The Shanwang fossil biota in eastern China: a Miocene *Konservat-Lagerstätte* in lacustrine deposits

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The Miocene Shanwang biota in eastern China is one of the taxonomically most diversified and extraordinarily well-preserved lacustrine fossil deposits in the world. This study provides the historical and geological background, documents the taxonomic diversity, and examines the preservational style of this unique *Konservat-Lagerstätte*. A 30 m thick diatomaceous shale (the lower part of the Shanwang Formation), deposited in a small and volcanically related lake basin under a warm temperate climate, hosts more than 500 fossil species, including fungi, diatoms, higher plants, insects, ostracodes, fishes, amphibians, reptiles, birds, and mammals. The excellent preservation of the fossils has yielded (1) non-mineralized organic tissues of animals and plants; (2) detailed morphology of delicate organs such as flowers, feathers, and hairs; (3) original coloration of plants and insects; and (4) completely articulated animal bodies with *in situ* teeth, skin, and even stomach contents. The highly diversified fossil biota shows a complex interrelationship of co-occurring organisms that once lived in a eutrophic water body with a dense forest nearby. The preservation of soft tissues among the Shanwang fossils provides feasible material for further molecular-level investigation of these Miocene organisms. □*Miocene, KONSERVAT-LAGERSTÄTTEN, lacustrine, taxonomic diversity, preservational style, Shanwang, China.*

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Extraordinarily well-preserved fossils (*Konservat-Lagerstätten*) not only provide detailed morphologic and molecular information of ancient life, but also offer nearly complete pictures of ancient communities that vanished millions of years ago. Fossilization of soft tissues results from rare depositional events, but such windows on ancient ecosystems, the Burgess Shale (Middle Cambrian) of Canada, the Solnhofen Limestone (Late Jurassic) and the Messel Oil Shale (Middle Eocene) of Germany, for example, are well known throughout the international scientific community, and they have considerably enriched our knowledge of the history of life.

Documentation of occurrences of *Konservat-Lagerstätten* of different age on various continents is scattered throughout the literature (see Allison & Briggs 1991a, b, for references). Among various sedimentary environments that favor soft-tissue preservation, Tertiary lacustrine deposits are well known for their exceptional fossils (Allison & Briggs 1991a). Grande (1984), for example, documented a high diversity of freshwater and terrestrial organisms from the Green River Formation (Late Paleocene to Late Eocene) in Wyoming, Colorado, and Utah. Smiley (1985) studied the Clarkia Miocene fossil deposits in northern Idaho and provided an example of team efforts on various fossil groups of a single exceptional fossil biota. In recent years, progress in molecular paleontology has yielded reports on the extraction and characterization of Miocene DNA from fossil plants preserved as soft tissue in the Clarkia lacustrine deposit (Golenberg *et al.* 1990; Soltis *et al.* 1992). Clearly, further prediction and re-evaluation of fossils with soft tissue demand a better understanding and world-wide search for fossil *Konservat-Lagerstätten*. Moreover, recent investigations of ancient terrestrial ecosystems and their changes through geologic time require more detailed knowledge of such well-preserved fossil biotas on different continents (Wing *et al.* 1992). However, there is little information available in English on extraordinarily well-preserved fossil biotas in China, mainly due to the language barrier and the lack of communication. A recent world-wide survey (Allison & Briggs 1991b) on Phanerozoic *Konservat-Lagerstätten* included only one Chinese site (the Early Cambrian Chengjiang fauna in Yunnan). Since the Shanwang fossil biota is one of the most diverse and extraordinarily well-preserved fossil deposits, and since more than one hundred papers (including two monographs and four M.S. theses) dealing with individual fossil groups

have been published (mainly in Chinese, except for a few in English) on the single site, it deserves comprehensive treatment with emphasis on data derived from a newly completed paleoecologic study. Our objective in this article is to provide geologic, paleontologic, and taphonomic information about the unique lacustrine *Konservat-Lagerstätte*, and we will focus on the taxonomic diversity and the preservational style of this fossil biota. A detailed interpretation of paleolimnological conditions in relation to the origin and taphonomic process of the Shanwang fossils will be published separately.

The Shanwang basin

Location

The Shanwang basin (36°N, 118°E) is located 22 km east of Linqu in the Shandong Peninsula (Shandong Province), eastern China (Fig. 1). The fossil area is an old mining district operated for diatomite ore during the 1950s. Because high-quality fossil material was discovered frequently during the mining operations, the Chinese government, on 17th February, 1980, declared a 1.5 km^2 National Preserved Area. Well-exposed fossil sites can be found in five locations within the preserved area and near the village of Xiejiahe. The abandoned open pit in the northwest foothill of the Jiaoyan Hill is the largest quarry, in which a large percent of Shanwang fossils were discovered (site 1). A smaller open pit to the west of the Xiejiahe village (site 2) exposes the upper part of the fossiliferous section, and fossil site 3 (the Shiliougou section) southwest of the Jiaoyan Hill along the Xiejia River reveals the basal part of the fossiliferous deposits. Fossil sites 4 and 5 have also provided well-preserved fossils, but not as abundant as sites 1–3.

