Relict distribution of land vertebrates and Quaternary glaciation in China

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Abstract The biogeographical relict phenomenon of extant land vertebrates at the species level has been considered in relation to climatic changes since the Quaternary. Three major relic patterns occurring in China have been illustrated. The results seemly are not in agreement with the theory of the East China Gaciation, a longstanding controversy [Acta Zoo-logica Sinica 50 (5): 841 - 851, 2004].

Key words Biogeographical relict, Land vertebrates, East China Quaternary glaciation

中国第四纪冰期与陆生脊椎动物残留分布

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摘 要 在第四纪冰期中,中国东部地区是否发生过冰川,长期存在争议。中国东部地区冰川说的创始人李四 光教授在提出该学说时,从古生物方面未得到冰期生物群的证据。现存生物种的地理残留现象可反映地质历史 时期的气候变化。本文作者依据中国陆生脊椎动物的北方残留、热带-亚热带残留、温带湿润带残留等现象, 推断: (1) 在冰期的冷期中喜暖动物南迁时,中国东部地区是一避难地; (2) 在中国东部地区未见有典型冰川 残留种的存在; (3) 一些湿润种的间断残留分布与中国北方黄土及干旱气候的发展有密切的关系。此结论似不 支持中国东部冰川说 [动物学报 50 (5): 841-851,2004]。

关键词 生物地理残留 陆栖脊椎动物 中国东部第四纪冰川

1 Introduction

In mainland Asia, major Pleistocene glaciations came into existence in the north, minor glaciations in the Central High Asia, where the huge Tibetan (Qinghai-Xizang) Plateau lies and the highest mountain ranges of the world, the Himalaya, Karkorum, Kunlun, Tianshan in the West China occur. Opinions have varied greatly concerning the extension of the glaciated areas in Siberia (Nilsson, 1983). Whether or not Quaternary glaciation ever existed in the medium and low mountains of East China is a long disputed question. The famous Chinese geologist, Prof. Li Si-Guang (J. S. Lee) and his followers claim that glacial relics were found at over 100 places, even on the hilly land 200 m a. s. l. at 22 N in East China. A group leaded by Prof. Shi Yafeng came to different conclusions. The main point is that apart from High Asia, where the glaciers have developed distinctly,

glaciers existed mostly in a few high mountains along the eastern margin areas of Tibetan Plateau. Mountains lower than 2 000 m over the area of East China were beyond the condition to glaciers during Quaternary (Fig. 1) (Shi et al., 1987).

In an early paper on East China Quaternary Glaciation, Prof. Li Si-Guang (1942) recognized that "based on palaontological evidence, other than a mixture of cold, temperate or tropical faunal elements, a particular glacial biota has not been known in the glaciated area hypothesized" (Li, 1975). Then, a theory of Ice age refugia—" Pantu Ground "of the East China was proposed (Kahlke, 1961). Recent studies on Quaternary palynology, mammals, loess, paleosols and cave deposits show that the climate oscillated from temperate to subtropical many times during the Quaternary in North China. A small number of relics of Mesozoic plants, as ginkgo Kinkgo bitoba, water fir Metasequoia glyptostroboides and a

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Fig. 1 Distribution of partial Quaternary glacier relics in Eastern China(Shi et al., 1987)

large number of Tertiary plants had been growing for a long time and survived several Quaternary cooling periods (Shi et al., 1987). The Yangze crocodile *Alligator sinensis* and the giant salamanders *Andris davidianus*, which are judged as species of the thermophilic Tertiary fauna (Illies, 1974), are still extant in the lower reaches of Changjiang River and over the most part of East China, respectively. The record of the Pleistocene zoogeographical evolution and its existing tendency indicate that there was a broad faunal transition zone between Oriental and Palaearctic realms in East China (Zheng and Han, 1991; Zhang, 2002). The results of these studies are in essential agreement with the theory of refugium rather than of glacial land in East China.

The synthesis presented herein is based on interpretations of relict distribution of extant land vertebrates in China. It is an attempt to assemble impressions accumulated during the author's long term studies on extant land vertebrate distribution of China that the relic phenomenon could serve as evidence for paleoenvironment changes; and providing information for the of East China Glaciation controversy.

