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A revision of *Sinaspideretes wimani* Young & Chow, 1953 (Testudines: Cryptodira: Trionychoidae) from the Jurassic of the Sichuan Basin, China

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Abstract – *Sinaspideretes wimani* Young & Chow, 1953 was based on a single shell from the Jurassic red beds of the Sichuan Basin. Originally referred to Trionychidae but later tentatively assigned to Carettochelyidae, it was long thought to be the oldest representative of those families. The re-examination of the carapace and further preparation of the plastron of the holotype of *S. wimani* revealed a number of important characters which clearly exclude this taxon from both Trionychidae and Carettochelyidae, but unite it with the primitive trionychoid *Yehguia tatsuensis* (Ye, 1963). *S. wimani* is therefore considered as the basalmost member of Trionychoidae. Our study adds to the evidence from the fossil record for the antiquity of Trionychoidae, thus is in agreement with the early split of Trionychia (Trionychidae and Carettochelyidae) among the crown Testudines suggested by the molecular phylogeny of turtles.

Keywords: Testudines, Trionychoidae, *Sinaspideretes wimani*, Jurassic, Sichuan Basin, China.

1. Introduction

The Jurassic deposits of the Sichuan Basin have yielded abundant turtle remains, which consist predominantly of archaic turtles (sichuanchelyids and bashuchelyids) in the Middle Jurassic and primitive eucryptodiran turtles (xinjiangchelyids) in the Upper Jurassic (Tong *et al*. 2012*a,b*), while trionychoid remains are scarce. Two trionychoid taxa have been hitherto described from that basin: *Sinaspideretes wimani* Young & Chow, 1953 and *Yehguia tatsuensis* (Ye, 1963). Both of them are based on a single specimen and both have a rather complex story. In 1953, Young and Chow studied a series of turtle specimens collected along the railway between Chengdu and Chongqing (Chengyu Railway) during its construction and the clearing away of building foundations in Datianwan, in the suburbs of Chongqing. The specimens from the Chengyu Railway are presumably of Middle or Late Jurassic age, but the exact location and horizon are unknown. One incomplete shell was named *Sinaspideretes wimani* and placed in the family Trionychidae based on the morphology of the neurals and the ornamentation on the shell surface (Young & Chow, 1953). This was long considered as the oldest member of that family (Young & Chow, 1953; Ye, 1963; Mlynarsky, 1976; Pritchard, 1979; Ernst & Barbour, 1989; Ye, 1994; Zhang, Zong & Ma, 1998; Lucas, 2001). Alternatively, *S. wimani* was placed in a separate family, Sinaspideretidae, and considered as intermediate between Adocidae and Trionychidae (Chkhikvadze, 1987). It was also thought to be intermediate between Trionychidae and Carettochelyidae, or even a primitive carettochelyid (de Broin, 1977). More than 30 years after the first description, Meylan and Gaffney examined a cast and the photographs of *S. wimani* and concluded that the specimen had been interpreted in an incorrect orientation, with the posterior end at the front. The new interpretation led to *S. wimani* being tentatively placed in the family Carettochelyidae (Meylan & Gaffney, 1992), a conclusion generally accepted (Sukhanov, 2000; Brinkman, Li & Ye, 2008), but contested recently (Tong, Zhang & Li, 2010).

The second trionychoid turtle from the Jurassic of the Sichuan Basin, *Yehguia tatsuensis* (Ye, 1963), was originally described as *Plesiochelys tatsuensis* Ye, 1963 (Plesiochelyidae), based on a shell with a poorly preserved carapace, complete plastron and other appendicular elements from the Upper Jurassic deposits of Dazu, between Chongqing and Chengdu (Ye, 1963). The systematic position of *P. tatsuensis* was first questioned by Nessov, who considered it as a member of Adocidae (Nessov & Julinen, 1977). It was even included in the adocid subfamily Shachemydinae, because a primitive hinge was supposed to be present between the epiplastra and entoplastron/hyoplastra (de Lapparent de Broin, 2004). Danilov & Parham (2006) re-studied *P. tatsuensis*. Their phylogenetic analysis placed it in a group of basal Trionychoidae named Adocusia, which comprised also Adocidae and Nanhsiungchelyidae, but a subsequent analysis placed this taxon within Adocidae,

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Original article

Lindholmemydid turtles (Cryptodira: Testudinoidea) from the Late Cretaceous of Shandong Province, China

Tortues Lindholmemydidés (Cryptodira: Testudinoidea) du Crétacé supérieur de la province de Shandong, Chine

