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Late Mesozoic entomofauna from Laiyang, Shandong province, China, with discussion of its palaeoecological and stratigraphical significance

Zhang Junfeng

Shandong Provincial Museum, Jinan, Shandong 250012, People's Republic of China

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A large collection of fossil insects has recently been recovered from the late Mesozoic Laiyang Formation in Shandong province, China, which contains many new taxa. Because many of these are geographically widespread, stratigraphic correlations are possible. The *Ephemeropsis* fauna, which is part of the Jehol biota, occurs in nonmarine rocks throughout eastern Asia. These insect-bearing strata are here regarded as Upper Jurassic. The overlying Lower Cretaceous strata contain few insect fossils. The *Ephemeropsis* fauna is divided into three assemblages characterized by the insects *Manlayamyia*, *Palaeogomphus* and *Mesolygaeus*. These assemblages indicate a warm, humid, lacustrine environment. The complex issues of the Jurassic-Cretaceous boundary within insect-bearing strata of eastern China are discussed; this boundary is here regarded to lie above the Laiyang Formation.

KEY WORDS: China; Jehol fauna; Laiyang entomofauna; *Ephemeropsis*; Upper Jurassic; Lower Cretaceous.

1. Introduction

The Jehol biota, first described by Grabau (1923), is a suite of fossil plants and animals which are characteristic of the Upper Jurassic and Lower Cretaceous strata of eastern and north-eastern Asia. The *Ephemeropsis* insect fauna is a significant component of the Jehol biota, of which many taxa have been studied from China, Mongolia, and the Trans Baikal region of the former Soviet Union since the 1930s (e.g. Grabau, 1923; Ping, 1928; Ponomarenko, 1961; Rasnitsyn, 1969, 1975; Lin, 1976, 1980, 1982a, 1982b; Joint Soviet-Mongolian Palaeontological Expedition (from now on JS-MPE), 1980, 1986; Hong, 1982, 1984a, 1984b; Hong & Wang, 1976; Kalugina & Kovalev, 1985; Arnoldi *et al.*, 1977; Zhang, 1986). Until recently, however, data have been insufficient to reveal the full biostratigraphic and palaeoecological potential of the Laiyang entomofauna.

The Laiyang Formation of Shandong province had yielded, prior to 1985, only 12 described fossil insect taxa (Grabau, 1923; Ping, 1928; Hong, 1984b). Currently 60 species have been described (Table 1; Grabau, 1923; Ping, 1928; Hong, 1984b; Hong & Wang, 1988; Yang & Hong, 1990; Zhang, 1985, 1987, 1988, 1989, 1990a, 1990b; Zhang *et al.*, 1986, 1989) which include, cockroaches, grasshoppers, leafhoppers, bugs, thrips, beetles, lacewings, scorpionflies, caddisflies, wasps, mosquitoes and flies. Recent collecting has recovered some 300 species from the following fourteen orders (currently under study by the author): Odonata, Blattaria, Orthoptera, Dermaptera, Homoptera, Heteroptera, Thysanoptera, Coleoptera, Neuroptera, Raphidioptera, Mecoptera, Tricoptera, Hymenoptera and Diptera (Table 1). This collection has significant implications for elucidating the stratigraphy and palaeoecology of the Upper Jurassic and Lower Cretaceous strata of eastern Asia.

The new fossil insect collection reported here was recovered from the Third Member of the Laiyang Formation, near the villages of Nanligezhuang, Tuanwang,

Table 1. Fossil insect taxa described from the Laiyang Formation, Shandong Province

BLATTARIA:	*Sinoblattaria laiyangensis*; *Laiyangia paradoxiformis*; *L. delicatula.*
ORTHOPTERA:	*Pseudoacrida* cf. *costata*; *Falsirameus ravus.*
HOMOPTERA:	*Mesoccus lutarius*; *M. advenus*; *Sinojassus brevispinatus*; *Archijassus? plurinevis*; *Paroviparosiphum opimum*; *P. camptotropum*; *Penaphis circa*; *Mesoviparosiphum tuanwangense*; *M. malacum*; *Sinaphidum epichare*; *Tartaraphis peregrina*; *Caudaphis spinalis*; *C. leptoneura*; *C. minulissima*
HETEROPTERA:	*Clypostemma xyphiale*; *Cl. petila*; *Karataviella shandongensis*; *Mesolygaeus laiyangensis*; *Schizopteryx shandongensis*; *S. lacustris.*
COLEOPTERA:	*Coptoclava longipoda*; *Proteroscarabaeus yeni*; *Mesostaphylinus laiyangensis*; *Laostaphylinus nigritellus*; *L. fuscus.*
NEUROPTERA:	*Allopterus luianus*; *Drakochrysa sinica.*
TRICOPTERA:	*Tuanwangia aethoneura.*
HYMENOPTERA:	*Palaeathalia laiyangensis*; *Stemmogaster celata*; *Tanchora sinensis*; *Polychorella magica*; *Oligoneuroides huadongensis*; *Mesomutilla aptera*; *Mataeosphex venulosus*; *Shandongodes lithodes*; *S. necrodes*; *Palcoapis beiboziensis.*
DIPTERA:	*Palaeolimnobis laiyangensis*; *Ceuthoneura dolichoptera*; *Chironomaptera gregaria*; *Ch. vesca*; *Mesochaoborus zhangsanyingensis*; *M. pallens*; *Coelochironoma xantha*; *Protobibio orientalis*; *Pleciomimella perbella*; *Aortomima shandogensis*; *Meconeura petrefacta*; *Palaeopetia laiyangensis*; *Mesopetia tuanwangensis*; *Lithopetia hirsula*; *Pseudopetia grandis*; *P. exilis*; *Sinolesta lata.*

