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

E.V. Syromyatnikova\(^a\),\(^{*}\), I.G. Danilov\(^a\), V.B. Sukhanov\(^b\)

\(^{a}\) Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 St. Petersburg, Russia

\(^{b}\) Borissyak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, 117997 Moscow, Russia

**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 Asian 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 Adocisia Danilov and Parham, 2006 (a clade unifying 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...
observations of YPM 782, holotype of A. punctatus Marsh, 1890), A. bossi Gilmore, 1919, A. kirtlandi 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 observations 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 Krasotzyk 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 et al. (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 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, Ekala, 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
Adocidae Cope, 1870
Genus Adocus Cope, 1868a
Adocus amtgai Narmandakh, 1985
Figs. 1–13
1985 Adocus amtgai Narmandakh: Narmandakh, p. 86, fig. 1;
2000 Adocides amtgai (Narmandakh): Sukhanov, p. 335, fig. 17.20
from the Late Jurassic of China (Danilov and Parham, 2006);
2006 Adocus 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;

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, trapezoidal 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 premaxilla, most of the pterygoids and basisphenoid, basioccipital and posterior end of the supraoccipital crest. Lateral parts of theotic 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
of the frontal with the postorbitals and the parietals are similar to *Adocus* sp. 1, except that the sutures in *A. amsi* are straight and without distinct interdigitations. The dorsal portion of the parietal is relatively narrow anteriorly and does not conceal the medial portion of the processus trochlearis oticum in dorsal view, similar to *Adocus* sp. 1, but differing from *A. amsi*, in which this portion is relatively wider. The parietals contact the frontals anteromedially and the postorbitals anterolaterally along long and short sutures, respectively. The parietals contact the prootic posterolaterally and the supraoccipital posteriorly. The lateral aspects of the descending parietal process (i.e., processus inferior parietalis) support the medial third of the processus trochlearis oticum. The ventral aspects of this process form the dorsal part of the anterior margin of the foramen nervi trigemini. Both postorbitals are preserved. The postorbital forms parts of the posterior orbital margin and the anterior rim of the upper temporal emargination. The contacts of the postorbital with the frontal and the parietal are at the level of the upper orbital margin. The contact of the postorbital with the frontal is equal to its contact with the parietal on the right side and longer than its contact with the parietal on the left side. The contact of the postorbital with the jugal is visible only on the right side. The jugal is almost complete on the right side, whereas on the left side its posterior part is broken off. The jugal forms the posterior margin of the orbit, the anterior part of the zygomatic arch and the dorsal part of the cheek emargination. The contacts of the jugal with the maxilla and the quadratojugal are not clear. The medial process of the jugal is either not visible or not preserved in both jugals. The quadratojugal and squamosal are preserved in the right side of the skull, but their sutures are not clear. The maxilla is preserved on both sides of the skull. The maxilla articulates with the premaxillae anteromedially and the prefrontals dorsally, but its contact with the jugal is unclear. The maxilla is long and low in lateral view, having no tooth-like projection, similar to *Adocus amsi*, whereas in *Adocus* sp. 1 the maxilla is higher and shorter, having the tooth-like projection. A ventral horizontal plate of the maxilla is partly visible in ventral view and forms the triturating surface. The vomer and palatines are missing.

**Table 1** Comparisons of skulls of *Adocus amsi* (ZISP PH 1/17), *A. amsi* (PIN 3640–3) and *Adocus* sp. 1 (CCM 60–15). "?" denotes impossibility of measuring.

<table>
<thead>
<tr>
<th>Characters</th>
<th>ZISP PH 1/17</th>
<th>PIN 3640–3</th>
<th>CCM 60–15</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior part of skull in dorsal view</td>
<td>Narrows gradually</td>
<td>Narrows gradually</td>
<td>Sharply constricted in preorbital region</td>
</tr>
<tr>
<td>Orbits</td>
<td>Directed anterolaterally under 30° to long axis of skull</td>
<td>Directed anterolaterally under 30° to long axis of skull</td>
<td>Directed anterolaterally under 40° to long axis of skull</td>
</tr>
<tr>
<td>Temporal emargination at dorsal view</td>
<td>Short and narrow (occupies about 50% of skull length, conceals medial portion of processus trochlearis oticum)</td>
<td>Long and wide (occupies more than 50% of skull length, medial portion of processus trochlearis oticum visible)</td>
<td>Long and wide (occupies more than 50% of skull length, medial portion of processus trochlearis oticum visible)</td>
</tr>
<tr>
<td>Snout profile in lateral view</td>
<td>Oblique, projected ventrally</td>
<td>Oblique, projected ventrally</td>
<td>Vertical</td>
</tr>
<tr>
<td>Prefrontal-frontal suture</td>
<td>Wedge between the prefrontals</td>
<td>Transverse</td>
<td>Transverse</td>
</tr>
<tr>
<td>Participation frontals into orbital margin</td>
<td>Form about one half of its length</td>
<td>Form about one half of its length</td>
<td>Form less than half of its length</td>
</tr>
<tr>
<td>Groove behind the foramen stapedio-temporale</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Maxilla</td>
<td>Long and low in lateral view</td>
<td>Long and low in lateral view</td>
<td>High and short in lateral view</td>
</tr>
<tr>
<td>Cheek emargination</td>
<td>Deepest in its medial part, without pocket anteriorly</td>
<td>Deepest in its medial part, without pocket anteriorly</td>
<td>Deepest anteriorly where it forms a pocket</td>
</tr>
<tr>
<td>Maxillary “tooth”</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>Ventral surface of basioccipital</td>
<td>With semicircular depression and groove</td>
<td>With semicircular depression</td>
<td>With semicircular depression with small crest, without groove</td>
</tr>
<tr>
<td>Postorbital</td>
<td>Does not contribute to zygomatic arch</td>
<td>?</td>
<td>Probably contributes to zygomatic arch</td>
</tr>
</tbody>
</table>

