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EVIDENCE OF THE EARLIEST FRESHWATER DECAPOD FOSSIL FROM SOUTHEAST ASIA (CRUSTACEA: DECAPODA: BRACHYURA)

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***ABSTRACT.* –** We report the first evidence for Miocene brachyuran freshwater crabs from Southeast Asia, a hotspot of extant freshwater crab biodiversity. This confirms the presence of potamoid freshwater crabs in Southeast Asia during the Miocene, as suggested by previous molecular clock estimates. The specimen (one claw fragment) originates from the Middle to Late Miocene site of Vieng Phouka, Lao People's Democratic Republic. Sedimentological and palaeontological data indicate the former existence of alternating swampy and lacustrine environments, inhabited by the crab and a low-diversity gastropod fauna.

***KEYWORDS.* –** Miocene, Laos, Vieng Phouka, Potamidae, Gecarcinucidae.

INTRODUCTION

The fossil record of freshwater decapod crustaceans is generally very sparse (Glaessner, 1969; Rode & Babcock, 2003; Klaus & Gross, 2010), especially in tropical Asia. In contrast, Southeast Asia represents a biodiversity hotspot for extant primary freshwater brachyurans (Yeo et al., 2008; Cumberlidge et al., 2009; Klaus et al., 2009). Primary freshwater crabs can be considered as those brachyuran families that lack any marine members (see Yeo et al., 2008), and occur in Southeast Asia as the families Potamidae and Gecarcinucidae, together comprising about 12% of the total number of currently described brachyuran species (Ng et al., 2008; Yeo et al., 2008; Cumberlidge et al., 2009).

However, the fossil record of these families is restricted to the geographic periphery regarding current regions of species richness. For example, *Potamon sivalense* was described by Glaessner (1933) from the Siwalik beds (Middle Miocene to Pliocene) in the northern part of the

Indian Subcontinent, but without information on the exact location and age. Several claw fragments originate from the Tatrot Formation within the Siwalik beds (2.5 Ma) that were attributed a closer relationship with the gecarcinucid genus *Sartoriana* Bott, 1969 (Klaus & Gross, 2010). Late Pleistocene subfossil specimens of the potamid freshwater crab genus *Geothelphusa* Stimpson, 1858 are known from clay sediments on Okinawa Island and Honshu (Karasawa, 1997; Naruse et al., 2003, 2006), and Holocene subfossil freshwater crabs (family Potamidae) were found in northern Vietnam (Rabett et al. 2008).

Fossils are of major importance for zoologists. They serve as direct evidence for past distribution patterns and thus contribute to biogeographic inferences. Although fossils can only supply minimum ages for taxa, they are a widely used tool for estimating mutation rates and calibrating molecular clocks (for freshwater crabs see Daniels et al., 2006; Klaus et al., 2010; Shih et al., 2009). Here, we report the first evidence of Neogene freshwater brachyurans in tropical Asia.

MATERIAL

***Description*. –** A single claw fragment, either part of propodus or dactylus, three conical teeth visible, one smaller tooth adjoined by two larger teeth to the left and right (see Fig. 1). A fourth tooth is only preserved in part. The length of the fragment is 2.3 mm. The specimen is stored in the paleontological collection of the University of Tuebingen (collection number: GPIT/CU/337).

***Location*. –** Vieng Phouka (or Viengpuka, Viengphoukha, Viangphouka) Coal Mine (coordinates: N 20.5833, E 101.0583), Luang Namtha Province, Lao People's Democratic Republic (see Fig. 2).