Beipozi, Huangyandi, Houzigou, Mareshan and Cuitan in the Laiyang basin (Figure 1). There are differing interpretations regarding the subdivision of the Laiyang Formation (=Laiyang Group of Gu, 1982, and Hong, 1984b), which are discussed in the Editorial Group of the Areal Stratigraphic Chart of Shandong (from now on, EGASCS, 1978), Chen *et al.* (1980) and Zhang (1985). The EGASCS (1978) divided the Laiyang Formation into six members within the Lower and Upper subformations, the former being absent in the Laiyang district. Chen *et al.* (1980) also divided this stratum into six members. In this paper the Laiyang Formation is divided into four members based on the stratigraphic section made by the 375th Team, Geological Bureau of the Ministry of Nuclear Industry; only the section containing the Third Member has been published (see Zhang, 1987, 1990a). The Third Member is here regarded as homotaxial with the Second Member of the Upper subformation of the EGASCS (1978) and the Fifth Member of Chen *et al.* (1980). The Nanligezhuang and Tuanwang localities yielded a great diversity of well-preserved fossil insects from the thin "paper" shales of the Third Member (Figure 2).

2. Laiyang entomofauna

Coleoptera are the most abundant taxa in the Laiyang entomofauna, with Hymenoptera and Diptera each having numerous species. Most of the taxa are new, especially the terrestrial forms, but also some aquatic species, and many appear to be geographically widespread. Several hundred, and even thousand, individuals of the species *Coptoclava longipoda*, *Mesolygaeus laiyangensis*, *Chironomaptera gregaria* and *C. vesca* have been recovered.

The backswimmer, *Clypostemma xyphiale* (Figure 3A), is known from the Baissa Formation near Baissa, Trans Baikal (USSR) (Popov, 1964), the Shouchang Formation, Zhejiang province (Lin, 1980), as well as from the Laiyang Formation (Zhang, 1985). It has also been reported from the Xinminpu Group near Yumen, Gansu province (Hong, 1982), and the Gurvaneren Formation at Gurvan-Ereniy-Nuru, Mongolia (JS-MPE, 1986).