The concept of relictness in this paper is that of a biogeographical relict (Udvardy, 1969), which occurs in isolation from its main center of distribution induced by climatic change. Two examples, well known in the biogeographical literature, are the azure-winged magpie *Cyanopica cyana* and the threetoed woodpecker *Picoides tridactylus*, which have been defined as temperate woodland relict and borealalpine relict respectively, induced by the vicissitudes of the Pleistocene climatic changes wiped out the species from the connecting areas (Voous, 1960, quoted from Udvardy, 1969). Their relic areas range separately in China and the Iberian Peninsula (Fig. 2). The following examples of most distinct relic patterns, which are characterized by disjunctive distribution at species level, would be obviously relating to the question arose in terms of evolution time in the Quaternary. In order to focus the question concerning to climatic fluctuation, big game mammals are not be included in this paper. A list of 87 species with those patterns has been attached (see Appendix).

The basic information of the animal distribution data of this paper have been quoted from following major contributions: (1) Amphibians and reptiles by Fei (1999), Zhao and Adler (1993), and Vorobev (1988); (2) Birds by Cheng (1987), Dementev et al. (1951 - 1954) and Zheng (2002); (3) Mammals by Zhang et al (1997), Wang (2003), Corbet (1978), Sokolov and Orlov (1980), Panteleev et al. (1990) and Flint et al. (1965).

2 Boreal-alpine relict

During climatically induced faunal displacements, disjunctions frequently developed in the coldadapting boreal-alpine species of Holarctica (Illies, 1974). Similar distribution patterns are known from



Fig. 2 Ranges of 1, three-toed woodpecker Picoides tridactylus; 2, azure-winged magpie Cyanopica cyana; 3, Ussuri large white-toothed shrew Crocidura lasiura

China. Southwards shift of the boreal fauna extended as far as the Central China mountains is indicated by number of species which have remained relic population there after the northwards retreat during the course of climatic fluctuation in the Quaternary. Examples of this include the by following species:

(1) Amphibians Siberian salamander Salamandrella keyselingii: its main range coincides almost completely with the area of taigas, and extents a bit further to the northeastern part of the Northeast China at about 45 %. A relic population of the species has been recorded further south, the Tongbai-Dabie mountains at about 32 % in Henan province, Central China (Fig. 3) (Wu and Qu, 1984).

(2) Reptiles Adder *Vipera berus*: the species is distributed mainly in the southwestern part of the taiga including northern part of North East China and Altai mountains, Xinjiang and further to the deciduous forest zone of Central Europe. A few records of relic population has been known to the south of Qinling mountains at about 33 °N in Central China (Fig. 3) (Song, 1989).

(3) Birds Ural owl *Strix uralensis*: the main range of the species crosses from northern Europe through Siberia reaching the coast of the Far East and including Sakhalin Island and Japanese islands. A relic population occurs in the northern Hengduan mountains at 30 - 34 °N in Southwest China (Fig. 4) (Cheng, 1987).

(4) Mammals Root vole *Microtus eoconomus*: the main range of the species covers most of the taiga and much of the tundra in the north and extend to the Central Mongolia and Tianshan mountains in the south where it spreads as alpine taiga and wooded steppe. A relic population exists in the northeastern margin of the Tibetan Plateau about 32 - 40 °N (Fig. 4). The narrow- skulled vole *Microtus gregalis* is distributed continually in the taiga of Siberia and spread southwards along the mountain chains of Da Xinganling and Tianshan in China. The relic population of the species occurs in Funiu mountains, about 32 - 35 N in Henan Province.

3 Tropical-subtropical relict

Palaeontological studies show that prior to the first cold period of the Quaternary, a thermophilic fauna most belonging to groups now occurring in the Oriental region associated with tropical-subtropical forests, was distributed over most of China (Zhou, 1984). As climatic deterioration progressed since the Pleistocene in China, the species were forced far southwards especially in the cold stages (Zheng and Han, 1991; Ji, 1985). In the course, relict populations may have remained in the north where refuge habitats existed, while the main ranges retreated to the areas reaching lower latitudes in different distance. The following species may be examples:

(1) Amphibians Large odorous frog



Fig. 3 Ranges of 1, Siberian salamander Salamandrella keyselingii; 2, adder Vipera berus; and 3, boreal digging frog Kaloula borealis



Fig. 4 Ranges of 1, Ural owl Strix uralensis; and 2, root vole Microtus economus

(*Odorrana livida* = *Rana livida*) maintains its relic population in the southeastern Shaanxi, to the south of Qinling at about 34 %, while the northern limit of its main range is laying to the south of the Changjiang River (Fig. 5) (Fei ,1999).