Research history

The earliest written record about Shanwang fossils appeared in the Official Linqu County Documentation, which was edited in the late 1800s (the Qing Dynasty). The unique occurrence of fossil material caught the attention of the local people, although no scientific explanation for the deposits was given. Scientific study of the fossils began in the middle 1930s, and, starting at that time, research about the Shanwang basin has gone through three phases: discovery in the 1930s, systematic description in the 1950s and early 1960s, and revision and paleoecologic synthesis in the 1980s and 1990s.

Young (1936a) surveyed the Shanwang area and completed the first geologic report in which he emphasized the excellent fossil material. He established the Shanwang Series, later changed into the Shanwang Formation, and recognized it as a Miocene deposit based upon the mammal fossils he studied (Young 1937). The fossils from the first Shanwang paleontologic expedition were studied by several specialists,

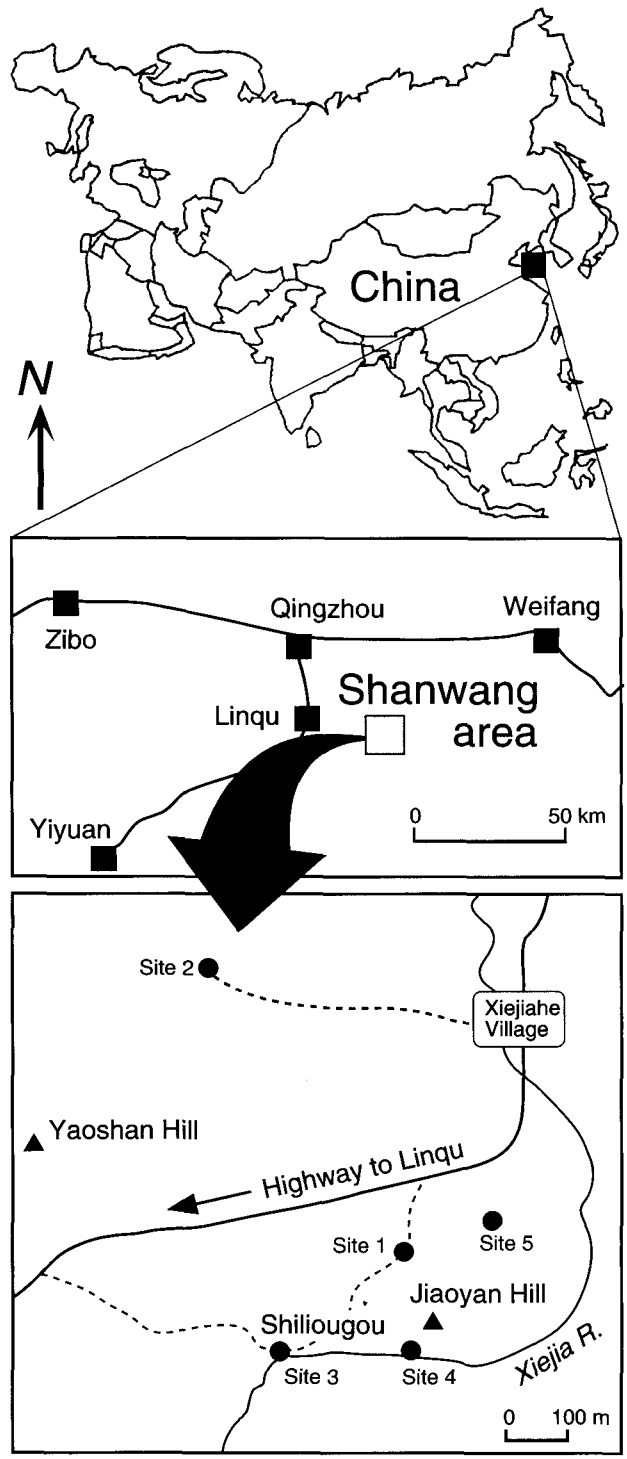

Fig. 1. Location map showing access to the Shanwang basin and different fossil sites. Dashed lines indicate unpaved roads.

and preliminary results on fossil frogs (Young 1936b), fish (Young & Tchang 1936), diatoms (Skvortzov 1937), deer (Teilhard de Chardin 1939), and plant megafossils (Hu & Chaney 1940) were then published. Juan (1937) studied the economic aspects of the diatomite ore in the Shanwang basin

and completed the first topographic map (1:2,000) of the region. Because of the Japanese invasion and the civil war in the late 1930s through 1940s, there was no further research in the Shanwang area until 1955.

Owing to the interest in diatomite ore by the local mining company, a detailed geological project, including several drilling holes, a 1:50,000 geological map, and a 1:10,000 topographic map were completed for the Shanwang basin in 1960. As a result of the mining operation, more fossils were discovered and described. Detailed studies of systematic paleontology of the Shanwang fossils resulted in the accumulation of a huge body of paleontologic information during the late 1950s to the middle 1960s, and the database was refined in the 1980s. The taxonomic documentation and revision of different fossil groups, from microfossils to large mammals, include fossil fungi (Wang 1991), diatoms (Li J.-y. 1982; Shi 1990), spores and pollen (Sung 1959; Song *et al.* 1964; Wang 1981; Liu & Leopold 1992), plant macrofossils (Sze 1951; Academia Sinica 1978; Li H.-m. 1982; Li & Zheng 1986; Yang 1988), insects (Hong 1979, 1983, 1985; Zhang 1986, 1989, 1990), ostracodes (Zheng 1986), fish (Zhou 1990); amphibians (Young 1965; Yang 1977; Gao 1986), reptiles (Sun 1961; Li & Wang 1987), birds (Yeh 1977, 1980, 1981; Yeh & Sun 1984), mammals (Hu 1957; Wang 1965; Li 1974; Chow & Shih 1978; Qiu 1981; Xie 1982; Yan 1983; Yan *et al.* 1983; Qiu *et al.* 1985a, b, 1986; Qiu & Sun 1988; Qiu 1990), and trace fossils (Guo 1991; Shipu Yang, unpublished data). The Shanwang Museum of Paleontology was built in downtown Linqu and opened to the public in 1985.