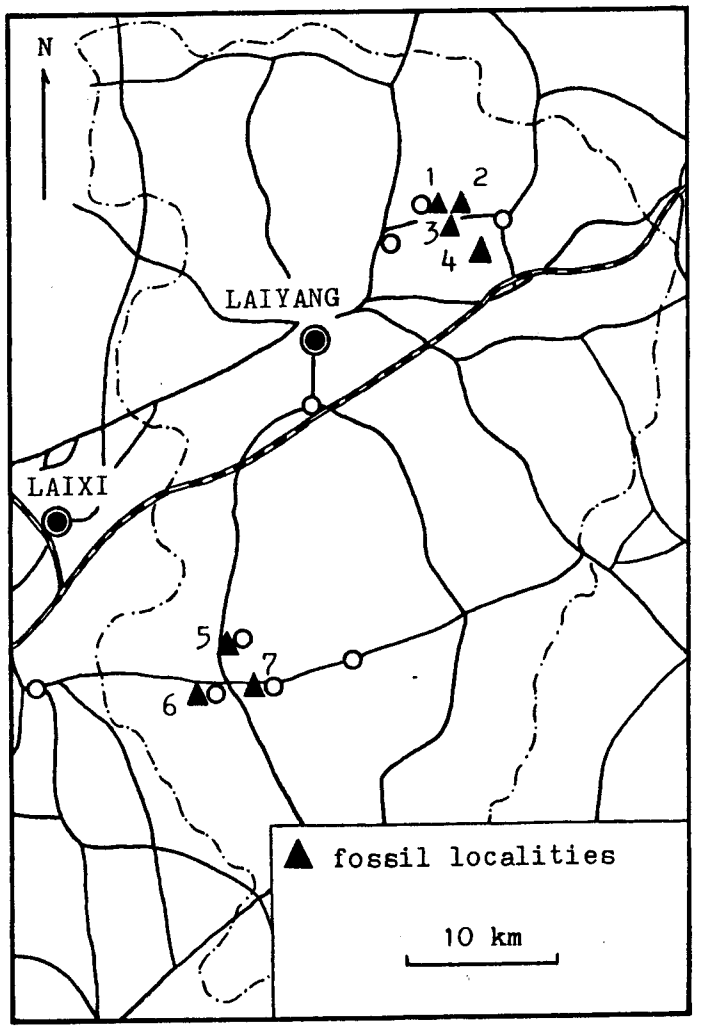

Figure 1. Locality map showing the Laiyang entomofaunal sites, Shandong province. 1–Beipozi, 2–Huangyandi, 3–Houzigou, 4–Mareshan, 5–Nanligezhuang, 6–Tuanwang, 7–Cuitan.

The large aquatic beetle, *Coptoclava longipoda* (Figure 3B, C), has been found in late Mesozoic strata throughout East Asia. This species was first described from the Laiyang Formation (Ping, 1928), the Shouchang Formation (Lin, 1980), the Jiufutang Formation, Liaoning province (Lin, 1976), the Guyang Formation in Nei-Monggol (Hong & Wang, 1976), the Chejinqiao Formation and Xinminpu Group, western Gansu (Hong, 1982), and the Liupanshan Group, Shaanxi-Gansu-Ningxia region (Lin, 1982a). In Mongolia this species has been found in the Mogotuin Formation, near Manlay, the Anda-Khuduk (or Odai Sair) Formation of Ubur-Khangai and the Gurvaneren Formation at Gurvan-Ereniy-Nuru and Khukh-

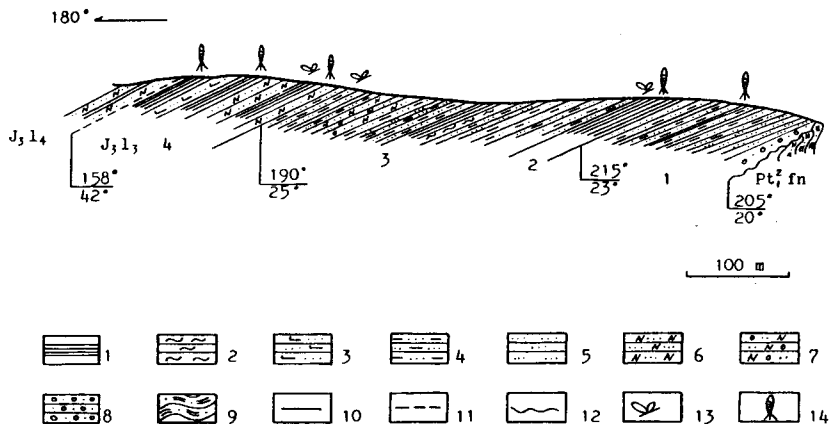

Figure 2. Stratigraphic section of the Third Member of the Laiyang Formation (J_3l_3; see text) at Nanligezhuang, Laiyang. Members 1 and 2 are missing at this locality. Key to lithologies: 1–shale, 2–mudstone, 3–calcareous sandstone, 4–siltstone, 5–fine-grained sandstone, 6–arkose, 7–gravel-bearing arkose, 8–conglomerate, 9–schist, 10–conformity, 11–disconfomity, 12–angular unconformity, 13-fossil plant fragments, 14–fossil insects.

Mort (JS–MPE, 1980, 1986). It has also been found in the Turga Formation at Baissa, Trans Baikal (Ponomarenko, 1961).

The phantom midge, *Chironomoptera gregaria* (Figure 3D), was originally described from the Laiyang Formation (Grabau, 1923), and has since been recorded from the Jiufutang Formation (Lin, 1976), the Mogotuin Formation in the southern Gobi of Mongolia (JS–MPE, 1980) and the Turga Formation of the Trans Baikal (Kalugina, 1977). Another species, *C. vesca,* is known throughout Mongolia (JS–MPE, 1986) and recently has been recognized in the Laiyang and Shouchang formations (Zhang, 1990a; see Figure 3E).

