

Cretaceous insects of China

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Recently collected insect fossils from 63 localities in Cretaceous strata in China comprise several thousand specimens, and permit a detailed analysis of Cretaceous insect evolution and palaeogeography in eastern Asia. The Cretaceous *Mesolygeus laiyangensis* and *Chironomaptera gregaria* are absent below 35°S. Their distribution is significant because it supports the existence of northern and southern palaeobiogeographic regions. During the Cretaceous three insect faunas of the northern region and four insect assemblages of the southern region are distinguished and different aspects of these faunas are discussed.

KEY WORDS: Cretaceous; insects; palaeobiogeography; biostratigraphy; China.

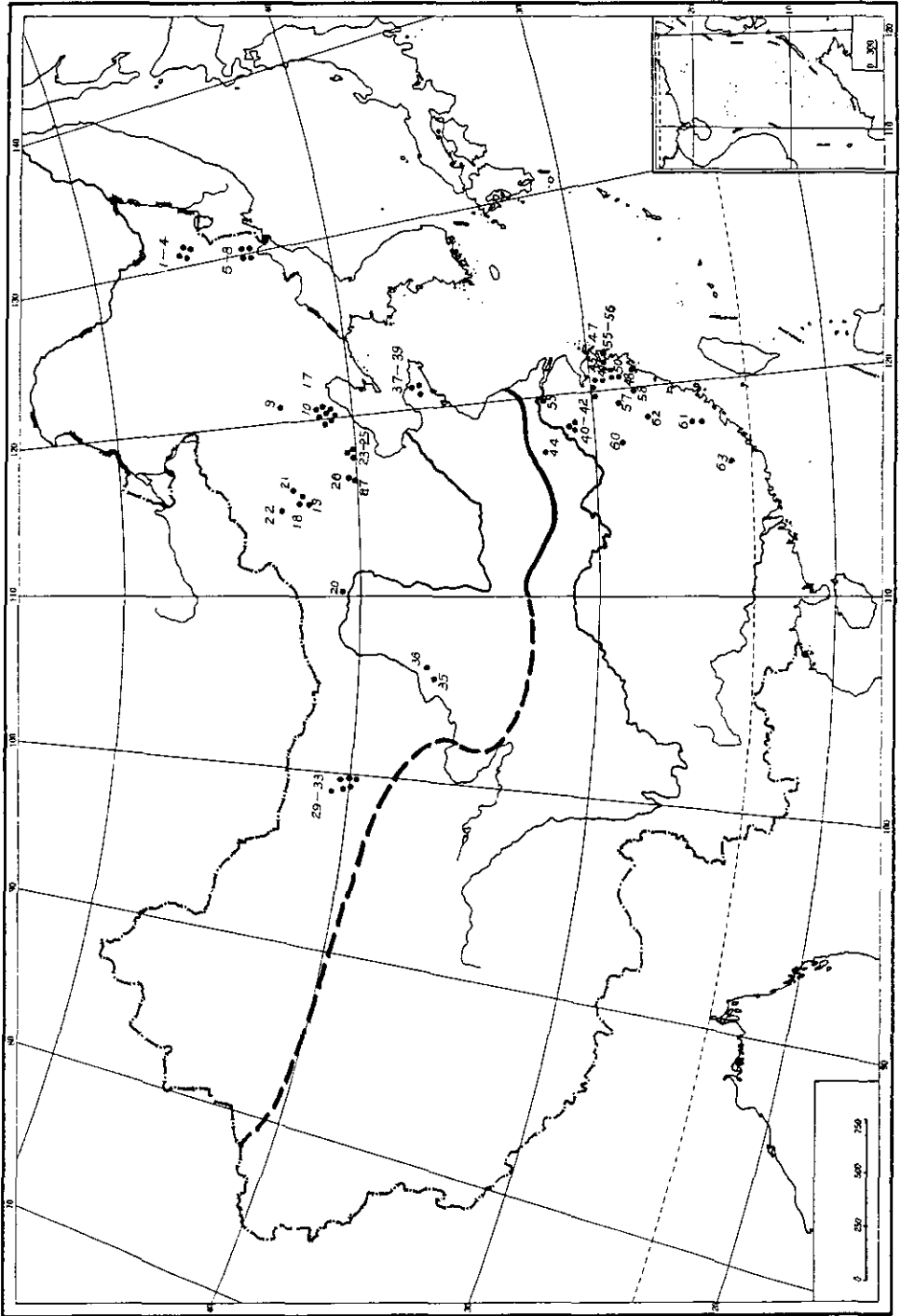
1. Introduction

Fossil insects from the nonmarine Lower Cretaceous *Lycoptera*-bearing beds around Laiyang, Shandong province, were first described by Grabau (1923). He identified the existence of Cretaceous strata in this region and described *Sinoblatta laiyangensis* Grabau, *Laiyangia paradoxiformis* Grabau, *Proteroscarabeus yeni* Grabau and *Samarura gregaria* Grabau. The Cretaceous age is determined by the occurrence of *Proteroscarabeus*, a post-Jurassic insect, and by a characteristic post-Jurassic flora from the Laiyang Formation. Later, Ping (1928) reviewed these specimens and complemented the fauna with rich material from Jehol in north-east China. Collections of fossil insects from 63 localities (Figure 1) have since been made, especially during the past decade (Chen & T'an, 1973; Lin, 1976, 1978, 1980, 1983, in press; Hong, 1965, 1982; Zhang, 1986, 1989, 1990, 1992), and they permit a thorough analysis of Late Jurassic–Cretaceous insect development, palaeobiogeography and palaeoclimate in eastern China.

2. Biogeography

Fossil insects of the Jehol fauna of northern China are characterized by lacustrine forms and some terrigenous forms. For example, *Sinoraphidia viridis* (snake fly) and *Mesolygeus laiyangensis* (water bug) are common in northern China, but not in the south; *Notocupes undatabdomenus* of southern China does not occur in the north. The phantom midge *Chironomaptera gregaria* and the waterboatman *Karataviella* sp. are found north of 35°N, thus play a significant role in correlating strata between northern China and Shandong, both of which lie north of this latitude. *Ephemeropsis trisetalis* is a dominant form in the northern region from the latest Jurassic. It then migrated into the southern regions in the earliest Cretaceous (Chen, 1988).