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Abstract

A new genus and new species of lindholmemydid turtle (Cryptodira: Testudinoidea), *Shandongemys dongwuica* n. g. and n. sp. are described on the basis of a partial skeleton with incomplete shell and skull, complete lower jaws and disarticulated limb bones from the Upper Cretaceous Wangshi Group of Zhucheng, Shandong Province, China. Among Lindholmemydidae, the new species is closely related to *Mongolemys elegans* from the Late Cretaceous of Mongolia. An incomplete shell from the same locality is referred as Lindholmemydidae indet. *Glyptops* sp. from the Upper Cretaceous Wang Group of Jingangkou, Laiyang, Shandong is revised and assigned to Lindholmemydidae.

Keywords: Testudines; Lindholmemydidae; Late Cretaceous; Shandong Province; China; Systematics

Résumé

Un nouveau genre et une nouvelle espèce de tortue Lindholmemydidae (Cryptodira: Testudinoidea), *Shandongemys dongwuica* n. g. n. sp. sont décrits à partir d'un squelette partiel composé d'une carapace incomplète associée avec un crâne incomplet, une mâchoire inférieure et des éléments des membres provenant du Crétacé supérieur du Groupe de Wangshi, Zhucheng, Province du Shandong, Chine. Au sein des Lindholmemydidae, le nouveau taxon est proche de *Mongolemys elegans* du Crétacé supérieur du Mongolie. Une

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Unbalanced food web in a Late Cretaceous dinosaur assemblage

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ABSTRACT

The rich assemblage of continental vertebrates from the Cenomanian Kem Kem Beds (Morocco) is one of the best known and most diversified for the mid Cretaceous period (Cenomanian). This assemblage, however, shows apparent ecological oddities, in particular the overabundance of theropod dinosaurs *versus* plant-eating dinosaurs. Several hypotheses have been proposed to explain this unbalanced ratio, including a peculiar ecosystem, non-systematic collecting, taphonomic factors, stratigraphic uncertainties and/or behavioral aspects of the dinosaur groups concerned. Except the comparison of proportions of taxa between field and shop data (McGowan and Dyke, 2009), the other hypotheses have not been tested so far because of the lack of accurately measured sections and systematically collected field data. Based on new field data, we test the above-mentioned hypotheses. The analysis is focused on the ratio of plant-eating versus carnivorous dinosaurs.

This dataset confirms the unbalanced ratio; moreover, the stratigraphic distribution of fossils is quantitatively not homogeneous and consequently important to avoid time-averaging, i.e. the mixing of fossils of different ages together into a single unit. The origin of the unbalanced food web among dinosaurs is related neither to non-systematic collecting, nor to stratigraphic biases. The palaeoenvironment seems to be the only likely factor to explain the significantly high proportion of carnivorous *versus* plant-eating dinosaurs. Indeed, the deltaic palaeoenvironment offered unfavourable conditions for the setting of stable terrestrial vegetation but favouring aquatic life. This aquatic life formed the basic level of an aquatic or semi-aquatic food web, which directly fed top predators, such as theropods in general and spinosaurs in particular.

1. Introduction

The fauna of the Kem Kem Beds (Cenomanian, Morocco) is the richest assemblage of terrestrial and freshwater vertebrates of that stage, with at least 54 taxa (Cavin et al., 2010). As in several mid Cretaceous North African sites, the Kem Kem Beds fauna is delineated by: 1) mostly scattered fossil vertebrate fragments; 2) specimens corresponding to large individuals, especially for fishes and dinosaurs; 3) abundant fish remains and abundant piscivorous predators; 4) few ornithischian dinosaurs compared to saurischians; and 5) few plant-eating dinosaurs compared to carnivorous dinosaurs, both in quantity and in diversity (Taquet, 1984; Russell, 1996; Sereno et al., 1998; Taquet and Russell, 1998; Russell and Paesler, 2003). These features, especially the unbalanced ratio in dinosaur composition is puzzling and difficult to understand, because it contradicts the manifest rule of dominance, in term of abundance, of plant-eating individuals over meat-eating individuals observed in continental vertebrate ecosystems, in particular for mammalian communities and for the likely endothermic dinosaurs (Bakker, 1972, 1975; Farlow, 1976, 1993; Seebacher, 2003; Naish et al., 2004; Pontzer et al., 2009; Farlow et al., 2010; Ganse et al., 2011; Sander et al., 2011a, b).

