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Ordosemys (Testudines: Cryptodira) from the Yixian Formation of Liaoning Province, Northeastern China: New Specimens and Systematic Revision

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ABSTRACT

The Yixian Formation, in Liaoning Province, northeastern China, has yielded abundant turtle remains which were described previously as *Manchurochelys liaoxiensis*. Study of a new collection in the Geological Museum of China and reexamination of previously studied IVPP collection allow us to assign this turtle to *Ordosemys*. Additional primitive features observed in *Ordosemys liaoxiensis* confirm its basal position among Centrocryptodira.

INTRODUCTION

The vertebrate-bearing beds of the Yixian Formation in the western part of Liaoning Province, northeastern China, are famous for the feathered dinosaurs and early birds they have yielded during the last decade. The study of the turtles from this formation started as early as the 1940s. In 1942, Endo and Shikama studied a turtle specimen, including

the posterior portion of a shell with pelvic girdle and hind limbs, from the so-called “Tsaotzushan Formation”, which is apparently what is now called Yixian Formation, near Tsaotzushan in the Yixian region, Liaoning Province. On the basis of this material, they erected the taxon *Manchurochelys manchoukuoensis* (Endo and Shikama, 1942; Ji, 1995). The material studied by

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Endo and Shikama cannot be located, neither in China nor in Japan, and was probably lost during the Second World War. Ji (1995) studied incomplete shells from the Yixian Formation of Bepiao, Liaoning Province, and described a new species of *Manchurochelys*, *M. liaoxiensis*. More recently, abundant turtle remains have been found at these localities, many of them being more-or-less complete articulated skeletons. In 1999, Li and Liu reported on material of *M. liaoxiensis* from the same region, in the collection of the IVPP. They described one skull (IVPP V11554) in detail and performed a cladistic analysis. The phylogenetic position of *Manchurochelys* among five primitive centrocryptodires was determined by these authors using 40 morphological characters (Li and Liu, 1999). All turtle remains described so far from the Yixian Formation of western Liaoning have been assigned to *Manchurochelys*.

In this paper, we report on the turtle remains from the Yixian Formation of Liaoning Province in the collection of the Geological Museum of China (Beijing). The purpose is to review the turtle material from that formation, to give a more complete description, and to discuss its systematic position. The material in the collection of the IVPP studied by Li and Liu (1999) was reexamined. Our study reveals that the turtle remains from the Yixian Formation, which were previously assigned to *Manchurochelys liaoxiensis*, closely resemble *Ordosemys leios*, a eucryptodiran turtle from the Early Cretaceous of Inner Mongolia, China (Brinkman and Peng, 1993a).

Turtle remains from the Yixian Formation in the collection of the Geological Museum of China consist of about 20 specimens. They are from two localities. Most of them are contained in thick-bedded sandstone from the Jianshangou locality. The others are in thin-bedded mudstone from the Sihetun locality. Both localities occur within the Yixian Formation. The deposits at Jianshangou are placed stratigraphically above those at Sihetun (Chiappe et al., 1999). Because of the hardness of the matrix surrounding the specimens, only some of them have been chosen for preparation and detailed study for the present paper.

INSTITUTIONAL ABBREVIATIONS

IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, Beijing
GM	National Geological Museum of China, Beijing

ANATOMICAL ABBREVIATIONS (for skull only)

bo	basioccipital
bs	basisphenoid
ex	exoccipital
fr	frontal
ju	jugal
mx	maxilla
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal

SYSTEMATICS

TESTUDINES LINNAEUS, 1758

EUCRYPTODIRA GAFFNEY, 1975

CENTROCRYPTODIRA GAFFNEY AND MEYLAN, 1988

Ordosemys Brinkman and Peng, 1993a

DIAGNOSIS (modified from Brinkman and Peng, 1993a): A cryptodire with a low domed shell and plastron loosely connected to the carapace as in macrobaenids, differing from all other macrobaenids in having a shell that is nearly as wide as long, in the presence of a preneural and in the presence of a medial fontanelle between the hypoplastron and xiphiplastron; differing from *Macrobaena* Tatarinov, 1959, *Anatolemys* Khozatskii and Nesov, 1979, *Hangaiemys* Sukhanov and Narmandakh, 1974, and *Kirgizemys* Nesov and Khozatskii, 1973 in that the vertebral scutes are wider than they are long; differing from *Sinemys* Wiman, 1930 and *Manchurochelys* Endo and Shikama, 1942 in having the posterior lobe of the plastron wider at the basis. Skull similar to *Macrobaena* and differing from *Hangaiemys* and *Dracochelys*

Gaffney and Ye, 1992 in having a wider triturating surface; canalis caroticus internus unfloored or with a thin floor, the foramina anterior canalis caroticus interni located close together at the base of the sella turcica, with sella turcica reduced in size, not reaching the dorsum sellae.

TYPE SPECIES: *Ordosemys leios* Brinkman and Peng, 1993a.

Ordosemys liaoxiensis (Ji, 1995)
Figures 1–9

REFERRED SPECIMENS: GM V3001, a nearly complete skeleton visible in ventral view (figs. 1, 2, 8, 9); GM V3002, a nearly complete shell and associated skull and limb bones visible in dorsal view (fig. 7); GM V3000-1, an incomplete skeleton in which a half carapace and plastron, skull, neck, and right forearm are preserved; GM V3000-2, a skeleton with skull, neck, carapace and plastron, part of tail and some limb bones (figs. 5, 6); GM V3000-3, a skull and partial neck visible in ventral view; GM V3000-4, a skull and partial neck (figs. 3, 4).

LOCALITY AND HORIZON: Yixian Formation, Liaoning Province, northeastern China.