In the Laocun Formation of Zhejiang, the predominant insect fossils are *Linicorixa odota*, *Mesopanorpa yaojiashanensis*, *M.?* *gambra*, *Lycoriomima mictis*,



Hemirysus leucus, and the chironomids *Tinactum solusum*, *Vidiauata otiosa*, *Orusa barba* (Lin, 1980). *Limicorixa odata* (waterboatmen) were microphagous feeders in small or shallow water bodies. *Tinactum solusum*, *Vidiauata otiosa* and *Orusa barba* were semiaquatic insects: modern adult forms do not feed and swarm gregariously, while larvae inhabit slow-moving water bodies. *Mesopanorpa yaojiashanensis* was terrestrial from that underwent metamorphosis in the soil; both larvae and imagoes were carnivorous. *Hemirysus leucus* used a long ovipositor for introducing eggs into prominent wood borings.

More than 12 dragonfly species have been identified from the Upper Jurassic to Lower Cretaceous strata in China. Eleven known taxa and two indeterminata occur in the north, for example *Pseudosamarura largina*, *Yixiangomphus labisus*, *Sinoaeschnidia heishankowensis*, *Dissurus tiayuanensis*, *Huaxiangomphus taushanensis* from the Yixian Formation of Liaoning; *Cercus clavus*, *Dissurus quinguanensis*, *Brunneaschnidia jiuquanensis*, and *Yixiangomphus* sp. from the Chijingqua Formation of western Gansu; *Hebeiaeschnidia fengningensis* from the Xiguayan Formation of Hebei; *Liupanshania sijiensis* and *Guyuanaeschnidia eximia* from the Liupanshan Group of Ningxia; and *Congqingia rhora* from the Laiyang Formation of Shandong. There is only one species, *Sinoaeschnidia huzouensis*, from southern China. Larvae of dragonflies inhabited slow-moving freshwater bodies, but the adults flew in surrounding areas. The abundance of dragonflies in northern China is indicative of warm and humid climates, and their scarcity in the south is considered to reflect an unfavourably hot and arid climate. This model is reflected also in the flora (e.g. Cao, 1982).

The above-mentioned differences indicate that a northern and a southern biogeographic province existed during the latest Jurassic and Cretaceous in China. The boundary between these provinces is tentatively placed along the Tianshan, Qinling, and Dabai range suture zone (approximately 35°–32°N) (Figure 1).

3. Insect faunas

3.1. North China

A succession of Upper Jurassic to Lower Cretaceous coal-bearing strata is well developed in Liaoning, Jilin and Heilongjiang provinces of north China, from which 39 rich fossil insect localities have been reported (Figure 1). Fossils from these beds are divided into three insect faunas:

