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Taxonomic Position of *Oxemys gutta* Nessov, 1977, a Problematic Turtle from the Upper Cretaceous of Uzbekistan, and Basisphenoid Morphology in Some Groups of Late Mesozoic Turtles of Asia

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Abstract—The holotype (basisphenoid) of *Oxemys gutta* Nessov, 1977, a problematic skull-based turtle taxon from the Khodzhakul Formation (Lower Cenomanian, Upper Cretaceous, Uzbekistan) is redescribed and its systematic position is reviewed. The literature and original morphological data on the basisphenoid complex of some Late Mesozoic turtles of Asia are discussed. A list of 14 characters of the basisphenoid complex, many of which have never been used in phylogenetic reconstructions, is provided. A comparison of *O. gutta* with other Late Mesozoic turtle taxa of Asia based on these characters shows that it is most similar to members of Macrobaenidae/Sinemydidae and Lindholmemydidae. The analysis of possible associations of *O. gutta* with shell-based turtle taxa known from the Khodzhakul Formation suggests that it most likely belongs to Macrobaenidae/Sinemydidae.

Keywords: *Oxemys gutta*, turtles, basisphenoid, Late Mesozoic, Asia
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INTRODUCTION

Oxemys gutta Nessov, 1977 is a member of the monotypic genus *Oxemys* Nessov, 1977, one of problematic species of Late Cretaceous turtles of Asia. It was described based on a single basisphenoid (holotype) from the Khodzhakul Formation (Lower Cenomanian, Upper Cretaceous) near Lake Khodzhakul, Uzbekistan (Nessov, 1977a). Nessov (1977a) assigned this taxon to the superfamily Chelonioidea Oppel, 1811 (sea turtles) sensu Gaffney, 1975 based on the close positions of anterior foramina of the canals of cerebral arteries (internal carotid arteries after Nessov, 1977a) relative to each other; the high dorsum sellae, which does not cover these foramina and is separated from them by the bone surface with the sagittal crest; and the presence of a posterior emargination of the basisphenoid. The taxonomic position of *O. gutta* at the family level was not determined, although it was proposed that it belongs "to a certain, previously unknown lineage within chelonioids" (Nessov, 1977a, p. 47). *O. gutta* was compared with members of the families Plesiochelyidae Baur, 1888, Macrobaenidae Sukhanov, 1964 (*Hangaiemys* Sukhanov et Narmandakh, 1974), Toxochelyidae Baur, 1895, and Cheloniidae Oppel, 1811, which in the 1970s were assigned to Chelonioidea or considered to be close to them (Gaffney, 1975; Nessov and Khosatzky, 1978). Subsequently, some of the above groups were placed at the base of radiation of all cryptodiran turtles (Plesiochelyidae; see Joyce, 2007) or some of them (Macrobaenidae; see Danilov, 2013) or combined with Cheloniidae (Toxochelyidae: Parham and Fastovsky, 1997; Hirayama, 1998). In any event, a number of other turtle groups known at that time from the Late Cretaceous of Asia were excluded from comparison with *O. gutta*, although Nessov (1977a) mentioned structural features of the basisphenoid of some of them in connection with the description of another turtle basisphenoid from the Khodzhakul Formation (Chelpyk locality), which was referred to *Kizylkumemys schultzi* Nessov, 1976 of the family Carettochelyidae Boulenger, 1887. Averianov (2002, pp. 138–139) reviewed subsequent mentions of *Oxemys gutta* and put in doubt the assignment of the basisphenoid of this species to the chelonioid type and also indicated that it is of uncertain taxonomic position and that chelonioid remains have not been recorded among thousands of shell specimens from the Khodzhakul locality. *O. gutta* was mentioned for the last time by Danilov (2004, p. 25), who proposed that *O. gutta* could have been assigned to the Xinjiangchelyidae–Macrobaenidae–Lindholmemydidae turtle group, because of the presence of peculiar processes on the ventral surface of the basisphenoid, which are only present in these families. In addition, he remarked that the poorly developed anterior part of the basisphenoid and open canals of the internal carotid arteries, which were among distinctive features of this genus, may result from underdevelopment of these structures in a juvenile. It is also noteworthy that some undescribed specimens from other localities of the Khodzhakul Formation (Khodzhakulsai and Sheikhdzheili II: Nessov, 1997, pp. 139, 140; Averianov, 2002, p. 139) were determined as cf. *Oxemys* sp. (Testudines indet.). The depository of these materials is not known.

Since the point of description of *O. gutta*, the knowledge of diversity and morphology of Late Mesozoic turtles of Asia expanded considerably (for reviews, see Sukhanov, 2000; Rabi et al., 2010, 2013). Several recent works are devoted to the morphology of the basisphenoid complex (basisphenoid and adjacent structures) of turtles, which is connected with structural features of canals of the internal carotid arteries and their branches which are of great significance for reconstruction of phylogenetic relationships of higher turtle taxa (Sterli and Fuente, 2010; Sterli et al., 2010; Brinkman et al., 2012; Rabi et al., 2013). Finally, new data on the composition of the basisphenoid complex in turtles from the Khodzhakul Formation were published (Nessov, 1978, 1981, 1997; Nessov and Krasovskaya, 1984; Danilov, 1999; Danilov and Averianov, 2003; Danilov and Syromyatnikova, 2008; Syromyatnikova and Danilov, 2009; Danilov et al., 2011; Syromyatnikova, 2011; Vitek and Danilov, 2014).

In the present paper, the holotype of *O. gutta* is redescribed and its systematic position is reviewed. For this purpose, published and original morphological data on the basisphenoid complex of some Late Mesozoic turtles of Asia are discussed. A list of characters of the basisphenoid complex, many of which have not been taken into account in previous phylogenetic reconstructions, is provided. *O. gutta* is compared with other taxa of Late Mesozoic turtles of Asia with reference to these characters. In addition, the composition of the turtle assemblage from the Khodzhakul Formation and the role of *O. gutta* in this assemblage are discussed.

The material mentioned in this paper is stored in the following institutions: (PIN) Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow; (TsNIGR Museum) Chernyshev Central Museum of Geological Exploration, St. Petersburg; (ZIN PH) Paleoherpetological Collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