Mesolygaeus laiyangensis is the dominant water bug of the Laiyang entomofauna, which has been considered as a terrestrial seed bug (Figure 3F; Ping, 1928; Hong, 1981; Lin, 1982a, 1982b). This species is also known from the Liupanshan Formation (Lin, 1982a), the Xinminpu Group (Hong, 1982) and the Lushangshufen Formation of the Xishan [Western Hills], Beijing. Hong (1981) regarded the fossils from the latter locality as a new taxon, *Xishania fusifirmis*, but this is not accepted here since no significant taxonomic differences can be identified. A single, poorly preserved specimen from the Jiufutang Formation was recognized by Lin (1976) as *M. laiyangensis*.

The locust, *Pseudoacrida costata*, was discovered first in the Liupushan Formation near Guyuan, Ningxia (Lin, 1982a), and has since been recorded from the Laiyang Formation (Figure 3G).

The winged aphid from Laiyang is extremely similar to *Panaphis circa* from the Shouchang Formation (Lin, 1980), which Zhang *et al.* (1989) regarded as conspecific (Figure 3H).

The remarkably primitive ichneumon fly, *Tanchora*, sharply differs from all extant and fossil ichneumons, and two species are known from the Zaza Formation of the Trans Baikal and the Anda-Khuk Formation of Mongolia (Townes, 1973a). A third new species, *T. sinensis* (Figure 4A), has been found in the Laiyang Formation. Specimens similar to the Russian species have been recorded from the Jiufutang