Figure 1. Map of China showing the distribution of Upper Jurassic and Lower Cretaceous fossil insect localities. The bold line marks the palaeontological province boundary, separating northern and southern China. Heilongjiang Province: 1, Chengzihe (near Jixi); 2, Jiazihe (near Boli); 3, Yilin (near Muqing); 4, Hegang, Jilin Province; 5, Tonghua; 6, Hunjiang; 7, Jiutai; 8, Dalazi (near Yanji), Liaoyuan. Liaoning Province: 10, Yixian; 11, Heichengzi (near Beipiao); 12, Zhaoyang; 13, Lingyuan; 14, Kazuo; 15, Fuxin; 16, Shaha; 17, Damingshan; 18, Naiman-qi. Nei-Monggol: 19, Damiao (near Chifeng); 20, Guyan; 21, Duolum; 22, Ayouqi. Hebei Province: 23, Weichang; 24, Zhouyingzi (near Luanping); 25, Fengning. Beijing: Xishan mountains; 27, Lushangfen. Henan Province: 28, Mashiping (near Nanshao). Gansu Province: 29, Yumen; 30, Chijingqiao; 31, Changma; 32, Sunan; 33, Shandan; 34, Hongliugou. Ningxia Province: 35, Shijizhen (near Guyuan); 36, Ordos. Shandong Province: 37–39, Tuanwang, Beipozi and Marshan (near Laiyang). Anhui Province: 40, Shexian; 41, Shangcaoshi; 42, Yantang; 43, Chuxian; 44, Hefei. Zhejiang Province: 45, Shouchang; 46, Laocun; 47, Linan; 48, Chenshan (near Zhenhai); 49, Xiakingjia (near Zhuji); 50, Qianjiawu; 51, Laozhu (near Lishui); 52, Grenting (near Yongjia); 53, Linhai; 54, Limei (near Jinhua); 55, Xiaoxisi; 56, Ziyanhuan; 57, Hejia (near lanxi); 58, Xitanghu (near Longyuo). Jiangsu Province: 59, Tianshenqio. Jiangxi Province: 60, Yiyang. Fujian Province: 61, Ninghua; 62, Shounin. Guangdong Province: 63, Xingning.