MATERIAL AND METHODS

We used published and original data on the following turtle taxa: **Meiolaniformes Sterli et Fuente, 2013**: *Mongolochelys efremovi* Khosatzky, 1998 (Late Cretaceous of Mongolia: Khosatzky, 1998; Sukhanov, 2000; Suzuki and Chinzorig, 2010; Rabi et al., 2013); **Xinjiangchelyidae Nessov in Kaznyshkin et al., 1990**: *Annemys latiens* Sukhanov et Narmandakh, 2006 (Late Jurassic of Mongolia: Sukhanov, 2000; Rabi et al., 2014); *A. levensis* Sukhanov et Narmandakh, 2006 (Late Jurassic of Mongolia: Sukhanov, 2000; Rabi et al., 2014); *A. wusu* Rabi et al., 2013 (Late Jurassic of China: Rabi et al., 2013); *Annemys* sp. (Middle Jurassic of China, Wucaiwan field area: Brinkman et al., 2012; Late Jurassic of China; Mesa Chelonia: Wings et al., 2012; Middle Jurassic of Krasnoyarsk Region: Danilov et al., 2013; original data); *Xinjiangchelys radiplicatoides* Brinkman et al., 2012 (Middle–Late Jurassic of China: Brinkman et al., 2012); *X. tianshanensis* Nessov, 1995 (Middle Jurassic of Kyrgyzstan: Kaznyshkin et al., 1990); **Carettochelyidae Boulenger, 1887**: *Kizylkumemys schultzi* Nessov, 1976 (Late Cretaceous of Uzbekistan: Nessov, 1977a, 1987; I.G.D., original data); **Trionychidae Gray, 1825**: *Gobiapalone orlovi* (Khosatzky, 1976) (Late Cretaceous of Mongolia: Danilov et al., 2014); *Khunnuchelys erinhotensis* Brinkman et al., 1993 (Late Cretaceous of China: Brinkman et al., 1993); *Kh. kizylkumensis* Brinkman et al., 1993 (Late Cretaceous of Uzbekistan: Brinkman et al., 1993; Vitek and Danilov, 2013); Trionychini indet. (Late Cretaceous of Uzbekistan: Vitek and Danilov, 2013); Trionychidae indet. (Late Cretaceous of Uzbekistan: Nessov, 1987; *Trionyx* sp., Dzharakuduk: Vitek and Danilov, 2013); "*Trionyx*" *kyrgyzensis* Nessov, 1995 (Early Cretaceous of Kyrgyzstan: Nessov, 1977b, 1986); **Adocidae Cope, 1870**: *Adocus aksary* Nessov in Nessov et Krasovskaya, 1984 (Late Cretaceous of Uzbekistan: Danilov and Parham, 2005); *Adocus* sp. (Late Cretaceous of the United States: Meylan and Gaffney, 1989; Rabi et al., 2013); *Ferganemys vezilini* Nessov et Khosatzky, 1977 (Early Cretaceous of Kyrgyzstan: Nessov, 1977b); *Shachemys laosiana* Lapparent de Broin, 2004 (Early Cretaceous of Laos: Lapparent de Broin, 2004); **Nanhsiungchelyidae Yeh, 1966**: *Zangerlia neimongolensis* Brinkman et Peng, 1996 (Late Cretaceous of China: Brinkman and Peng, 1996); **Macrobaenidae Sukhanov, 1964/Sinemydidae Yeh, 1963**: *Dracochelys bicuspis* Gaffney et Ye, 1992 (Early Cretaceous of China: Gaffney and Ye, 1992; Rabi et al., 2013); *Changmachelys bohlini* Brinkman et al., 2013 (Early Cretaceous of China: Brinkman et al., 2013); *Judithemys sukhanovi* Parham et Hutchison, 2003 (Parham and Hutchison, 2003; Gaffney et al., 2007; Rabi et al., 2013); *Kirgizemys dmitrievi* Nessov et Khosatzky, 1981 (Early Cretaceous of Transbaikalia: Danilov et al., 2006); *K.* (=*Hangaiemys*) *hoburensis* (Sukhanov et Narmandakh, 1974) (Early Cretaceous of Mongolia:

Sukhanov, 2000; Rabi et al., 2007); *Manchurochelys manchoukuoensis* Endo et Shikama, 1942 (Early Cretaceous of China: Zhou, 2010); *Ordosemys brinkmania* Danilov et Parham, 2007 (Early Cretaceous of China: Danilov and Parham, 2007); *O. leios* Brinkman et Peng, 1993 (Early Cretaceous of China: Brinkman and Peng, 1993a); *O. liaoxiensis* (Ji, 1995) (Early Cretaceous of China: Li and Liu, 1999; Tong et al., 2004); *Ordosemys* sp. (Early Cretaceous of China: Brinkman and Wu, 1999); *Sinemys brevispinus* Tong et Brinkman, 2013 (Early Cretaceous of China: Tong and Brinkman, 2013); *S. gamera* Brinkman et Peng, 1993 (Early Cretaceous of China: Brinkman and Peng, 1993b; Rabi et al., 2013); *S. lens* Wiman, 1930 (Late Jurassic of China: Brinkman and Peng, 1993b); **Lindholmemydidae Chkhikvadze in Shuvalov et Chkhikvadze, 1975**: *Mongolemys elegans* Khosatzky et Mlynarski, 1971 (Late Cretaceous of Mongolia: Cadena et al., 2013; I.G.D., original data); *Lindholmemys elegans* Riabinin, 1935 (I.G.D., original data); and **Cryptodira fam. indet.**: *Basilochelys macrobios* Tong et al., 2009 (Late Jurassic–Early Cretaceous of Thailand: Tong et al., 2009; Rabi et al., 2013).

We follow the terminology for canals and foramina of the internal carotid arteries and their branches developed by Rabi et al. (2013; abbreviations are given in brackets after Latin terms): canalis caroticus internus (*cci*), internal carotid canal (up to the divisions into branches); foramen posterius canalis carotici interni (*fpcci*), posterior foramen of the internal carotid canal; foramen anterius canalis carotici interni (*facci*), anterior (exit) foramen of the internal carotid canal; canalis caroticus cerebralis (*ccc*), cerebral artery canal (medial branch of the internal carotid artery); foramen posterius canalis carotici cerebralis (*fpccc*), posterior foramen of the cerebral artery canal; foramen anterius canalis carotici cerebralis (faccc), anterior foramen of the cerebral artery canal; canalis caroticus palatinum (*ccp*), palatine artery canal (lateral branch of the internal carotid artery); foramen posterius canalis carotici palatinum (*fpccp*), posterior foramen of the palatine artery canal; foramen anterius canalis carotici palatinum (*faccp*), anterior foramen of the palatine artery canal; fenestra carotica (*fca*), bony window on the ventral surface of the basicranium, limited posteriorly by the anterior foramen of the internal carotid canal and, anteriorly, by the posterior foramen of the cerebral artery canal and posterior foramen of the palatine artery canal or interpterygoid fossa.

The terminology for other elements of the basisphenoid complex follows Gaffney (1979).

DESCRIPTION OF THE HOLOTYPE OF *OXEMYS GUTTA*

Holotype. TsNIGR Museum, no. 2/11478, basisphenoid; Khodzhakul locality (SKh-20), precipices north of dried Lake Khodzhakul, southwestern Kyzyl Kum Desert, Karakalpakstan, Uzbekistan; lower or middle part of the Khodzhakul Formation, Lower Cenomanian, Upper Cretaceous.

Description (Fig. 1). The basisphenoid is almost complete (only anterior parts of the trabeculae are broken off), consists of round body narrowing slightly anteriorly (true basisphenoid) and parasphenoid adjoining ventrally in the shape of a narrow, longitudinally extended pentagon (one corner directed anteriorly), projecting significantly anteriorly and posteriorly beyond the basisphenoid body. The ventral part of the basisphenoid seen externally (in articulated condition) occupies the central part of the abovementioned pentagon and approaches in shape an extended triangle, the anterior corner of which apparently reaches the anterior corner of the pentagon. The posterior side of the triangle (which is the posterior side of the pentagon) is concave and provides contact with the basioccipital. A pair of symmetrically positioned transverse ridges (basisphenoid ridges), each of which is formed of two fused tubercles, is observed at the level of the posterior quarter of the triangle. Longitudinally extended pits (basisphenoid pits) are located posterior to these ridges. The anterior part of the pentagon is limited laterally by wide canals (grooves) of cerebral arteries open completely ventrally. In articulated condition, these canals, like lateral parts of the basisphenoid, were covered ventrally by the pterygoids. The points of division of canals of the internal carotid arteries into canals of the cerebral and palatine arteries were apparently located beyond the basisphenoid (in the pterygoids); it remains uncertain whether or not the fenestrae carotica were present. The dorsal (internal) surface of the basisphenoid is strongly concave. Its anterior part displays a pair of posterior foramina of the canalis nervi abducentis and, anterior to the dorsum sellae, there is the sagittal crest separating pits for the retractor bulbae muscles. The sella turcica is located anterior to the sagittal crest. The basisphenoid rostrum is reduced. The clinoid processes are absent or broken off (Nessov (1977a) indicated that these processes were poorly developed). The medial tubercle (basis tuberculi basalis) at the basioccipital boundary is absent. In anterior view, the dorsum sellae, sagittal crest, large pits for the retractor bulbae muscles (lateral to which, there are anterior foramina of the canalis nervi abducentis), and sella turcica separating anterior foramina of the cerebral arteries canals are visible. In lateral view, it is seen that the posterior foramen of the cerebral artery canal is positioned close to the middle of the basisphenoid thickness and the anterior foramen of the cerebral artery canal is at the level of its lower quarter. It is also seen that the dorsum sellae does not overhang the sella turcica.