DIAGNOSIS (modified from Ji, 1995, Li and Liu, 1999): A species of *Ordosemys*, differing from *O. leios* in having a slight ornamentation on the shell surface, a large semi-circular lateral fontanelle on the bridge, and in having the first peripheral not contacting or barely contacting the first costal plate.

MEASUREMENTS: See tables 1 and 2.

DESCRIPTION AND COMPARISON

SKULL

PRESERVATION: The skull is visible in dorsal view in GM V3000-1 and GM V3000-2, both with the skull roof damaged. In GM V3001, the skull is complete but dorsoventrally crushed and visible only in ventral view (fig. 2). GM V3000-4 is the most complete skull. It has been fully prepared, but is somewhat dorsoventrally crushed (figs. 3, 4).

GENERAL ASPECT: The skull roof is decorated with vermiculated grooves, preserved on both GM V3000-1 and GM V3000-4.

The skull is low and has a triangular outline as seen from above. The apertura narium

externa faces anterodorsally. The orbit is large and oval-shaped and faces dorsolaterally. The temporal emargination is shaped like an inverted V and is moderate in size; its anterior margin is anterior to the foramen stapedio-temporale, but the processus trochlearis oticum is not fully visible though the emargination. The crista supraoccipitalis extends posteriorly nearly up to the level of the posterior end of the squamosal. In lateral view, there is a shallow cheek emargination with its upper margin slightly above the level of the lower margin of the orbit. The general aspect of GM V3000-4 and GM V3001 is similar to V11554 (Li and Liu, 1999). The size of our specimens is slightly larger. The slight differences between them, including the wider skull of GM V3001 and V 11554, the more anteriorly facing apertura narium externa, and the more laterally facing orbits of IVPP V11554, are mainly due to post-mortem deformation.

In comparison with *Ordosemys* sp. (Brinkman and Wu, 1999), the size of the Liaoning specimens is much smaller, but the general aspect is similar, although the Liaoning specimens have a narrower skull as seen from above. *Sinemys* and *Dracochelys* have a lower skull and larger temporal emargination through which the processus trochlearis oticum is fully visible.

NASAL: Both nasals are preserved in GM V3000-4. The left nasal is preserved in GM V3000-1. Similar to that of *Ordosemys* sp., the nasal is a small element forming the upper margin of the apertura narium externa. In GM V3000-4, due to postmortem crushing, the nasal is a little shifted posteriorly. It contacts the other nasal along the midline, the frontal posteromedially, and the prefrontal posterolaterally. The nasal/maxilla contact is not clearly preserved in this specimen. The nasal of GM V3000-1 is larger and its contacts with the maxilla, the prefrontal, and the frontal and its mate are well preserved. Li and Liu (1999) described a small nasal probably not meeting the maxilla in IVPP V11554. There is no nasal/maxilla contact indicated in *Ordosemys* sp. (Brinkman and Wu, 1999).

PREFRONTAL: The prefrontals are complete in GM V3000-4. Only the left prefrontal is preserved in GM V3000-1. The prefrontal



Fig. 1. *Ordosemys liaoxiensis* (Ji, 1995), GM V3001, Yixian Formation, Liaoning, China. Skeleton in ventral view. Scale bar = 50 mm.

TABLE 1
Measurements of Skull of *Ordosemys liaoxiensis*
(Ji, 1995), Yixian Formation, Liaoning, China
(in mm)

Specimen	Length ^a	Width (max.)
GM V3001	56	54
GM V3000-4	57	43

^aFrom snout to occipital condyle.

agrees with that of *Ordosemys* sp. and *Sinemys* (Brinkman and Peng, 1993b). This is an anteroposteriorly elongated element forming the anteromedial margin of the orbit. They do not meet on the midline, but are separated by the frontals. The midline meeting with the prefrontals of IVPP V11554 indicated by Li and Liu (1999) is incorrect. The prefrontal contacts the maxilla anterolaterally, the nasal anteriorly, and the frontal medially. In *Hangaemys* (Sukhanov and Narmandakh, 1974; Sukhanov, 2000), *Draconchelys* (Gaffney and Ye, 1992), and *Macrobaena* (Tatarinov, 1959), the prefrontal is larger and meets its counterpart along the midline.

FRONTAL: Both frontals are complete in GM V3000-4. The left frontal is complete in GM V3000-1, while the right one is damaged. Together, the frontals form an inverted T-shaped element which agrees with that of *Ordosemys* sp. and *Sinemys*. The frontals meet each other on the midline by a long suture and send an anterior process between the prefrontals to meet the nasals. They prevent the midline meeting of the prefrontals. The frontal forms a small portion of the orbital margin between the prefrontal and the postorbital. Posteriorly, the frontal contacts the parietal by an anteriorly convex suture, as in *Ordosemys* sp. In *Sinemys*, the frontal-parietal suture is straight. The heart-shaped frontal not reaching the orbital margin in IVPP V11554, as indicated by Li and Liu (1999), is incorrect.