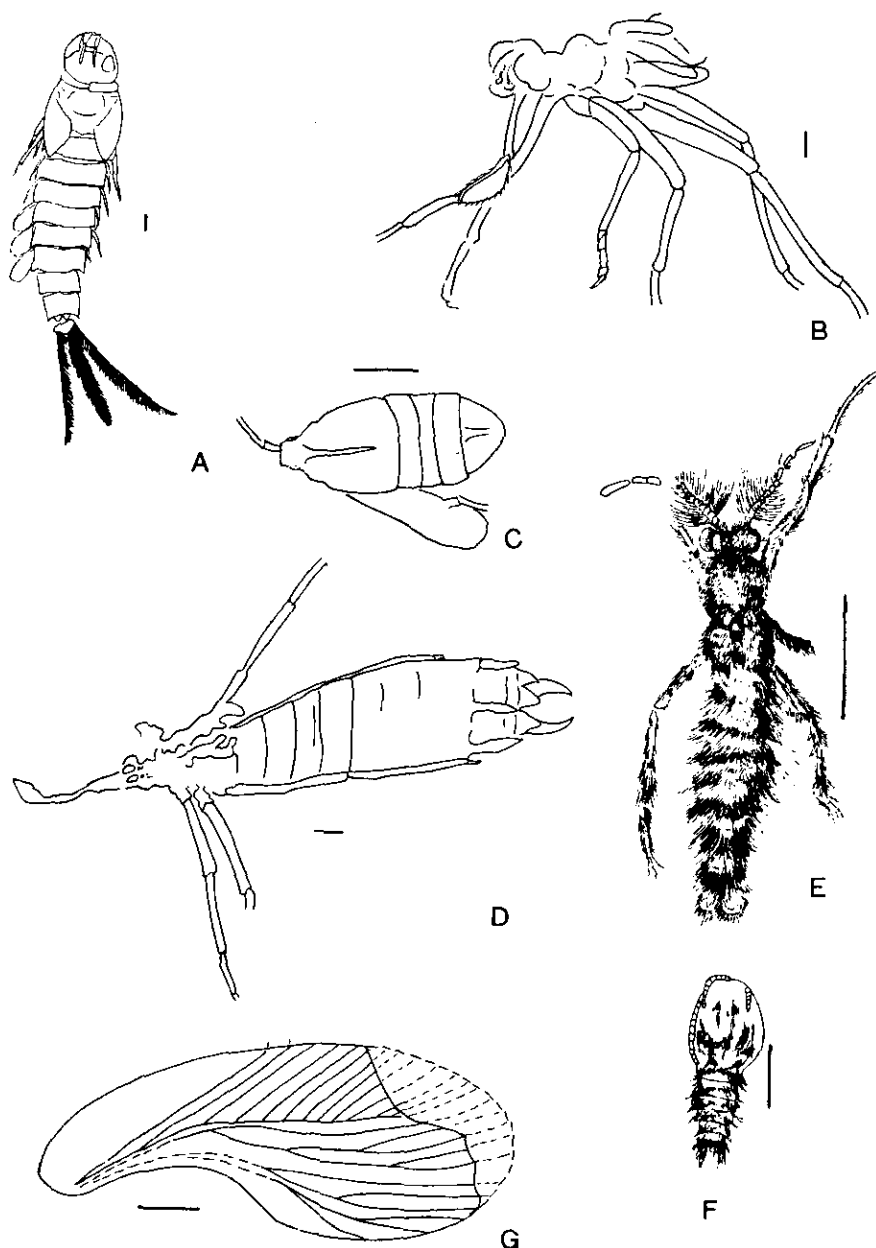


Figure 2. *Ephemeroptera* fauna from the northern China region. A, *Ephemeroptera trisetalis* Eichwald (nymph: 19528) from the Yixian Formation, Beipiao, western Liaoning; B, *Pseudosamarura largina* Lin (larva: 20074) from the Yixian Formation, Yixian, western Liaoning; C, *Mesolygeus laiyangensis* Ping (adult: 20076) from the Jiufotang Formation, Kazuo, western Liaoning; D, *Yixiangomphus labius* (Lin) (larva: 19529) from the Yixian Formation, Yixian, western Liaoning; E, F, *Chironomaptera gregaria* Ping (E, imago, 20088; F, prepupa, 20099) from the Jiufotang Formation, Kazuo, western Liaoning; G, *Rhipidoblattina? fuxinensis* Lin (tegmen: 20075) from the Shapai Formation, Fuxin, western Liaoning. All specimen numbers refer to collections at the Nanjing Institute of Geology and Palaeontology. Scale bars are 2 mm.

Ephemeroptera Fauna (Tithonian–Valanginian). This fauna belongs to the classic Jehol fauna defined by Grabau (1923) and comprises many lacustrine and terrestrial forms. This fauna has been divided into three assemblages based on stratigraphic and geographic distribution (Zhang, 1992). The first assemblage

contains abundant *Manlayanyia hebeiensis*, *Ephemeropsis trisetalis* and *Coptoclava longipoda* from the Dabeigou Formation, Hebei province. The second assemblage consists primarily of *Yixiangomphus labius* (= *Archaeogomphus labirus* Lin, 1976, or *Palaeogomphus labirus* Zhang, 1992; figure 2D) and *Ephemeropsis trisetalis* (Figure 2A), with additional forms in different localities. This assemblage is known principally from the Yixian Formation and coeval strata in northern China. The third assemblages includes *Mesolygeus laiyangensis*, *Chironomoptera gregaris* (Figure 2E, F), *C. vesca*, *Coptoclava longipoda*, *Pseudoacrida costata*, *Palaeopetia laiyangensis*, *Mesopetia tuanwangensis*, *Lithopetia hirsuta*, *Clypostemma xyphiale*, *Penaphis circa*, and *Petiolatendipes shouchangensis*. The last three forms are from the Shouchang Formation of Zhejiang (Lin, 1980), which is Valanginian in age. The first two are here regarded as Tithonian in age.

Mesolygeus laiyangensis is extremely abundant in the Laiyang (Figure 2C), Luohandong, Madongshan and Xiagou formations. This water bug is found only in northern China and eastern Mongolia, and is absent in southern China.

Chironomoptera gregaria was described by Ping in 1928 (Figure 2E, F), but its systematic position remained unclear until Kalugina (1974, 1977) described specimens with well-preserved genitalia and body hairs which clarified its position. Zhang (1990) recorded two species of *Chironomoptera* from Laiyang, and considers *C. vesca* and *Petiolatendipes shouchangensis* to be synonymous. My research shows that *P. shouchangensis* does not have the particular genitalia and body hairs characteristic of *C. vesca* from the Laiyang Formation, thus *P. shouchangensis* is a chironomid midge, while *C. vesca* is referred to the Chaoboridae. *C. gregaria* is not known from southern China.

Parahagloopsis Fauna (Hauterivian-Barremian). Succeeding the *Ephemeropsis Fauna* are the forest insects *Parahagloopsis posteria*, *Rhipidoblattina jilinensis* (Figure 3) *R. shulanensis*, and *R? fuxiensis* (Figure 2G), and the terrestrial insects *Jiutanina erroranusa*, *Liutaiprosbole aeschrosis* (Figure 4B), and *Liutaipsychops borealis* (Figure 4A).

Parahagloopsis posteria is very similar to *Parahagla sibirica* known from the Tyurkina Formation of the Transbaikalian region of Russia (Sharov, 1968). *Rhipidoblattina jilinensis*, *R. shulanensis* and *R? fuxinensis* bear a close resemblance to *R. gurvaniensis* from the Lower Cretaceous Gurvaneren Formation of western Mongolia (Vishniakova, 1986). These *Parahagloopsis* and *Rhipidoblattina*-bearing rocks, such as the Yincheng and Fuxin formations of Jilin and western Liaoning in NE China, contain abundant fossil plants, palynomorphs, ostracods and conchostracans which indicate an approximately Valanginian to Hauterivian age (Ye & Zhong, 1990). *E. trisetalis* has not been reported in typical insect-bearing strata, such as the Qingshila Formation in northern Hebei, the Tuoli Formation near Beijing, the Zhidan and Liupanshan groups in the Shaanxi, Gansu, Ningxia region, and the Xiagou Formation of western Gansu. One or two isolated and incomplete specimens possibly attributable to *E. trisetalis* have been reported from the Shapai or Yincheng formations. This indicates a reduced extent of lacustrine environments during the latest Jurassic to earliest Cretaceous.