Besides systematic paleontology, local stratigraphy was refined, and detailed lithostratigraphic units were established by Yan *et al.* (1983) and later modified by Yang (1988) and Li (1991). Petrographic studies of Shanwang basalts were conducted by Wang *et al.* (1981), Wang & Jin (1985), and Wang (1986). Geophysical and geochemical properties of the diatomite and basalt were reported by Ye & Yuan (1980), Zhao *et al.* (1983), Liu & Shi (1989), and Zhi (1990). Several K–Ar dates from various basalt flows in the Shanwang basin have been obtained (Wang *et al.* 1981; Chen & Peng 1985; Jin 1985; Zhu *et al.* 1985). The accumulation of paleontologic and geologic data has led to the current paleoecologic project focusing on the paleocommunity and taphonomy of the fossil biota.

Geological setting

The Shanwang basin is one of the small basins within the Tertiary lake-basin system in eastern China. The important geologic features of the Shanwang basin are:

1 The Tertiary olivine tholeiite (the Niushan Formation), resting above Precambrian metamorphic rocks and Cretaceous pyroclastic rocks, makes up the lake basin floor.

2 The Shanwang Formation, the widely spread rock unit and the main body of the Shanwang Miocene lake, overlies the Niushan Formation and consists of breccia, sandstone, diatomite, mudstone, volcanic ash, phosphorous nodules, and basalt interbeddings; the diatomaceous shale (about 30 m in thickness) hosts the diverse fossil biota (Fig. 2)

3 The Yaoshan Formation, consisting of mainly Tertiary alkalic olivine basalt, tops the Tertiary sequence in the study area. Similar Tertiary lacustrine sequences can be found in Baojiahe, north of Shanwang; in Dachegou, south of Shanwang; and in Qingshan, northwest of Shanwang (Yang 1988; Li 1991).

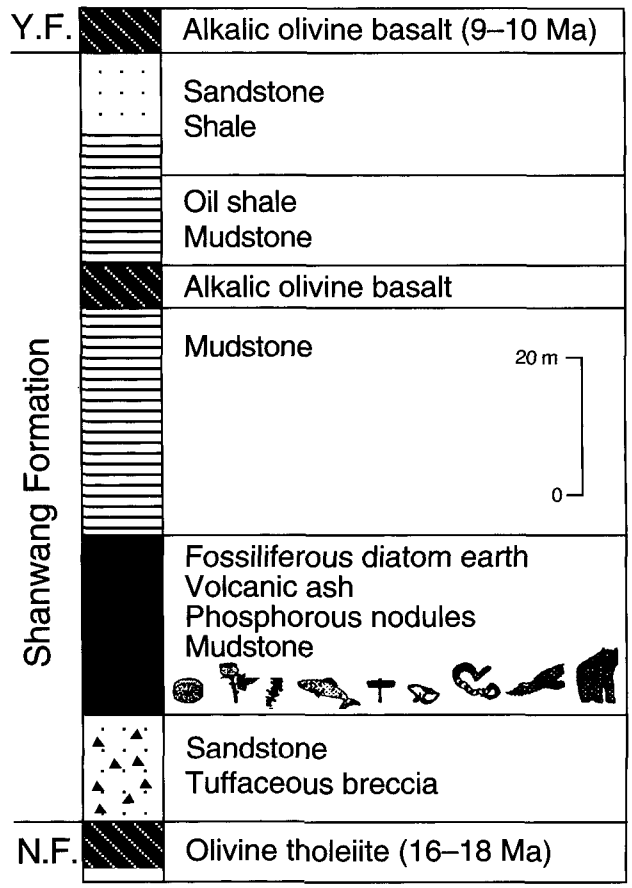

Fig. 2. Generalized stratigraphic sequence of the Shanwang basin showing the fossiliferous diatomaceous unit at the lower part of the Shanwang Formation. Y.F. Yaoshan Formation; N.F. Nushan Formation.

Although this paper does not focus on a detailed analysis of depositional environments of the Shanwang basin, the paleoclimatic and paleolimnologic features of the area are summarized below: (1) A warm temperate climate with mild winters but distinct seasonality is indicated by both fossil assemblages and sediment types; the weather was similar to that in the present-day lower Yangtze River (Changjiang) Valley in southeastern China or in the southeastern US (Yang 1988; Yang & Smiley 1991). (2) The Shanwang Miocene lake, in which the soft-tissue fossils were deposited, was a small basin resting on a lava depression created by the

eruptions of Tertiary basalt (the Niushan Formation) (Yang 1988). (3) The lake had a round-shaped configuration and was probably too shallow to be stratified. (4) Large amounts of biogenous sediments (diatomite) were deposited with a high sedimentation rate in a nearly neutral pH and eutrophic water body (Yang 1993).