(2) Reptiles Green pit-viper Trimeresurusstejnegeri has a relic population recorded in Changbai Mountain at about 42 % in North East China, where



Fig. 5 Ranges of 1, large odorous frog Rana livida; 2, green pit-viper Trimeresurus stejnegeri; and 3, rhesus monkey Macaca mulatta

a temperate zone is situated (Zhao, 1979) (Fig. 5). These Oriental species are mainly distributed in southeast Asia, with a northern limit approximately coincided with the northern boundary of the north subtropical zone. In contrast to the green pit-viper, the Banded coral snake *Calliophis macclellandi* has a relic population in the border area at about 33 % in Gansu and Shaanxi (Zhao and Adler, 1993) (Fig. 6), along the most northern limit of north subtropical zone and, the northern limit of its main range is bounded by the central subtropical zone.

(3) Mammals South China hare Lepus sinensis distributed mainly in central subtropical zone of East China, a relic population record has been known at about 42 N in Changbai mountain, North East China (Fig. 6) (Luo, 1988). Probably it belongs to the relic population of the same species in the Korean peninsula. An isolated population of rhesus monkey Macaca mulatta occurred at about 41 °N in the north of Beijing, which population was at the northernmost edge of the species in Asia. A few individuals of the population disappeared due to human impact in the end of 1980s (Fig. 5) (Zhang et al., 1989). Now, the main range of this species in the area of subtropical zone in China is more or less continuous in terms of geographical distribution on a small scale map, an insolated population laying just north of the Yellow River at about 35 °N in border area of Henan and Shanxi. The black giant squirrel Ratufa bicolor

could be an example of those species, which have retreated farther south. The main range of this species is in the Indo-China Peninsula, but remains on a margin of it in southern Yunnan Province and a relic population in Hainan island (Fig. 6) both belong to the tropical zone of China.

4 Temperate-humid relict

Deposition of loess indicating a tendency of change toward a of dry and cold climate, began in the early Pleistocene, but its distribution was limited to the north of the Qinling mountains in China. By the Late Pleistocene, it had become much more widespread, reaching as far as the middle and lower reaches of the Changjiang River. The widespread deposition of loess disturbed the previous humid forest land (Liu and Ding, 1984). The species of strict mesophytes, adapted to humid-temperate habitats disappeared in the main part of the deteriorated areas and may have remained relic population scattered in locally suitable habitats outside or inside of the arid land. Examples of this pattern are given by following species:

(1) Amphibian Boreal digging frog Kaloula borealis is distributed mainly around the eastern part of north China, a semi-humid area, while a relict population occurs in Wenxian of southwestern Gansu Province (Fig. 3) (Fei et al., 1999), where is within the margin of the humid subtropical zone.



Fig. 6 Range of 1, banded coral snake Calliophis macclellandi; 2, South China hare Lepus sinensis; 3, black giant squirrel Ratufa bicolor

(2) Reptiles *Takydromus amurensis* is mainly distributed in the eastern part of North East China, but a relic population has been recorded in southeastern Gansu Province (Fig. 7) (Yao and Chang, 1981), in a location near the relict population of boreal digging frog (see above).

(3) Birds the Reed parrot bill *Paradoxornis heudei* has two separate ranges, one of them in the north, the central area of North East China, the arrother in the south, in Zejiang Province (Fig. 7) (Cheng, 1987).