Geotrupoides Fauna (formerly *Coptoclava Assemblage*) (Aptian-Albian). This fauna is found in the Dalazi Formation and includes two ecological groups: the terrestrial and aquatic or semi-aquatic groups. The former is represented mainly by Coleoptera, and includes the carnivorous carabid beetles *Protorabus minisculus* and *Ensicupes dalaziensis*; the saprophagous scarabaeid beetles *Geotrupoides saxosus* and *Proteroscarabaeus dalaziensis*; the phytophages such as



Figure 3. *Rhipidoblattina jilinensis* Lin (imago) from the Yincheng Formation, Liutai, Jilin (Nanjing Institute of Geology and Palaeontology No. J19511). Scale bar: 2 mm.

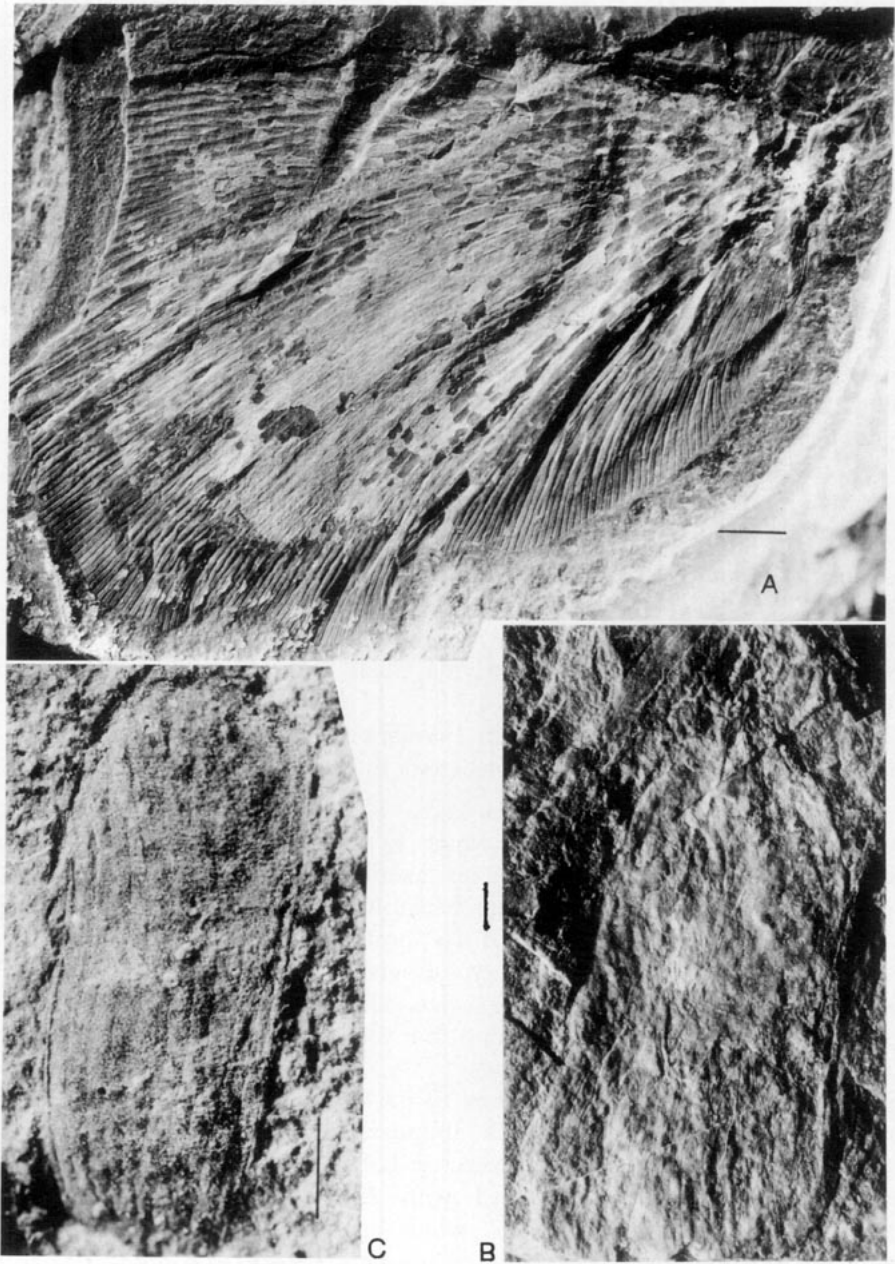


Figure 4. *Parahagloopsis* fauna of northern China. A, *Liutaipsychops borealis* Lin (forewing: J19512); B, *Liutaiprosbole aechronensis* Lin (forewing: J19513); C, Curculionidae indet. (elytron: J19514). All specimens, housed in the collections of the Nanjing Institute of Geology and palaeontology, are from the Yincheng Formation, Luitai, Jilin. Scale bar: 2 mm.

