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

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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 Manchoumysia, Palaeosymphyla, and Mesophila. These assemblages indicate a warm, humid, lacustrine environment. The complex issues of the Jurassic-Cretaceous boundary within insect-bearing strata of eastern Asia 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, Hemiptera, Heteroptera, Thyanopter, 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 Liaiyang Formation, Shandong Province

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<th>Taxon</th>
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<tr>
<td>BLATTARIA</td>
<td><em>Sinooblattaria layangensis</em>, <em>Laiyangia paradoxiformis</em>, <em>L. delicatula</em></td>
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<tr>
<td>ORTHOPTERA</td>
<td><em>Pseudocoridae cl. costata</em>, <em>Faltracium revus</em></td>
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<tr>
<td>HOMOPTERA</td>
<td><em>Mecozetes latarus</em>, <em>M. adenura</em>, <em>Sinusaurus brevignatus</em>, <em>Archipsius plicarinus</em>, <em>Parasphenopus epiphanum</em>, <em>P. campiotropus</em>, <em>Panaphis cirrus</em>, <em>Mesosparopsis tuanfangensis</em>, <em>M. malacum</em>, <em>Siphopterus ephialte</em>, <em>Tartaraphes perigrina</em>, <em>Caudaphis spinalis</em>, <em>C. leptoneura</em>, <em>C. minutissima</em></td>
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<tr>
<td>HETEROPTERA</td>
<td><em>Chysostemma xiphale</em>, <em>Cl. perla</em>, <em>Karoternula shandongensis</em>, <em>Mesolycogas layangensis</em>, <em>Schizopteryx shandongensis</em>, <em>S. lacustris</em></td>
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<tr>
<td>COLEOPTERA</td>
<td><em>Coptocleta longipoda</em>, <em>Proteroschizara bueti</em>, <em>Mesostethus layangensis</em>, <em>Laonolophus nigritus</em>, <em>L. fusca</em></td>
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<td>NEUROPTERA</td>
<td><em>Aletopterus buatianus</em>, <em>Drakochrysa sinica</em></td>
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<td>TRICOPTERA</td>
<td><em>Tuananga antheaeura</em></td>
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<td>HYMENOPTERA</td>
<td><em>Palacanthula layangensis</em>, <em>Stenomantis exulata</em>, <em>Tachinella sinensis</em>, <em>Polycheurella magica</em>, <em>Oligomerides haudogenisi</em>, <em>Mecanotus apera</em>, <em>Melaenochares samuelis</em>, <em>Shandongodes tichodes</em>, <em>S. mordax</em>, <em>Palaeospilus becosiensis</em></td>
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<tr>
<td>DIPTERA</td>
<td><em>Palaeolimnophila layangensis</em>, <em>Geothoneura delichoptera</em>, <em>Chironomaptera gregaria</em>, <em>Ch. vesca</em>, <em>Mesochorbonia shangshuyangensis</em>, <em>M. pallens</em>, <em>Coelochirona xunhua</em>, <em>Prothepha orientalis</em>, <em>Phloeomyia bellii</em>, <em>Atrontima shandongensis</em>, <em>Mesocera petriformis</em>, <em>Palaeocephalina layangensis</em>, <em>Mesopetra tuangensis</em>, <em>Lithoptera kirsula</em>, <em>Pseudopetra grandis</em>, <em>P. exilis</em>, <em>Sinoleta latea</em></td>
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Beipozi, Huangyandi, Houzigu, Mareshan and Cuitan in the Liaiyang basin (Figure 1). There are differing interpretations regarding the subdivision of the Liaiyang 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 Liaiyang Formation into six members within the Lower and Upper subformations, the former being absent in the Liaiyang district. Chen et al. (1980) also divided this stratum into six members. In this paper the Liaiyang 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 Nanlizezhuan and Tuanwang localities yielded a great diversity of well-preserved fossil insects from the thin "paper" shales of the Third Member (Figure 2).

2. Liaiyang entomofauna

Coleoptera are the most abundant taxa in the Liaiyang 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 *Coptocleta longipoda*, *Mesolycogas layangensis*, *Chironomaptera gregaria* and *Ch. vesca* have been recovered.

The backswimmer, *Chyphostemma xiphale* (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 Liaiyang Formation (Zhang, 1985). It has also been reported from the Xinminpu Group near Yimen, Gansu province (Hong, 1982), and the Gurvaneren Formation at Gurvan-Ereyi-Nuru, Mongolia (JS-MPE, 1986).

Figure 1. Locality map showing the Liaiyang entomofaunal sites, Shandong province. 1-Beipozi, 2-Huangyandi, 3-Houzigu, 4-Mareshan, 5-Nanlizezhuan, 6-Tuanwang, 7-Cuitan.