**Palatal elements.** The premaxilla is visible in ventral and anterior aspects; its posterior part is missing. Laterally, the premaxilla meets the maxilla to form the triturating surfaces; medially, both premaxillae meet on the midline and enter dorsally into the palatoquadrate and braincase. The ventral portion of the premaxilla forms the anterior-most portion of the poorly preserved labial ridge and triturating surface. The contact of the premaxilla with the vomer is not observable. The maxilla is preserved on both sides of the skull. The maxilla articulates with the premaxillae anteromedially and the prefrontals dorsally, but its contact with the jugal is unclear. The maxilla is long and low in lateral view, having no tooth-like projection, similar to *Adocus amsi*, whereas in *Adocus* sp. 1 the maxilla is higher and shorter, having the tooth-like projection. A ventral horizontal plate of the maxilla is partly visible in ventral view and forms the triturating surface. The vomer and palatines are missing.

**Cranial foramina.** The foramen stapedio-temporale is preserved on both sides of the skull. As in other *Adocus*, it is large and well developed, formed by the prootic medially and the quadrato laterally. There is a shallow groove directed posteriorly from the foramen. A similar groove is known in *A. amsi* but seems deeper and directed more medially; this groove is absent in *Adocus* sp. 1. The foramen posterior canalis caroticus interni is missing. Part of the canalis caroticus internus is exposed on the left side due to a breakage of the basisphenoid–pterygoid region. It is directed from the posterior edge of the pterygoid anteromedially and probably was formed by the pterygoid. The foramen basisphenoidale is not observable.

**Palatoquadrate and braincase.** The quadrate is partially preserved on the left side of the skull only. The cavum tympani is only partially preserved and the incisura columella auris is missing. The processus trochlearis oticum is well developed and visible on both sides of the skull. It is formed by the quadrate laterally, and more medially by the prootic and the inferior process of the parietal. The process is trough-like, strongly concave dorsally and anteriorly, and protrudes into the adductor fossa. The contribution of the pterygoid to this process is about one-third of the total, but seems to be greater than in other *Adocus*. The opisthotic is preserved on both sides and visible externally in dorsal and posterior views. It contacts the prootic anteriorly, the quadrate laterally, the supraoccipital anteromedially, and the exoccipital posteromedially. The opisthotic is relatively shorter than in *Adocus amsi* and *Adocus* sp. 1. The fenestra postotica is not preserved. The foramen nervi trigemini is visible on the left side, with the prootic forming its dorsal margin, the parietal forming its anterior margin, and the pterygoid forming its ventral margin. Similar morphology of the foramen nervi trigemini is known in *Adocus* sp. 1. The occipital bones are represented by the supraoccipital and the exoccipitals, whereas the basisphenoid is not preserved. The supraoccipital forms the supraoccipital crest and dorsal margin of the foramen magnum. The exoccipitals are not discernible, but probably formed the lateral margins of the foramen magnum. The basisphenoid is represented only by two isolated fragments which do not show any morphological features.
Lower jaw. The lower jaws are represented by both rami. The left ramus and anterior part of the right ramus were separated from the skull during the preparation, whereas the middle portion of the right ramus was left articulated with the skull. The triturating surface of the dentary is only slightly concave in the posterior part, unlike Adocus sp. 1. The presence of the dentary pocket known in Adocus sp. 1 is unclear. The coronoid process is relatively low and reaches its greatest height in the posterior part of the lower jaw. In Adocus sp. 1, the coronoid process is much higher and reaches its greatest height in the middle of the lower jaw. The coronoid, surangular and angular are visible in lateral view. Other elements of the lower jaw are missing.
Shell (Figs. 3–5). The estimated length of the shell is ~400 mm, whereas its width is hard to estimate due to deformation. The plastron is estimated to approximate 75% of the carapace length and almost reach the carapace rim anteriorly. The surface of the shell is covered by typical adocid sculpturing, consisting of relatively small and regular grooves and pits (see Danilov et al., 2011). The scute sulci are narrow and shallow.