Distenorrhinus magnus. Mesoblattinid cockroaches such as *Rhipidoblattina magna* and *R. decoris*, and the pygidicranids such as *Geosoma prodroma*, were polyphagous and were typically forest dwelling insects in tropical to subtropical humid climates. The hymenopterid *Ovigoster cephalotus* Zhang, was a parasitic insect. The ecological complexity and diversity of this community is greater than for the *Parahagloopsis* Fauna.

The aquatic and semi-aquatic group has a low diversity, but contains abundant *Cristosorixa dalaziensis* H. Zhang, *Coptoclava longipoda*, and *Chironomoptera* cf. *gregaria*. The cockroach *Umenocoleus* sp., which previously had been referred to the Coleoptera (Chen & T'an, 1973), first appears in this fauna and occupies an evolutionary position between the Umenocleidae and the Corrydiidae or Euryrrhapidae. A form similar to *Umenocolius* sp. is reported from the Santana insect assemblage in the Crata Crato Member (Aptian–Albian) in Brazil (Grimaldi, 1991).

The *Geotrupoides* Fauna consists of 17 genera in 15 families and 7 orders, and the genera *Cristocorixa*, *Protorabus*, *Proteroscarabaeus*, *Geotrupoides*, *Chironomoptera* and *Rhipidoblattina* are also recorded from Lower Cretaceous strata in western Mongolia.

The *Mongolocypis yanjiensis*–*Cypridea coninaformis* ostracod assemblage and the palynomorphs *Cicatricosisporites*, *Shizaeosporites* and *Tricolpites* are known from the Aptian–Albian Dalzi Formation (Gou, 1983; Yu & Miao, 1984).

3.2. South China

Mesopanorpa Fauna (*Berriasian*). This fauna includes *Linicorixa odota*, *Tinactum solusum*, *Viduata otiosa*, *Orusa barba*, and terrestrial insects such as *Lycoriomoma mictis*, *Mesopanorpa yaojiashanensis*, *M. ?gambra*, and *Humiryssus leucus* (Lin, 1980). These forms inhabited low-lying areas with common shallow water bodies.

This fauna is found in the Laocun Formation of western Zhejiang province, which comprises the lowest Cretaceous strata in southeastern China.

Penaphis Fauna (*Valanginian*). This fauna is characterized by the abundant waterboatman *Vulcanicorixa dorylis*, which is a phytophage that lived in small lakes feeding off diatoms and algae. This taxon is similar to *Baissocorixa* from the Neocomian Baissa Formation in Trans-baikal Russia. Homoptera are represented by the aphid *Penaphis circa* (Figure 5F), a form that appears in the lower part of the Weald Clay Group of southern England (Jarzembowski, 1989). The chironomid midges *Petiolatendipes shouchangensis* (Figure 5E) and *Baishulingella micris* (Figure 5D) are commonly found, but the hexagenitid mayfly, cockroaches and primitive katydids are absent.

Strata containing these forms belong to the upper member of the Shouchang Formation in Zhejiang, from which abundant ostracods, conchostracans, bivalves, fish, and plant mega- and microfossils have been recorded. Insects from this fauna are generally associated with *Ephemeropsis trisetalis*, *Coptoclava longipoda*, and *Clypostemma xyphiale*, which are also reported from the Third Assemblage of the Laiyang Formation in northern China. This indicates that the Shouchang and Laiyang formations are approximately equivalent in age. *Huizhougenia orbicularis* (Figure 5C) and *Ratiticorixa stenorhynchis* (Figure 5A, B) from the Yantang Formation in southern Anhui are referred to this fauna since this formation can be correlated with the Shouchang Formation in neighbouring Zhejiang.