***Geology, palaeoenvironment and stratigraphy*. –** The opencast mine of Vieng Phouka exposes an 85 metre thick section of lignites, dark lignitic marls, grey marls, and bodies of fine sand (Fig. 3). Occasionally, allochthonous carbonized tree-trunks (>2 m in length, up to 1.2 m in diameter) occur in the lignite seams. The bases of several marl levels that overly lignite seams show root traces and the development of stump horizons (bed # 2, 5, 7), and often contain fossil resin. The partly fine-laminated and pyrite-bearing grey marls contain small freshwater gastropods (e.g., *Bithynia* Leach, 1818; Bithyniidae) in moderate abundance. The crab claw fragment is also derived from one of these marl horizons (lower part of bed # 5). The fine sands, which are locally rich in plant debris, usually show erosional bases, while ripple-marks may occur at their top. Altogether, these data indicate a swamp environment driven by a periodically pending groundwater level. During high stand periods, the swamp was flooded, forming a shallow lake (gastropod and crab-bearing grey marl) that was supplied with fine-grained sandy sediments by inflowing rivers.

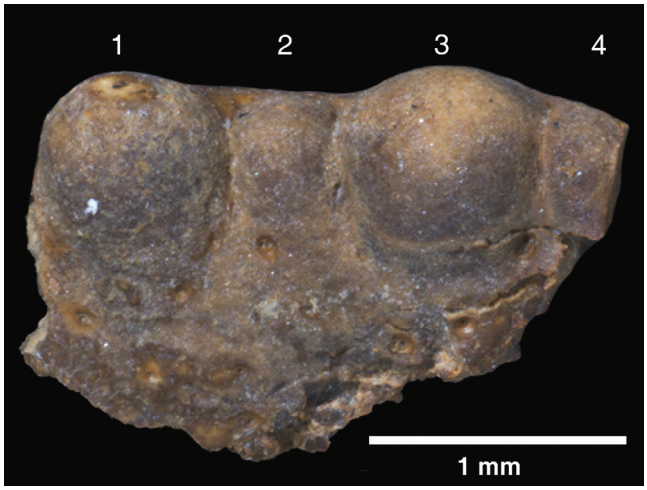

Fig. 1. Fragment of the brachyuran chela (either propodus or dactylus). Two larger teeth (no. 1 and 3) and one intertooth (no. 2) are completely preserved, with evidence of a fourth tooth. The specimen is stored in the paleontological collection of the University of Tuebingen (collection number: GPIT/CU/337).

Reliable age indicators are absent from the sediments. However, the Vieng Phouka Basin obviously is structurally related to the N-S to NE-SW striking Neogene rift basins of Northern Thailand (Morley, 2001), as it is positioned in their direct prolongation. Assuming a similar tectonostratigraphic evolution for the basins along these major Southeast-Asian fault systems, a mid to late Miocene age may be suggested for the sediments at Vieng Phouka. This estimation already implies a potential age gradient between western and eastern basins, as previously emphasized (Morley, 2001, Songtham et al., 2003) or neglected (Chaimanee et al., 2007).

DISCUSSION

The critical question concerning the claw specimen is its taxonomical assignment. There have been efforts to assign chelae fragments of fossil freshwater crabs to extant species by means of dentition patterns (Pretzmann, 1971; Bachmayer & Pretzmann, 1971), and by using rigorous morphometric analyses (Ashkenazi et al., 2005). However, for both approaches large sample sizes, entire propodi and dactyli, and especially a priori knowledge about extant relatives for comparison are required. None of these criteria are fulfilled

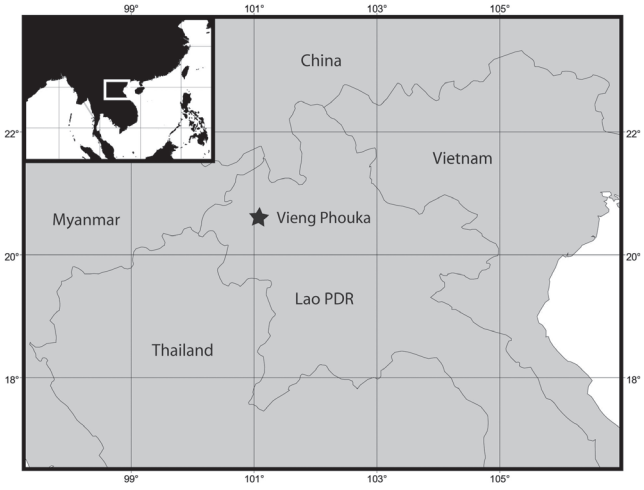

Fig. 2. Location of Vieng Phouka in northwestern Laos.

with the present fragment. Thus we can only give a broad delimitation of taxonomic identity of the claw fragment, mainly based on the distribution pattern of extant groups and their known fossil record.