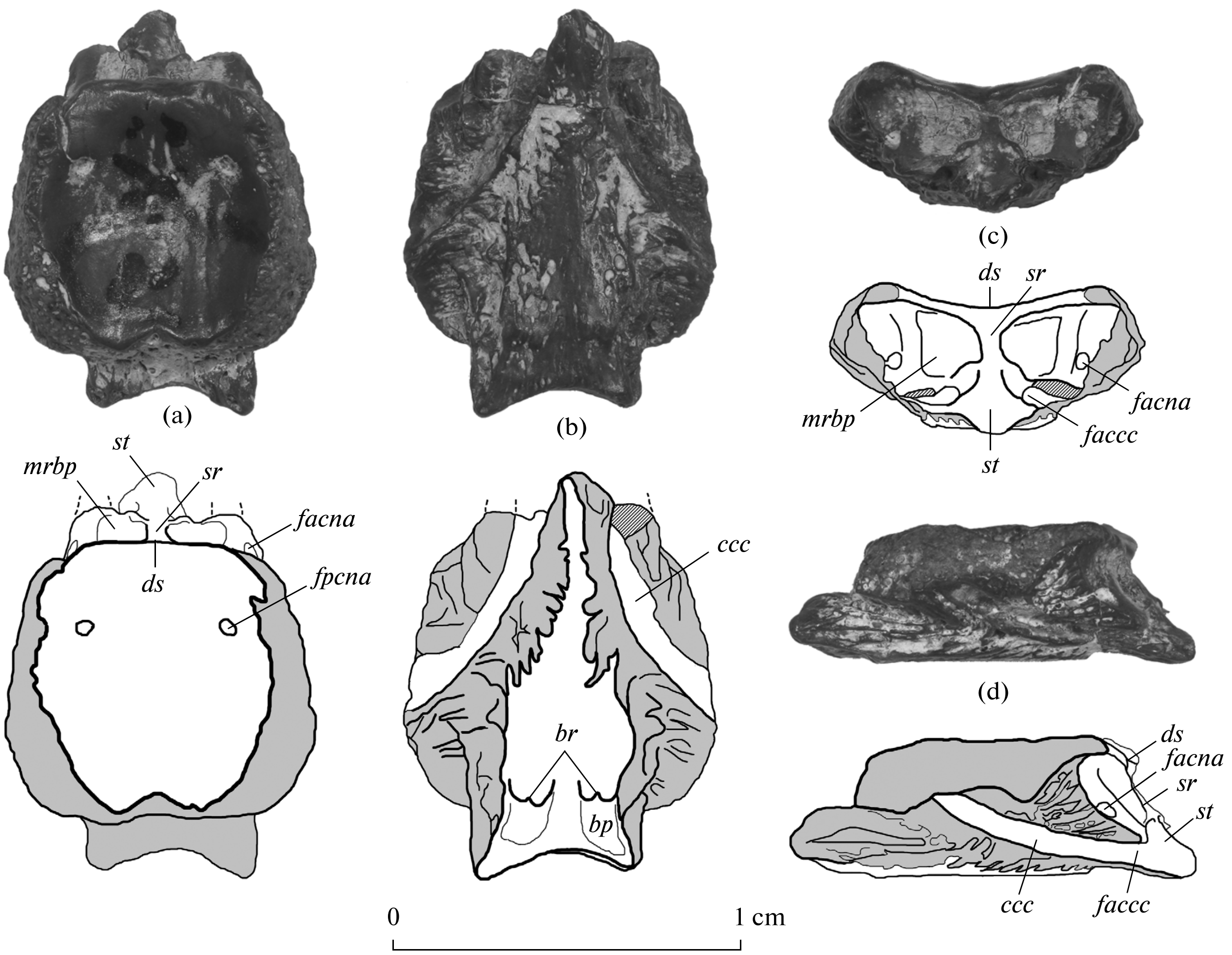

Fig. 1. Basisphenoid of *Oxemys gutta*, holotype TsNIGR Museum, no. 2/11478, photographs (at the top) and explanatory figures (at the bottom): (a) dorsal, (b) ventral, (c) anterior; and (d) left lateral views; Uzbekistan, Karakalpakstan, southwestern Kyzyl Kum, precipice north of dried Lake Khodzhakul, Khodzhakul locality (SKh-20); lower or middle part of the Khodzhakul Formation, Lower Cenomanian, Upper Cretaceous. Hatching shows breaks, gray color is sutures, and dashed lines are reconstructed parts. Designations: (*bo*) basioccipital, (*bp*) basisphenoid pit, (*bpt*) basipterygoid process, (*br*) basisphenoid ridge, (*bs*) basisphenoid, (*btb*) basis tuberculi basalis, (*ccc*) cerebral artery canal, (*cci*) internal carotid canal, (*ccp*) palatine artery canal, (*ds*) dorsum sellae, (*facna*) anterior foramen of the canalis nervi abducentis, (*faccc*) anterior foramen of the cerebral artery canal, (*facci*) anterior foramen of the internal carotid canal, (*fca*) fenestra carotica, (*fpccc*) posterior foramen of the cerebral artery canal, (*fpcci*) posterior foramen of the internal carotid canal, (*fpccp*) posterior foramen of the palatine artery canal, (*fpcna*) posterior foramen of the canalis nervi abducentis, (*itf*) intertrabecular pit, (*mrbp*) fossa for the retractor bulbae muscle, (*sr*) sagittal crest, (*pal*) palatine, (*pcl*) clinoid process, (*pt*) pterygoid, (*st*) sella turcica, (*tr*) trabecula.

STRUCTURE OF THE BASISPHENOID IN SOME LATE MESOZOIC TURTLE GROUPS OF ASIA

In the Late Mesozoic (from the Middle Jurassic to Cretaceous) of Asia, members of 12 turtle groups have been recorded: Meiolaniformes*, Bashuchelyidae Tong et al., 2012, Xinjiangchelyidae*, Sichuanchelyidae Tong et al., 2012, Sinochelyidae Chkhikvadze, 1973, Carettochelyidae*, Trionychidae*, Adocidae*, Nanhsiungchelyidae*, Macrobaenidae/Sinemydidae*, Lindholmemydidae* (=Haichemydidae Sukhanov et Narmandakh, 2006), Chelonioidea (Sukhanov, 2000; Averianov, 2002; Sterli and Fuente, 2012; Tong et al., 2012). The basisphenoid structure has been described more or less thoroughly in Late Mesozoic representatives of eight of the groups listed, which are marked here by "*". In addition, the basisphenoid structure is known in *Basilochelys macrobios* (Cryptodira fam. indet.; Tong et al., 2009). The modern understanding of phylogenetic relationships and paleobiogeography of these groups have recently been reviewed by Danilov (2013).

In the Late Mesozoic, the clade Meiolaniformes is represented in Asia by a single genus and species, *Mongolochelys efremovi* from the Upper Cretaceous (Maastrichtian) of Mongolia. The structure of its basisphenoid was only described and figured in the external (ventral) view within complete skulls (Fig. 2a; Khosatzky, 1998; Sukhanov, 2000; Suzuki and Chinzorig, 2010; Rabi et al., 2013). The basisphenoid is longitudinally extended and widened posteriorly; its anterior one-third has more or less developed triangular basipterygoid processes, which are directed ventrolaterally. Along the midline of the basisphenoid, there is a triangular, posteriorly widened thickening, which apparently corresponds to the parasphenoid. Lateral to this thickening, there are ventrally open canals of the internal carotid arteries and points where they are divided into canals of the cerebral and palatine arteries. At the level of the basipterygoid processes, there are large posterior foramina of canals of the cerebral arteries and, at the anterior edge of the basisphenoid, along the boundary with the pterygoids, there are similar large posterior foramina of canals of the palatine arteries. The posterior edge of the basisphenoid is straight or slightly convex; just anterior to it, there is a pair of symmetrical transverse ridges and depressions (pits) located posterior to them and restricting posteriorly the above-mentioned thickening of the basisphenoid.