Carapace. Although the carapace is missing some parts in its middle–posterior portion, it can be almost fully reconstructed. The

Fig. 1. Skull (A–F) and lower jaw fragment (G, H) of Adocus amtgai (PIN 3640–3): A – dorsal view, B – ventral view, C – right lateral view, D – left lateral view, E – anterior view, F – posterior view, G – lateral view, H – dorsal view.
Fig. 2. Skull (A–F) and lower jaw fragment (G, H) of Adocus amtgai (PIN 3640–3), explanation drawings of Fig. 1: A – dorsal view, B – ventral view, C – right lateral view, D – left lateral view, E – anterior view, F – posterior view, G – lateral view, H – dorsal view. See Fig. 2 for abbreviations and designations. Abbreviations: ac – acetabulum; acrp – acromion process; ang – angular; bs – basisphenoid; c – costal; cci – canalis caroticus internus; ce – cervical; ch – caput humeri; cor – coronoid; den – dentary; ectf – ectepicondylar
carapace is oval-shaped, widened anteriorly (as wide anteriorly as posteriorly), with a shallow nuchal emargination that formed by the nuchal and anterior part of the peripherals similar to those in *Adocus aksary* and *A. bossi*. The carapace is low-domed, as in other *Adocus*, its anterior part in lateral view looks more steep than the posterior one. The anterior part of the carapace has a strongly upward free border.

The nuchal is relatively wide (wider than long) hexagonal and slightly emarginated anteriorly. Its free edge is rounded and upturned in the cross-section. The anterior border of the nuchal is relatively wide (ratio of the nuchal anterior width to its maximal width is seven-tenths, that is the same as in *A. aksary*). The anterolateral and posterolateral borders of the nuchal are nearly straight or slightly convex and about of the same length. As in other *Adocus*, the posterior border of the nuchal is concave and contacts with neural 1.

The neural formula is typical for most of the Adocidae: neural 1 is hexagonal short-sided posteriorly, neural 2 is tetragonal, neurals 3-5 are hexagonal and short-sided anteriorly and neural 6 is heptagonal. Neural 2 is relatively short as seen in *A. beatus* and *A. aksary*. Neural 6 is relatively elongated with an angled posterior border which slightly wedges between costals 7. Most other species of *Adocus* (*A. aksary*, *A. beatus*, *A. bossi*, and *A. kirtlandius*) have six neurals, however, among them, the similarly elongated heptagonal neural 6 is present only in *A. beatus*.

There are two suprapygalss. Suprapygal 1 is a relatively small, elongated, oval-shaped element. Suprapygal 2 is a relatively wide.
octagonal element that contacts suprapygal 1 along concave anterior borders, costals 8 along straight anterolateral borders, peripherals 10 along convex lateral borders, peripherals 11 along slightly convex posterolateral borders, and the pygal along a convex posterior border. Similar suprapygals are known in other Adocus, except A. bossi, which has no suprapygal 1.

The pygal is a slightly longer than wide, trapezoidal (ratio of the anterior pygal width to its posterior width is about three-fifths), and has straight lateral borders. The free edge of the pygal is slightly upturned. The described pygal morphology is similar to that in other members of the Adocidae.

The costals are represented by eight pairs, which are nearly complete, except that most of left costals 6 and 7 are missing. Ribheads and rib thickenings of the costals are weak as in other adocids, except Yehguia tatsuensis. On the internal surface of costal 1, scars of thoracic ribs 1 and 2 lie close to each other. Costals 7 contact each other along the midline. Costals 8 contact each other along the midline at the anterior half of their medial length and separated by suprapygal 1 at the posterior half of their medial length. Among adocids, similar posterior-costal morphology is seen in Adocus beatus.

The peripheral series is represented by almost complete peripherals 1—11 on the right side and peripherals 1—6, 10 and 11 on the left side. The anterior peripherals (1—3) appear trapezoidal in dorsal view with short medial and long lateral borders. Their free edges are upturned and angled in the cross-section. The bridge peripherals (4—8) are mostly rectangular and partly broken along the free edges. The posterior peripherals are wider than the anterior ones with upturned and angled free edges. There is some variation in peripherals of the right and left sides. Peripheral 1 on the right side fused with peripheral 2 forming a single wide element, which at least half as wider than peripheral 1 of the left side. Peripheral 3 on the left side contacts only with costal 1, whereas on the right side it reaches costal 2 as well. Peripheral 4 on the left side is longer medially than laterally and contacts with costals 1—3, whereas on the right side it is shorter medially than laterally and contacts only costal 2. Peripheral 5 on the left side is shorter medially than laterally and contacts only costal 3, whereas on the right side it is longer medially than laterally and contacts costals 2—3. Peripherals 6—9 have convex medial borders that slightly wedge between the corresponding costals. Peripheral 10 contacts costals 7 and 8 and suprapygal 2 medially. Peripheral 11 is shorter than peripheral 10.