Age determination

A Middle Miocene age (15.5–17 Ma) for the Shanwang fossil biota is determined based on both paleontologic and radiometric evidence.

1 Biostratigraphic studies of the fossil deposit indicate that the fossil flora (both megafossils and microfossils) is comparable with Middle Miocene floras in other parts of China, Japan, and North America (Hu & Chaney 1940; Song *et al.* 1964; Li H.-m. 1982; Yang 1988; Liu & Leopold 1992).

2 Abundant mammalian fossils from the site provide detailed chronological correlations for mammalian stages among Shanwang, Europe, and North America, and the Shanwang fauna is believed to be equable to the European early Middle Miocene mammalian stage (MN5, 15.5–17 Ma) (Yan *et al.* 1983; Qiu 1990).

3 The radiometric dates (K–Ar method) of basalt flows below and above the fossiliferous diatomite show that the age of the Niushan Formation (immediately below the fossiliferous diatom earth) is clustered around 16–18 Ma, and the Yaoshan Formation basalt, above the fossiliferous layers, is around 9–10 Ma (Wang & Jin 1985; Chen & Peng 1985; Zhu *et al.* 1985).

Taxonomic diversity

The diverse Shanwang biota in diatomite deposits has yielded more than 500 fossil species from more than ten major groups. Table 1 shows the taxonomic diversity of the biota for each fossil group at the genus level, and a tentative taxonomic list of the fossil biota derived from published systematic studies is available upon request from the senior author. Insects and plant macrofossils are the two most diversified groups in this fossil biota. However, fossil diatoms, although containing only 15 genera, is the most abundant organism in specimen number, and the concentration of diatoms produced a rich diatomite ore deposit, which was the major interest of the local mining company.

Fungi. – A recent preliminary study on fungal fossils from the Shanwang deposit has provided a list of 8 genera and 12 species (Wang 1991). The microfossil flora is dominated by members of Microthyriaceae, a common family in Tertiary non-marine deposits, and *Multicellaesporites* and *Inapertisporites* are dominant genera in the microflora.

Table 1. Taxonomic diversity of the Miocene Shanwang fossil biota.

Taxonomic group	Genera	Species
Fungi	8	14
Diatoms	15	85
Higher plants		
Macrofossils	97	136
Microfossils	63	–
Insects	169	266
Ostracodes	4	6
Fishes	7	10*
Amphibians	4	4
Reptiles	3	3*
Birds	4	5
Mammals	17	12*
Trace fossils	3*	1

*including unpublished specimens.

Diatoms. – The diatom flora comprises 15 genera and 85 species (Skvortzov 1937; Li J.-y. 1982; Shi 1990). The genus *Melosira*, both benthic and planktic species, dominates this diatom flora, and species of *Cymbella*, *Fragilaria*, and *Navicula* are also common. The modern forms of the majority of this diatom assemblage are living in shallow, normal salinity, nutrient-rich, and still water bodies under warm temperate climates.

Higher plants. – The Shanwang flora (both macrofossils and microfossils) is one of the most diverse Tertiary plant fossil deposits in China. A revision of the macrofossils was completed by Yang (1988), and 136 species from 97 genera and 47 families were documented. The flora is dominated by deciduous plants such as members of Betulaceae, Fagaceae, Juglandaceae, Saliaceae, Tilaceae, and Ulmuaceae; they are mixed with evergreen families (e.g., Lauraceae, Magnoliaceae, and Sapindaceae). The ratio between evergreen and deciduous elements is about 1:12. At the genus level, Leguminosae (10 genera), Rosaceae (9 genera), and Betulaceae (5 genera) have higher diversity, but *Acer*, *Carpinus*, *Carya*, *Ceratophyllum*, *Fothergilla*, *Populus*, *Juglans*, *Hamamedis*, *Ulmus*, and *Zelkova* exhibit high abundance in numbers of specimens. The macrofossils record a forest type of vegetation containing 58.8% trees, 25.2% shrubs, 9.0% vines, and 7.0% herbs (Yang 1988). In addition, a rich microfossil flora, consisting of at least 63 genera of spore/pollen, from the diatomaceous unit has been reported (Sung 1959; Song *et al.* 1964; Wang 1981; Liu & Leopold 1992). Members of important families are represented by both macro- and microfossils, although some genera (mainly wind-pollinated gymnosperms and aquatic plants) have not been recorded in the macrofossil collection. On the other hand, a few taxa that are well represented by macrofossils (e.g., Salicaceae, Rosaceae, and Leguminosae) are not shared by pollen record (Liu & Leopold 1992).

Insects. – A rich insect fauna is represented by 169 genera and 266 species (from 50 families and 12 orders) in the Shanwang

site (Hong 1979, 1983, 1985; Zhang 1986, 1989, 1990). The fauna is dominated by the orders of Coleoptera (68 genera, 100 species), Hymenoptera (54 genera, 84 species), and Heteroptera (13 genera, 20 species). At least 70% of Shanwang insect fossils can be classified into modern genera without much difficulty (Zhang 1986). In addition, the fauna is dominated by forest-type insects, and their modern relatives are largely found in the Yangtze River Valley. The ratio between terrestrial forms and aquatic forms is about 14:1 at the genus level (Zhang 1986, 1989). The aquatic insects (12 genus and 14 species) are represented by members of Heptageniidae, Leptophlebiidae, Nepidae, Notonectidae, Corixidae, Dytiscidae, and Hydrophilidae (Zhang 1986, 1989).