Family Xinjiangchelyidae. In this group, the structure of the basisphenoid (in ventral view) within complete skulls or braincases is known in representatives of the genera *Annemys* Sukhanov et Narmandakh, 2006 and *Xinjiangchelys* Yeh, 1986 (Fig. 2; Kaznyshkin et al., 1990; Sukhanov, 2000; Wings et al., 2012; Brinkman et al., 2013; Rabi et al., 2013, 2014). In the basisphenoid proportions, the Xinjiangchelyidae are similar to *Mongolochelys efremovi* and differ from it in the less massiveness and less developed thickening of the ventral surface. In addition, the posterior parts of canals of the internal carotid arteries are usually covered by ventral contacts between the basisphenoids and pterygoids. In some members of the genus *Annemys* (*A. latiens, A. levensis, A. wusu*), the anterior part of the basisphenoid retains the foramen interpreted as the interpterygoid fossa, which extends along the boundary with the pterygoid (Rabi et al., 2013, 2014; intertrabecular fossa in our work, see below). In other Xinjiangchelyidae, this foramen is absent and this site contains the posterior foramina of canals of the palatine arteries. The posterior edge of the basisphenoid is more or less straight (*Annemys* spp.) or concave (*Xinjiangchelys radiplicatoides*), with a pair of transverse basisphenoid ridges and pits (only recorded in some species), which are located just anterior to it. We investigated the structure of an isolated basisphenoid of Xinjiangchelyidae in *Annemys* sp. from the Middle Jurassic of the Krasnoyarsk Region (Figs. 2c–2e). This basisphenoid displays the following features: the basisphenoid ridges and pits are located at the posterior edge of the basisphenoid; the posterior foramina of canals of the cerebral arteries are located in the anterior one-third of the basisphenoid; anterior to them, parallel grooves of the palatine arteries are observed; close to this level, there are relatively small asymmetrical basipterygoid processes; on the dorsal surface of the bone, close to the middle of the basisphenoid body, there are posterior foramina of the canalis nervi abducentis and on either side of the dorsum sellae, there are relatively small clinoid processes; the dorsum sellae overhangs the sella turcica, the lateral parts of which contain the anterior foramina of canals of the cerebral arteries; the pits for the retractor bulbae muscles are separated by the dorsum sellae; the lateral parts of these pits contain the anterior foramina of the canalis nervi abducentis; the trabeculae were apparently short; the space anterior to the sella turcica does not ossify, forming an incisure between the trabeculae; basis tuberculi basalis is absent.

Family Carettochelyidae. The structure of the basisphenoid has only been described in *Kizylkumemys schultzi* from the Late Cretaceous (Cenomanian) of Uzbekistan (Nessov, 1977a). In this description, it was indicated that the bone is longitudinally extended; the dorsum sellae is relatively low, strongly overhanging the sella turcica and covering the anterior foramina of very large cerebral arteries; the bone has posterior foramina of the canalis nervi abducentis, which are located somewhat anterior to the level of the posterior foramina of canals of the cerebral arteries; it was proposed that the basisphenoid was connected anteriorly to the palatines (as in the majority of Trionychoidea). It is possible to add the following characteristics (Figs. 2f–2h): the ventral surface of the basisphenoid is pear-shaped (narrowed anteriorly and expanded posteriorly) and lacks ridges or pits; the posterior foramina of canals of the internal carotid arteries are located in the pterygoids at the level of the middle of the basisphenoid; canals of the internal carotid arteries are completely formed by the pterygoids; anteriorly, the basisphenoid comes in contact with the palatines.

Family Trionychidae. The basisphenoid structure is known in individual members of this family from the Cretaceous of Asia (Figs. 2i, 2j: *Gobiapalone orlovi, Khunnuchelys* spp., “*Trionyx*” *kyrgyzensis*, Trionychini indet., Trionychidae indet.: Nessov, 1977b, 1987; Brinkman et al., 1993; Vitek and Danilov, 2013; Danilov et al., 2014) and closely resembles that of living Trionychidae (see Gaffney, 1979; Meylan, 1987). The Trionychidae, like Carettochelyidae (which are united in the superfamily Trionychoidea Gray, 1825), have very large canals of the cerebral arteries and the dorsum sellae strongly overhangs the sella turcica (Gaffney, 1975); the ventral surface of the basisphenoid is smooth, canals of the internal carotid arteries are formed by the pterygoids. Cretaceous Trionychidae differ from *Kizylkumemys schultzi* in the greater elongation of the ventral basisphenoid surface, the absence of a strong narrowing in the anterior part, and in the position of the posterior foramina of the internal carotid arteries in the posterior parts of the pterygoids (posterior to the basisphenoid).

Family Adocidae. The basisphenoid structure of complete skulls is known in the Cretaceous Asian species *Adocus aksary, Ferganemys verzilini*, and *Shachemys laosiana* (Figs. 2k–2n: Nessov, 1977b; Lapparent

