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Fossil frogs (Anura) from Shanwang (Middle Miocene; Shandong Province, China)☆

Les grenouilles fossiles (Anura) de Shanwang (Miocène moyen ; Province de Shandong, Chine)

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Abstract

The early middle Miocene biota from the Shanwang locality in eastern China is one of the most diverse and well preserved in the world. This overall richness contrasts with its low diversity of anuran amphibians. The most abundant anurans are representatives of the family Ranidae, which remains the dominant group in the extant anuran fauna of China. Besides *Rana basaltica* Young, some other ranids can be recognised at the locality, and are clearly distinguishable from *R. basaltica* based on their larger size and different proportions. Ranids are also represented by a developmental series of tadpoles, ranging from approximately Nieuwkoop-Faber (NF) stage 43 to a metamorphosing tadpole of NF stage 57. This is the first known developmental series of fossil non-pipoid Anura outside the Pelobatidae. In addition to the ranids, *Bufo shandongensis* nov. sp. (replacement name for *B. linquensis*), represented by one of the earliest known articulated bufonid skeletons, is described and illustrated. Another large toad, *Macropelobates linquensis* (Yang) nov. comb., is re-described; it can be assigned to the Pelobatoidea, with a possible relationship to the Scaphiopodidae, and can be considered, based on the presence of a large spade, a tibiofibula shorter than the femur, and a short astragalus and calcaneus, to be the earliest known anuran burrower.

Keywords: Anura; Neogene; *Bufo*; *Macropelobates*; *Rana*; Tadpole; East Asia

Résumé

Le biotope d'âge Miocène moyen ancien de la localité de Shanwang, en Chine orientale, est l'un des plus diversifiés et des mieux préservés dans le monde. Sa richesse totale contraste avec sa faible diversité en amphibiens anoures, les plus abondants d'entre eux appartenant à la famille des Ranidae, qui reste le groupe dominant dans la faune actuelle d'anoures en Chine. À côté de *Rana basaltica* Young, quelques autres ranidés peuvent être identifiés dans cette localité ; ils se distinguent nettement de *R. basaltica* par leur plus grande taille et des proportions différentes. Les ranidés sont également représentés par une série ontogénétique de têtards s'étalant approximativement du stade 43 de Nieuwkoop-Faber (NF) au stade NF 57 (têtard en cours de métamorphose). C'est la première série ontogénétique connue d'anoures non pipoïdes en dehors des Pelobatidae. En plus des ranidés, *Bufo shandongensis* nov. sp. (nom de remplacement pour *B. linquensis*), représenté par un des plus anciens squelettes articulés de bufonidé, est décrit et illustré. Un autre grand crapaud, *Macropelobates linquensis* (Yang) nov. comb., est re-décrit ; il peut être attribué aux Pelobatoidea, possiblement relié aux Scaphiopodidae, et peut être considéré, sur la base de la présence d'un grand tubercule métatarsien, d'un tibiofibula plus court que le fémur, et d'un astragale et calcanéum courts, comme le plus ancien anoure fouisseur connu.

Mots clés : Anura ; Néogène ; *Bufo* ; *Macropelobates* ; *Rana* ; Têtard ; Asie orientale

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1. Introduction

The Shanwang Basin is approximately 700 m long and 500 m wide, and is located in central Shandong Province, about 22 km east of the town of Linqu (Fig. 1). The first geological report on Shanwang was published by Young (1936b), who later established the age of the Shanwang deposits as Miocene on the basis of fossil mammals (Young, 1937). Recent investigations (Deng et al., 2003) have recognised three formations in the Shanwang Basin, named in ascending order, the Niushan Formation, the Shanwang Formation, and the Yaoshan Formation. The Shanwang Formation consists of six beds, the second of which is diatomaceous and contains abundant fossils (Yan et al., 1983: fig. 4). Most of the fossil frogs discussed in this paper, especially ranids, comes from this second bed. Fossils also occur in the first and fourth beds (tuffaceous sandy gravels and sandy conglomerate intercalated with arenaceous mudstone, respectively; Yan et al., 1983) but are limited to scarce large bones, possibly due to less favourable preservational conditions. Li (1991) and Deng et al. (2003) basically accepted the stratigraphic division proposed by Yan et al. (1983), but Deng et al. (2003) combined the original third and fourth beds and divided the sixth bed into two. The age of the Shanwang Formation is generally considered to be early middle Miocene (equivalent of the European MN5 mammalian unit; Steininger et al., 1996), or 17–15.2 Ma old in numerical terms (Yang et al., 2007). Recently, Deng et al. (2003) suggested that the age of the Shanwang fauna may be slightly greater at about 18 Ma, which is comparable to MN4 of Europe.