Ostracodes. – The biota apparently lacks a large benthic invertebrate fauna. An intensive search since 1936 has yielded only 4 genera and 6 species of ostracodes in the Shanwang Formation; the ostracode fauna is monotonous and very low not only in diversity but also in abundance. *Ilyocypris* and *Potamocypris* are the two common genera in this fauna (Zheng 1986).

Fish. – The Shanwang site is famous for its diverse vertebrate fossils, which include well-preserved fish (7 genera), amphibians (4 genera), reptiles (3 genera), birds (5 genera), and mammals (17 genera). Although a part of the fish collection remains unstudied, a tentative list of the fish fauna has yielded 6 genera and 9 species belonging to different subfamilies of Cyprinidae (minnows and carps) (Young & Tchang 1936; Zhou 1990). The fossil specimens differ from all known living cyprinids in number of vertebrae, body size, and pharyngeal dental morphology. Therefore, they are believed to represent an extinct primitive cyprinid fauna, which resembles modern assemblages living in southern China, indicating a warm temperate lake water (Zhou 1990).

Amphibians. – Shanwang's amphibian fossils represent one genus of salamander, one genus of frog, and two genera of toads; each genus has only a single species (Young 1936b, 1965; Yang 1977; Gao 1986). The salamander (*Procynops miocenicus* Young, 1965) is very similar to the modern form *Cynops orientalis* but much smaller (Young 1965). The frog (*Rana basaltica* Young, 1936) is thought to be similar to the living species *Rana asiatica* although the fossil species is smaller and has thicker limb bones (Young 1936b). Yang (1977) established a toad species (*Bufo liquensis* Yang, 1977) based on two well-preserved specimens from Shanwang; one of them was later reclassified as *Macropelobates cratus* Gao, 1986. The fossil species of *Bufo* is believed to be similar to the modern species *Bufo gargarzans* living in China. *Macropelobates* (Pelobatidae) is a fossil genus that was first established on the basis of material from Mongolia and is recognized as the ancestor of the modern *Megophrys* group now living in Asia (Gao 1986).

Reptiles. – Two genera of fossil reptiles, a snake and an alligator, have been reported from the Shanwang Formation. The snake (*Mionatrix diatomus* Sun, 1961) is represented by several well-preserved specimens belonging to Colubridae, one of the largest snake families in the subtropical regime. The animal is of medium size (about 1 m long) and comparable with the modern genus *Natrix* (a water snake) and related forms in southern China (Sun 1961). Recently, a crocodilian skull (*Alligator luicus* Li & Wang, 1987) was discovered from the diatomaceous unit. It represents an extinct species showing some similarities to the modern species *Alligator sinensis*, a famous 'living fossil' in the lower Yangtze River Valley in China (Li & Wang 1987). While working on the site in 1987, we found a fossil turtle in the lower part of the Shanwang Formation, but it is still unstudied (Fenglin Li, personal communication, 1993).

Birds. – Shanwang is one of the rare places where fossil birds are completely preserved. Of the four genera of birds reported from the site, two belong to Phasianidae (Galliformes) (Yeh 1977, 1980). One of these, *Shandongornis shanwanensis* Yeh, 1977, represents a medium-sized bird and shares some similar features with the modern genus *Perdix*. The other, *Linquornis gigantis* Yeh, 1980, is a large fossil bird (estimated about 1–1.5 m tall) with long and strong legs and is similar to the size of a peacock. *Sinanas diatomas* Yeh, 1980 was a duck-like species belonging to Anatidae (Anseriformes), and resembling modern *Anas*, although the fossil has a larger body size and stronger bones (Yeh 1980). In addition, the small bird *Youngornis gracilis* Yeh, 1981, belonging to the family Rallidae (Gruiformes), preserves a complete skeleton with well-rounded gizzard stones that are distinguished from the matrix diatomite (Yeh 1981).

Mammals. – The Shanwang site is well known for its highly diversified and completely preserved Miocene mammalian fossils. Qiu (1990) summarized the mammal fauna as 17 genera belonging to 6 orders. These include one species of fossil bat (*Shanwangia unexpectuta* Yang, 1977, Chiroptera), four members of Rodentia, including one skeleton of mountain beaver (*Ansomys shanwangensis* Qiu & Sun, 1988), two well-preserved squirrels (*Plesiosciurus* aff. *sinensis* Qiu & Liu, 1986, and *Diatomys shantungensis* Li, 1974), and a flying squirrel (*Meinia asiatica* Qiu, 1981) (Li 1974; Qiu 1981; Yang 1977; Qiu & Sun, 1988).