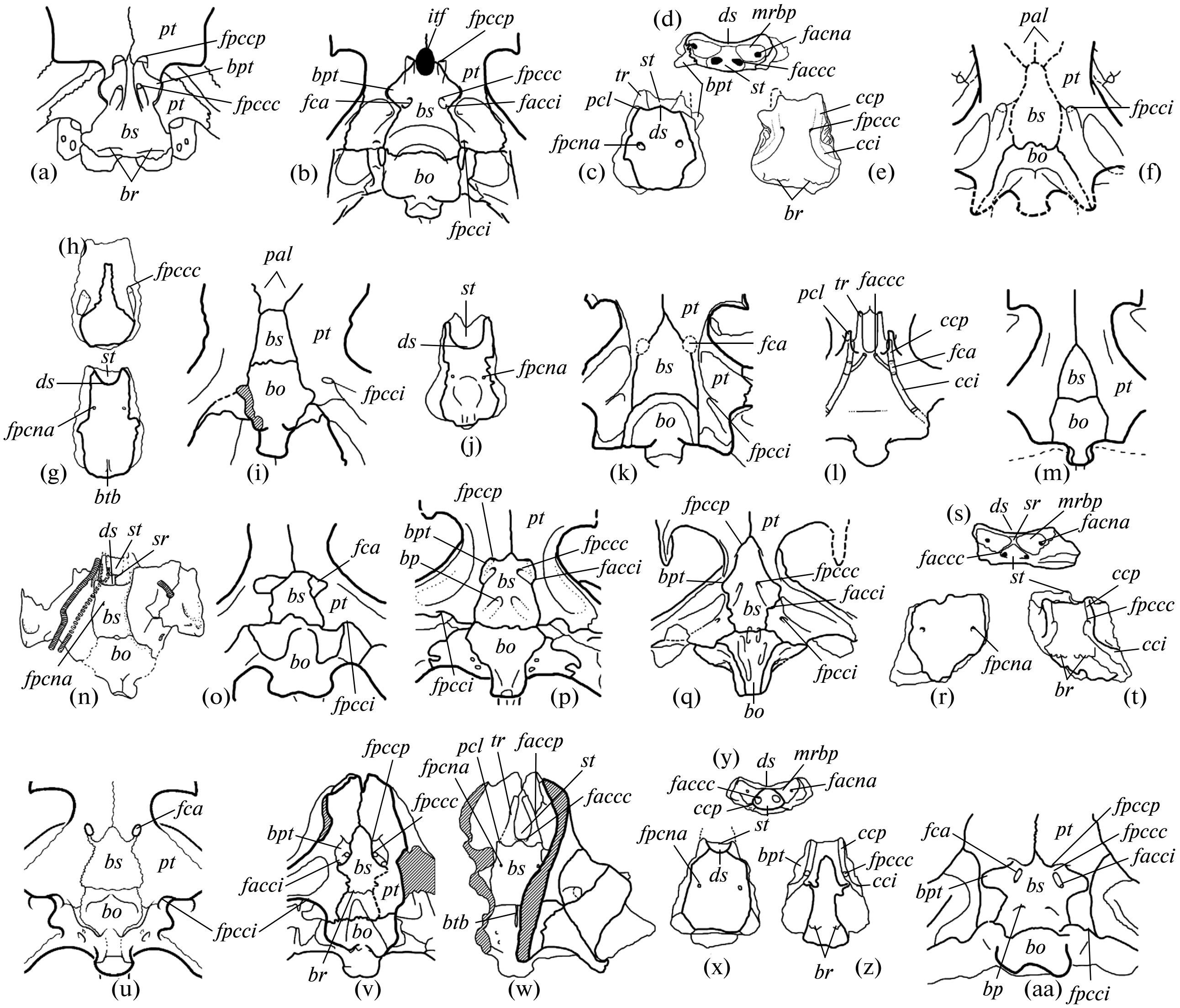

Fig. 2. Structure of the basisphenoid and (or) basisphenoid complex in some Late Mesozoic turtles of Asia and North America: (a) *Mongolochelys efremovi*, skull fragment, ventral view (after Rabi et al., 2013); (b) *Annemys wusu*, skull fragment, ventral view (after Rabi et al., 2013); (c–e) *Annemys* sp., specimen from collection ZIN PH, no. 178, basisphenoid; Middle Jurassic of the Krasnoyarsk Region: (c) dorsal, (d) anterior, and (e) ventral views; (f–h) *Kizylkumemys schultzi*: (f) skull fragment, ventral view (reconstruction based on a specimen from collection ZIN PH, no. 179); (g, h) specimen TsNIGR Museum, no. 1/11478, basisphenoid: (g) ventral and (h) dorsal views; (i) *Gobiapalone orlovi*, skull fragment, ventral view (after Danilov et al., 2014); (j) Trionychidae indet., basisphenoid, dorsal view (after Nessov, 1987); (k) *Adocus aksary*, skull fragment, ventral view (after Danilov and Parham, 2005); (l) *Adocus* sp. from the Late Cretaceous of the United States, reconstructed skull fragment, dorsal view (after Meylan and Gaffney, 1989); (m, n) *Ferganemys verzilini*, skull fragment, ventral view (reconstructed), and dorsal view (after Nessov, 1977b); (o) *Zangerlia neimongolensis*, skull fragment, ventral view (after Brinkman and Peng, 1996); (p) *Kirgizemys hoburensis*, skull fragment, ventral view (after Sukhanov, 2000); (q–s) *Ordosemys leios*, basisphenoid: (q) dorsal, (r) anterior, and (s) ventral views (after Brinkman and Peng, 1993a); (t) *Dracochelys bicuspis*, skull fragment, ventral view (after Rabi et al., 2013); (u) *Judithemys sukhanovi*, reconstructed skull fragment, ventral view (after Gaffney et al., 2007); (v–z) *Lindholmemys elegans*: (v, w) specimen ZIN PH, no. 2/17, skull fragment: (v) ventral and (w) dorsal views; (x–z) specimen ZIN PH, no. 3/17, basisphenoid: (x) dorsal, (y) anterior, and (z) ventral views; (aa) *Basilochelys macrobios*, skull fragment, ventral view (after Tong et al., 2009, with additions from Rabi et al., 2013). For designations, see Fig. 1.

de Broin, 2004; Danilov and Parham, 2005). In *A. aksary*, only the ventral basisphenoid surface has been described; as in other Adocidae, it is elongated triangular in outline; the posterior edge of the bone is concave; the anterior one-third contains the fenestra carotica close to the boundary of the pterygoids; the ventral surface of the bone lacks ridges or pits (Fig. 2k: Danilov and Parham, 2005, text-figs. 1B, 3B). The internal structure of the basisphenoid of the genus *Adocus* was described in *Adocus* sp. from the Upper Cretaceous of the United States. Its canals of the cerebral arteries are somewhat narrower than the canals of the palatine arteries; the sella turcica is elongated; the trabeculae of the basisphenoid are relatively widely spaced (Fig. 2l: Meylan and Gaffney, 1989, text-fig. 8A). The posterior edge of the basisphenoid of *Adocus* sp. is straight (Meylan and Gaffney, 1989, text-fig. 5), in contrast to that of *A. aksary*. The basisphenoid of *F. verzilini* is in the shape of an elongated equilateral triangle in ventral view; the ventral surface of the basisphenoid lacks ridges or pits; its posterior edge is almost straight; the canals of the internal carotid arteries are completely covered by the pterygoids; the canal of the palatine artery is very narrow, and the canal of the cerebral artery is wider; anterior to the dorsum sellae, there is a gently sloping surface with a weak medial crest (Figs. 2m, 2n: Nessov, 1977b, text-fig. 2). In *Sh. laosiana*, only the shape of the external (ventral) basisphenoid surface has been described; it is elongated triangular; the posterior bone edge is straight; canals of the internal carotid arteries are covered completely ventrally; the ventral bone surface lacks ridges or pits (Lapparent de Broin, 2004, text-figs. 1N, 1O).

Family Nanhsiungchelyidae. The basisphenoid structure (only the ventral side within a complete skull) is known in only one species of this family, *Zangerlia neimongolensis* from the Upper Cretaceous of China (Fig. 2o: Brinkman and Peng, 1996, text-fig. 5B). The basisphenoid was apparently elongated triangular or quadrangular (this is uncertain because of distortion); its posterior edge is concave; in the anterior one-third, at the boundary with the pterygoids, there is the fenestra carotica; the posterior foramina of canals of the internal carotid arteries are located in the posterior part of the pterygoids close to the level of the posterior edge of the basisphenoid; the ventral surface of the basisphenoid lacks ridges or pits.

Group Macrobaenidae/Sinemydidae. The basisphenoid structure was described more or less thoroughly in many members of Macrobaenidae/Sinemydidae (Figs. 2p–2u: Gaffney and Ye, 1992; Brinkman and Peng, 1993a, 1993b; Brinkman and Wu, 1999; Sukhanov, 2000; Parham and Hutchison, 2003; Tong et al., 2004; Danilov et al., 2006; Danilov and Parham, 2007; Zhou, 2010; Brinkman et al., 2013; Tong and Brinkman, 2013). It is generally similar to that of Xinjiangchelyidae, differing in the more anterior position of ridges and pits on the ventral surface of the basisphenoid. In *Kirgizemys hoburensis*, the basisphenoid (within a complete skull) is almost rectangular in ventral view; the posterior edge is slightly convex; basisphenoid ridges and pits are well-developed; the fenestrae carotica are small, located at the boundary between the basisphenoid and pterygoids (Fig. 2p: Sukhanov, 2000, text-fig. 17.10B). In *Ordosemys* sp., the basisphenoid is widened strongly posteriorly; at the level of its posterior third, there is a united transverse ridge, with the pits located posterior to it; the posterior edge of the basisphenoid is concave (Brinkman and Wu, 1999, text-fig. 2). *Dracochelys bicuspis* is characterized by a long rhomboid basisphenoid, with a straight posterior edge; the system of ridges and pits is poorly developed or absent (Fig. 2q; Gaffney and Ye, 1992, text-figs. 3, 5; Rabi et al., 2013, text-fig. 11D). In *Judithemys sukhanovi*, the basisphenoid is triangular; the fenestrae carotica are located in the pterygoids and separated from the main body of the basisphenoid; basisphenoid ridges and pits are well-developed (Fig. 2u: Parham and Hutchison, 2003, text-figs. 3B, 5; Gaffney et al., 2007, text-fig. 13B; Rabi et al., 2013, text-fig. 11G). The internal basisphenoid structure of Macrobaenidae/Sinemydidae has been described in *Judithemys sukhanovi, Kirgizemys dmitrievi, K. hoburensis*, and *Ordosemys leios* (Brinkman and Peng, 1993a; Parham and Hutchison, 2003; Danilov et al., 2006). In *O. leios*, the sella turcica is reduced in size and the anterior foramina of canals of the cerebral arteries are located close to each other at the base of the sella turcica; the pits for the retractor bulbae muscles are large, located on either side of the sella turcica, and, above it, approach each other with the formation of the sagittal crest connecting the sella turcica and dorsum sellae. These pits contain the anterior foramina for the canalis nervi abducentis; canals of the cerebral and palatine arteries are approximately equal in diameter (Figs. 2r–2t: Brinkman and Peng, 1993a, text-fig. 6). The close position of the pits for the retractor bulbae muscles, with the formation of the sagittal crest was also recorded in *K. dmitrievi*, whereas in *J. sukhanovi* and *K. hoburensis*, these pits are smaller and separated by the dorsum sellae (Parham and Hutchison, 2003, text-fig. 6; Danilov et al., 2006).