(4) Mammals Japanese mole Mogera wogura is mainly distributed in the Korean Peninsula, Liaodong peninsula and Japanese islands. Two relic populations occur in lower reaches of Yellow River and Changjiang River (Fig. 7). Chinese birch mouse Sicista concolor has five separate relic ranges located in mountain areas: Sikhote Alin-Sungari in the east, Nanshan-Qinling, West Tienshan, Hindu Kush and Caucasus in the west (Fig. 7) (Flint et al., 1965; Corbet, 1978; Zhang et al., 1997). Ussuri large white toothed shrew Crocidura lasiura has a main range in Korea Peninsula-Ussuri area and eastern mountains of North East China, and one relic population occurs in lowest reaches of Changjiang River, (Fig. 2) separated by vast arid-semihunid land. De Winton's shrew Soriculus hypsibius is mainly distributed in the mountains stretching along the northern margin of Sichuan Basin and a relic population occurs near Beijing (Fig. 7).

5 Discussion

During the last glaciation of the Quaternary, stimulated by glacial episodes, arctic tundra faunas evolved in the northern hemisphere. A few mammals of strongly tundra-specific, the polar bear Ursus maritimus, polar fox Alopex lagopus, reindeer Rangifer tarandus, collared lemming Dicrostonyx and narrow-skulled vole *Microtus gregalis* are represented. To the southern front of the glacial land, the region of coniferous forest, the taiga, which though not quite as extreme climatically is still characterized by a distinctly low temperature. The fauna of the taiga includes all the tundra animals, but with the addition of most of more temperate latitudes (Illies, 1974; Marain, 1984). Among them the wolverine Gulo gulo and polar hare Lepus timidus stretch a little southwards, reaching the northernmost area of China, associating with the taiga zone in North East China and Altai mountains, Xinjiang. The root vole Microtus oeconomus and narrow- skulled vole Microtus gregalis spread much further to the south and remained relic populations. The relic range of root vole occurs in the northeastern margin of Tibetan Plateau where periglacial habitats and alpine glaciers still exist. The relic range of narrow-skulled vole occurs in much lower elevation where is within the area of Pleistocene glaciation suggested by the scholar Prof.



Fig. 7 Ranges of 1, Takydromus amurensis; 2, De Winton's shrew Soriculus hypsibius; 3, Chinese birch mouse Sicista concolor; 4, Japanese mole Mogera wogura; and 5, reed parrot bill Paradoxornis heudei

Li. So far known, in Central Europe, these two species of voles survived the individual stadials at the lower elevations, denoted warmer periods, characterized by a disjunct occurrence, differing from typically northern tundra species (Povolny, 1966). No doubt, the relics of the two species of voles and other taiga faunal species would be the evidence for the experience of relatively cold climate of the areas in the past when the taiga extended southwards, but not necessarily under conditions of glaciation. And, even much of Siberia, where the taiga originated, shows no geologic evidence of glaciation in the Pleistocene (Brown and Gibson, 1983). Obviously, the changes of southern limits ranging from the boreal relic in China may indicate the extent of cold climate during cold stages of the Pleistocene. The animals of the taiga could migrate southwards at least along cold ridges with alpine coniferous of the mountains in northern China. The occurrence of the boreal - alpine relic species have reached mainly to the Qinling-Dabie mountains in the east and to eastern margin of the Tibetan Plateau, the Hengduan mountains, in the west, between 30 - 40 N.

During maximum glaciation, the Tibetan Plateau was never covered by ice sheets, but under periglacial environment with different scale of valley-pediment glaciers mainly (Shi and Zheng, 1995). Palynological studies show that since the Pliocene the general trend of environmental changes of the plateau has been from

warm humid to cold arid climate and the forests have retreated from the interior to the southeastern margin in lower elevation. In the course of the uplift of the plateau, alpine tundra faunas have evolved and formed a distinct highland pattern in distribution (Hs ü, 1978; Zhang and Zheng, 1981). Among mammals, the black-lipped pike Ochotona curzoniae, Himalayan marmot Marmota himalayana, Blyth's vole Pitymys leucurus white -lipped deer Cervus albirostris, etc. are specialized for periglacial alpine meadow habitats. Their fossils have been known firstly in southern Tibet in the strata of early Holocene (Guo, 1976). Neither fossil nor relic population of them have been known from East China, but their ranges extend to the eastern margin of the Tibetan plateau, around Hengduan mountains, where glaciation has been confirmed occurring in few high mountains during the Pleistocene, even now.