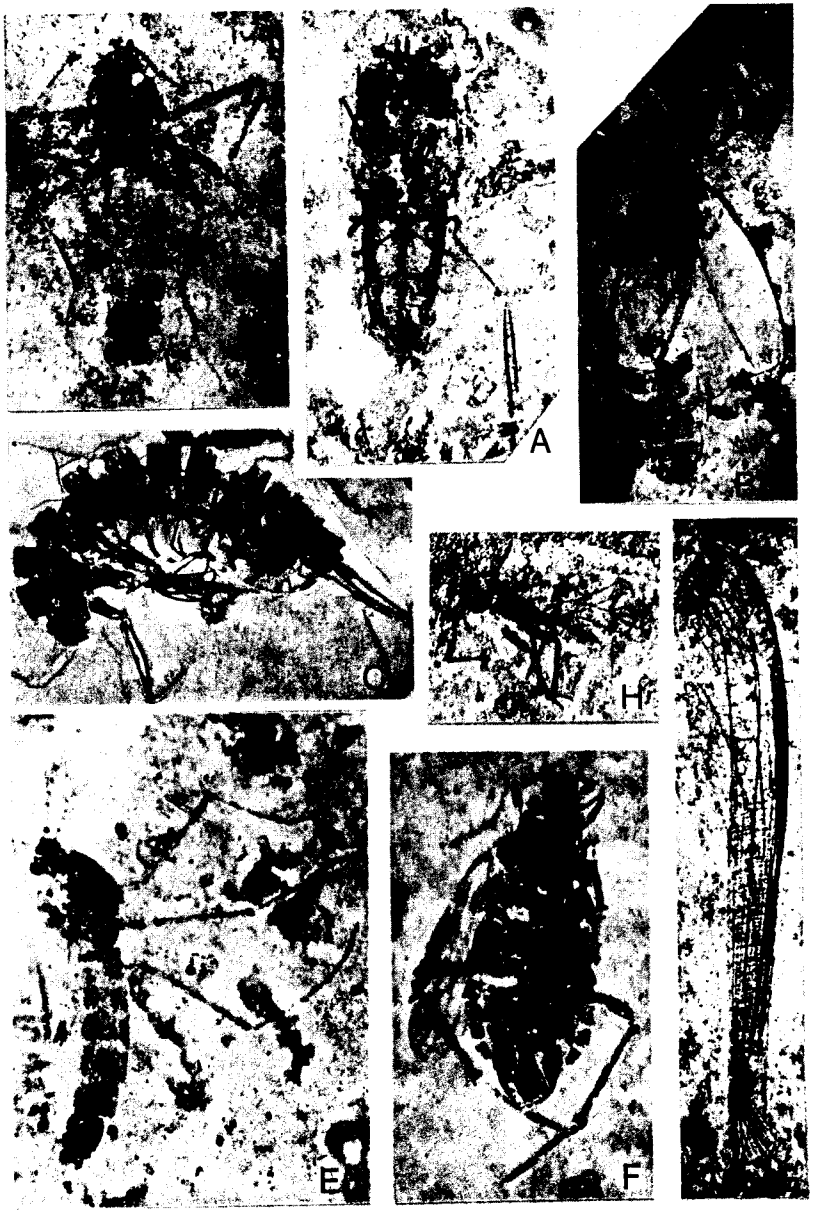

Figure 3. Fossil insects from the Laiyang Formation near Laiyang, Shandong province, China. All specimen numbers refer to the collections at the Shandong Provincial Museum, Jinan City, Shandong. A—*Clypostemma xyphiale*, adult (×3.9), L84996, from Beipozi; B—*Coptoclava longipoda*, adult (×1.1), L87649, from Nanligezhuang; C—*Coptoclava longipoda*, larva (×1.5), L87662. from Nanligezhuang; D—*Chironomaptera gregaria*, adult (×7.3), L86414; E—*Chironomaptera vesca*, adult (×7.3), L84285, from Nanligezhuang; F—*Mesolygaeus laiyangensis*, adult (×7.3), L88222, from Nanligezhuang; G—*Pseudoacrida costata*, front and hind wings (×3.6), L84985, from Tuanwang; H—*Panaphis circa*, adult (×8.8), L84127, from Tuanwang.

Figure 4. Fossil insects from the Laiyang Formation near Laiyang, Shandong province, China. All specimen numbers refer to the collections at the Shandong Provincial Museum, Jinan City, Shandong. A—*Tanchora sinensis*, adult, holocype (×6.0), L84984, from Nanligezhuang; B—*Clypostemma petila*, adult, holotype (×3.9), L84997, from Beipozi; C—*Karataviella shandongensis*, adult, holotype (×5.8), L84999, from Naligezhuang; D—*Schizopteryx shandongensis*, adult, holotype (×5.5), L88245, from Tuanwang; E—*Schizopteryx lacustris*, adult, holotype (×6.6), L88255, from Nanligezhuang; F—*Chironomaptera gregaria*, pupa (×5.8), L86305, from Tuanwang; G—*Chironomaptera vesca*, pupa (×7.3), L86313, from Nanligezhuang.

Formation by Hong (1988), who regarded the stratum as the Sahai Formation (see Figure 6). It is believed that several *Tanchora* species existed in the continental basins throughout eastern Asia for a brief period during the late Mesozoic.

3. Palaeoecology

The Third Member of the Laiyang Formation consists of 250–705 m of calcareous sandstone, siltstone and fine-grained sandstone intercalated with thin, paper-like, insect-rich shales representing facies of a large (several hundred km^2) lake in the Laiyang basin. In addition to the abundant entomofauna, plant fossil fragments, fish and a single bird feather also have been found. Water plants were apparently rare, and at the centre of the lake I have found no plant or animal fossils.

According to the EGASCS (1978), Cao *et al.* (1982) and Vakhrameev (1988), the Laiyang Formation plant assemblage comprises *Thinnfeldia* sp., *Zamites* sp., *Otozamites linguifolia*, *Baiera* cf. *australis*, *Araucarites* sp., *Brachyphyllum obesum*, *Pagiophyllum* sp., *Sphenolepis kurriana*, *Palaeocyparis* sp., *Equisetites* sp., *Ruffordia goepperti*, *Elatocladus* sp., *Elatides* sp., *Cupressinocladus elegans*, *Sagenopteris mantelli* and *Onychiopsis elongata*. Vakhrameev (1988) pointed out that this assemblage belonged to the northernmost East Asia province, reflecting a warm, humid subtropical climate. Since these fossils are fragmented close to the shoreline, and the dominant conifers lived at some distance from the shoreline, it is presumed that substantial transport mechanisms existed for this plant debris. However, the predominantly fine-grained sediments of the Laiyang Formation suggest a subdued topography with hydrophilous equisetalean marshland around the lake margin.

There existed a large number of phytophagous, parasitic, predatory and saprophagous insects throughout the forest and marsh zones, among which phytophilic components were especially diverse and numerically abundant (Zhang, 1985; Zhang *et al.*, 1986). The aquatic insects appear to have lived close to the shoreline and are represented by the following taxa: the large, rapacious beetle, *Coptoclava longipoda* (Figure 3B, 3C), the predaceous bugs, *Clypostemma xyphiale* (Figure 3A), *C. petila* (Figure 4B), *Karataviella shandongensis* (Figure 4C), *Mesolygaeus laiyangensis* (Figure 3F), *Schizopteryx shandongenesis* (Figure 4D), *S. lacustris* (Figure 4E), and larvae and pupae of the phantom midges, *Chironomaptera gregaria* (Figure 4F) and *C. vesca* (Figure 4G).

The food cycle in this lake system is evident. Phantom midge larvae and pupae were microphagous or saprophagous, and were fed upon by water bugs. At the top of the food chain were the large aquatic beetles, of which the adults and larvae were strong predators on other insects, even small fish.