Solusipanorpa Fauna (*Aptian–Albian*). This fauna is characterized by highly diverse terrestrial insects, such as the monkey grasshoppers (Eumastacidae) and cockroaches (e.g., *Taphacris turgis* and *Zhujiblatta anofissilis*; Figure 5 I, J). They indicate a tropical or subtropical leaf-litter environment (Imms, 1960; Fujiyama, 1973). The following tropical or subtropical plant megafossils occur in associated beds of the Gantou Formation (Aptian–Albian) in Zhejiang: *Onchiopsis elongata*,

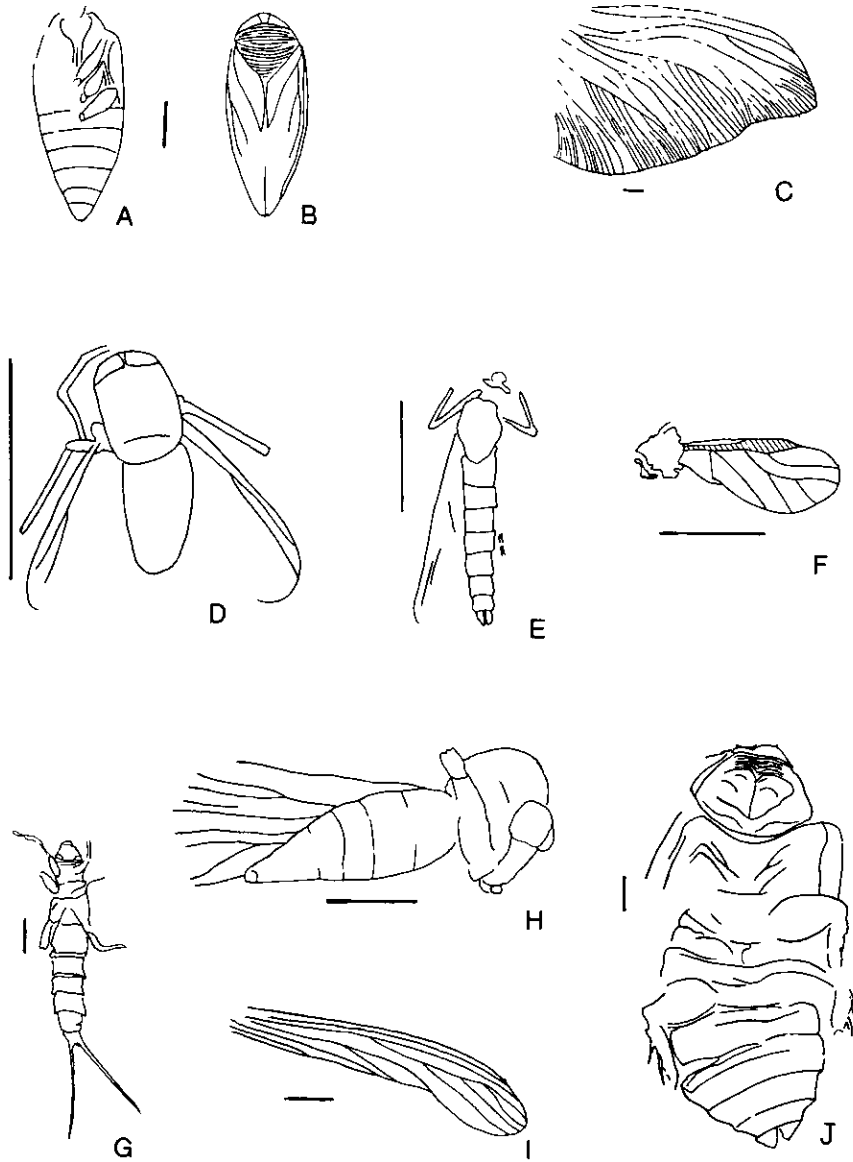


Figure 5. *Penaphis* fauna (A–F) and *Solusipanorpa* fauna (G–J) from southern China (A–F): A, B, *Ratiticorixa stenorhinshis* Lin (imago: 38581) from the Yantang Formation, Shexian, Anhui; C, *Huizhougentia orbicularis* Lin (forewing: 38556) from the Yantang Formation, Shexian, Anhui; D, *Baishuilingella micris* Lin (imago: 38597) from the Upper Member of the Shouchang Formation, Shouchang, Zhejiang; E, *Petiolatendipes shouchangensis* Lin (imago: 38596) from the Upper Member of the Shouchang Formation, Shouchang, Zhejiang; F, *Penaphis circa* Lin (imago: 38582) from the Upper Member of the Shouchang Formation, Shouchang, Zhejiang; G, *Fluminiperla hastis* Lin (nymph: 38573) from the Guantou Formation, Zhuji, Zhejiang; H, *Solusipanorpa gibbidorsa* Lin (adult: 38585) from the Chaochuan Formation, Zhuji, Zhejiang; I, *Taphacris turgis* Lin (tegmen: 38586) from the Chaochuan Formation, Zhuji, Zhejiang; J, *Zhujiblatta anofissilis* Lin (imago: 38562) from the Chaochuan Formation, Zhuji, Zhejiang. All specimens are in the Nanjing Institute of Geology and Palaeontology.