The shape and pattern of the preserved teeth clearly indicate a brachyuran origin of the fragment. Astacid crayfish comprise the oldest known Asian freshwater decapods (Upper Jurassic of the Jehol Group in Northern China, see Taylor et al., 1999). However, they do not possess comparably toothed chelae. Moreover, both extant and fossil astacids of East Asia are restricted to more temperate climates.

The present fossil may be attributed to different taxa within the Brachyura. Many Asian species of the Grapsoidea, for example, invade or even wholly inhabit the freshwater habitat (see Yeo et al., 2008). The genera *Eriocheir* De Haan, 1835 and *Varuna* H. Milne Edwards, 1830 (Varunidae) enter estuaries, and are also found further up in rivers. The sesarmid genera *Sesarmoides* Serène & Soh, 1970, *Labuanium* Serène & Soh, 1970 and *Karstarma* Davie & Ng, 2007 can be completely freshwater adapted, the latter being semi-terrestrial (see Cumberlidge et al., 2009; Davie & Ng, 2007; Ng, 2004). Finally, *Geosesarma* De Man, 1892, is found in terrestrial habitats (Ng, 1988; 2004). Also several species of Gecarcinidae (land crabs), Hymenosomatidae and semiterrestrial Ocypodoidea can be regarded as potential origin of the claw fragment, as these can disperse far into the inland (Ng, 2004; Yeo et al., 2008). However, chelae morphologies differ from the present claw fossil (P. K. L. Ng; T. Naruse, pers. comm.). These brachyuran groups have virtually no fossil record, although fossils of marine Sesarmidae (*Sesarma* Say, 1817) and Varunidae (*Miosesarma* Karasawa, 1989; *Cyclograpsus* H. Milne Edwards, 1837; *Helice* De Haan, 1833; but also freshwater adapted, Pliocene *Eriocheir* De Haan, 1835) have been reported from Miocene and Pliocene sediments of Japan (Karasawa & Narita, 2000; Karasawa & Kato, 2001). Assuming that the transition