PARIETAL: Both parietals are complete in GM V3000-4; they are a little damaged in GM V3000-1. The parietal is a large element forming most of the temporal emargination and contacting the frontal anteriorly, the postorbital anterolaterally. Posterolaterally, the parietal sends a process to meet the squa-

TABLE 2
Measurements of Shell of *Ordosemys liaoxiensis*
(Ji, 1995), Yixian Formation, Liaoning, China
(in mm)

Specimen	Carapace		Plastron	
	Length	Width	Length	Width
GM V3001	213	200	(180) ^a	175
GM V3002	120	120	—	—
GM V3000-1	(170)	(150)	(111)	(104)
GM V3000-2	165	140	108	(101)

^aMeasurements in parentheses are estimates.

mosal, preventing the exposure of the post-orbital in the temporal emargination. Parietal/squamosal contact is present on both sides in GM V3000-4 and it is well preserved on the left side of GM V3000-1. Such a process is present in *Ordosemys* sp. (Brinkman and Wu, 1999: fig. 2), but the squamosal is not preserved in this specimen. The very small parietal of IVPP V11554 described by Li and Liu (1999) is incorrect. Parietal/squamosal contact is present in *Hangaemys* (Sukhanov and Narmandakh, 1974; Sukhanov, 2000) and chelonioids (Cheloniidae, some Protostegidae, and some Dermochelyidae [Hirayama 1994, 1998]). There is no parietal/squamosal contact in *Sinemys* (Brinkman and Peng, 1993b).

POSTORBITAL: The postorbitals are complete in both GM V3000-4 and GM V3000-1. The postorbital is a large anteroposteriorly elongated element which agrees with that of *Ordosemys* sp. It forms the posterior margin of the orbit but does not reach the temporal emargination. The exclusion of the postorbital from the temporal emargination can be observed on both sides in GM V3000-4 and on the left side of GM V3000-1. Whether the postorbital is exposed on the temporal emargination in *Ordosemys* sp. is uncertain, but if it is, the exposure would have been small, as indicated by Brinkman and Wu (1999). The postorbital contacts the frontal anteromedially, the parietal posteromedially, the jugal anterolaterally, and the quadratojugal and the quadrate lateroventrally. The region where the postorbital meets the squamosal in GM V3000-4 is damaged. However, the postorbital/squamosal contact is well preserved on the left side in GM V3000-1, and it is partly

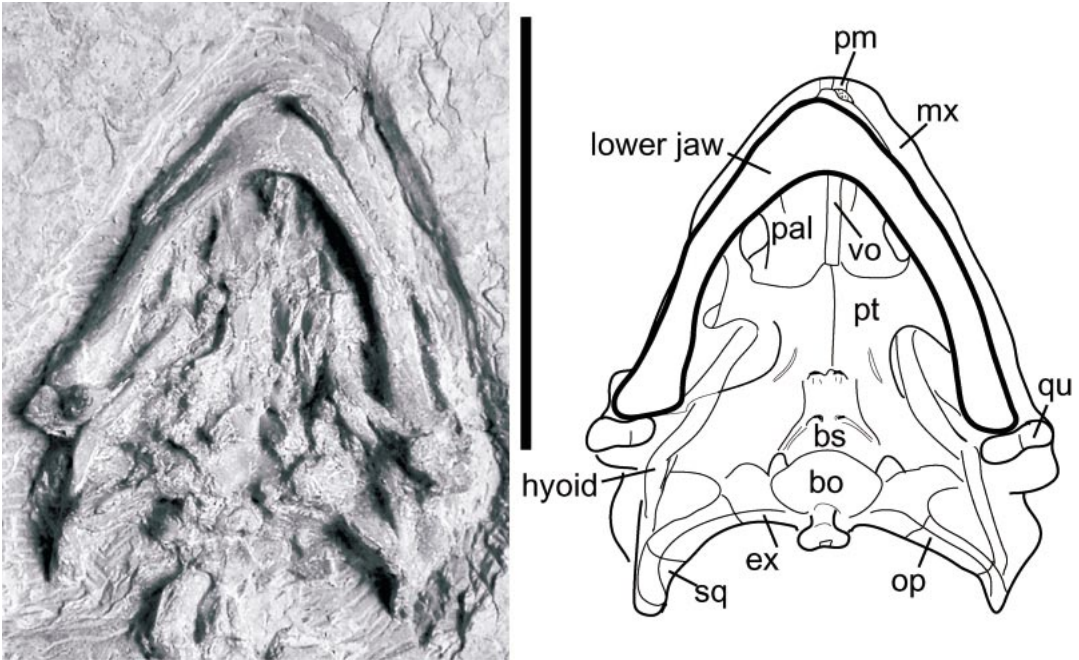


Fig. 2. *Ordosemys liaoxiensis* (Ji, 1995), GM V3001, Yixian Formation, Liaoning, China. Skull in ventral view. Scale bar = 50 mm.

preserved on its right side. Li and Liu (1999) indicated a postorbital/prefrontal contact in IVPP V11554, but reexamination of this specimen shows that this contact is absent.

JUGAL: The jugals are complete in GM V3000-4. The jugal agrees with that of IVPP V11554 and *Ordosemys* sp.: it is a small element forming the posteroventral margin of the orbit and the anterior portion of the cheek emargination. It extends more posteriorly than that of *Ordosemys* sp. It contacts the postorbital dorsally and the maxilla anteriorly. Posteriorly, the jugal barely meets the quadratojugal above the cheek emargination.

QUADRATOJUGAL: Both quadratojugals are complete in GM V3000-4. The quadratojugal is a C-shaped element forming the posterior half of the cheek emargination, as in *Ordosemys* sp. It contacts the postorbital dorsally, the quadrate posteriorly, and barely reaches the jugal anteriorly.

SQUAMOSAL: Both squamosals are complete in GM V3000-4. The squamosal is a cone-shaped element forming the posterolateral part of the skull roof and the lateral portion of the temporal emargination. Ventrally

the squamosal contacts the quadrate and anterodorsally the postorbital. There is no squamosal/quadratojugal contact, as mentioned by Brinkman and Wu (1999) for *Ordosemys* sp. A short squamosal/parietal contact is present along the temporal emargination. The left squamosal is well preserved in GM V3000-1, which confirms the squamosal/parietal contact.

