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The skeletal morphology and phylogenetic position of *Adocus amtgai*, an adocid turtle from the Late Cretaceous of Mongolia

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ABSTRACT

This paper presents the description of the skeletal morphology of *Adocus amtgai*, an adocid turtle from the Late Cretaceous of Mongolia, based on an almost complete skeleton from the upper part of the Bainshire Formation (late Turonian–Santonian) of the Bayshin Tsav locality. Examination of this specimen, which is the best preserved among Asian *Adocus* species, reveals some previously unknown and misunderstood characters of *A. amtgai* and expands our understanding about variation within *Adocus*. The phylogenetic analysis of Adocusia (Adocidae + Nanhsiungchelyidae) places *A. amtgai* within the *Adocus* clade as a sister taxon to *A. aksary* from the Late Cretaceous of Uzbekistan.

1. Introduction

Adocidae Cope, 1870 are a group of freshwater cryptodiran turtles, known mainly from the Cretaceous and Paleogene of Asia and North America (Hutchison, 2000; Sukhanov, 2000; Danilov et al., 2011). Although the adocid record is rather extensive (see Danilov et al., 2011 for the latest review of the Asiatic record of the Adocidae), it is represented mainly by shell material, whereas skulls and elements of non-shell postcrania are known only for four taxa. These are *Adocus* sp. from the Late Cretaceous of the USA, represented by most parts of the skeleton (Meylan and Gaffney, 1989), *A. aksary* Nessov in Nessov and Krasovskaya, 1984 from the Late Cretaceous of Uzbekistan, represented by isolated shell fragments and the skull (Danilov and Parham, 2005; Syromyatnikova and Danilov, 2009), *Ferganemys verzilini* Nessov and Khosatzky, 1977 from the early–middle Albian of Kyrgyzstan, represented by several incomplete skulls and numerous shell fragments (Nessov, 1977; Nessov and Khosatzky, 1977), and *Shachemys laosiana* Lapparent de Broin, 2004 from the Aptian–Albian of Laos, represented by several partial shells, skulls, posterior cervical vertebrae, remains of the girdles, fore- and hindlimbs (Lapparent de Broin, 2004). All these taxa are important for phylogenetic studies of adocids and turtles in general (Meylan and Gaffney, 1989; Lapparent de Broin, 2004; Danilov and Parham, 2005, 2006; Joyce, 2007; Danilov and Syromyatnikova, 2009a, b; Tong et al., 2009; Sterli, 2010; Syromyatnikova, 2011; Anquetin, 2012). One more adocid taxon known from an almost complete skeleton is *A. amtgai* Narmandakh, 1985 from the Late Cretaceous of Mongolia (Danilov et al., 2011). This species was described based on a partial shell, including a plastron with an incomplete carapace (Narmandakh, 1985). Later, based on the shell morphology of a second specimen, represented by an almost complete skeleton, this species was placed in the monotypic genus *Adocoides* Sukhanov and Narmandakh, 2006 (Sukhanov, 2000; Sukhanov and Narmandakh, 2006). To date, only an incomplete carapace of the second specimen has been figured (Sukhanov, 2000, fig. 17.20B). Some preliminary results of the study of the second specimen of *A. amtgai* were reported by Syromyatnikova et al. (2011) and were used in the phylogenetic analysis of other *Adocus* species (Syromyatnikova and Danilov, 2013; Danilov et al., 2013). In this paper, we present a detailed description of this specimen, include *A. amtgai* in the phylogenetic analysis of Adocusia Danilov and Parham, 2006 (a clade uniting Adocidae and Nanhsiungchelyidae Yeh, 1966) and discuss the systematic position of this species.

2. Material and methods

In addition to the material of *Adocus amtgai* described below, our study relies on published data and personal observations on the following taxa of the Adocidae: *Adocus agilis* Cope, 1868a, *A. beatus* (Leidy, 1865) (Hay, 1908; White, 1972; IGD personal

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observations of YPM 782, holotype of *A. punctatus* Marsh, 1890), *A. bossi* Gilmore, 1919, *A. kirtlandius* Gilmore, 1919, *Adocus* sp. (Meylan and Gaffney, 1989; photos of skull CCM 60-15 by J.F. Parham; hereafter *Adocus* sp. 1), *Adocus* sp. (EVS personal observation of UCMP 129732; hereafter *Adocus* sp. 2), *A. syntheticus* Cope, 1870 from the Late Cretaceous, *A. annexus* Hay, 1910 (Hay, 1910; Gilmore, 1919) and *A. substrictus* Hay, 1908 from the Paleocene of the USA (Hay, 1908); *A. aksary* Nessov in Nessov and Krasovskaya, 1984 from the Late Cretaceous of Uzbekistan (see Syromyatnikova and Danilov, 2009); *A. bostobensis* Syromyatnikova and Danilov, 2009 from the Late Cretaceous of Kazakhstan (Syromyatnikova and Danilov, 2009, 2013), *A. foveatus* Nessov and Khosatzky in Khosatzky and Nessov, 1977 from the Late Cretaceous of Tajikistan (see Syromyatnikova and Danilov, 2009); *A. kizylkumensis* Nessov, 1981 from the Late Cretaceous of Uzbekistan (see Syromyatnikova and Danilov, 2009); "*Adocus*" *orientalis* Gilmore, 1931 from the late Eocene of China and Mongolia (Gilmore, 1931; Danilov et al., 2011); *A. planus* (Sukhanov and Narmandakh, 2006) from the Late Cretaceous of Mongolia (see Syromyatnikova et al., 2012); *Adocus* sp. from the Late Cretaceous of Canada (EVS personal observations of RTM 99.63.1; hereafter *Adocus* sp. 3); *Yehguia tatsuensis* (Yeh, 1963) from the Late Jurassic of China (Danilov and Parham, 2006).

