatively short and curved R2+3 terminating near the tip of R1, and the absence of the so-called 'diagonal' vein, exclude this genus from the Nemestrinidae. Also, R1-4 not fused apically exclude it from Acroceridae.

In many ways, *Sinonemestrius* (Figure 1) resembles extant *Heterostomus* Bigot, 1857 (curved R2+3 terminating near the tip of R1, sigmoidal R4, and shape of discal cell; Figure 2) and extant *Exeretoneura*

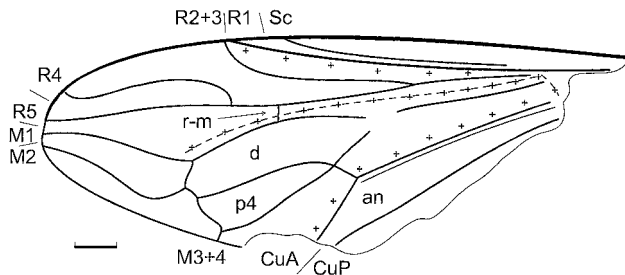


Figure 1. Wing venation of *Sinonemestrius akirai* sp. nov., holotype. Crosses indicate convex areas in the wing; broken lines in all figures indicate convex folding. Scale bar represents 1 mm.

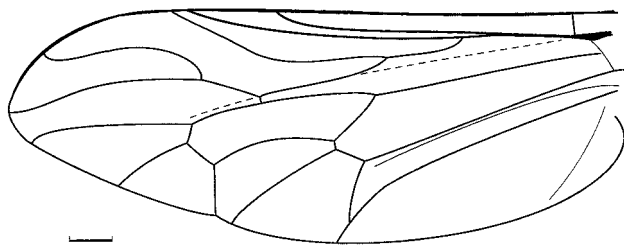


Figure 2. Wing venation of *Heterostomus curvipalpis*, Recent, Chile. Scale bar represents 1 mm.

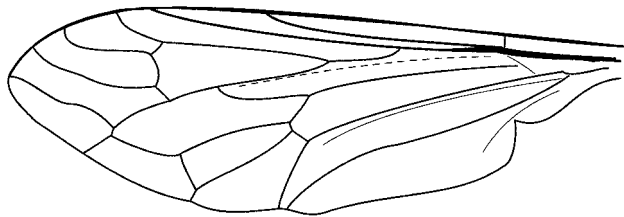


Figure 3. Wing venation of *Exeretoneura maculipennis*, Recent, Tasmania (after Mackerras, 1925, with modification).

Macquart, 1846 (curvature of R2+3, R4 and M1; tendency of vein apices to be displaced towards the anterior margin of the wing; petiolate p4 and open anal cell; Figure 3). *Exeretoneura* was included in the Nemestrinidae until Nagatomi (1977) erected a new monobasic family for this genus. Later, he considered that *Exeretoneura* and *Heterostomus* were related (based on the male genitalia and some other characters) placing them in Xylophagidae *sensu lato* in separate subfamilies (Nagatomi, 1984, 1985, 1992).

Our investigation of wing folds in *Coenomyia ferruginea* (Scopoli) (Xylophagidae *s.l.* = Coenomyiidae auct.), *Heterostomus curvipalpis* Bigot, *Exeretoneura maculipennis* Macquart and *Sinonemestrius akirai* sp. nov. provides new evidence concerning their system-

atic positions. The folding observed in *Coenomyia* and *Heterostomus* [R5 convex on a convex fold forming the additional supporting spar of Ennos (1989) running along M1+2 distally to r-m] seems to be more primitive than that of *Exeretoneura* and Nemestrinidae. In the latter, the spar coincides with a diagonal vein composed of Rs, R4+5, M1+2 (the latter two often fused replacing r-m) and M2 [in *Exeretoneura* and also undescribed Rhagionemestriinae from the Upper Jurassic of Kazakhstan and Lower Cretaceous of Spain (Montsec) and Mongolia (Bon-Tsagaan)] or M2+3 and M3+4 (Nemestrinidae). In *Sinonemestrius*, the spar is represented by a strong convex fold running between the radial and medial branches (following Rs and R4+5 basal to r-m, and M1+2 distal to r-m) resembling *Coenomyia* more than *Heterostomus* in not coinciding with R4+5.

The nemestrinoids (superfamily Nemestrinoidea excluding family Bombyliidae) retain a pulvilliform empodium and so are often placed in the lower Brachycera as a group phylogenetically distinct from other superfamilies (e.g., Steyskal, 1953; Nagatomi, 1992). *Exeretoneura* differs from extant nemestrinids in its primitive antennal structure and other primitive features. The advanced wing folding in this genus and Rhagionemestriinae suggests, however, an 'annectent' position between Xylophagidae *s.l.* and Nemestrinoidea, and even a relationship with the latter. *Heterostomus* and *Sinonemestrius* belong to a separate group. Nagatomi & Yang (1998) even placed the latter in its own family, Sinonemestriidae, which they considered to be the sister-group of Nemestrinidae based only on the position of veins M1 and M2. We retain this higher grouping only as a tribe within Heterostominae.