The overabundance of carnivorous dinosaurs in the mid Cretaceous North African assemblages was firstly thought to reflect a regional ecological trend, caused either by the attraction to the stream courses as a source of prey, or by a peculiar food chain linked with aquatic environments (Russell, 1996). Recent studies, however, suggest various alternative scenarios, including (a) biases in non-systematic collecting, (b) taphonomic factors, (c) stratigraphic uncertainties, and/or (d) idiosyncratic biological features of the dinosaur groups concerned (Cavin et al., 2010; Dyke, 2010). McGowan and Dyke (2009) compared the proportions of taxa between field data and shop data and concluded that the collecting activity constitutes a bias, but other hypotheses have not yet been tested so far.

Here, the composition of a systematic collection of vertebrate remains from the Cenomanian Kem Kem Beds, SE Morocco, is analysed,

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A new species of *Cuora* (Testudines: Geoemydidae) from the Miocene of Thailand and its evolutionary significance

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Abstract – A new species of *Cuora*, *Cuora chiangmuanensis* sp. nov., is described on the basis of a nearly complete shell with limb bones from the late Middle – early Late Miocene Chiang Muan Mine, Phayao Province (Northern Thailand). *C. chiangmuanensis* is distinguished from other fossil and living *Cuora* species mainly on the basis of its plastral morphology. Among fossil and extant *Cuora* taxa, the new species appears to be a missing link between the taxa from Southeast Asia and those from East Asia. It represents the earliest record of the genus and demonstrates that by 11–12 Ma, Asian box turtles were already present in Southeast Asia.

Keywords: *Cuora*, Geoemydidae, Miocene, Thailand, evolution, Southeast Asia.

1. Introduction

Cuora Gray, 1855 is a living and fossil genus of Geoemydidae, which is geographically restricted to Asia. Living species of *Cuora* are found in both continental areas and insular regions of Southeast and East Asia (Iverson, 1992; Parham *et al*. 2001) as shown in Figure 1. During the last three decades, the genus has received scientific interest in terms of systematics and taxonomy (Parham *et al*. 2004; Stuart & Parham, 2004; Blanck, McCord & Le, 2006; Spinks, Thomson & Shaffer, 2009; Spinks *et al*. 2012). Hypotheses regarding phylogenetic relationships within the genus are diverse (Yasukawa, Hirayama & Kikida, 2001; Honda *et al*. 2002; Stuart & Parham, 2004; Spinks & Shaffer, 2007; Zhang *et al*. 2008; Spinks, Thomson & Shaffer, 2009; Spinks *et al*. 2012). Among major findings, recent phylogenetic studies (Spinks, Thomson & Shaffer, 2009) suggest that the genera *Pyxidea* Gray, 1863 and *Cistoclemmys* Gray, 1863 should be included in *Cuora* for the genus to be monophyletic, a position that we adopt here. In addition to uncertainties regarding the phylogeny of the genus, species delimitation hardly reaches a consensus: the number of recognized species within the genus *Cuora* still varies from author to author from 10 living species (Fritz & Havas, 2006) to 12 or 13 living species (Iverson, 2008; Spinks, Thomson & Shaffer, 2009; Turtle Taxonomy Working Group, 2011). Taxonomy and systematics is rendered difficult for at least three reasons:

(1) Some species have a small geographical range or are unknown in the wild. For instance, *Cuora yunnanensis* was considered extinct until it was recently rediscovered (Zhou & Zhao, 2004; Blanck, 2005; He *et al*. 2007); species such as *C. mccordi* were for a long time unknown in the wild (Zhou *et al*. 2008).

(2) The presence of nuclear mitochondrial pseudogenes has led to misinterpretations in molecular-based phylogenies (Spinks, Thomson & Shaffer, 2009).

(3) Incomplete lineage sorting and introgression seems common between species of *Cuora* and between *Cuora* and other geoemydid genera (Stuart & Parham, 2007; Spinks, Thomson & Shaffer, 2009). This complexity is well illustrated by the species *C. serrata* Iverson & McCord, 1992. This species was thought to result from hybridization in a turtle farm for the pet trade since it was not known in the wild (Parham *et al*. 2001; Stuart & Parham, 2004, 2007). This taxon was later discovered in the wild and analysed showing that the hybridization was not necessarily driven by farming practices only (Shi *et al*. 2005; Spinks, Thomson & Shaffer, 2009).

Thanks to an increasing number of studies, the systematics of *Cuora* has nevertheless progressed, but problems in species delimitation still impact the way we understand it. Different genes provide different signals, possibly owing to introgression and hybridization (Spinks, Thomson & Shaffer, 2009). Recently, Spinks *et al*. (2012) provided one of the most detailed molecular studies, which resulted in much clearer and better supported nodes within the *Cuora* genus.