All carapacial scutes are observable, however the shape of the cervical and vertebrais 3—5 are partially reconstructed as narrow and trapezoidal, slightly expanded anteriorly. Among other Adocus, a similar cervical is known in A. aksary and A. beatus. Vertebral 1 is trapezoidal, widened anteriorly and in contact with marginals 2, as in all other Adocus. Vertebrails 2—4 are longer than wide. Vertebral 2 seems to be shorter than vertebral 3 which is longer than others. Vertebral 4 is shorter than vertebrails 2 and 3 and narrowed posteriorly. Vertebral 5 is small and ovate as in A. aksary and A. bossi. In other species of Adocus, vertebral 5 is usually wider (A. kirtlandius
and *A.* hesperius) or as wide as more anterior vertebrae (*A.* beatus). The pleurals are longer than wide and getting narrower from the anterior to the posterior ones. Pleural 1 is anomalous and differs in shape on the left and right sides. The left pleural 1 is wide posteriorly and overlaps peripheral 4; its lateral border has a strong indentation due to the invasion of marginal 4. The right pleural 1 is narrowed in posterior part and does not reach peripheral 4; the indentation of its lateral border is absent. Pleurals 2–4 are extremely narrow (ratio of the pleural width to its length is about three-tenths). In other *Adocus*, the pleurals are relatively wider (ratio of the pleural width to its length is usually ~0.6; see Table 2).

The marginals are represented by a virtually complete set of scutes (12 pairs) except for the left marginals 8–11. Marginals 1–3 are restricted to the peripherals and cover approximately half of their external surface. Marginal 4 overlaps onto the costals. The left marginal 4 overlaps costal 1 only by its anteromedial part; whereas its posteromedial part does not reach the costals. The right marginal 4 overlaps costal 2 by its posteromedial part. Thus, the overlapping of the marginals onto costals begins with marginal 4. In most other species of *Adocus*, overlapping begins with marginal 5, whereas in *A.* aksary it also begins with marginals 4 (or even 3). Marginals 5–10 overlap the corresponding costals (2–8), covering about one-third of their width. Marginals 11 and 12 cover more than half of the length of costals 8 and suprapygal 2.

The skin-scute sulcus lies very close to the free edge of the nuchal and in the middle part of the peripherals.

**Plastron.** The plastron is almost completely preserved. The anterior lobe of the plastron is wider than long (length of anterior lobe is about one half of its width), truncated anteriorly and does not reach the anterior carapace rim. In other species of *Adocus*, the anterior lobe is either rounded (*A.* annexus, *A.* bossi, *A.* kirtlandius, and *A.* substrictus) or truncated (*A.* aksary, *A.* beatus, *A.* syntheticus, and “A.” orientalis) anteriorly. The length of the anterior lobe makes up 30% of the plastron length. In other *Adocus*, the length of the anterior lobe varies from 22 to 23% (*A.* beatus and *A.* kirtlandius) to 27% (*A.* annexus) of the plastron length. The posterior lobe narrows posteriorly and is longer and narrower at the base than the anterior one. The length of the plastral bridge is ~40% of the plastron length. The gular and anal notches are absent as in other *Adocus.* The epiplastron has a relatively wide and straight (truncated) anterior border, which is greater than the length of the epiplastral symphysis that is also known from *A.* beatus and *A.* foveatus. The dorsal surface of epiplastron is concave. The entoplastron is a large hexagonal element, wider than long and with poorly developed lateral borders. The similar hexagonal entoplastron is characteristic of all *Adocus* species. On the dorsal surface of the entoplastron, a Y-shaped system of ridges is poorly visible. The hypoplastra and hypoplastra have no peculiarities and make equal contributions to the bridge length. The left hypoplastron and the right hypoplastron have a long contact that separates the right hypoplastron from the left hypoplastron. The xiphiplastron is longer than wide, narrowed posteriorly and with a rounded lateral border. The length of the xiphiplastron is ~75% of the posterior lobe length along the midline. Internally, it bears an oval area for the pelvic attachment.