Palaeobiology. The only living species of *Heterostomus* is known from Chile; four species of *Exeretoneura* occur in temperate Australia and Tasmania, i.e., both genera have a Gondwanan distribution. The discovery of fossil Laurasian relatives (*Sinonemestrius* and Rhagionemestriinae) implies a wider distribution of their subfamilies in previous epochs (cf. Eskov, 1992). The biology and immature stages of *Heterostomus* are unknown. However, the larvae of Coenomyiinae and Xylophaginae are predatory and develop either in soil (the former) or in decaying wood (the latter); the adults imbibe plant fluids (Krivoshchina & Zaitsev, 1989). The larvae of *Exeretoneura* and their biology are similar to Coenomyiinae (Palmer & Yeates, 1998), including DNA sequences (B. M. Wiegmann, pers. comm., 1999). The concentration and upturning of the apical wing veins in *Sinonemestrius* is suggestive of hovering ability (cf. Grimaldi, 1999).

Stratigraphy and brachyceran assemblages. The genus *Simonemestrius* is typically known from the famous insect-bearing Laiyang Formation in Shandong Province, People's Republic of China. The age of this formation is controversial. Zhang (1987, 1992) regarded it as either Late Jurassic or Tithonian–Berriasian, based mainly on a radiometric date of 127 Ma for the Qingshan Formation, which lies disconformably above the Laiyang Formation. The latter was correlated with the Jiufutang Formation in Liaoning and Hebei provinces by Zhang (1992) in which the Jurassic/Cretaceous boundary was recognised by Ren *et al.* (1995). Analysis of ostracod, bivalve, conchostracan and insect assemblages (Zherikhin, 1978; Hong & Wang, 1990; Lin, 1995; Li & Xie, 1997) supported by palaeobotany (Liu, 1990) and palynology (Yu, 1990) would place the Laiyang Formation firmly in the Lower Cretaceous and correlate it with the lower Wealden in Europe (Lin, 1995). It may be noted that there are no typical Late Jurassic brachyceran flies in the Laiyang Formation, but Platypezoidea (represented by Platypezidae and Ironomyiidae: Sinolestinae) do occur (Zhang, 1987; Hong & Wang, 1988, 1990). Platypezoidea are characteristic of Neocomian deposits in Siberia and the Aptian of Mongolia (Mostovski, 1995a, b) but are absent in the lowermost Cretaceous of Mongolia where empidids are abundant (43% of determinate Brachycera) and rhagionids are subdominant (31%). Such a high percentage of rhagionids is unusual for the Lower Cretaceous where 11–14% is more common. Platypezoids are also absent from the Purbeck and Wealden where true empidids do occur (Jarzembowski, 1984; Coram *et al.*, 1995) unlike in the Laiyang Formation. However, rhagionids are uncommon in the latter as in the Purbeck and Wealden (Jarzembowski & Coram, 1997).

On balance, the Laiyang Formation is evidently of Early Cretaceous age, probably a little younger than the lowermost Cretaceous deposits of Asia, and possibly Valanginian. However, the distribution and relative abundance of Platypezidae/Empididae may have been influenced by palaeoenvironmental as well as temporal considerations, as suggested in the Neocomian of Baissa (Transbaikalia) where fossil insects were collected bed-by-bed.

Palaeoecology. The palaeoecology of the Laiyang Basin has been reviewed by Zhang (1992). The predominantly fine-grained sediments of the Laiyang Formation were deposited in a large lake, with an area of several hundred square kilometres, in a lowland

setting. In addition to insects, fossil plants, fish and a bird feather have also been found. Aquatic insects are well represented. The plant assemblage is of the northernmost East Asian type and is considered to indicate a warm, humid (subtropical) climate (Vakhrameev, 1988). The basin was included by Zharkov *et al.* (1998) in the northern mid-latitude warm humid zone based on sedimentary facies. The lake margin supported equisetalean reedswamp, with conifers growing away from the shoreline. The fragmentation of plant matter suggests some transport of terrestrial biota to the site of deposition.

Simonemestrius akirai sp. nov.

Figure 1

1987 cf. *Heterostomus*: Jarzembowski, pp. 289–291, fig. 12.19.

Derivation of name. After the entomologist (dipterist) Dr Akira Nagatomi of Kogoshima, Japan.

Material. Holotype specimen registration number MNEMG 2000.39 a, b, Jarzembowski coll.: length 13.2 mm; width 4.7 mm.