The large aquatic beetle, *Coptocleta longipoda* (Figure 3B, C), has been found in late Mesozoic strata throughout East Asia. This species was first described from the Liaiyang Formation (Ping, 1928), the Shouchang Formation (Lin, 1980), the Jiufutang Formation, Liaoning province (Lin, 1976), the Guyang Formation in Nei-Mongol (Hong & Wang, 1976), the Chejinjiao 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-Ereyi-Nuru and Khukh-
Mort (JS–MPE, 1980, 1986). It has also been found in the Turga Formation at Baissa, Trans Baikal (Ponomarenko, 1961).

The phantom midge, Chromonemoptera 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).

Mesobygaeus 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 Lushangshuen Formation of the Xishan [Western Hills], Beiji. Hong (1981) regarded the fossils from the latter locality as a new taxon, Xishania fusiformis, 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 Zaaz 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 2. Stratigraphic section of the Third Member of the Laiyang Formation (J3 4, see text) at Nanligezhuan, 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–gravelbearing arkose, 8–conglomerate, 9–schist, 10–conformity, 11–disconformity, 12–angular unconformity, 13–fossil plant fragments, 14–fossil insects.

Figure 3. Fossil insects from the Laiyang Formation near Laiyang, Shandong province, China. All specimens numbers refer to the collections at the Shandong Provincial Museum, Jinan City, Shandong. A—Chytopsoma xiphidae, adult (×3.9), L84996, from Beipizi; B—Coxopodema longipoda, adult (×1.1), L87649, from Nanligezhuan; C—Coxopodema longipoda, larva (×1.5), L87662, from Nanligezhuan; D—Chromonemoptera gregaria, adult (×7.3), L84844, from Nanligezhuan; E—Chromonemoptera vesca, adult (×7.3), L84285, from Nanligezhuan; F—Mesobygaeus laiyangensis, adult (×7.3), L88222, from Nanligezhuan; G—Pseudoacrida costata, front and hind wings (×3.6), L84985, from Tuanwang; H—Panaphis circa, adult (×8.8), L84127, from Tuanwang.
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 km²) 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 Thrinclisporites sp., Zamites sp., Otozamites linguliformia, Baiera cf. australis, Araucarites sp., Brachypityllum omanum, Pagiophyllum sp., Sphenolepis kurriana, Palaeoeyptis sp., Equitesites sp., Ruffordia goepertii, Elatocladus sp., Elatides sp., Cupressinocladus elegans, Sagenopteris mantelli and Onychites 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 equinalean 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, Copoelophas longispina (Figure 3B, 3C), the predacious bugs, Cephalostoma sp., (Figure 3A), C. petita (Figure 4B), Karataula shandongensis (Figure 4C), Mesobryo ayangensis (Figure 3F), Schizapteryx shandongensis (Figure 4D), S. laccatus (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 Manlayanmyia, Palaeoentomatus and Mesobryo. The first contains abundant Manlayanmyia dabeigouensis (Diptera, Chironomidae), Ephemeropsis tristalis (Ephemerida, Hexagenitidae) and Copoelophas longispina (Coleoptera, Copoelophasidae), and was first identified from the Dabeigou Formation, Hebei province. The second assemblage consists principally of Palaeoentomatus labii (=Archaemoschus labius
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4. Ephemeropsina fauna

The *Ephemeropsina* 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 *Ephemeropsina* fauna into three assemblages based on stratigraphic and geographic distribution, and characterized by the genera *Manlayamia*, *Palaeeomphus* and *Mesolygaena*. The first contains abundant *Manlayamia dabsiguisensis* (Diptera, Chironomidae), *Ephemeropsina tristails* (Ephemeroidea, Hexagenidae) and *Coptocleava longipoda* (Coleoptera, Coptocladidae), and was first identified from the Daibigou Formation, Hebei province. The second assemblage consists principally of *Palaeeomphus labius* (= *Archaeomphus labius*).
Lin, 1976) (Odonata, Gomphidae) and *Ephemeropsis tristatales*, 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 Nanzha Formation, Henan province (Cao et al., 1986). The *Mesolygaeus* assemblage is diverse and includes principally *M. layangensis*, *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 tristatales* and *Coptoclava longipoda*, had a persistent duration.

In northern Hebei, late Mesozoic strata are divided into seven formations: Zhangjiakou, Dabeigou, Dadianzi, Huaijiying, Nandian, Qingshila and Tujingzi.
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 *Copocelata 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 Xingan 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, Huangjiang, 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, *Manlayamya*, *Palagopodus* 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 (*Manlayamya* and *Palagopodus*), and the Mogotuin and Gurvanerlen 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 peninsula (Kalugina, 1974, 1977; Remm, 1976; Alekseyev & Rasnitsyn, 1981; Townes, 1973b).

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References


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Kalugin, N. S. 1974. Changes in the subfamily composition of chironomids (Diptera, Chironomidae) as an indicator of possible eutrophication of bodies of water during the late Mesozoic. *Moscow Society of Biology* 79, 45–56. [In Russian].


Rasnitsyn, A. P. 1975. Mesozoic higher Hymenoptera. *Proceedings of the USSR Palaeontological Institute* 147, 1–140. [In Russian].