The plastral scutes are represented by a complete set including two pairs of gulars, extragulars, humerals, pectorals, abdominals, femorals, anals and four pairs of inframarginals. The gulars are relatively wide (anterior width of the gular is more than the length of the epiplastral symphysis), like in *A.* beatus. The gulars slightly overlap the entoplastron as in most other species of *Adocus* (except *A.* planus and sometimes *A.* aksary and *A.* beatus). The extragulars are relatively small covering about one-fourth of the external surface of the epiplastra, with short medial borders that comprise about three-fifths of length of the epiplastral symphysis. The short medial borders of the extragulars are known in *A.* beatus, whereas in other species they are usually longer. The lateral borders of the extragulars are strongly elongated reaching the epi-hyoplastral.
suture posteriorly similar to cf. “Adocus” orientalis (see Danilov et al., 2011). The pectorals are strongly shortened (their medial length is about eight hundredth of the plastron length), longer medially than laterally and slightly overlapping the entoplastron. They contribute to the rim of the axillary notch, as in other adocids. The pectorals of other species of Adocus are variable: overlapping (A. annexus and A. beatus) or not overlapping the entoplastron (A. agilis, A. bossi, A. kirtlandius, “A.” orientalis, and A. substrictus). The abdominals are long and contribute to the rim of the inguinal notch. The femoral–anal sulcus is S-shaped. The inframarginals are relatively wide and partly extend onto the peripherals. Their size and shape are variable; there are three inframarginals on the right side and five inframarginals on the left side. On the right side, inframarginals are similar to those of PIN 3640–2: inframarginal 1 is large, narrowed medially and widened laterally, and does not contribute to the pectoral rim; inframarginal 2 is about twice as longer as inframarginal 1, spans the hyo-hypoplastral suture; inframarginal 3 contributes to the rim of the inguinal notch. On the

![Fig. 6. Cervical vertebrae of Adocus amtgai (PIN 3640–3), photographs: A – cervical 4, B – cervical 5, C – cervical 7, D – cervical 8. Lateral views of C and D are mirror images.](image-url)
left side, inframarginal 1 is relatively short and widely contributes to the pectoral rim; inframarginal 2 is longer than the others, spans the hyo-hypoplastral suture only by its most posterior part; inframarginal 3 is slightly shorter than inframarginal 2; inframarginal 4 seems short and contribute to the rim of the inguinal notch. An additional inframarginal scute is present on the left side of the plastron between the abdominal and inframarginals 2 and 3. It spans the hyo-hypoplastral suture. In other *Adocus*, the inframarginals are usually represented by four pairs, except for *A. bossi* which has three. The midline sulcus is strongly sinuous. The skin-scute sulcus lies close to the free edge of the plastral lobes.

**Cervical vertebrae** (Figs. 6, 7). The cervical series is incomplete and represented only by the partly preserved cervical vertebrae 4, 5, 7 and 8. All cervicals are opisthocoelous as in *Adocus* sp. 1. Centra 4, 5 and 7 are at least twice as long as they are wide; centrum 8 is as

---

**Fig. 7.** Cervical vertebrae of *Adocus amtgui* (PIN 3640−3), explanation drawings of Fig. 6: A – cervical 4, B – cervical 5, C – cervical 7, D – cervical 8.
Fig. 8. Left pectoral girdle of *Adocus amtgai* (PIN 3640-3): A — scapula, anterior view, B — explanation drawing of the same, C — scapula, posterior view, D — explanation drawing of the same, E — coracoid, dorsal view, F — explanation drawing of the same, G — coracoid, ventral view, H — explanation drawing of the same. See Fig. 2 for abbreviations and designations.
Fig. 9. Left humerus (A–H) and left manus (I–L) of Adocus antiquai (PIN 3640–3): A – posterior view, B – explanation drawing of the same, C – dorsal view, D – explanation drawing of the same, E – ventral view, F – explanation drawing of the same, G – anterior view, H – explanation drawing of the same, I – ventral view, J – explanation drawing of the same, K – dorsal view, L – explanation drawing of the same. See Fig. 2 for abbreviations and designations.
Fig. 10. Pelvic girdle of Adocus amtgai (PIN 3640–3): A – dorsal view, B – explanation drawing of the same, C – left lateral view, D – explanation drawing of the same, E – ventral view, F – explanation drawing of the same. See Fig. 2 for abbreviations and designations.
wide as long. Centrum 4 has a single convex anterior articular surface; the posterior surface is partly missing but seems to be single concave. Centrum 5 has a single convex anterior articular surface; its posterior surface is missing. Centrum 7 has a doubled convex anterior articular surface; its posterior surface is missing. Centrum 8 has a doubled concave posterior articular surface; the anterior surface is partly missing but appears to be doubled convex. Partial ventral keels are present on centra 4 and 5. They are represented by small, thin fragments which do not allow their shape to be restored. The neural arches have widely separated pre- and postzygapophyses. The postzygapophyses become more robust posteriorly.