In addition, fossils representing four ursid (Carnivora) genera have been reported: A right lower jaw of the large *Amphicyon confucianus* Young, 1937, with *in situ* teeth; several isolated teeth belonging to the large *Hymicyon youngi* and an unnamed member of Thaumastocyoninae (Qiu *et al.* 1986); and a complete skeleton with *in situ* teeth of the small *Ursavus orientalis* Qiu *et al.*, 1985, the smallest species of this genus and believed to be the ancestor of the modern bears (Qiu *et al.* 1985a). The Perissodactyla are represented by one genus of tapir (*Palaeotapirus xiejiaheensis* Xie, 1982), two genera of rhinoceros (*Plesiaceratherium gracile* Young, 1937, and *Brachypotherium* sp.), and an unstudied perissodactyl skeleton. An undescribed specimen believed to be *Chalico-*

therium grande is also present in the mammalian fauna (Qiu 1990). Various fossil deer (Artiodactyla) are the most abundant mammalian fossils. *Lagomeryx*, with permanent horns, is the most common deer found in Shanwang, and this genus is represented by teeth, horns, and complete skeletons (Teilhard de Chardin 1939; Hu 1957; Chow & Shih 1978). A complete deer skeleton belonging to *Palaeomeryx*, a genus between modern deer and giraffe, has been documented (Qiu *et al.* 1985b). Moreover, an unstudied specimen believed to be a member of Suinae has been reported (Qiu 1990). The Shanwang mammalian fossils exhibit a diverse ecologic spectrum covering different habitats of the Miocene forest near the lake basin.

Trace fossils. – Two types of trace fossil were found in the Shanwang site. Trail-like traces, likely created by benthic invertebrates or insect larvae, were collected from the southern rim of the basin (Shipu Yang, unpublished data). Insect borings in the bark of Miocene plants were reported as a rare occurrence (Guo 1991). In addition, insect mining and feeding traces on angiosperm leaves are also commonly found in the Shanwang Formation (Yang 1988).

Preservational style

The Shanwang fossils are exceptionally well preserved. A combination of preservational features makes the taphonomic facies of the Miocene biota a unique type among *Konservat-Lagerstätten*. We will put our emphasis on documenting these features; a detailed interpretation of taphonomic processes and controlling factors of the soft-tissue fossils will be published elsewhere.

Macrofossil breakage. – The ratio of broken to unbroken megafossils is very low in the Shanwang fossils. Many plant leaves, shoots, and reproductive organs are preserved with little physical damage. Many compound leaves are preserved with leaflets (Yang 1988), and complete insects with hair impressions and other morphological details are clearly observable (Fig. 3A). Most fish are preserved with whole skeletons and body outlines, though a few isolated scales and disturbed skeletons are also found. Completely preserved frogs, salamanders, and snakes have been found with little deformation, yet an alligator skull and a fragmented turtle were found in the site. Most mammals from Shanwang are preserved as complete skeletons with *in situ* skulls, teeth, and skin (Fig. 4A–B). Shanwang's fossil plants seldom show evidence of physical abrasion. However, damage by insects was common on angiosperm leaves (Yang 1988). No trace of damage caused by benthic scavengers was found.

Articulation. – The majority of the plant megafossils are isolated vegetative or reproductive organs, although attached fruits and leaflets are frequently reported (Li & Zheng 1986). Most fossil fish are preserved as articulated skeletons, and many fish bones are attached at small joints (Fig. 3B). Most insect fossils show detailed articulation, and their wings, bodies, and even hairs are articulated in fine detail. Most frogs, toads, and tadpoles are preserved complete with soft tissues or skin impressions (Fig. 3C), and several fossil snakes also reveal fine articulation. Four out of five bird specimens are complete articulated skeletons. Among the fossil mammals, a flying squirrel (*Meinia asiatica*) has a fairly large helm-type tail preserved (Qiu 1981), and many deer (*Palaeomeryx* spp.) and rhinoceroses (*Plesiaceratherium* sp.) are preserved as whole skeletons. A complete skeleton of a primitive bear (*Ursavus*) with skull and *in situ* teeth was reported as a rare occurrence revealing the complete body architecture (Qiu *et al.* 1985a).

Coloration. – Leaves and insects found in the Shanwang site usually showed original colors when they were first unearthed. Many leaves had brown, reddish brown, yellow, and even green colors (Yang 1988); similarly, some beatles showed bright metallic-green color on their bodies or yellowish green color on their hair when first uncovered. The color would change into black within several days of being exposed (Zhang 1986). Most fossil fish showed black or dark-brown colors; likewise, many large vertebrate skeletons had a dark-brown color, sometimes with brownish-colored skin *in situ*. Young (1936b) noticed that the general outline of frog bodies was clearly indicated in brown on the light-colored diatomite, and the bones distinctly marked in the body by a darker coloration. Qiu *et al.* (1985b) reported that a thin brownish 'hard shell' covered the surface of some deer bones.

Preservation of ultrastructure and delicate organs. – Delicate parts of organisms such as flowers, hairs, and feathers, rarely reported from ordinary fossil sites, are commonly found in the Shanwang fossil site (Fig. 3D). The preservation of Shanwang plant megafossils permitted the removal of *in situ* pollen grains from intact inflorescence and male cones (Li & Zheng 1986). The microfossils, including fungi, diatoms, and spore/pollen grains, show well-preserved ultrastructure, as observed under the SEM. Colorful hairs can be seen on fossil insects under light microscopy, and multiple-eyes of some fossil insects are clearly distinguishable under high-powered microscopy (Hong 1979; Zhang 1986). Furthermore, fossil frogs and salamanders usually preserve detailed skin patterns around the skeletons. Eyes of tadpoles are also well preserved (Young 1936b). In addition, bird feathers and animal hairs are commonly preserved in the Shanwang fossils. For instance, Li (1974) reported that a fossil squirrel (*Diatomys shantungensis*) preserved its thick brownish hair impressions. Moreover, skin details can be seen on some rhinoceroses in which stomach contents, such as plant fragments, were also uncovered (Fenglin Li, personal communication, 1988).