Cladophlebis browniana, *Otozamites* cf. *staenstrupi*, *Dictyozamites* sp., *Zamites* sp., *Cupressinocladus elegans*, *Brachyphyllum obesum* and *Sagenopteris shouchangensis*. The scorpionfly *Solusipanorpa gibbidorsa*, and the stonefly *Fluminiperla hastis* reflect a more open, grassy environment with proximity to freshwater (Riek,

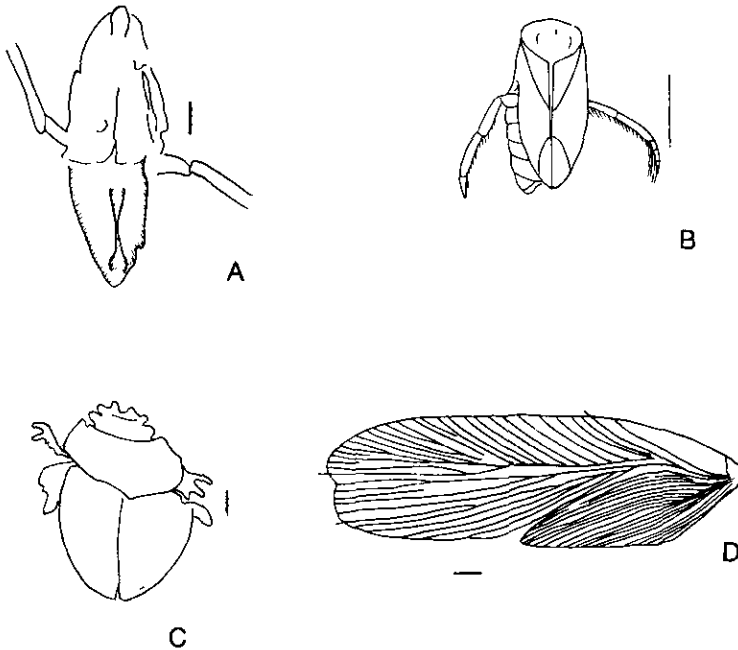


Figure 6. *Siculicorixa* fauna from southern China. A, *Clypostemma limna* Lin (imago: 38564); B, *Siculicorixa estria* Lin (imago: 38580); C, *Prionocephale deplanate* Lin (adult: 38602); A–C from the Lanxi Formation, Lanxi, Zhejiang; D, *Strictiblatta longanusis* Lin (tegmen: 38563) from Upper Cretaceous, Hefei, Anhui. All specimens are in the collections of the Nanjing Institute of Geology and Palaeontology.

1979). *Anaglyphites laximandibule* Lin is a specialized wood-feeder. The insects of this fauna are from two formations in Xiaoxisi near Zhuji, Zhejiang. *Zhujiblatta anofissilis*, *Fluminiperla hastis* (Figure 5G) have been reported from the Gantou Formation, while *Taphacris turgis*, *Solusipanorpa gibbidorsa*, and *Anaglyphites laximandule* are from the Chaochuan Formation (Lin, 1980).

Siculocorixa Fauna (Turonian?–Santonian). Late Cretaceous insect fossils are rare, but five localities in the Lanxi Formation of Zhejiang are reported. The dominant form is *Siculocorixa estria* (Figure 6B), with *Prionocephale deplanate* (Figure 6C) and *Clypostemma limna* (Figure 6A). *S. estria* is a more specialized waterboatman that inhabited small lakes. Nymphs and adults of *C. limna*, like *C. xyphiale*, was an aquatic form. This fauna indicates that swamp or lake environments were widespread in the Jinhua–Quxian basin during the Late Cretaceous.

The age of this assemblage is determined from fossil ostracods (*Cypridea* (*Pseudocypridea*) *porrecta*, *C. (P.) aversa*, *Cristocypridea triangulata*) and conchostracans (*Zhestheria*, *Sinoestheria*) (Ye, 1983).

4. Conclusions

Seven faunas and two biogeographic regions in China are identified based upon the distribution of insect fossils during the Cretaceous.

Fossil insects from strata adjacent to the Jurassic–Cretaceous boundary have been reviewed by Chen (1988) and Zhang (1992 and references therein). Here I divide the insects of the Jehol biota into three distinct faunas in the north, and four faunas in the south. Earliest is the *Ephemeropsis* fauna, here regarded as Tithonian to Valanginian in age, and is the closely related genus *Mongologenites*

Sinitshenkova of the Gurvaneren Formation of western Mongolia (Sinitshenkova, 1986). The abundance of *E. trisetalis* declined significantly at the top of the Jiufutang Formation, and does not persist into the Shahai, Yinchang, and Xiagou formations across northern China; it is present in small numbers in the lower member of the Shouchang Formation (Zhejiang), but is absent in the upper member.

Ponomarenko & Popov (1980) and Pritykina (1986) indicated that in the Early Cretaceous western Mongolia and the Trans-baikal lay outside the East Asiatic province of the Indo-European region. My research confirms both this observation, and that the fact that most nonmarine fossil insects from the Upper Jurassic and Cretaceous strata in China belong to the East Asiatic province of the Indo-European region.

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