**Pectoral girdles** (Fig. 8). Both right and left pectoral girdles are almost completely preserved. The scapular and acromion processes of the scapula meet at an angle of \( 90^\circ \). The scapular process is rod-like and rounded in cross-section. The acromion process is slightly flattened and bowed downwards. It is shorter than the scapular process (ratio of its length to length of the scapular process is 0.7), like in *Adocus* sp. 1. The coracoid is long, flat, and relatively wide (its length is approximately one-third of its width) with a truncated distal edge. It is longer than the acromion process of the scapula and only slightly shorter than the body of the scapula. In *Adocus* sp. 1, the coracoid is about the same proportion, but has a rounded distal edge.

**Forelimb** (Fig. 9). The left and proximal part of the right humeri are almost complete. The caput humeri are large and oval in dorsal view. It is located at an angle of \( 90^\circ \) to the shaft of the humerus. The medial process of the humerus is about three times larger than the lateral process; between them is a well-developed intertubercular fossa. The medial process extends posteriorly from the shaft at an angle of \( 40^\circ \), and extends as far medially as does the caput humeri. The lateral process diverges anteriorly from the shaft at an angle of \( 10^\circ \) and does not extend medially to the level of the caput humeri. The two distal trochanters, the capitellum and trochea, are approximately equal in size. The ectepicondylar foramen is closed. Dorsally under the caput humeri, there is a concave

---

**Fig. 11.** Right femur of *Adocus amgai* (PIN 3640–3): A – anterior view, B – explanation drawing of the same, C – dorsal view, D – explanation drawing of the same, E – ventral view, F – explanation drawing of the same, G – posterior view, H – explanation drawing of the same. See Fig. 2 for abbreviations and designations.
attachment for mm. latissimus dorsi et teres major. The described morphology of the humerus is similar to that of Adocus sp. 1.

Other elements of the forelimb are represented by the complete left radius, small distal part of the ulna and metacarpal with phalanges which are encased in the sediment and have shifted from their original natural position. The distal part of the ulna is flattened distally and seems to be widened distally. The manus is like those of many other turtles and has a primitive number of elongated metacarpals and phalanges. The carpus is not preserved. The metacarps and phalanges are represented partly for 1–4 digits. The phalanges are 2–3–3–3–3 with claws apparently present on all five digits.

Pelvic girdle (Fig. 10). The pelvic girdle is incomplete and has been distorted. The ilia form the dorsal third of the acetabulum and extend posterodorsally at an angle of nearly 120°. The thelial processes are represented by the virtually complete right element, whereas the left element is absent. The thelial process is weak as in Adocus sp. 1. The pubes make up one-third of the acetabulum. They are slightly narrowed anteriorly with broad interpubic contact that extend anteriorly well beyond the pectineal processes. Whether the pubic projected a process into the thyroid fenestra at the midline is unclear, but probably absent in contrast to Adocus sp. 1. The pectineal processes are large and elongate, lying at nearly right angles to the midline; however, such a position is reconstructed and could be incorrect. In Adocus sp. 1, the pectineal processes appear to be somewhat shorter. The ischia comprise the posterodorsal third of the acetabulum; the ventral portions of ischia are missing. The metischial processes are long, as in Adocus sp. 1. The thyroid fenestra is not divided.

Hindlimb (Figs. 11–13). The femur is represented by both elements, but their distal ends are damaged. The estimated length of the femur is 73 mm. The femur is slightly curved and expanded medially. There are two large proximal trochanters which are about the same size and separated by the well-defined and deep intertrochanteric fossa. The trochanter minor does not extend proximally as much as the trochanter major and does not extend medially beyond the head. The femoral head is oval, longer than narrow. The distal end of the femur is partly damaged and represented only by part of the tibial condyle. The distal articular surface appears to face ventrally and is divided into two distinct condyles. The tibia is represented by the complete right and proximal part of the left elements; its length is 55 mm. The tibia is expanded to bear the articulation with the femur proximally and tapers distally. The shaft of the tibia bows away from the fibula as in other turtles. The proximal articular surface has a medial concavity and a weak lateral convexity for the articulation with the condyles of the femur. The patellar tendon attachment site (=cnenial crest) is identifiable as a rugose area with a concavity on the dorsal surface of the tibia. In Adocus sp. 2,
the patellar tendon attachment site looks weakly developed and smooth. At the proximal part along the shaft of the tibia, there is a rugose protuberance for attachment of the flexor tibialis internus.