Oxidation and compaction. – The Shanwang fossil biota was likely preserved in an anoxic state. Plant compressions, insect bodies, and vertebrate skeletons from the site show original

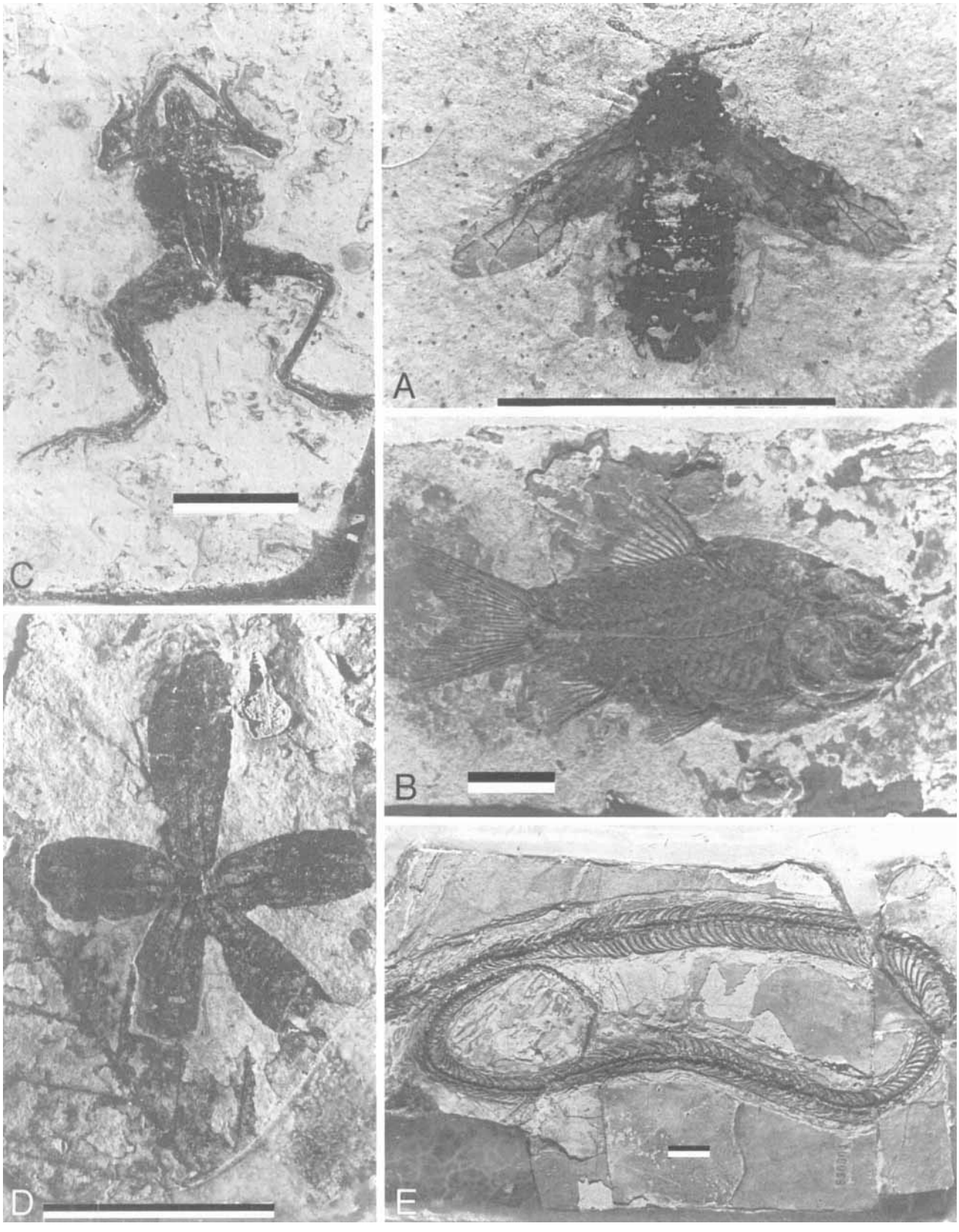

Fig. 3. Examples of Shanwang fossils showing states of preservation (scale bar 2 cm). □A. Preservation of organic tissues in fossil insect (*Clavellaria bicolor*). □B. Fully articulated fossil fish (Cyprinidae). □C. Fossil frog (*Rana basaltica*) showing the complete skeleton with well-preserved soft tissues and body outline. □D. Delicate flower (?*Astronium* sp.). □E. Coiled snake (*Mionatrix diatomus*).