PREMAXILLA: Both premaxillae are complete in GM V3000-4. They are visible in ventral view in GM V3001. The premaxilla agrees with that of *Ordosemys* sp. and IVPP V11554; it is a very small element forming the middle portion of the triturating surface. There is a pair of "teeth" formed at the suture of the premaxilla and maxilla on the labial ridge, which is less developed than that of *Dracochelys* (Gaffney and Ye, 1992). It is formed only by a smooth undulation of the ventral margin of the labial ridge with a midline notch on the premaxillary midline suture. This structure is preserved on the right side of both GM V3000-4 and GM V3001, with the left one being damaged on both of them. Such undulation of the labial ridge can

be seen in *Ordosemys* sp. (Brinkman and Wu, 1999: fig. 2C). The premaxilla contacts the maxilla posterolaterally. The posterior part of the premaxilla and its contact cannot be seen in either specimen because of the attached lower jaw.

MAXILLA: Both maxillae are complete in GM V3000-4 and they are visible in ventral view in GM V3001. This element agrees with that of *Ordosemys* sp. Anteriorly, the maxilla forms the anteroventral margin of the orbit and contacts the nasal and prefrontal dorsally, the premaxilla anteriorly, and the jugal posteriorly. Together with the premaxillae, the maxillae form the triturating surface and its labial ridge. The triturating surface is hidden by the attached lower jaw on both GM V3000-4 and GM V3001 and is not visible; its width seems to be more similar to that of *Ordosemys* sp. than to *Dracochelys*, according to the lower jaw (Brinkman, 2001), with the latter being narrower. Anteromedially, the maxilla contacts the premaxilla and medially it meets the palatine in ventral view. It is uncertain whether the maxilla enters into the lateral margin of the foramen palatinum posterius because of the attached lower jaw, but at most, the contact would have been small. Posteromedially, the maxilla would contact the pterygoid as in *Ordosemys* sp., but this region is hidden by the lower jaw.

PALATINE: The palatines are complete in both GM V3000-4 and GM V3001. As in *Ordosemys* sp., it is an anteroposteriorly elongated element. There is a shallow groove along its medial margin from the apertura narium interna to the palatine/pterygoid suture, where the palatine/vomer suture is located. The palatine sends an anterolateral process between the apertura narium interna and the foramen palatinum posterius to contact the maxilla, but this contact is hidden by the attached lower jaw. The palatine forms most of the foramen palatinum posterius which is similar in size to that of *Ordosemys* sp. In *Sinemys*, *Haigaiemys*, and *Dracochelys*, this foramen is larger. Posteriorly, the palatine contacts the pterygoid by a W-shaped suture.

VOMER: The vomer is complete in GM V3000-4 and GM V3001. It is a ridgelike internarial septum extending far posteriorly

to reach the pterygoid and separating the palatines. Its anterior end is covered by the lower jaw and it becomes narrower posteriorly as in *Ordosemys* sp.

QUADRATE: The quadrates are complete in GM V3000-4 and GM V3001. Laterally the quadrate forms a deep cavum tympani which is triangular in shape. The almost straight upper margin of the cavum in GM V3000-4 is clearly due to crushing; the original shape of the cavum can be observed in GM V3000-1 where it is taller. The structure of the cavum tympani of GM V3000-4 is very similar to that of *Ordosemys* sp.: the incisura columellae auris is a posteroventrally opened slit, with a small tubercle on the lateral end of the ventral margin; the precolumellar fossa is absent, and only a slight depression is present anteroventral to the incisura columellae auris; the antrum postoticum is large. Ventrally, the quadrate forms the low condylus mandibularis. With the lower jaw of GM 3001 being pushed forward, the condylus mandibularis is visible, which has a transversally elongated and concave facet. The contact of the quadrate with the surrounding bones agrees with that of *Ordosemys* sp.

PTERYGOID: Both pterygoids are complete in GM V3000-4; the posterior end is a little damaged in GM V3001. It generally agrees with that of *Ordosemys* sp. in structure and relationships. The ventral surface of the pterygoid of GM V3000-4 and GM V3001 is wider than that of *Ordosemys* sp. and is concave along the midline suture. Anterolaterally the pterygoid constitutes the processus pterygoideus externus which is similar to that of *Ordosemys* sp. in size. In GM V3001, the pterygoid forms the posterolateral rim of the foramen palatinum posterius as in *Ordosemys* sp., while in GM V3000-4 it seems not to reach the foramen, with the palatine/maxilla contact preventing it. Therefore the bones surrounding the foramen palatinum posterius seem to be variable among *O. liaoxiensis*, as in the specimens from the Ordos Basin (Brinkman and Peng, 1993a; Brinkman and Wu, 1999), being the palatine, maxilla, and pterygoid in IVPP V11554 (Li and Liu, 1999) and GM V3001, and the palatine and maxilla, excluding the pterygoid, in GM V3000-4.