The fibula is preserved by an almost complete right element with length 56 mm. The fibula is relatively straight, its distal end expanded and the proximal one slightly larger than the shaft. The plane of distal expansion is twisted from the plane of the proximal expansion for $\sim 30^\circ$ as in most other turtles. The distal part of the fibula shaft is flat on its dorsal side but there is a thickened ridge on the ventral side that ends at an expanded part of the distal articulation surface. The tarsals and part of metatarsals are missing from the pes. The preserved metatarsals and phalanges are disarticulated and do not allow identifying its exact position in the pes. However, it is clear that they are distinctly larger than the corresponding bones of the manus.

4. Discussion

The newly described material of an almost complete Adocus amtgai skeleton, allows us to emend the diagnosis of this species (see Systematic paleontology section).

Adocus amtgai is assigned to Adocidae based on the following characters (following Danilov and Syromyatnikova, 2008): (1) adocid-type of sculpturing, (2) narrow and shallow scute sulci, (3) weak ribheads, (4) weak rib thickenings of the costals, (5) longer than wide pygal, (6) relatively short plastral bridges (<50% of plastron length), (7) relatively long posterior plastral lobe (>30% of plastron length), (8) presence of the pectoral contribution to the axillary rim, (9) ventromedial edge of marginal 6 not expanded, and (10) absence of overlapping scutes onto the dorsal surface of plastral lobes. Adocus amtgai is assigned to the genus Adocus based on the marginals that overlap onto the costals in the middle and posterior parts of the carapace. Most of the described characters of the skull and shell (see Tables 1 and 2) indicate that A. amtgai is most similar to A. aksary. One of these characters is the extension of the marginals onto the costals beginning with marginals 4. In A. aksary, such an extension begins with marginals 3 or 4, whereas in most other species of Adocus it begins with marginals 5 (see also Syromyatnikova and Danilov, 2013; Danilov et al., 2013). Another important character of A. amtgai is a very narrow vertebral 5 (narrower than anterior vertebrae). Among other species of Adocus, the similar narrow vertebral 5 is known in A. aksary and A. bossi.

Previously, Adocus amtgai was placed in its own genus Adocoides based on the following characters identified by Sukhanov (2000) and Sukhanov and Narmandakh (2006): reduction of the cervical; presence of relatively wide vertebrae 2–4; significantly wider marginals 4–12; very narrow pleurals 2–4; very narrow vertebral 5; larger size of the plastron; smaller size of gulars and extragulars; strongly shortened of pectorals and correspondingly elongated abdominals, greater width of inframarginals. New data on Adocus amtgai’s morphology allow us to comment on these characters. Our observation of PIN 3640–3 does not confirm the presence of an “almost complete, reduction of the cervical and the appearance of a contact between the first marginals” (Sukhanov, 2000, p. 336). Actually, A. amtgai has a narrow cervical that excludes a contact between marginals 1. Vertebrae 2–4 of A. amtgai are similar in width to those of A. aksary (the length of vertebral 3 is same as its width in both species). The narrow vertebral 5 is known in some other species of Adocus (see above). The ratio of the length of the plastron to the length of the shell varies among Adocus: A. aksary – 76%; A. beatus – 65%; A. planus – 80%; Adocus sp. 2 – 70%; A. substictus – 78%. In A. amtgai it is $\sim 75\%$ that is almost the same as in A. aksary. The gulars of A. amtgai are relatively large; their width is more than length of the epiplastral synphysis. The extragulars of A. amtgai are relatively small but similar in size to those of A. beatus and Adocus sp. 3. The inframarginals of A. amtgai are relatively wide that is also known in some other species of Adocus. Thus, the above-mentioned characters are highly variable.

![Fig. 13. Pes of Adocus amtgai (PIN 3640–3): A – dorsal view, B – explanation drawing of the same. See Fig. 2 for abbreviations and designations.](image_url)
within *Adocus* and insufficient to assign *A. amtgai* to a separate genus. On the other hand, other characters of *A. amtgai* (wide lateral and posterior marginals and very narrow pleurals 2–4; the shorter of the pectorals) are unique for this species and may represent its autapomorphies. According to criteria used for *Adocus*, the differences between *A. amtgai* and other species of this genus (see Table 2) reflect mere species-level differences.

Our study also presents new observations on *Adocus* morphology in general, including the detailed morphology of the skull and elements of the non-shell postcrania. Some elements (femur, tibia, fibula, bones of the pes) were previously unknown for the genus. The morphology of the non-shell postcranial elements of *A. amtgai* on the whole is similar to that of *Adocus* sp. 1, which is another taxon of *Adocus* with known morphology of the non-shell postcranium. The only difference between these taxa in the morphology of the non-shell postcranium is the presence of the truncated distal edge of coracid in *A. amtgai*, whereas in *Adocus* sp. 1 it is rounded. As a result, this study makes *A. amtgai* the best-known Asian representatives of the genus and one of the best-known members of the genus in general.