The phylogenetic analysis of the clade Adocusia was performed based on a modified character/taxon matrix of Danilov and Syromyatnikova (2009a,b) with additions from Syromyatnikova (2011) and Syromyatnikova et al. (2012). The following modifications to this character/taxon matrix were made: we added *Adocus amtgai* and one additional character: 78, marginals overlapping onto the costals: (0) beginning with marginal 5; (1) beginning with marginals 3 or 4 (see Appendix 1 for distribution of this new character and Appendix 2 for characters coded for *A. amtgai*). The final data matrix includes 78 osteological characters for 27 taxa. Our updated matrix was assembled using NDE 0.5.0 (Page, 2001) and analyzed with NONA ver. 2 and Winclada ver. 1.00.08 by Ratchet algorithm with 1000 iterations. Characters were left unordered and considered reversible and of equal weight. Bremer supports were calculated using Autodecay 4.0.1 (Eriksson, 1998).

Institutional abbreviations. CCM, Carter County Museum, Ekalaka, Montana, USA; PIN, Borissyak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; RTM, Royal Tyrrell Museum of Paleontology, Drumheller, Canada; UCMP, University of California Museum of Paleontology, Berkeley, USA; YPM, Yale Peabody Museum, New Haven, USA.

3. Systematics section

Testudines Batsch, 1788
Cryptodira Cope, 1868b
Adocusia Danilov and Parham, 2006
Family Adocidae Cope, 1870
Genus *Adocus* Cope, 1868a

Adocus amtgai Narmandakh, 1985
Figs. 1–13

1985 *Adocus amtgai* Narmandakh: Narmandakh, p. 86, fig. 1;
2000 *Adocoides amtgai* (Narmandakh): Sukhanov, p. 335, fig. 17.20 (nomen nudum);
2006 *Adocoides amtgai* (Narmandakh): Sukhanov and Narmandakh, p. 124;
2009 *Adocus amtgai* Narmandakh: Syromyatnikova and Danilov, p. 76; Syromyatnikova et al., p. 77;
2011 *Adocus amtgai* Narmandakh: Danilov et al., p. 103, 105, 127; Syromyatnikova et al., p. 202; 2013 *Adocus amtgai* Narmandakh: Syromyatnikova and Danilov, 2013, p. 198–200.

Holotype. PIN 3640–2, a partial shell, including plastron with incomplete carapace; Amtgai locality (=Amtgai Khuduk), Dornogov Aimag, Mongolia; upper part of the Bainshire Formation, upper Turonian–Santonian.

Referred material. PIN 3640–3, an almost complete skeleton from the Bayshin Tsav locality, Dornogov Aimag (Eastern Gobi), Mongolia; upper part of the Bainshire Formation, upper Turonian–Santonian. Previously, this specimen was erroneously indicated to come from the Amtgai locality (Sukhanov, 2000, p. 335, fig. 17.20b; Syromyatnikova et al., 2009, p. 77; Danilov et al., 2011, p. 105; Syromyatnikova et al., 2011, p. 202).

Emended diagnosis. *Adocus amtgai* can be differentiated from other *Adocus* species by narrower pleurals 2–4 (width is ~30% of its length) and accordingly wide lateral and posterior marginals, shorter pectorals; marginals overlapping onto costals beginning with marginal 4 (except *A. aksary*), longer anterior lobe of the plastron (except *A. annexus*). In addition, it can be differentiated from *A. aksary* by its relatively longer and wider temporal emargination, transverse prefrontal–frontal suture, more elongated neural 6, trapezoid cervical, wider anterior border of epiplastron and gulars, and shorter extragulars; from *A. planus* by extension of gulars onto entoplastron; from *A. beatus* by narrower vertebral 5 and wider inframarginals. See Tables 1 and 2 for a more detailed comparison.

Description of PIN 3640–3.

Skull (Figs. 1, 2). The skull is incomplete and deformed. Part of the left zygomatic arch is missing along with the vomer, palatine, most of the palatal parts of the maxilla and premaxillae, most part of the pterygoids and basisphenoid, basioccipital and posterior end of the supraoccipital crest. Lateral parts of the otic capsules are damaged or not preserved. Viewed from above, the anterior part of the skull is slightly constricted in the preorbital region. The similar constriction is observed in *Adocus aksary*, whereas in *Adocus* sp. 1 this constriction is more strongly developed. The orbits seem to be slightly depressed and placed in the anterior third of the skull. They are directed anterolaterally, forming an angle of ~30° with the long axis of the skull. Similar shape and orientation of the orbits is known in *A. aksary*, whereas in *Adocus* sp. 1 the angle formed by the orbits with the long axis of the skull is slightly greater. The upper temporal emargination is relatively long and wide, occupying more than half of the skull length. The processus trochlearis oticum is well developed. The lower temporal emargination is well developed, deepest in its medial part and without a pocket in its anterior part similar to *A. aksary*.

Skull roof. There is no indication of nasal bones. The prefrontals form the anterior margin of the skull roof and roof the fossa nasalis. Anteriorly, the prefrontals do not form the medial projection present in *A. aksary*. The contact between the prefrontal and maxilla lies at the level of the upper border of the orbit. The ventral process of the prefrontal is broken. The prefrontal–frontal suture is perpendicular to the midline of the skull as in *Adocus* sp. 1, whereas in *A. aksary* this suture extends slightly posterolaterally from the midline. The frontals enter the orbital margin forming about one half of its length in dorsal view. In *A. aksary*, the degree of frontal contribution to the orbital margin is similar, whereas in *Adocus* sp. 1 it is distinctly smaller (approximately one-third of the dorsal orbital margin). The contacts