4. *Ephemeropsis* fauna

The *Ephemeropsis* fauna forms part of the Jehol biota, which has been identified throughout eastern Asia, from eastern China to the Trans Baikal (Figure 5). It is possible, and useful, to divide the *Ephemeropsis* fauna into three assemblages based on stratigraphic and geographic distribution, and characterized by the genera *Manlayamyia*, *Palaeogomphus* and *Mesolygaeus*. The first contains abundant *Manlayamyia dabeigouensis* (Diptera, Chironomidae), *Ephemeropsis trisetalis* (Ephemerida, Hexagenitidae) and *Coptoclava longipoda* (Coleoptera, Coptoclavidae), and was first identified from the Daibeigou Formation, Hebei province. The second assemblage consists principally of *Palaeogomphus labius* (=*Archaeogomphus labius*

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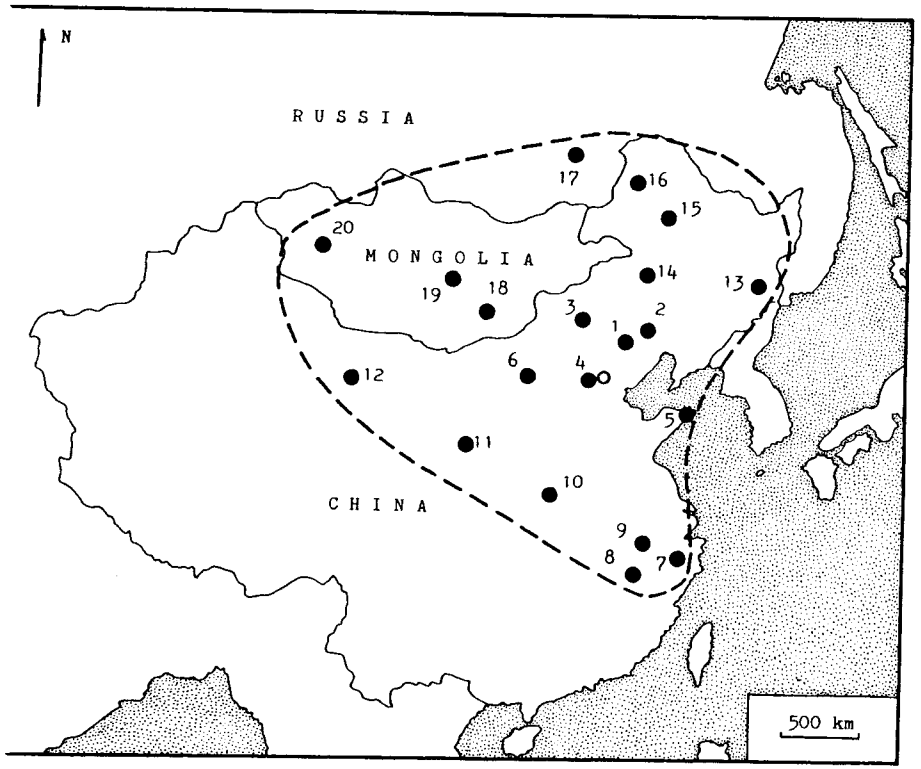

Figure 5. Distribution of the principal *Ephemeropsis* faunal sites in eastern Asia. 1–Luanping, Hebei; 2–Yixian, Liaoning; 3–Abagaqi, Nei-Monggol; 4–Fangshan, Beijing; 5–Laiyang, Shandong; 6–Guyang, Nei-Monggol; 7–Shouchang, Zhejiang; 8–Shixi, Jiangxi; 9–Shexian, Anhui; 10–Nanzhao, Henan; 11–Guyuan, Ningxia; 12–Yumen, Gansu; 13–Jiutai, Jilin; 14–Keyouzhongqi, Nei-Monggol; 15–Longjiang, Heilongjiang; 16–Geyouqi, Nei-Monggol; 17–Baissa, Trans Baikal (USSR); 18–Manlay, Mongolia; 19–Andakhuduk, Ubur-Khangai (Mongolia); 20–Gurvan-Ereniy-Nuru, Mongolia.

Lin, 1976) (Odonata, Gomphidae) and *Ephemeropsis trisetales*, with additional forms in different localities and horizons. This assemblage was originally recorded from the Yixian Formation, Liaoning (Lin, 1976), but has subsequently been discovered from the Nanzhao Formation, Henan province (Cao *et al.*, 1986). The *Mesolygaeus* assemblage is diverse and includes principally *M. laiyangensis*, *Chironomaptera gregaria*, *C. vesca* and *Coptoclava longipoda*, is found throughout eastern Asia, and reflects the acme of the *Ephemeropsis* fauna.