The pterygoid/palatine/vomer suture is W-

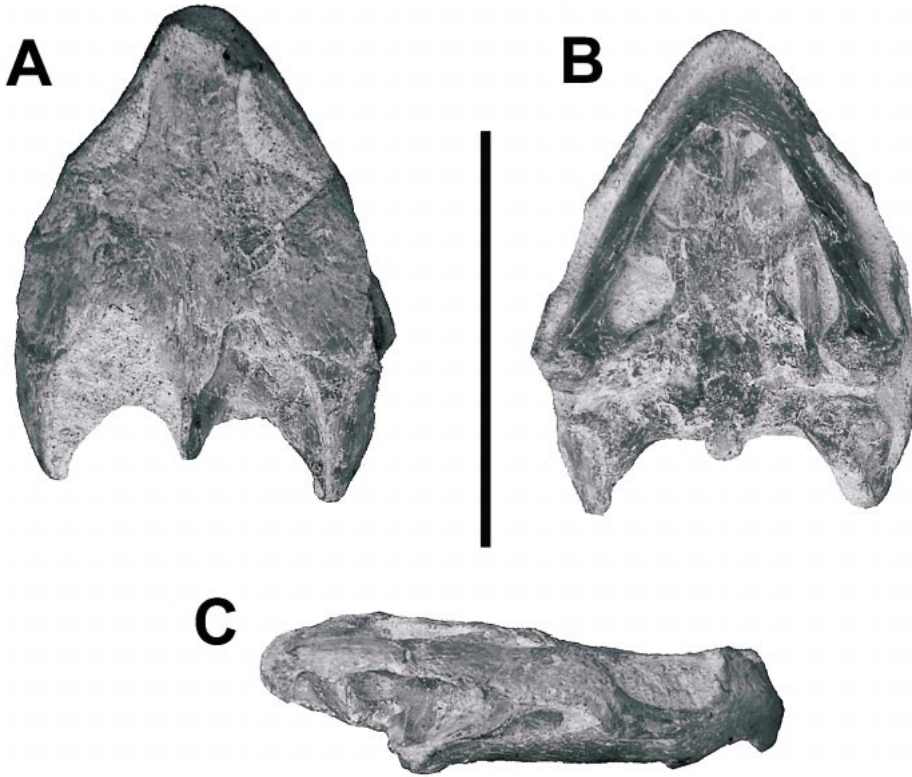


Fig. 3. *Ordosemys liaoxiensis* (Ji, 1995), GM V3000-4, Yixian Formation, Liaoning, China. Skull in dorsal (A), ventral (B) and right lateral (C) views. Scale bar = 50 mm.

shaped as in *Ordosemys* sp. and IVPP V11554. It is different from that of *Dracochelys* and *Hangaiemys* in which this suture is nearly straight. The pterygoid contacts the basisphenoid posteromedially by a serrated suture. There is a shallow and medially convex groove along the lateral margin of the pterygoid, lateral to the foramen caroticum lateral. This groove is clearly visible in GM V3001 and GM V3000-4. Posterolaterally, the quadrate ramus of the pterygoid contacts the quadrate at the base of the condylus mandibularis and posteromedially the exoccipital. A distinct concavity is present along the posterior portion of the quadrate ramus, as in *Ordosemys* sp. Posteriorly, the pterygoid forms the anterior margin of the fenestra postotica.

BASISPHEOID: The basisphenoid is complete in both GM V3001 and GM V3000-4, but the ventral surface is a little damaged in the latter. The basisphenoid of the Liaoning

specimens is similar to that of *Ordosemys* sp. It is an arrow-shaped element in ventral view, pointed anteriorly and divided into two parts by a pair of pits: a triangular anterior portion and a wider posterior part. The foramen caroticum basisphenoidale, through which enters the internal carotid artery, is located within these pits in GM V3001. In GM V3000-4, due to damage and crushing of the basisphenoid surface, the position of the foramen is not clear—it seems to be slightly lateral to the pit, but not within it. A shallow groove, in which the internal carotid artery was located, extends from the foramen caroticum basisphenoidale posterolaterally toward the foramen posterius canalis carotici interni. In *Ordosemys* sp., the foramen caroticum basisphenoidale is more anteriorly placed, located near the basisphenoid/pterygoid suture, and the groove for the internal carotid artery follows the pterygoid/basisphenoid suture. The foramen basispheno-