Horizon and locality. Lower Weald Clay, Clockhouse Brickworks, Surrey (latitude 51°8'N, longitude 0°19.5'W); upper Hauterivian.

Diagnosis. *Simonemestrius* with transverse crossvein r-m present at the middle of the anterior margin of the discal cell; cell p4 petiolate; vein CuP not curved.

Description. The species is known from the part and counterpart of an isolated forewing lacking the anal lobe. The costal (C) before the wing tip, the subcostal (Sc) and first radial (R1) veins are somewhat thickened. R2+3 and R4+5 separate basally of the discal cell. R4 is weakly sinuous. The transverse crossvein r-m is located at the middle of the anterior margin of the discal cell (d). The medial stem before its fork and M1+2 and M3+4 just after the fork appear a little weakened. A strong convex fold runs between the radial and medial fields (Figure 1: broken line). Cell p4 has a short petiole. Vein CuP is straight. All the veins are dark brown and the wing membrane is dusky especially distally.

Remarks. The geology of the Clockhouse Brickworks has been summarised by Jarzembowski (1991); for stratigraphy, see Ross, in Rasnitsyn *et al.* (1998). The insects occur mainly as disarticulated remains in scour fills of well-cemented siltstone in a mudstone sequence. The unique type of Wealden *Simonemestrius* is

associated with other insect orders including Odonata (dragonflies), Coleoptera (beetles) and Blattodea (cockroaches). The remains are thought to have been transported during the wet season by rivers flowing off denuded uplands and emptying into basinally low-lying, muddy wetland/shallow open water. Aquatic insects are generally uncommon in the Weald Clay. As in the Laiyang Formation, there would have been some fringing horsetail reedbeds and woodland along the rivers but also *Bevhalstia* mat amongst the former; the climate is considered to have been subtropical/warm temperate and generally more humid after the dry phase represented by the Purbeck beds (e.g., Jarzembowski, 1995; Allen, 1998).

Acknowledgements

Our thanks to Dr D. E. Shcherbakov (Palaeontological Institute, Moscow) for helpful discussion, and Dr B. R. Pitkin (The Natural History Museum, London) for the loan of Recent Diptera. The work was partly supported by the European Science Foundation (Fossil Insect Network), Royal Society (EAJ) and the International Science Foundation (grant nos. a97-181 and RGO-822-7 to MBM): we are grateful to them all. This is PRIS contribution no. 811 for EAJ.