On the other hand, the fossil record of the genus is poorly documented, especially for pre-Neolithic times. A better knowledge of fossil *Cuora* can certainly help form a better understanding of the systematics and

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Original article

A new nanhsiungchelyid turtle from the Late Cretaceous of Neixiang, Henan Province, China

Un nouveau chélonien nanhsiungchelyidé du Crétacé supérieur de Neixiang, Province du Henan, Chine

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Abstract

A new genus and species of Nanhsiungchelyidae (Testudines: Cryptodira), *Yuchelys nanyangensis* n. g. n. sp., are described on the basis of a partial skeleton from the Late Cretaceous Gaogou Formation of Neixiang, Nanyang Basin, Henan Province. It is the first nanhsiungchelyid record in the east-central part of China and fills the geographical gap between the western (Uzbekistan, Mongolia, Northern and Southern China) and eastern (Japan) distribution areas of the family Nanhsiungchelyidae.

Keywords: Testudines; Nanhsiungchelyidae; Late Cretaceous; Henan Province; China; Systematics

Résumé

Un nouveau genre et une nouvelle espèce de Nanhsiungchelyidae (Testudines : Cryptodira), *Yuchelys nanyangensis* n. g. n. sp., sont décrits à partir d'un squelette partiel provenant de la formation Gaogou (Crétacé supérieur) à Neixiang, Bassin de Nanyang, Province du Henan, Chine. C'est le premier nanhsiungchelyidé découvert dans le centre-est de la Chine, comblant la lacune géographique entre l'Ouest (Ouzbékistan, Mongolie, Chine du Nord et du Sud) et l'Est (Japon) de la zone de répartition de la famille.

Mots clés : Testudines ; Nanhsiungchelyidae ; Crétacé supérieur ; Province du Henan ; Chine ; Systématique

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SENCKENBERG

ORIGINAL PAPER

A new species of *Sinemys* (Testudines: Cryptodira: Sinemydidae) from the Early Cretaceous of Inner Mongolia, China

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Abstract A new species of *Sinemys* (Testudines: Cryptodira: Sinemydidae), *S. brevispinus* n. sp. is described on the basis of three skeletons from the Early Cretaceous Luohandong Formation, Chabu Sumu, Ordos Basin, Inner Mongolia. The new taxon is characterised by an elongate carapace with a pair of distinct but short lateral spines, a sculptured shell surface, closed lateral carapacial fontanelles and an open incisura columellae auris. A nearly complete turtle skeleton from the Early Cretaceous of Hedaochuan, Huanxian, Gansu Province which was previously referred to *S. lens* is revised and assigned to *S.* cf. *brevispinus*. The systematics of Sinemydidae is discussed and the family is restricted to the genus *Sinemys*. *S. brevispinus* likely lived in a fluvial environment with the spines acting as a stabiliser to limit the rolling of the carapace, as in *S. gamera*, but the difference in the shape of the shell suggests that these two species were adapted to different hydrodynamic regimes. The distribution of *Sinemys* adds to the evidence for biogeographically distinct aquatic communities in eastern and western China during the Early Cretaceous.

Keywords Testudines · Sinemydidae · *Sinemys* · Early Cretaceous · Inner Mongolia · China

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Introduction

Sinemys is a highly aquatic turtle with a flat shell and a seventh peripheral that is laterally expanded, resulting in a lateral process that varies in size from a small process to a large spine. Two species of *Sinemys* are recognised: *S. lens* Wiman, 1930 from the Late Jurassic or Early Cretaceous of the Mengyin Formation of Shandong and *S. gamera* Brinkman and Peng, 1993 from the Early Cretaceous Luohandong Formation of Inner Mongolia (Brinkman and Peng 1993a; Wiman 1930; Ye 1963). Here we report a new species of *Sinemys* from the Early Cretaceous of Inner Mongolia. The material was collected by the Sino-Canadian expedition from the vicinity of Chabu Sumu, west of Otog Qi, Ordos Basin, Inner Mongolia in 1990, together with several specimens of the champsosaur *Ikechosaurus sunailinae*, near a major footprint track site (Brinkman and Dong 1993; Dong 1993).

This description is based on three skeletons, one of which is fully prepared. This latter specimen was mentioned by Gaffney and Ye (1992) and used for comparisons. A nearly complete *Sinemys* skeleton reported by Ye (1963) from the Early Cretaceous of Hedaochuan, Huanxian, Gansu Province is revised. All specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Academia Sinica, Beijing, China.