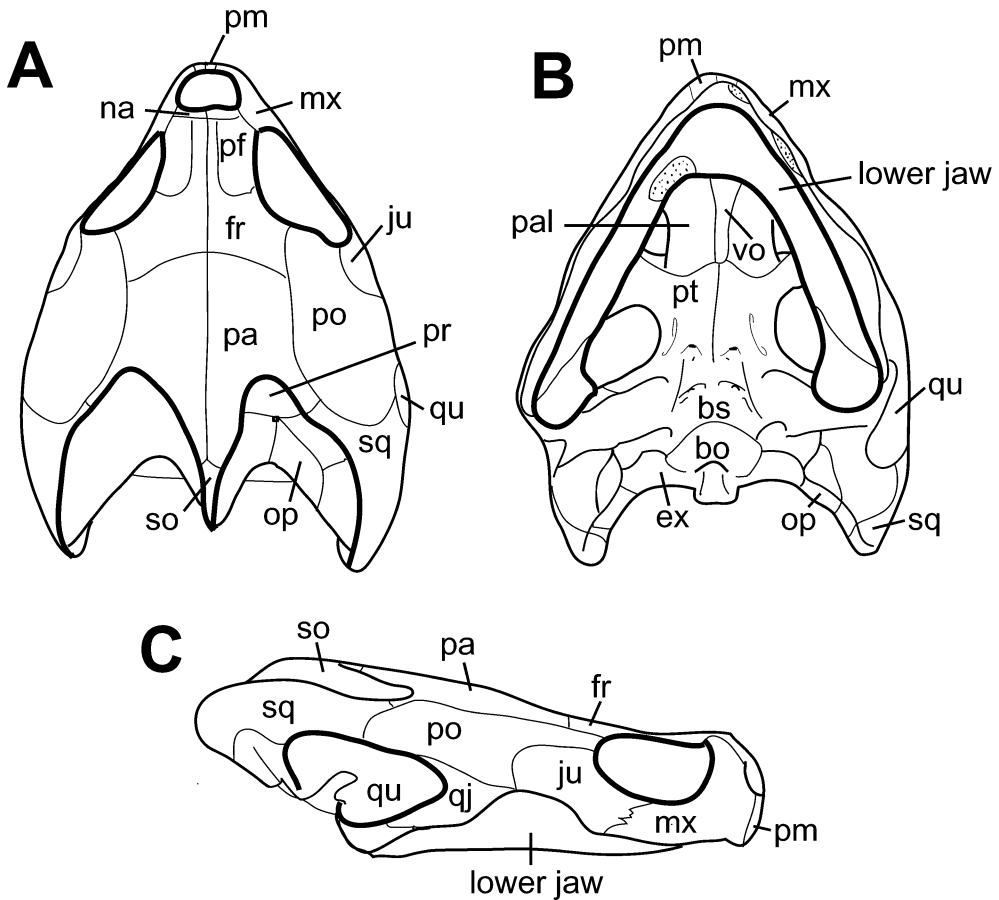


Fig. 4. *Ordosemys liaoxiensis* (Ji, 1995), GM V3000-4, Yixian Formation, Liaoning, China. Skull in dorsal (A), ventral (B) and right lateral (C) views. Key for figure 3.

dale, located in the middle of the basisphenoid in the Liaoning specimens, is somewhat more similar to the condition in *Dracochelys*, as mentioned by Li and Liu (1999), than to *Ordosemys* sp.

The region of the foramen posterius canalis carotici interni is not well preserved in either GM V3001 or GM V3000-4. The foramen seems to be more posteriorly located in our specimens than that of *Ordosemys* sp., being placed where the basisphenoid/pterygoid/basioccipital meet, posterolaterally to the basisphenoid pits. In *Ordosemys* sp., this foramen is more anteriorly located, on the basisphenoid/pterygoid suture, lateral to the basisphenoid pits. The posterior portion of the canalis carotici interni is damaged in both GM V3001 and GM V3000-4. It seems to be

covered by thin bone as in *Ordosemys* sp. Posteriorly, the basisphenoid forms a pair of large tubercles and contacts the basioccipital by an anteriorly convex suture, as in *Ordosemys* sp., but the posterior part of the basisphenoid is narrower and longer than that of *Ordosemys* sp.

Anteriorly and laterally, the basisphenoid contacts the pterygoid, but the lateral suture with the pterygoid is not clear. The anterior pterygoid/basisphenoid suture is serrated. The pair of foramina carotica laterale is placed on this suture, through which enters the palatine artery (Gaffney, 1979).

BASIOCCIPITAL: The basioccipital is complete in GM V3001; it is nearly complete in GM V3000-4 but its ventral surface is a little damaged. As in *Ordosemys* sp., the basioc-

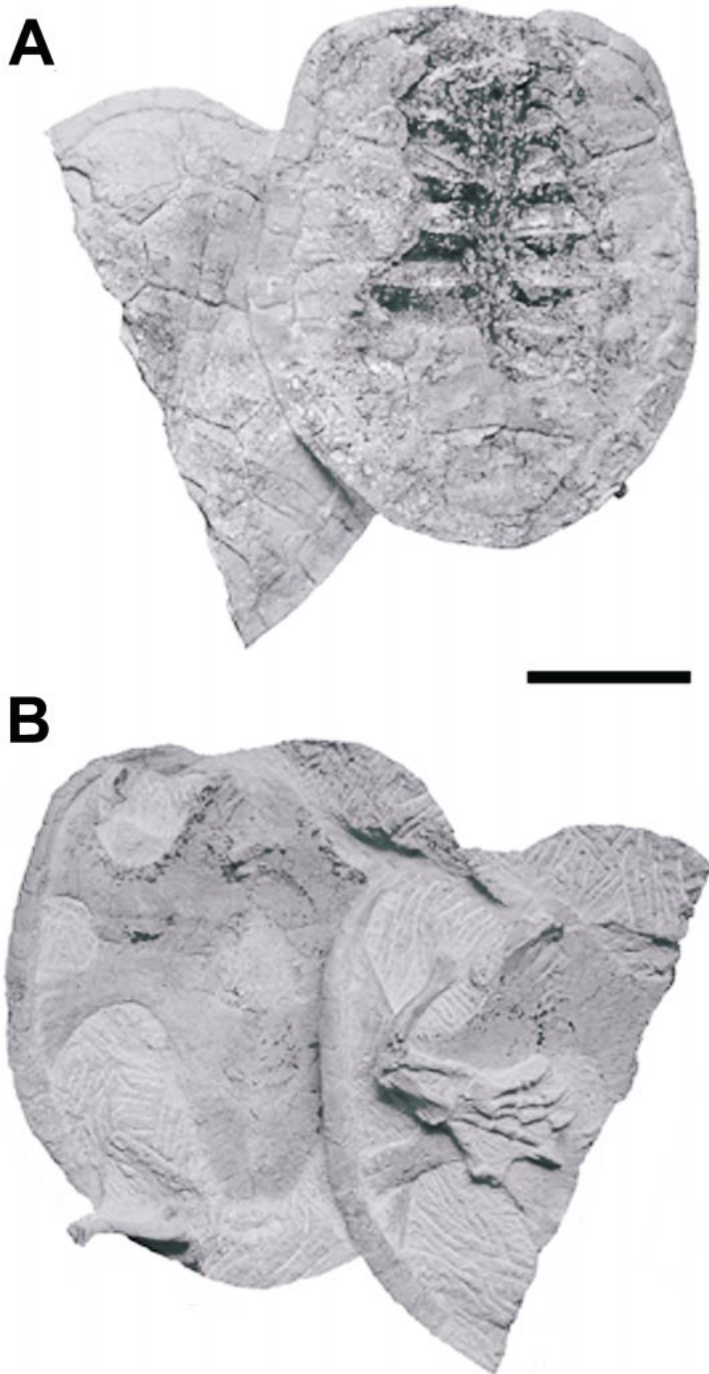


Fig. 5. *Ordosemys liaoxiensis* (Ji, 1995), GM V3000-1 and GM V3000-2, Yixian Formation, Liaoning, China. Shell in dorsal (**A**) and ventral (**B**) views. Scale bar = 50 mm.