References

- Allen, P. 1998. Purbeck-Wealden (early Cretaceous) climates. *Proceedings of the Geologists' Association* **109**, 197–236.
- Coram, R., Jarzembowski, E. A. & Ross, A. J. 1995. New records of Purbeck fossil insects. *Proceedings of the Dorset Natural History and Archaeological Society* **116**, 145–150.
- Ennos, A. R. 1989. Comparative functional morphology of the wings of Diptera. *Zoological Journal of the Linnean Society* **96**, 27–47.
- Eskov, K. 1992. Archaetid spider from Eocene Baltic amber (Chelicerata: Araneida: Arachnida) with remarks on the so-called "Gondwanan" ranges of Recent taxa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **185**, 311–328.
- Grimaldi, D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* **86**, 373–406.
- Hong, Y. & Wang, W. 1988. Sinolestinae, an early Cretaceous new subfamily of Platypezidae (Insecta, Diptera) from the Laiyang Basin, Shandong Province. *Geoscience* **2**, 386–392.
- Hong, Y. & Wang, W. 1990. Fossil insects from the Laiyang Basin, Shandong Province. In *Stratigraphy and paleontology of the Laiyang Basin, Shandong* (Regional Geological Surveying Team), pp. 44–189 (Geological Publishing House, Beijing).
- Jarzembowski, E. A. 1984. Early Cretaceous insects from southern England. *Modern Geology* **9**, 71–93. pls 1–4.
- Jarzembowski, E. A. 1987. Early Cretaceous insects from southern England. Unpublished PhD thesis, University of Reading, 421 pp.
- Jarzembowski, E. A. 1991. The Weald Clay of the Weald: report of 1988/89 field meetings. New insects from the Weald Clay of the Weald. *Proceedings of the Geologists' Association* **102**, 83–108.
- Jarzembowski, E. A. 1995. Early Cretaceous insect faunas and palaeoenvironment. *Cretaceous Research* **16**, 681–693.
- Jarzembowski, E. A. & Coram, R. 1997. New fossil insect records from the Purbeck of Dorset and the Wealden of the Weald. *Proceedings of the Dorset Natural History & Archaeological Society* **118**, 119–124.
- Krivoshchina, N. P. & Zaitsev, A. I. 1989. Phylogenesis and evolutionary ecology of dipteran insects. *Itogi Nauki i Tekhniki Seriya Entomologiya* **9**, 162 pp. [In Russian]
- Li, S. & Xie, C. 1997. A discussion on the age of the Laiyang Formation in Laiyang Basin, Shandong. *Journal of Stratigraphy* **21**, 233–238.
- Lin, Q. 1995. On *Penaphis* Lin, 1980 from the Cretaceous (Callaphididae, Homoptera) and its coevolutionary relationships. *Acta Palaeontologica Sinica* **34**, 194–204.
- Liu, M. 1990. The stratigraphy and palaeontology of the Laiyang Formation, Laiyang Basin. Fossil plants. In *Stratigraphy and palaeontology of the Laiyang Basin, Shandong* (Regional Geological Surveying Team), pp. 196–211 (Geological Publishing House, Beijing).
- Mackerras, I. M. 1925. The Nemestrinidae of the Australasian Region. *Proceedings of the Linnean Society of New South Wales* **50**, 489–561.
- Mostovski, M. B. 1995a. New representatives of the Platypezidae (Diptera) from the Mesozoic and the main directions in the evolution of the family. *Paleontological Journal* **1995** (2), 106–118.
- Mostovski, M. B. 1995b. New taxa of ironomyiid flies (Diptera, Phoromorpha, Ironomyiidae) from Cretaceous deposits of Siberia and Mongolia. *Paleontological Journal* **1995** (4), 86–103.
- Mostovski, M. B., Jarzembowski, E. A., Coram, R. A. & Ansoerge, J. 2000. Curious snipe-flies (Diptera: Rhagionidae) from the Purbeck of Dorset, the Wealden of the Weald and the Lower Cretaceous of Spain and Transbaikalia. *Proceedings of the Geologists' Association* **111**, 153–160.
- Nagatomi, A. 1977. Classification of lower Brachycera. *Journal of Natural History* **11**, 321–335.
- Nagatomi, A. 1984. Male genitalia of the lower Brachycera. *Beiträge zur Entomologie* **34**, 99–157.
- Nagatomi, A. 1985. Redescription of *Heterostomus curvipalpis* (Diptera, Heterostomidae) and some notes on my paper of the male genitalia of the lower Brachycera. *Kontyû* **53**, 699–710.
- Nagatomi, A. 1992. Notes on the phylogeny of various taxa of the orthorrhaphous Brachycera (Insecta: Diptera). *Zoological Science* **9**, 843–857.
- Nagatomi, A. & Yang, D. 1998. A review of extinct Mesozoic genera and families of Brachycera (Insecta, Diptera, Orthorrhapha). *Entomologist's Monthly Magazine* **134**, 95–192.
- Palmer, C. M. & Yeates, D. K. 1998. Immature stages and relationships of the genus *Exeretoneura* Macquart (Brachycera). In *Abstracts Volume, Fourth International Congress of Dipterology*, Oxford, 6–13 Sept. 1998 (ed. Ismay, J. W.), pp. 166–167.
- Rasnitsyn, A. P., Jarzembowski, E. A. & Ross, A. J. 1998. Wasps (Insecta: Vespida=Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research* **19**, 329–391.
- Ren, D., Lu, L. W., Guo, Z. G. & Ji, S. 1995. *Faunas and stratigraphy of the Jurassic-Cretaceous in Beijing and adjacent areas*, 223 pp. (Seismic Publishing House, Beijing).
- Steyskal, G. C. 1953. A suggested classification of the lower brachycerous Diptera. *Annals of the Entomological Society of America* **46**, 237–242.
- Vakhrameev, V. A. 1988. *Jurassic and Cretaceous floras and global climate*, 160 pp. (Nauka, Moscow). [In Russian]
- Yu, J. 1990. Palynological assemblages from the Laiyang and Qingshan formations of eastern Shandong Province. In *Stratigraphy and palaeontology of the Laiyang Basin, Shandong* (Regional Geological Surveying Team), pp. 211–225 (Geological Publishing House, Beijing).
- Zhang, J.-F. 1987. Four new genera of Platypezidae. *Acta Palaeontologica Sinica* **26**, 595–603.

Zhang, J.-F. 1992. The late Mesozoic entomofauna from Laiyang, Shandong Province, China, with discussion of its palaeoecological and stratigraphical significance. *Cretaceous Research* **13**, 133–145.

Zharkov, M. A., Murdmaa, I. O. & Filatova, N. I. 1998. Palaeogeography of the Berriasian-Barremian stages of the Early

Cretaceous. *Stratigraphy and Geological Correlation* **6**, 49–72. [In Russian]

Zherikhin, V. V. 1978. Evolution and changes in the Cretaceous and Cenozoic faunistic assemblages. *Transactions of the Paleontological Institute of the Academy of Sciences of the USSR* **165**, 197 pp. [In Russian]



Rev. P. B. Brodie