Before the middle Pleistocene, the subtropical zone extended northwards, reaching to the south at 42 N in North East China (Liu, 1984). Associated with the climatic optimum, the northern distribution limit of the warm-preferring animal species during that time could be shown by the northernmost locations of their relics. A few of them occur at latitude of 42 N to the north of the Korea Peninsula, coinciding with the northern limit of middle Pleistocene subtropical zone and is close the present northern margin of warm-temperate zone. During southwards retreats of the subtropical zone in the cold stage since middle Pleistocene, numbers of the warm-preferring species remained relic population in different places depending on their ability to adapt to the cold-resistant and habitat conditions in the areas retreated. The northern limits of the main ranges of those species lie at different latitudes with various contours coinciding with suitable optimal environments. Some of them have withdrawn from the subtropical areas or only remain in the islands of Hainan and Taiwan, even out of the territory of China. The tropical-subtropical relics could indicate that in East China since the Middle Pleistocene to the Later Pleistocene, the climatic conditions have fluctuated from temperate to subtropical within the limit of cold-tolerant of the warm-preferring relic species.

The progressive development of arid climate and loess deposition as mentioned above resulted in an arid land of so called "North West Arid Region "in China, which includes desert and steppe. To the east, the region connects the forest-steppe region of the North China and forms a relatively arid zone crossing northern China. The former scale of the zone could be indicated by distribution of a few representative species, such as sand lizards (*Phrynocephalus* spp.) in reptiles and zokors (Myospalax spp.) in mammals, which range continuously over most land of North China, eastern Inner Mongolia and the east of North East China; no data in terms of biogeographical relic have been learned from them. On the contrary, the remarkable phenomenon of the extant widely discontinuous gaps of the humid-temperate relic species (Fig. 7) could not be originated by crossing the barrier of Po Hai Sea or vast loess plateau, except the possible migration by chance of the reed parrotbill, but because the population disappeared in the North China plain, and points at a general tendency of intensive climatic deterioration of cold and arid with minor fluctuation since early Pleistocene during the evolution of the loess plateau. The same could be true of all the other two cases of mesophytic species. Obviously, arid condition is one of the most important negative factors for glacier formation.

6 Conclusions

This elucidation suggests that since the Quaternary, the following events could be identified. (1) Eastern China has become a refugium for survival of temperate and tropical-subtropical faunas during their southwards retreat in the cold stage; (2) a number of taiga fauna have extended to the middle reaches of Changjiang River, but no typically glacial relic has been found in the lower lands of East China; (3) among the faunal species of southwards northwards extension associated with taiga and temperate forests, the numbers of mesophytic specialized species have been become discontinuous in distribution by the development of the loess arid and semi-arid zone. This conclusion seemly is not in agreement with Prof. Li's hypothesis of East China Glaciation.

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Appendix : Biogeographical relic list of extant land vertebrates in China