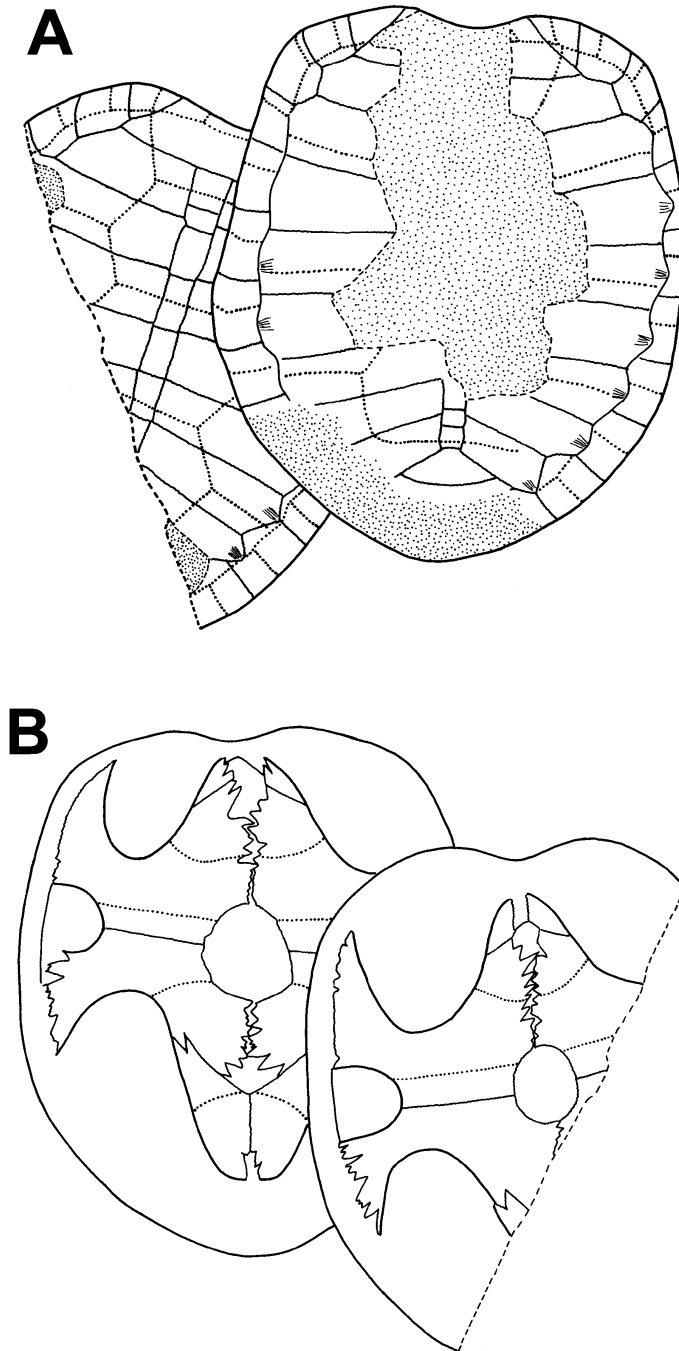


Fig. 6. *Ordosemys liaoxiensis* (Ji, 1995), GM V3000-1 and GM V3000-2, Yixian Formation, Liaoning, China. Shell in dorsal (A) and ventral (B) views. Key for figure 5.

cipital has a nearly flat ventral surface which is slightly wider than the posterior end of the basisphenoid. The posterolateral edge of the basioccipital is thickened to form a pair of basioccipital tubercles. The occipital condyle is placed at a distinctly more dorsal level than the anterior part, as in *Ordosemys* sp. According to Brinkman and Wu (1999), there is no distinct change in elevation between the ventral surface of the anterior portion of the basioccipital and that of the occipital condyle in *Sinemys* and *Dracochelys*. The basioccipital contacts the basisphenoid anteriorly by an anteriorly convex suture, as in *Ordosemys* and *Dracochelys*. It is different from *Sinemys* and *Hangaiemys* in which the basioccipital/basisphenoid suture is straight. Anterolaterally the basioccipital contacts the pterygoid and laterally the exoccipital.

EXOCCIPITAL: The exoccipital is complete in GM V3001 and GM V3000-4; it agrees with that of *Ordosemys* sp. Medially, it meets the basioccipital. Laterally, the exoccipital sutures to the opisthotic for its whole length. In ventral view, it reaches anteriorly the pterygoid but seems not to contact the basisphenoid. Dorsally, the exoccipital forms the lateral margin of the foramen magnum and contacts the supraoccipital dorsomedially. Two foramina nervi hypoglossi can be seen at the left side of GM V3000-4, both within the exoccipital.

SUPRAOCCIPITAL: The supraoccipital is complete and visible only in GM V3000-4. It agrees with that of *Ordosemys* sp. The supraoccipital forms the crista supraoccipitalis which extends posteriorly to the level of the posterior end of the squamosal. It contacts the parietal anterodorsally, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally.

PROTIC: Only a small portion of the right prootic is visible through the temporal emargination in GM V3000-4. It forms the anterior margin of the large foramen stapedio-temporale and contacts the supraoccipital medially and the quadrate laterally.