Systematic palaeontology

Testudines Linnaeus, 1758
Cryptodira Cope, 1868
Eucryptodira Gaffney, 1975
Sinemydidae Ye, 1963
Sinemys Wiman, 1930
Sinemys brevispinus n. sp.
(Figs. 1, 2, 3)

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Geoemydid turtles from the Late Eocene Maoming basin, southern China

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Key-words. – Turtle, Geoemydidae, Eocene, China, Guangdong province.

Abstract. – The fossil record of testudinoid turtles of China during the Eocene-Oligocene is poorly documented. The Maoming basin is one of the few Paleogene basin in southern China having yielded a rich turtle fauna including Trionychidae, Carettochelyidae and Geoemydidae (Testudinoidea). Testudinoids were known in this basin by a single, supposed aquatic species, *Isometremys lacuna* CHOW and YEH, 1962. The examination of the new material collected since the first description, and a reexamination of the type material provide additional data on the morphology of that species. In addition, a second geoemydid, *Guangdongemys pingi* nov gen. nov sp., is described on the basis of shell material. Both species are supposed to be aquatic, and have a probably basal position in the geoemydid phylogeny.

Les tortues geoemydidés du bassin éocène de Maoming au Sud de la Chine

Mots-clés. – Tortues, Geoemydidae, Eocène, Chine, Province de Guangdong.

Résumé. – Le registre fossile des tortues testudinoïdes n'est pas bien documenté dans l'Eocène et l'Oligocène en Chine. Le bassin sédimentaire de Maoming est une des rares localités du sud de la Chine à avoir livré plusieurs espèces de tortues appartenant aux Trionychidés, Carettochelyidés et Geoemydidés. Dans ce bassin, les testudinoides étaient connus par une seule espèce de la famille des Geoemydidés, *Isometremys lacuna* CHOW et YEH, 1962, décrite sur la base de moules internes. L'étude de matériel nouveau et la révision du matériel type permettent de mieux comprendre la morphologie de cette espèce. Par ailleurs, la présence d'un second et nouveau genre de Geoemydidés est attestée dans le bassin, basée sur des carapaces permettant la définition du taxon *Guangdongemys pingi* nov. gen nov. sp. Les deux espèces étaient probablement aquatiques, et leur position phylogénétique est probablement basale au sein de la radiation des Geoemydidés.

INTRODUCTION

Turtles are currently very diversified in the eastern and southern parts of the Eurasian supercontinent with at least two continental clades – Testudinoidea and Trionychia. Molecular phylogenies demonstrate that diverse lineages within these clades live in South-East Asia and in eastern Asia [Diesmos *et al*., 2005; Engstrom, 2004; Spinks *et al*., 2004; Le *et al*., 2007; Praschag *et al*., 2006, 2007], suggesting either that this place may have played a major role in their initial radiation, or that it is today a refuge for turtle diversity. Analysing the fossil record in these places at key periods is therefore of interest for better understanding the origin and evolution of this modern diversity. It has been shown that the Eocene was a key period for the radiation of testudinoids [Claude et Tong, 2004; Claude *et al*., 2007]. However, although well known in Europe, Eocene herpetological assemblages are still poorly known in the eastern and southern parts of the Eurasian supercontinent.

The Maoming basin located in Guangdong province of China has yielded one of the richest turtle faunas, including different aquatic turtle families. In 1955, *Anosteira maomingensis*, a carettochelyid turtle was first described from the basin [Chow and Liu, 1955], rapidly followed by the description of a testudinoid species which was named *Isometremys lacuna* by Chow and Yeh in 1962. A year later, Yeh described *Aspideretes impressus,* a trionychid turtle from the same locality [Yeh, 1963]. Based on additional material, Tong *et al.* [2010] recently redescribed and redefined *Anosteira maomingensis*. *Isometremys lacuna* was described on the basis of internal molds and nearly nothing was known concerning the scute pattern exhibited by this species. This taxon represents, however, one of the very few Eocene-Oligocene testudinoid taxa in southern and eastern Asia (see discussion, table I, and figure 1). This work provides a revision of the holotype and a description of additional material of *Isometremys lacuna* that was collected and gathered by several institutions (Institute of Vertebrate Palaeontology of Beijing, Natural History Museum of Guangxi Zhuang Autonomous Region, Nanning, Beijing Museum of Natural History, and Natural History Museum of Tianjin) since the early discoveries of the fifties. The

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