1. Boreal-alpine relict

- A: Siberian salamamder Salamamdrella keyserlingii (To).
- R: adder Vipera berus (Qs).
- B: Chinese grouse Bonasia bonasia (H), boreal owl Aegolius funereus (T), long-eared owl Asio otus (T), U-ral owl Strix uralensis (T), three-toed woodpecker Picoides tridactylus (H), white-backed woodpecker Picoides leucotos (H, Fuj, It), Siberian rubythroat Luscinia calliope (H), dusky warbler Phylloscopus fuscatus (H), Pallas's leaf warler Phylloscopus proregulus (H), yellow-browed warler Phylloscopus proregulus (H), red crossbill Loxia curvirostra (H), common rosefinch Carpodacus erythrinus (H), Chinese nuthatch Sitta vilosa (T, wt).
- M: northern hedgehog *Erianceus europaeus* (subt., Eu), east Siberian shrew *Sorex minutissimus* (H), pygmy shrew *Sorex minutus* (H), Laxmann's shrew *Sorex caecutiens* (T), common shrew *Sorex araneus* (H, subt.), northern pika *Ochotona alpina* (wt), Siberian flying squirrel *Pteromys volans* (To), Eurasian red squirrel *Sciurus vulgaris* (To), northern red-backed vole *Cletheionomys rutilus* (wt), narrow-skulled vole *Microtus gregalis* (To), root vole *Microtus oeconomus* (T), common vole *Microtus arvalis* (T).
- 2. Tropical-subtropical relict (most in the northern margin of the subtropical zone)
- A: black knobby newt *Tylototriton asperrimus* (To), bonyheaded toad *Bufo galeatus* (Ih), South China tree toad *Hyla simplex* (Z), large odorous frog (Q) red-webbed treefrog *Rhacophorus rhodopus* (D), beautiful pygmy frog *Microhyla pulchra* (W).
- R: Trionys steindachneri (N. subt.), Sacalia bealei (C., subt.), banded coral snake Calliophis maccellandi (W), Achalinus rufescens (Qs), Trachischium tenuiceps (Qs), red-necked keelback Rhabdophis subminiata (wt), green pit viper Trimeresurus stejnegeri (t), Pareas monticola (Fj. subt.)
- B: black-browed barbet Megalaima oorti (D., Ih-t), blue-rumped pitta Pitta soror (D, Ih), maroon oriole Oriolus traillii (Ih, It), black drongo Dicrurus macrocercus (H, Ih, It), bronzed drongo Dicrurus aeneus (H, Ih, It), greater racket-tailed drongo Dicrurus paradiseus (Ih), short-tailed green magpie Cissa thalassina (D, subt., Ih), spot-necked babbler Stachyris striolata (Ih), yellow-browed tit Sylviparus modestus (H, Fj, Gus), sultan tit Melanochlora sultanea (H, Gus, Fj, Ih).
- M: common European white-toothed shrew Crocidura russula, Hodgson's brown-toothed shrew Soriculus caudatus (H, Qs, It), Horsfield's shrew Crocidura horsfieldi (Qs, H, Ih. t), Indian flying fox Pteropus giganteus (Qs. T), greater false vampire Megaderma lyra (n. subt), little Japanese horseshoe bat Rhinolophus cornutus (wt), Schreiber's long-fingered bat Miniopterus schreibersi (wt), wrinkle-lipped bat Tadarida plicatta (wt), hairy-winged bat Harpiocephalus harpia (H. It), Chinese hare Lepus sinensis (t.), rhesus macaque Macaca mulatto (wt, h), black gibbon Hylobates concolor (Ih), hairy-footed flying squirrel Belomys pearsoni (To), red giant flying squirrel Petaurista petaurista (W, Qs, It), red-and-white flying squirrel Petaurista alboruf us (H, W, Qs, It), Himalayan striped squirrel Tamiops macclellandi (To), black giant squirrel Ratufa bicolor (Ih), Chinese bamboo rat Rhizomys sinensis (Qn) Chinese porcupine Hystrix hodgsoni (wt), palm mouse Vandeleuria oleracea (H), pencil-tailed tree mouse Chiropodomys gliroides (D, Ih), black rat Rattus rattus (wt).
- 3. Temperate humid relict (relic population occurring in monsoon regions separated by loess arid area.)
- A: oriental bell taod bombina orientalis, boreal digging frog Kaloula borealis (W).
- R: Takydromus amurensis (t. W), Takydromus wolteri (subt., t.) Takydromus septentrionalis (Subt., t.).
- B: reed parrotbill Paradoxornis heudei (subt.,t.).
- M: Natterer's bat Myotis natterei (t., ct., Eu.), water bat Myotis daubentoni (t., ct., Eu.), long-fingered bat Myotis capaccinii (subt., t,. Eu.), particolored bat Vespertilio murinus (t., ct., Eu.), Chinese water deer Hydropotes inermis (subt., t.) Chinese birch mice Sicista concolor (H, Tianshan, t.), Ussuri large white toothed shrew Crocidura lasiura, De Winton's shrew Soriculus hysibius.

A: amphibian. R: reptile. B: birds. M: mammals.

Relic areas. ct : Cold temperate zone. D : Dayaoshan, Guangsi. Eu. Europe. Fj : Fujian. Gus : Guangxi. H :

Hengduan mountains. Ih: Hainan Is. It: Taiwan Is. Q: Qinling mountains (Qs: southern flank; Qn: northern flank). subt.: Subtropical zone. t: Temperate zone. T: Tibetan plateau. To: Tongbai-Dabie mountains, Henan. tr: Tropic zone. W: Wenxian, Gansu (to the west of Qinling mountains). wt: Warm temperate zone. Z: Zheijiang.