Family Lindholmemydidae. The basisphenoid structure (in ventral view of the braincase) is known in *Lindholmemys elegans* from the Upper Cretaceous of Uzbekistan (Figs. 2v–2z: Nessov, 1986, pl. I, fig. 1 [as *Anatolemys maximus* Khos. et Ness. (?)]: Danilov, 2004) and *Mongolemys elegans* from the Upper Cretaceous of Mongolia (Danilov, 2001; Cadena et al., 2013, text-figs. 4A, 4B). The morphology of the basisphenoid of Lindholmemydidae is generally similar to that of Macrobaenidae/Sinemydidae. The basisphenoid of *Lindholmemys elegans* (Figs. 2v–2z) is described below: an isolated basisphenoid is elongated trapezoid; the main body of the basisphenoid is covered ventrally with a narrower thickening in the shape of an elongated narrow pentagon, which is a part of the basisphenoid (parasphenoid) seen externally in a complete skull; this thickening projects significantly posteriorly beyond the edge of the main basisphenoid body and is restricted posteriorly by the basioccipital and, laterally and anteriorly, by the pterygoids; the ventrally open canals of the internal carotid arteries are located in the middle one-third of the basisphenoid and directed anteromedially towards the posterior foramina for the cerebral arteries; the grooves of canals of the palatine arteries are almost parallel, extending anteriorly from the level of the posterior foramina for the cerebral arteries; the basipterygoid processes are poorly developed; the posterior foramina of for the internal carotid artery are located at the posterior edges of the pterygoids in the fenestrae postotica; the fenestrae carotica are large, located in the anterior one-third of the basisphenoid, at its contact with the pterygoids; the fenestrae carotica display the foramina of anterior canals of the internal carotid arteries and posterior foramina of canals of the cerebral and palatine arteries, which are approximately equal in diameter; at the level of the posterior one-third or one-fourth, the ventral surface has a pair of transverse ridges and pits located posterior to them; posteriorly, the ventral surface of the basisphenoid is overlapped by a triangular depression of the basioccipital; the basisphenoid rostrum formed by ossifying trabeculae is long; the trabeculae extend anteromedially from the main body of the basisphenoid and closely approach the midline; the dorsum sellae overhangs the sella turcica only slightly, if at all; the clinoid processes are present; on the dorsal surface of the main basisphenoid body, close to the midlength, there are posterior foramina of the canalis nervi abducentis and, at its boundary with the basioccipital, there is a low medial crest (basis tuberculi basalis); in anterior view, the anterior foramina of canals of the cerebral arteries located on either side of the sella turcica are visible; the pits for the retractor bulbae muscles contain the anterior foramina of the canalis nervi abducentis; these pits are separated by the dorsum sellae.

Cryptodira fam. indet.: *Basilochelys macrobios*. This species has very large basipterygoid processes; the interpterygoid fossa is absent; the posterior parts of canals of the internal carotid arteries are closed ventrally; the ridges and pits on the ventral basisphenoid surface are positioned at the level of the posterior one-third of the bone; and the posterior edge of the basisphenoid is concave (Fig. 2aa: Tong et al., 2009, text-fig. 2; Rabi et al., 2013, text-fig. 11F). Thus, in the structure of the basisphenoid complex, *B. macrobios* is at the level of Macrobaenidae/Sinemydidae, while in the shell structure, it is more similar to Xinjiangchelyidae and Trionychoidea (Tong et al., 2009).

DISCUSSION

Remarks on the Basisphenoid Complex Structure of Late Mesozoic Turtles of Asia

In phylogenetic studies of turtles, the basisphenoid complex has attracted particular attention (Joyce, 2007; Sterli, 2008; Sterli et al., 2010; Rabi et al., 2013). The above review of its structure in some Late Mesozoic turtles of Asia allows the improvement of its characteristics.

1. Medial contact of pterygoids (after Joyce, 2007: Character 44: Pterygoid G) is present (0) or absent (1). In the majority of turtles, the pterygoids (even if the interpterygoid fossa is present) come in contact at the midline anterior to the basisphenoid; however, in the Pleurosternidae, Carettochelyidae, and Trionychidae, the pterygoids lack such a contact because the basisphenoid adjoins the palatines. The condition of this character in *Oxemys gutta* is not known.

2. Thickening on the ventral surface of the basisphenoid (parasphenoid: Sterli et al., 2010): is restricted by its medial part (0) or expands onto the entire ventral surface of the basisphenoid (1). The primitive condition of this character is observed in *Mongolochelys efremovi*, Xinjiangchelyidae, Macrobaenidae/Sinemydidae, Lindholmemydidae, and *Oxemys gutta*; the derived condition is in Carettochelyidae and Trionychidae. The condition of this character in Adocidae, Nanhsiungchelyidae, and *Basilochelys macrobios* is not known.

3. The thickening on the ventral surface of the basisphenoid projects beyond its posterior edge: no (0); yes (1). The primitive condition of this character is observed in Xinjiangchelyidae, Carettochelyidae, and Trionychidae; the derived condition is characteristic of Lindholmemydidae and *Oxemys gutta*. In *Mongolochelys efremovi*, Adocidae, Nanhsiungchelyidae, Macrobaenidae/Sinemydidae, and *Basilochelys macrobios*, the condition of this character is not known.

4. The posterolateral parts of the basisphenoid are widely covered by the pterygoids: no (0); yes (1). The primitive condition of this character is observed in *Mongolochelys efremovi*, Xinjiangchelyidae, Carettochelyidae, Trionychidae, and some Macrobaenidae/Sinemydidae (*Dracochelys bicuspis, Ordosemys* spp., *Sinemys* spp.); the derived condition is in some Macrobaenidae/Sinemydidae (*Kirgizemys* spp.), Lindholmemydidae, and *Oxemys gutta*. The condition of this character in Adocidae, Nanhsiungchelyidae, and *Basilochelys macrobios* is not known.

5. The basipterygoid processes (after Sterli, 2008: 41. Pterygoid B, modified) are present (0) or absent (1). The basipterygoid processes are retained in many primitive turtles, including *Mongolochelys efremovi*, *Xinjiangchelyidae, Macrobaenidae/Sinemydidae,* and *Basilochelys macrobios* and are independently lost in members of some other groups, including Carettochelyidae, Trionychidae, and Adocidae (Brinkman et al., 2012; Rabi et al., 2013). In addition, it has been reported that the basipterygoid processes are absent in members of Lindholmemydidae (*Mongolemys elegans*: Rabi et al., 2013). However, according to our data, reduced basipterygoid processes are retained in the other member of this group, *Lindholmemys elegans*.