5. Stratigraphic correlation

The short reproductive cycle, rapid evolution and swift geographic dispersal of insects ensured their usefulness for regional biostratigraphic correlation. Some species, however, such as *Ephemeropsis trisetales* and *Coptoclava longipoda*, had a persistent duration.

In northern Hebei, late Mesozoic strata are divided into seven formations: Zhangjiakou, Dabeigou, Dadianzi, Huajiying, Nandian, Qingshila and Tujingzi

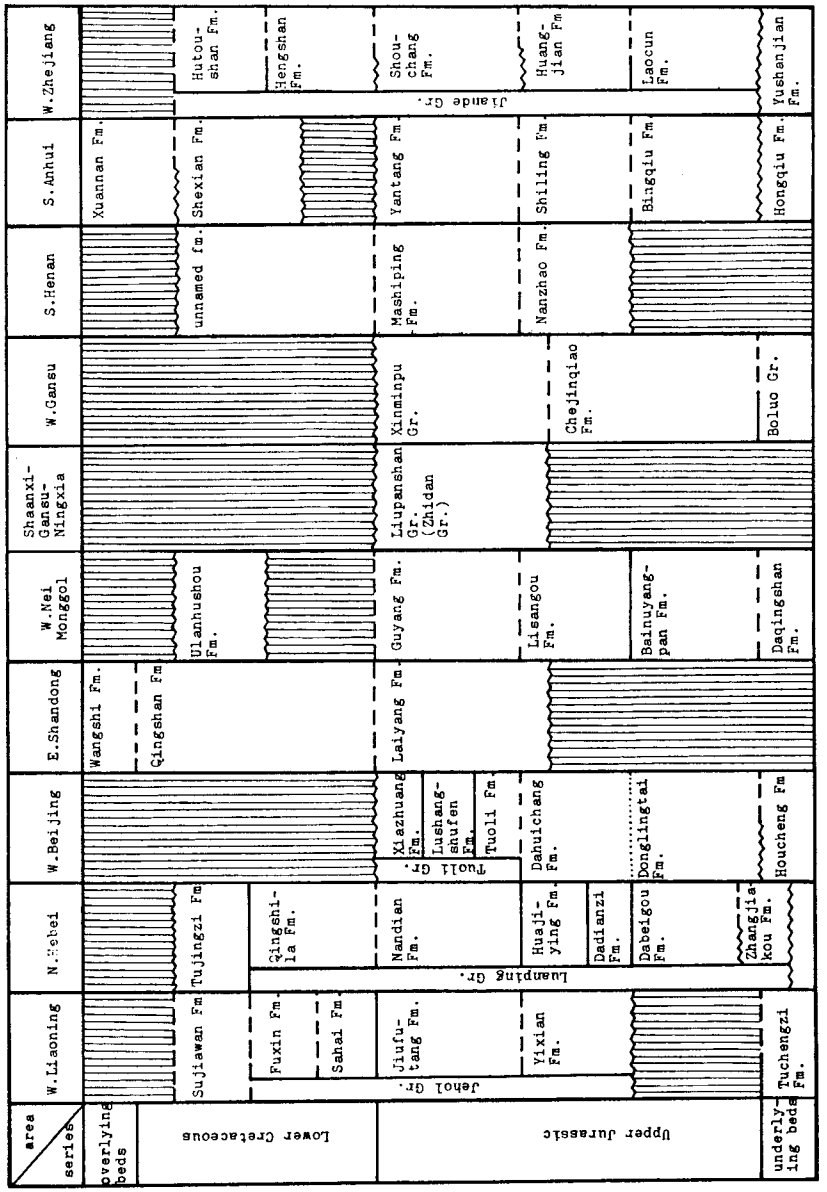

Figure 6. Correlation chart of the principal Upper Jurassic and Lower Cretaceous insect-bearing strata in China.

(Figure 6). The lowermost insect-bearing strata occur within the Daibeigou Formation, which contains a well-defined *Manlayamyia* assemblage. This chironomid midge has also been identified by the author from the Chejinqiao Formation of Gansu based on photographs published by Hong (1982, plate 36, figure 1–3; plate 37, figure 1, 7), which were there recorded as *Chironomaptera gregaria* and *C. melanura*. Representatives of the *Palaeogomphus* assemblage have also been recorded from the Chejinqiao Formation (Hong, 1982), as well as from the Yixian Formation of Liaoning and the Nanzhao Formation of Henan (Cao *et al.*, 1986).