The examination of both specimens of *Adocus amtgai* (PIN 3640–2 and PIN 3640–3) allows us to note variation of this species in the following shell characters: presence/absence of the cervical, shape of the extragulars, shape and number of the inframarginals, and degree of sinuosity of the midline sulcus. The cervical in PIN 3640–3 is narrow and trapezoidal, slightly expanded anteriorly, whereas in PIN 3640–2 it seems to be absent (Narmandakh, 1985). The extragulars are more elongated posterolaterally and medially in PIN 3640–3 than in PIN 3640–2. The inframarginals in PIN 3640–2 are represented by three pairs (Sukhanov, 2000, p. 336), whereas in PIN 3640–3 there are three inframarginals on the right side and five inframarginals on the left side. In PIN 3640–2, the right side the inframarginal 1 almost does not contribute to the pectoral rim and is separated from it by a small contact of the pectoral and marginal 4. The small additional inframarginal separating abdominal from the rim of the inguinal notch is mistakenly shown (Narmandakh, 1985, fig. 1g; Sukhanov, 2000, fig. 17.20A). On the left side of PIN 3640–2, inframarginal 1 contributes broadly to the pectoral rim. In PIN 3640–3, the right side of the inframarginals are similar to those of PIN 3640–2 in the presence of three elements and inframarginal 1 separated from the pectoral rim. However, on the left side of PIN 3640–3 the inframarginals differ from PIN 3640–2 in presence of five elements. The midline sulcus is strongly sinusus in PIN 3640–2 along the whole length of the plastron, whereas in PIN 3640–2 it is sinusous only along the pectorals.

All the data obtained on *A. amtgai* allow us to undertake a phylogenetic analysis. The result of our phylogenetic analysis consists of 85 trees with 151 steps, consistency index is 0.56, and retention index is 0.76. The resulting strict consensus tree is given in Fig. 14. This tree demonstrates that *A. amtgai* is placed within the *Adocus* where it forms a clade with *A. aksary*. This result supports the assignment of *A. amtgai* to the genus *Adocus*. The clade unifying *A. amtgai* and *A. aksary* (both from the Late Cretaceous of Asia) is supported by a single synapomorphy, the overlapping of the marginals onto the costals beginning with marginals 3 or 4. Two other species of *Adocus* (*A. bostobensis* and a new species from the Late Eocene of China) known to have the overlapping of the marginals onto the costals beginning with marginals 3 or 4 also belong to this clade (Syromyatnikova and Danilov, 2013; Danilov et al., 2013). In addition to the members of this clade, there are other species of *Adocus* in Asia characterized by the overlapping of the marginals onto the costals beginning with marginal 5 (*A. foveatus, A. kizylkumensis*) or unknown for this and other important characters (see Syromyatnikova and Danilov, 2009). In all North American *Adocus*, in which this character is observable, the marginals overlap onto the costals beginning with marginal 5. The character of costal overlap beginning with marginal 5 is considered to be primitive in our analysis. *Adocus planus*, the third Asiatic species of *Adocus* in our analysis is placed outside the *A. amtgai* + *A. aksary* clade in polytomy with other species of *Adocus*. The topology of the rest part of the tree agrees with previous analyses (Danilov and Syromyatnikova, 2009a,b; Syromyatnikova, 2011; Syromyatnikova et al., 2012).

![Phylogeny of Adocusia showing the hypothesized position of Adocus amtgai.](image)

**Fig. 14.** Phylogeny of *Adocusia* showing the hypothesized position of *Adocus amtgai*. This is a strict consensus of 85 phylogenetic trees resulting from this study (see Discussion for description of the tree). Numbers designate Bremer support indices.

5. Conclusions

The virtually complete skeleton of *Adocus amtgai*, the best preserved among Asian species of the genus, is described in detail. This material of *A. amtgai* allows us to mend the diagnosis of the species. The result of our study confirms the assignment of *A. amtgai* to the genus *Adocus* based on the marginals that overlap onto the costals in the middle and posterior parts of the carapace. Most of the described characters of the skull and shell indicate that *A. amtgai* is most similar to *A. aksary*. Our study also presents new observations on *Adocus* morphology in general, especially in the detailed morphology of the skull and elements of the non-shell.
postcrania. The morphology of some elements (femur, tibia, fibula, bones of the pes) were previously unknown for the genus.

Acknowledgments

The authors thank J.F. Parham for offering photographs of the skull of Adocus sp. 1 (CCM 60–15), Julien Claude (Institut des sciences de l’évolution, Montpellier, France) and an anonymous reviewer for reviewing the manuscript and useful comments. This study was done with financial support from Grants of the President of the Russian Federation to the Leading Scientific Schools (NSh-6560.2012.4), Russian Foundation for Basic Research 12-05-31015_mol_a to EVS.

References