6. The pterygoids do not participate in the formation of canals of the internal carotid arteries (0); participate in the formation of the posterior parts of these canals, the fenestrae carotica are present (1); or form completely these canals, fenestrae carotica are absent (2). The pterygoids do not participate in the formation of canals of the internal carotid arteries in *Mongolochelys*

efremovi and some Xinjiangchelyidae (*Annemys* sp.), participate in the formation of the posterior parts of these canals (fenestrae carotica are present) in some Xinjiangchelyidae, some Adocidae, Nanhsiungchelyidae, Macrobaenidae/Sinemydidae, Lindholmemydidae, and *Basilochelys macrobios*, or completely form these canals (fenestrae carotica are absent or confined to the pterygoids) in Carettochelyidae, Trionychidae, some Adocidae, Macrobaenidae/Sinemydidae, and *Oxemys gutta*.

7. Canals of the cerebral arteries are enclosed in the basisphenoid (0) or open ventrally (1). In the majority of turtles, canals of the cerebral arteries are enclosed in the basisphenoid and covered from below. In *Oxemys gutta*, these canals are not enclosed in the basisphenoid and are represented by open grooves on its ventral surface. These grooves were covered ventrally by the pterygoids. The condition of this character in the Nanhsiungchelyidae and *Basilochelys macrobios* is not known.

8. Canals of the cerebral arteries are much greater in diameter than canals of the palatine arteries: no (0); yes (1). Canals of the cerebral arteries are approximately equal in diameter to canals of the palatine arteries in *Mongolochelys efremovi*, Xinjiangchelyidae, Adocidae, Macrobaenidae/Sinemydidae, and Lindholmemydidae, whereas in the Carettochelyidae and Trionychidae, they are considerably greater in diameter than canals of the palatine arteries (Gaffney, 1975). The condition of this character in Nanhsiungchelyidae, *Basilochelys macrobios*, and *Oxemys gutta* is not known.

9. The dorsum sellae strongly overhangs the sellae turcica: no (0); yes (1). The dorsum sellae strongly overhangs the sellae turcica in the Carettochelyidae and Trionychidae (Gaffney, 1979). In the other groups considered (Xinjiangchelyidae, Adocidae, Macrobaenidae/Sinemydidae, Lindholmemydidae, *Oxemys gutta*), it only slightly overhangs the sellae turcica, if al all. In *Mongolochelys efremovi*, Nanhsiungchelyidae, and *Basilochelys macrobios*, the condition of this character is not known.

10. The pits for the retractor bulbae muscles are positioned close to each other, with the formation of the sagittal crest: no (0); yes (1). The pits for the retractor bulbae muscles are usually located on either side of the sella turcica and do not prevent contact of the sella turcica and dorsum sellae. This pattern is observed in the majority of the turtle groups under consideration, Xinjiangchelyidae, Carettochelyidae, Trionychidae, some Adocidae (*Adocus* sp.), Macrobaenidae/Sinemydidae (*Judithemys sukhanovi, Kirgizemys* spp.), and Lindholmemydidae. In some Adocidae (*Ferganemys verzilini*), Macrobaenidae/Sinemydidae (*Ordosemys leios*), and *Oxemys gutta*, these pits are positioned close to each other and form the sagittal crest separating the sella turcica from dorsum sellae. The condition of this character in *Mongolochelys efremovi*, Nanhsiungchelyidae, and *Basilochelys macrobios* is not known.

11. The intertrabecular fossa is absent (0) or present (1). Many basal turtles have an interpterygoid fossa, an open space (fissure) between the pterygoids; in members of the crown turtle group, the interpterygoid fossa is absent, since the pterygoids are connected at the midline (see Joyce, 2007: Character 40: Pterygoid C). In recent studies of Rabi et al. (2013, 2014), the presence of the interpterygoid fossa was recorded in some representatives of the family Xinjiangchelyidae (*Annemys latiens, A. levensis, A. wusu*), which are usually considered to belong to basal cryptodirans. Our data on the morphology of isolated basisphenoids of *Annemys* sp. from the Middle Jurassic of the Krasnoyarsk Region show that, in this taxon, the space anterior to the sella turcica does not ossify, resulting in the formation of an incisure between the trabeculae. At the connection of the basisphenoid with pterygoids, a foramen that should be named the intertrabecular fossa is retained. Apparently, in other Xinjiangchelyidae, we also deal with the intertrabecular (rather than interpterygoid) fossa, the presence of which should be regarded as either an ontogenetic stage or derived feature. In other investigated turtle groups, an intertrabecular fossa is absent.

12. The basisphenoid rostrum is reduced: no (0); yes (1). The basisphenoid rostrum of turtles is a part of the basisphenoid anterior to the sella turcica, which is formed of ossified trabeculae and space between them (Gaffney, 1979). Among the taxa under consideration, the basisphenoid rostrum is reduced only in *Oxemys gutta*, although the condition of this character in *Mongolochelys efremovi*, Nanhsiungchelyidae, and *Basilochelys macrobios* is not known.

13. Ridges and pits on the ventral basisphenoid surface (Joyce, 2007: Character 51: Basisphenoid B) are present (0) or absent (1). Paired pits on the ventral basisphenoid surface have been recorded in some primitive cryptodirans (Xinjiangchelyidae, Macrobaenidae/Sinemydidae, Lindholmemydidae, *Basilochelys macrobios*: see Joyce, 2007; Tong et al., 2009). It is proposed that they are connected with the cervical retractors and homologous to V-shaped ridges of Cheloniidae (Brinkman and Wu, 1999; Joyce, 2007). The absence of these structures in some Xinjiangchelyidae (*Annemys latiens, A. levensis, A. wusu*; Rabi et al., 2013, 2014) has recently been noticed. Our studies of Late Mesozoic turtles of Asia have shown that it would be more properly to consider transverse ridges and pits located posteriorly of them rather than the pits alone. These structures are present in the above-mentioned groups as well as in *Mongolochelys efremovi* and *Oxemys gutta* and, apparently, some other groups of primitive turtles.

Table 1. Taxon–character matrix based on characters of the basisphenoid complex in some taxa of Late Mesozoic turtles of Asia; for descriptions of characters, see the text

Taxon	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Mongolochelys efremovi	0	0	?	0	0	0	0	0	?	?	0	?	0	0
Xinjiangchelyidae	0	0	0	0	0/1	0/1	0	0	0	0	0/1	0	0	0
Carettochelyidae	1	1	0	0	1	2	0	1	1	0	0	0	1	–
Trionychidae	1	1	0	0	1	2	0	1	1	0	0	0	1	–
Adocidae	0	?	?	?	1	1/2	0	0	0	0/1	0	0	1	–
Nanhsiungchelyidae	0	?	?	?	?	1	?	?	?	?	0	?	1	–
Macrobaenidae/Sinemydidae	0	0	?	0/1	0	1/2	0	0	0	0/1	0	0	0	1
Lindholmemydidae	0	0	1	1	0/1	1	0	0	0	0	0	0	0	1
Basilochelys macrobios	0	?	?	?	0	1	?	?	?	?	0	?	0	1
Oxemys gutta	?	0	1	1	1	2	1	?	0	1	0	1	0	1

14. Ridges and pits on the ventral basisphenoid surface are located close to the posterior edge (0) or far from it (1). In *Mongolochelys efremovi* and Xinjiangchelyidae, these structures are located very close to the posterior edge of the basisphenoid and sometimes hardly discernible. In the Macrobaenidae/Sinemydidae, Lindholmemydidae, and *Basilochelys macrobios*, they are at a distance of one-fourth or one-third of the bone length from the posterior edge of the basisphenoid. In other cryptodires, the basisphenoid lacks ridges or pits on the ventral surface.

All of the above 14 characters of the basisphenoid complex are used for construction of the taxon–character matrix, including ten taxa of Late Mesozoic turtles of Asia (Table 1).