The Dabeigou Formation is older than the Yixian and Nanzhao formations, and the thicker Chejinqiao Formation contains both *Manlayamyia* and *Palaeogomphus* assemblages; this is correlated with the combined Dabeigou, Dadianzi and Huajiying (Yixian) formations (Figure 6). The Yixian and Nanzhao formations are coeval. The *Mesolygaeus* assemblage has been recorded from the Laiyang Formation, the Shouchang Formation, the Xinminpu Group, the Liupanshan Group, the Guyang Formation, the Lushangshufen Formation and the Jiufutang Formation (Figure 6). It is suggested that these formations are approximately coeval.

6. Geological age and the Jurassic-Cretaceous boundary

The age of the Jehol biota has been the focus of much discussion among Chinese geologists and palaeontologists. Gu (1980, 1982) regarded the entire Jehol biota to be of Middle to Late Jurassic age, but others have argued that this biota is Late Jurassic to Early Cretaceous (Chen *et al.*, 1980; Ye & Li, 1982; Wang, 1986, 1990; Cao *et al.*, 1986). Some researchers, such as Hao *et al.* (1986) regard the entire biota as Early Cretaceous in age.

A drop in temperature during the Tithonian has been recorded in many parts of eastern Asia (Liu *et al.*, 1986), and it is here believed that the virtual disappearance of the *Ephemeropsis* fauna is at least an indirect result of that climate change. Only a few taxa, including *Coptoclava longipoda*, persisted after this event. Substantial tectonic and volcanic activity in many parts of eastern Asia (Gu, 1980; Hao *et al.*, 1986; Wang, 1990) may have disturbed the prevailing ecologies during the Late Jurassic and may have contributed to this disappearance. The radiometric age of the Dabeigou Formation is 152.3 Ma (Wang, 1990), which is Oxfordian according to the time scale of Odin (1982). In western Liaoning, the Yixian Formation has been dated as 142.5 Ma according to Wang & Diao (1984), placing it within the Kimmeridgian to Tithonian. Gu (1980) regards the lower formations (Laocun, Huangjian, and Shouchang) of the Jiande Group of Zhejiang as Late Jurassic based on palaeontological and radiometric data, which have revealed an age of 143 Ma. A radiometric date of 127 Ma (Gu, 1980) from the Qinshan Formation, which overlies the Laiyang Formation, further suggests that the Laiyang Formation might have been deposited during the Tithonian and Berriasian. Furthermore, a 130 Ma age from the Fuxin Formation of Liaoning supports this assessment (Wang, 1990). The top of the Jiufutang Formation is sharply eroded by the overlying Sahai Formation (Wang, 1990) and thus can be considered as being substantially older than 130 Ma, but younger than 142.5 Ma.

The foregoing indicates that the Jurassic-Cretaceous boundary lies between the Laiyang and Qingshan formations in Shandong, the Jiufutang and Sahai formations of western Liaoning, the Nadian and Qingshila formations of Hebei, and the Shouchang and Henshan formations of Zhejiang. Because the Mashiping Formation in southern Henan may be correlated with the Laiyang Formation (Cao *et al.*, 1986), it is regarded as Late Jurassic in age; the overlying, unnamed unit may in large part be Cretaceous in age; thus this area could provide an additional Jurassic-Cretaceous boundary site.

7. Conclusion

The *Ephemeropsis* entomofauna is found in south-eastern, north-eastern and north-western China, Mongolia and the Trans Baikal region of southern Siberia. According to this paper it is restricted to the uppermost Jurassic strata. This fauna is divided into three assemblages, *Manlayamyia*, *Palaeogomphus* and *Mesolygaeus*, which, based on insect fossils, occur in rocks of early, middle and late Late Jurassic age, respectively. The distinction between the three assemblages becomes blurred further to the west: the Chejinqiao Formation contains forms from both the first and second assemblages (*Manlayamyia* and *Palaeogomphus*), and the Mogotuin and Gurvaneren formations of Mongolia contain elements of all three assemblages (JS–MPE, 1980, 1986).

This entomofauna appears to have originated in the early Late Jurassic throughout the region ranging from northern Hebei to western Gansu, including Mongolia, and thereafter quickly spread throughout eastern Asia. Terrestrial sedimentary basins in much of China, Mongolia and southern Siberia contain abundant finely-laminated lacustrine mudstone facies in which insect fossils are commonly found.

Lower Cretaceous strata in China, for example the Qingshan (Shandong), Hengshan (Zhejiang), Dalazi (Jilin) and Fuxin (Liaoning) formations, typically contain few, if any, insect fossils owing to a decrease in temperature and lake availability. By Late Cretaceous time, the entomofauna took on a very different character from earlier assemblages, showing a greater affinity with Tertiary forms as seen in a fauna from the Taymyr peninsular (Kalugina, 1974, 1977; Remm, 1976; Alekseyev & Rasnitsyn, 1981; Townes, 1973b).

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