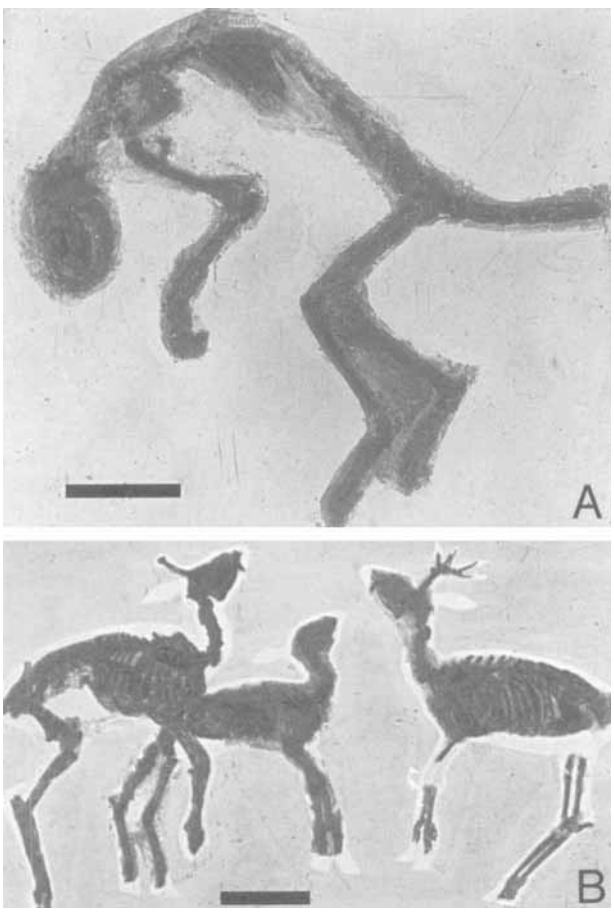

Fig. 4. Preservation of mammalian fossils of Shanwang. □A. Complete fossil bear (*Ursavus orientalis*) with teeth *in situ*. □B. 'Family' of deer (*Lagomeryx colberti*).

colors, black-colored soft tissues, and dark outlines of impressions of soft-parts. On the other hand, most fossil material, especially vertebrates, exhibit some degree of compaction. Three-dimensional fossils are found, but with a strong tendency of vertical flattening. Most skeletons are found flat in the bedding planes, and many vertebrate skeletons, such as frog heads and mammal skulls, usually suffered compaction and are preserved at two dimensional level. No special orientation is observed in any type of macrofossil.

Ecological co-occurrence. – The Shanwang fossil biota contains a mixture of both autochthonous and allochthonous organisms. Evergreen and deciduous plant fossils are preserved together, and there is no distinctive 'leaf layer' or 'fruit layer'. The plants show some degree of overlapping, and most vertebrates are found flat on the bedding planes. Most fossil insects are mature terrestrial taxa that associate with immature body forms. Moreover, fossil frogs of different stages of maturity (frogs with tails and tadpoles) were also reported (Yang 1977), and fossil snakes are usually found with their bodies coiled (Sun 1961) (Fig. 3E). In addition, many fossil deer are preserved within a very close distance, sometimes in contact with each other (Fig. 4B). According to the museum technician who prepared the specimens in Fig. 4B, the distances between the three deer were arranged as found in the field. Both fossil leaves and fish fins penetrate several laminae. It is not uncommon that vertebrate skeletons and plant megafossils are preserved on the same bedding surface. The co-occurring fossils provide an opportunity to examine the ecologic spectrum and the trophic structure that once co-existed within and surrounding the ancient lake.

Discussion

The Shanwang Miocene biota offers an excellent example of a soft-tissue fossil deposit formed in a volcanically influenced small lake basin under a warm temperate climate. Seilacher *et al.* (1985) grouped the occurrences of exceptional fossils into two main categories: concentration deposits and conservation deposits (*Konservat-Lagerstätten*). The following characters of the Shanwang biota make it different from known lacustrine *Konservat-Lagerstätten*. First, the fossil biota is highly diversified and contains more than 500 fossil species, consisting of a mixture of aquatic organisms (diatoms, ostracodes, fish, amphibians, and water reptiles) and terrestrial forms (plants, insects, birds, and mammals). Second, the preservation of the fossil material is truly exceptional. The fossil deposits are characterized by a low degree of macrofossil breakage and abrasion; completely articulated vertebrate skeletons are the common rule rather than exceptions. The original coloration and detailed ultrastructures found in both fossil plants and animals make this biota a remarkable fossil *Lagerstätte*. Finally, the high diversity and fine preservation of this biota provide information on a wide range of habitats that were occupied by various ancient co-occurring organisms under a warm temperate climate during the Miocene.

One of the main objectives of evolutionary paleoecology is to understand ancient ecosystems and their long-term responses to biotic and abiotic changes through geologic time (Wing *et al.* 1992). Documentation and analysis of ancient fossil biotas, especially *Lagerstätten*, on different continents at different time intervals are a necessary step toward the establishment of a global model. Our efforts on the Shanwang biota add information to the database of Miocene nonmarine ecosystems, especially in eastern Asia, from where information is difficult to retrieve because of the language barrier. Even though the biota cannot be taken as a 'frozen' Miocene biocoenosis, the overwhelming abundance and diversity of the fossil deposit provide a rare opportunity for a qualitative reconstruction of the ecologic habits and the interaction of Miocene organisms. The potential of obtaining paleobiological information from ancient biomolecules has recently been recognized (Eglinton & Logan 1991). The

preservation of soft tissues among various plant and animal fossils in the Shanwang site may offer excellent material for the extraction of various biomolecules that seldom are available from ordinary fossil biotas. The quality and quantity of the Shanwang biota sets it apart from other known non-marine *Konservat-Lagerstätten*, and both paleoecologic and geologic evidence suggests that the extraordinary preservation of the fossil biota was caused by a combination of various limnologic and taphonomic factors. Besides systematic studies, further research on taphonomic processes in relation to sedimentological and geochemical parameters of the basin and comparisons with other similar lake deposits will further elucidate the paleoenvironmental conditions required for the formation and preservation of lacustrine *Konservat-Lagerstätten.*

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