Taxonomic Position of O. gutta

Nessov (1977a) assigned *O. gutta* to the superfamily Chelonioidea sensu Gaffney, 1975, which comprises the families Plesiochelyidae, Toxochelyidae, Protostegidae, Dermochelyidae, and Cheloniidae (Gaffney, 1975). According to the modern concept, the superfamily Chelonioidea sensu stricto is restricted to the last four groups; at the same time, representatives of Toxochelyidae are transferred to Cheloniidae, and the Protostegidae are sometimes removed from Chelonioidea (Hirayama, 1998; Joyce, 2007; Parham and Pyenson, 2010). The Chelonioidea sensu stricto are characterized by close position of the anterior foramina for the cerebral arteries and high dorsum sellae separated from the sella turcica and anterior foramina of the cerebral arteries (Hirayama, 1998), whereas in *Oxemys gutta*, the anterior foramina for the cerebral arteries are located at a greater distance from each other and the dorsum sellae is separated from the sella turcica to a lesser extent. In addition, remains of Chelonioidea have not been recorded among thousands of shell fragments extracted from the Khodzhakul Formation (Averianov, 2002). The family Plesiochelyidae is only known from the Late Jurassic–Early Cretaceous of Europe (Danilov, 2005). Thus, based on available data, it is possible to reject with confidence the assignment of *O. gutta* to Chelonioidea sensu stricto and sensu Gaffney (1975).

Oxemys gutta is distinguished from all turtles (in which the basisphenoid structure has been described) by the canal of the cerebral artery not enclosed in the basisphenoid and by the poorly developed site anterior to the dorsum sellae (basisphenoid rostrum). These features may be the unique derived characters (autapomorphies) of this species, which reflect an early ontogenetic stage or even result from abnormal development. A comparison of *O. gutta* with other Late Mesozoic turtles of Asia shows that it is most similar in derived characters to members of Macrobaenidae/Sinemydidae and Lindholmemydidae (Table 1). These characters include the ventral thickening of the basisphenoid projecting beyond its posterior edge (character 3), the posterolateral parts of the basisphenoid strongly overlapped by the pterygoids (4), and the ridges and pits on the ventral surface of the basisphenoid positioned far from its posterior edge (14). In addition to the above characters, *Oxemys gutta* differs from Macrobaenidae/Sinemydidae (except for *Judithemys sukhanovi*), and Lindholmemydidae, in the pterygoids forming completely the canals of the internal carotid arteries; it additionally differs from Macrobaenidae/Sinemydidae and some Lindholmemydidae in the absence of basipterygoid processes and from Lindholmemydidae in the connection of the pits for the retractor bulbae muscles, with the formation of the sagittal crest. Among Macrobaenidae/Sinemydidae, *O. gutta* is apparently close to the taxa, such as *Judithemys sukhanovi*, in which the points of division of the internal carotid arteries into branches (and fenestrae carotica) are located in the pterygoids (beyond the basisphenoid). The differences of *O. gutta* from other Late Mesozoic turtle groups of Asia are more essential or they are impossible to compare based on the majority of characters (Table 1).

In addition to *Oxemys gutta*, the turtle assemblage from the Khodzhakul Formation includes the following taxa: *Adocus kizylkumensis* Nessov, 1981, "*Ferganemys*" *itemirensis* Nessov, 1981 (Adocidae), *Kizylkumemys schultzi* Nessov, 1976 (Carettochelyidae), *Khodzhakulemys occidentalis* (Nessov in Nessov et Krasovskaya, 1984) (Lindholmemydidae), *Anatolemys oxensis* Nessov et Khosatzky in Nessov, 1977 (Macrobaenidae), Macrobaenidae indet., Nanhsiungchelyidae indet., "*Trionyx*" cf. *kyrgyzensis*, "*Trionyx*" sp. nov. (Trionychidae), *Tienfucheloides undatus* Nessov, 1978 (Eucryptodira inc. superfam. et fam.), and Testudines indet. (Nessov, 1997; Vitek and Danilov, 2014). The majority of the above-listed taxa are only represented by shell specimens; *Kizylkumemys schultzi* is known from shell and cranial remains, and *O. gutta* is only represented by cranial material (basisphenoid). Since the basisphenoid of *O. gutta* is most similar to that of Macrobaenidae/Sinemydidae and Lindholmemydidae, it is possible to restrict the consideration of its probable associations with shell turtle taxa from the Khodzhakul Formation to *Anatolemys oxensis*, Macrobaenidae indet., *Tienfucheloides undatus*, and *Khodzhakulemys occidentalis*.

Anatolemys oxensis is known from fragmentary shell specimens from the Khodzhakulsai locality; the reconstructed shell is about 40 cm long (Khosatzky and Nessov, 1979). Certain undescribed shell specimens from contemporaneous localities of the southwestern and central Kyzyl Kum Desert also belong to this species (Nessov, 1986, 1997). Other members of the genus *Anatolemys* are known from later deposits of the Dzharakuduk locality (central Kyzyl Kum, Uzbekistan; Bissekty Formation; Upper Turonian) and localities of southwestern Fergana (Tajikistan; Yalovach Formation; Lower Santonian) and the northeastern Aral Region (Kazakhstan; Bostobe Formation, Santonian–Lower Campanian). Cranial remains of this genus have not been recorded. A braincase from the Dzharakuduk locality that was referred to as *Anatolemys maximus* actually belongs to *Lindholmemys elegans* (Lindholmemydidae: Danilov, 2004). It is noteworthy that, in the level of shell development, the turtle genus *Anatolemys* is similar to *Judithemys sukhanovi*.

Macrobaenidae indet. from the Khodzhakul Formation was mentioned in the literature as *Kirgizemys* sp., Toxochelyidae, Toxochelyidae?, *Kirgizemys* (?) sp., and cf. *Kirgizemys* sp. (Nessov, 1977c, 1981, 1997). The specimens assigned to this form are represented by several shell fragments (Nessov, 1981, tax-fig. III, figs. 14, 15; 1997, pl. 29, fig. 36, pl. 30, figs. 1, 2). Judging from the size, this form was smaller (the shell was about 20 cm long) than *Anatolemys oxensis*.

Tienfucheloides undatus was described based on shell fragments from localities of the Khodzhakul Formation (Nessov, 1978). The genus *Tienfucheloides* was originally assigned to Testudinata incertae sedis, although it was indicated that it is similar in some characters to Asian members of the genus *Plesiochelys* (presently Xinjiangchelyidae) and members of the genera *Kirgizemys* (Macrobaenidae) and *Sinemys* (Sinemydidae). Later, it was indicated that *Tienfucheloides* is similar to Sinemydidae (Nessov, 1987; Brinkman and Peng, 1993b). Taking into account the similarity of *Tienfucheloides* to the above-mentioned turtle groups, it is possible to propose more or less confidently that this genus belongs to basal Eucryptodira.

Khodzhakulemys occidentalis is described based on a few shell fragments from several localities of the Khodzhakul Formation (Nessov and Krasovskaya, 1984; Danilov, 1999). This species is rather similar to members of the genus *Lindholmemys* in the shell structure and possibly belongs to this genus. It is highly improbable that unique structural features of the basisphenoid of *Oxemys gutta* are attributable to intrageneric variation.

Thus, *O. gutta* is most similar to the turtles Macrobaenidae/Sinemydidae and Lindholmemydidae and probably belongs to the first group. A more precise establishment of the taxonomic position of this species and its relationships with shell taxa from the Khodzhakul Formation requires new, more complete materials.

CONCLUSIONS

This study has shown significant gaps in our knowledge of the structure of the basisphenoid complex in Late Mesozoic turtles of Asia, even in the groups the skull morphology of which is generally believed to be well understood. The condition of certain characters of this complex is possible to determine only in isolated bones (basisphenoid, pterygoids), whereas the determination of other characters requires articulated braincases. The determination of conditions of the characters considered here of the basisphenoid complex in the main large taxa of ancient turtles will allow to use them more widely in future phylogenetic studies.

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