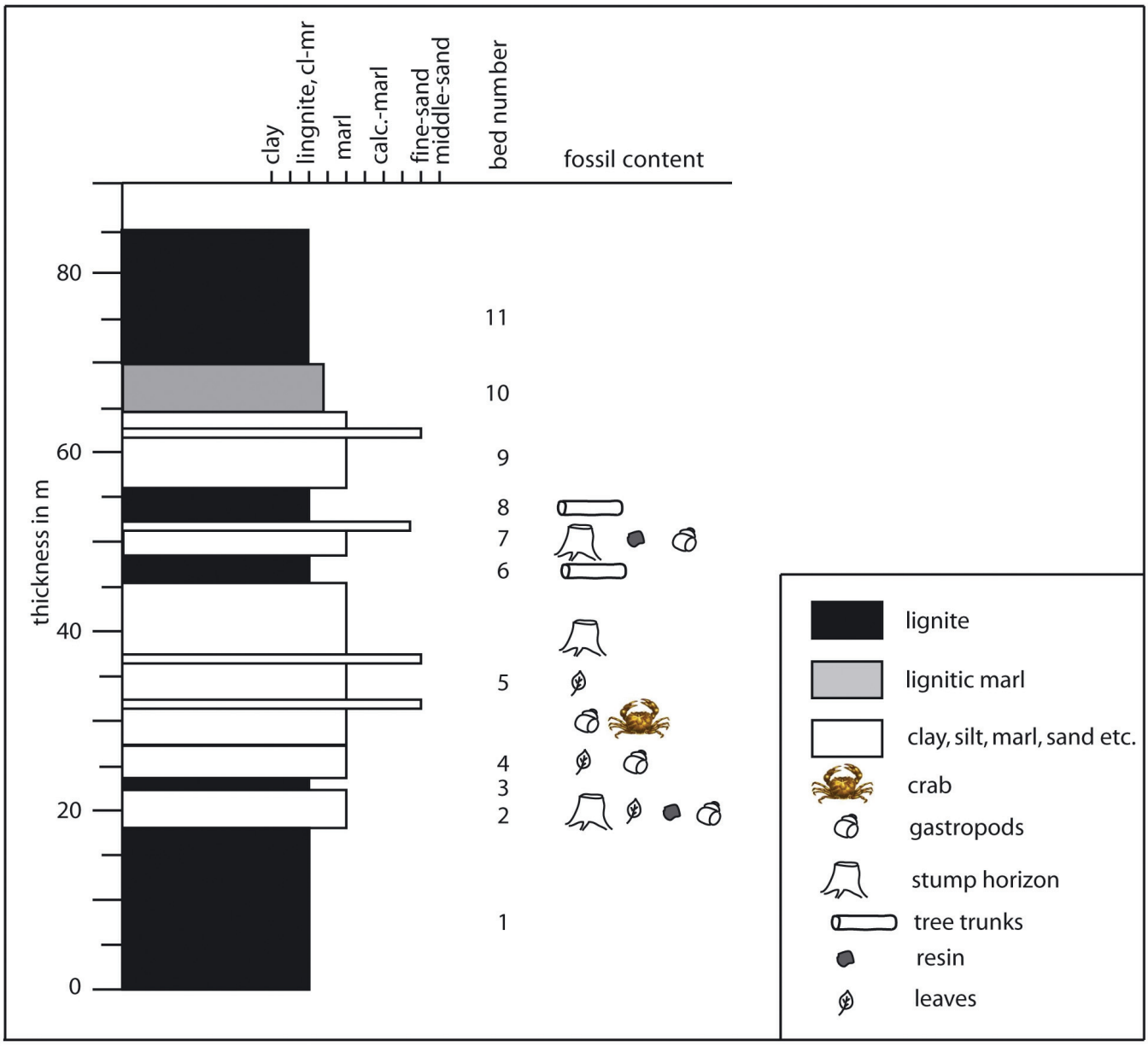

Fig. 3. Sedimentologic profile and fossil content of the Vieng Phouka coal mine.

into freshwater and terrestrial environments within these euryhaline, secondary freshwater species may represent a rather recent, post-Miocene, phenomenon (Yeo et al., 2008), the present claw fragment is more likely to be of primary freshwater crab origin. Although the ontogenetic age and final adult size of the fossil crab remains elusive, the small size of the claw fragment could indicate that it belongs to a sub-adult specimen that originated not far away from the Vieng Phouka site. In contrast, most secondary freshwater brachyurans have a marine larval development and would reach inland habitats more likely as adults.

Primary freshwater crabs are present in Eurasia as two families, the Potamidae and the Gecarcinucidae, and both have their maximum of species diversity in tropical Asia (Yeo et al., 2008; Cumberlidge et al., 2009; Klaus et al., 2009). The preserved rounded crushing teeth resemble the character state found in several Southeast Asian gecarcinucid genera, while potamids tend to have sharper teeth. Also the palaeoenvironment of the Vieng Phouka site, as inferred from the sedimentological and palaeontological data, suggests that a gecarcinucid affiliation is more likely: extant potamids occur predominantly at higher elevations in clear streams, while gecarcinucid freshwater crabs dominate lowland habitats, like floodplains or lacustrine environments (Ng, 1988).

Divergence time estimates of potamid (Shih et al., 2009) and gecarcinucid (Klaus et al., 2010) phylogenies, based on molecular clock approaches, do not conflict with the age of the present fossil, as Southeast Asian lineages presumably predate the Pliocene. On the contrary, the claw fragment provides independent evidence for the presence of primary freshwater crabs in Southeast Asia during the Miocene. Nevertheless, for an unambiguous morphological assignment to one of these families further material will be necessary, ideally with preserved carapaces.

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