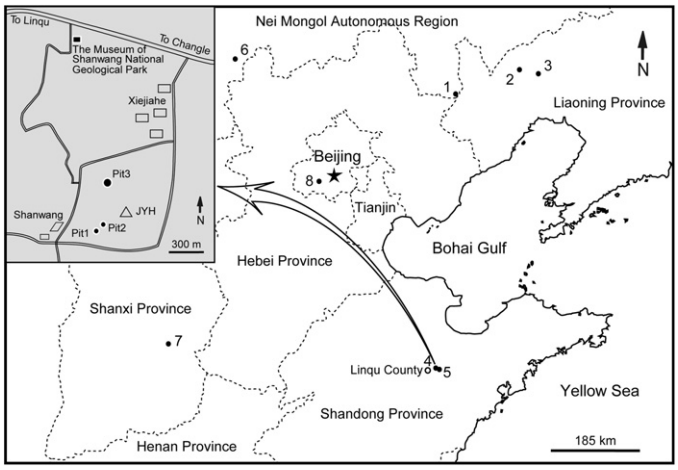

Fig. 1. Main anuran fossil localities of China, with Shanwang area shown as inset. **1**. Daohugou Locality (Anura indet.)? Upper Jurassic; near Chifeng City, Ningcheng County, Nei Mongol Autonomous Region. **2**. Sihetun Locality (*Callobatrachus sanyanensis* Wang and Gao, 1999; *Liaobatrachus grabaui* Ji and Ji, 1998), Lower Cretaceous; Heitizigou Locality (*Mesophryne beipiaoensis* Gao and Wang, 2001), Lower Cretaceous; both near Beipiao City, Liaoning Province. **3**. Xierhuqiao Locality (Anura indet.), Lower Cretaceous; Hejiaxin Locality (*Yizhoubatrachus macilentus* Gao and Chen, 2004), Lower Cretaceous; both Yixian County, Liaoning Province. **4**. Shanwang Locality (*Rana basaltica* Young, 1936; *Bufo shandongensis* nov. sp.; *Macropelobates linquensis* (Yang, 1977), Middle Miocene; near Weifang City, Linqu County, Shandong Province. **5**. Jijiazhuang Locality (*R. basaltica* Young, 1936), Middle Miocene; near Weifang City, Changle County, Shandong Province. **6**. Ertemete Locality (?*Rana hipparionum* Schlosser, 1924), Upper Miocene/Lower Pliocene; near Ulanqab City, Huade County, Nei Mongol Autonomous Region. **7**. Zhangcun Locality (*Rana yushensis* Liu, 1961), Lower Pliocene; Wuxiang County, Shanxi Province. **8**. Zhoukoudian Locality (*Rana nigromaculata* Hallowell, 1861; *Rana asiatica* Bedriaga, 1898; *Bufo gargarizans* Cantor, 1842 and *Bufo raddei* Strauch, 1876), Middle Pleistocene; SW vicinity of Beijing. Inset: Pit 1 and 2, deserted diatomite mine pits; Pit 3, largest mine pit in Shanwang Basin, containing what is now the main stratigraphic section in the Shanwang Geopark; JYH, Jiaoyan Hill, the highest point in the basin; Shanwang and Xiejiahe, the nearest villages to the fossil localities of the Shanwang Basin.

The Shanwang Formation was deposited in a maar lake on a basalt platform (Luo et al., 1992; Li et al., 2000). Many ancient craters still can be recognised around the Shanwang Basin. Volcanic activity supplied sufficient silica-containing material for diatoms to thrive. Taxonomic analysis of the diatoms in the Shanwang strata suggests that they may have lived in a highland (alpine) lake (Yang et al., 2007). Hu and Chaney (1940) also came to the conclusion that, in the Miocene, Shanwang was located on a highland not less than 1000 m above sea level. Current altitude of the basin does not exceed 300 m. Plant macrofossils and palynoflora indicate that today's Shanwang Basin was to a great extent a lake-side wooded habitat (which contained abundant dicotyledonous trees and rare palms) with different types of open-habitat grasses; this suggests that open patches were interspersed with the woodland vegetation (Strömberg et al., 2007).

Climatic inferences from palaeobotanical methods are somewhat variable – the mean annual temperature has been variously estimated at 9.5–11.2 °C (Sun et al., 2002a), 10.9–14.5 °C (Yang et al., 2007) or 15.3–17.2 °C (Sun et al., 2002b; Liang et al., 2003; Liang, 2004), and mean annual precipitation at 1107.3–1880.0 mm (Yang et al., 2007) or 1162–1281 mm (Liang, 2004). Data obtained from the palynoflora suggest that stable climatic conditions persisted throughout the entire period of deposition (Liang, 2004). Generally, the Shanwang Miocene palaeoclimate is classified as warm and humid.

According to Guo et al. (2007), volatiles were emitted in the Shanwang volcanic region in much greater quantities than in some eruptions elsewhere that are known to have had a substantial effect on the climate and environment. The volatile-rich basaltic volcanism at Shanwang could have resulted in mass mortality by triggering abrupt environmental changes and altering lake chemistry. Subsequently, falling volcanic ash would have covered and buried the dead animals and plants, forming well-preserved fossils in Shanwang maar sediments.

The list of fossil taxa that have so far been recognised at Shanwang includes 400 insect species and 23 spiders (Zhang, 1989; Zhang et al., 1994), six ostracods (Zheng, 1986), 11 fishes (Young and Tchang, 1936; Zhou, 1990, 1992; Chen et al., 1999), three anurans and one caudate (Wang et al., 2008), one snake (Sun, 1961), one crocodile (Li and Wang, 1987), undescribed turtles (Yan et al., 1983), five birds (Li et al., 2008), and a variety of mammals including one insectivore, one bat, six rodents, four carnivorans, one indeterminate elephant, seven perissodactyls including chalicotheres, rhinoceros and tapirs, and eight artiodactyls including deer, giraffes and pigs (data on mammalian fauna from Qiu and Qiu, 1995; Yang and Sun, 2000; Liu et al., 2002; Qiu and Yan, 2005). Thus, the Miocene Shanwang biota is one of the most taxonomically diverse and