OPISTHOTIC: The opisthotic is similar to that of *Ordosemys* sp. in structure, but only its anterior portion is visible dorsally, while in *Ordosemys* sp. the opisthotic is visible dorsally for its full length. The opisthotic forms the posterior margin of the foramen

stapedio-temporale dorsally and the posterior margin of the fenestra postotica ventrally. The fenestra postotica is located lateral to the exoccipital and anteroventral to the opisthotic; it is not visible in occipital view, as in *Ordosemys* sp. The opisthotic contacts the supraoccipital dorsomedially, the quadrate laterally, and the exoccipital ventromedially.

LOWER JAW

The lower jaw is complete in GM V3001 and GM V3000-4, both preserved in connection with the skull, so the dorsal side is not visible. The ventral side of the lower jaw agrees with that of IVPP V11554. The two rami form an angle of about 65°. The symphysis is short.

In comparison with *Dracochelys*, the lower jaw of our specimens is clearly narrower; the rami are nearly straight, forming together a triangle, while in *Dracochelys* the rami are more convex laterally, forming together a rounded and much wider arc (Brinkman, 2001).

HYOID BONE

The cornu branchial I is complete in GM V3001 and GM V3000-3 and is partly preserved in GM V3000-4. All are visible in ventral view. This is a long, curved, rodlike element with a flattened posterior end (fig. 2).

SHELL

CARAPACE (figs. 5–7): The shell is very low. It has an oval outline, with its length slightly larger than its width. The lateral margin of the carapace is slightly divergent posteriorly, with the widest point being at the level of the seventh peripherals. The nuchal emargination is shallow and wide and is well preserved in GM V3000-1. A midline depression is present along the neural region, as in *Ordosemys leios* (Brinkman and Peng, 1993a), some *Xinjianchelys* and *Chengyuchelys* (Ye, 1994), and *Siamochelys* (Tong et al., 2002). The lateral fontanelle is nearly closed in GM V3000-1 and GM V3000-2, so there is little space between the lateral margin of the costals and the peripherals. However, the rib ends of the second to seventh costals are clearly visible in dorsal view,

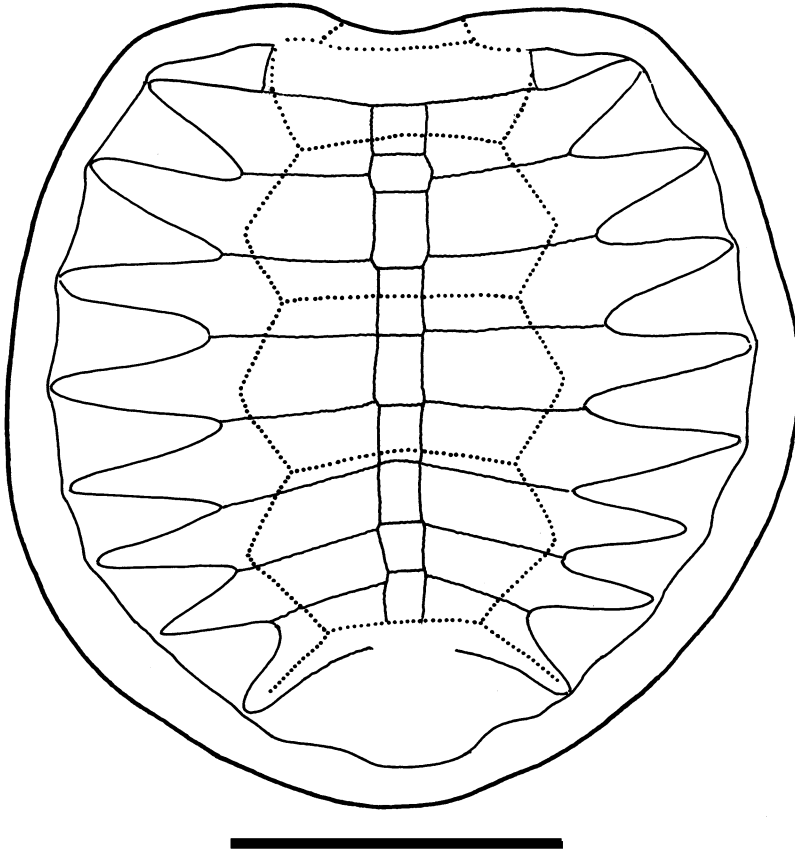


Fig. 7. *Ordosemys liaoxiensis* (Ji, 1995), GM V3002, Yixian Formation, Liaoning, China. Shell in dorsal view. Scale bar = 50 mm.

even in GM V3000-1, where the lateral fontanelle is more closed. In other specimens, the size of this fontanelle varies according to the age of the individual. In GM V3000-2, it is very narrow, extending from the second costal plate to the seventh. In GM V3002, the lateral fontanelle is wider. There is no gutter along the anterolateral margin of the carapace, which is different from the condition in *Xinjianchelys* and *Siamochelys*, but a groove is clearly present anterolaterally, along the marginal/pleural sulcus. The shell surface is not perfectly smooth, but is slightly rugose with very light vermiculated grooves.

The nuchal plate is preserved in GM V3000-1. It is a wide trapezoidal plate with the width being about twice the length. The series of neurals is well preserved in GM V3002 and is incomplete in GM V3000-1.

As in *O. leios*, a preneural and the first neural are present between the first costal plates. The preneural, preserved in both GM V3000-1 and GM V3002, is a rectangular-shaped plate that is longer than the first neural. The first neural is a subrectangular plate which is wider than long. The second to eighth neurals tend to be rectangular and are all longer than wide. The eighth neural in GM V3000-2 is divided into two small plates, with the intervertebral sulcus between the fourth and fifth vertebrae crossing the posterior one. The neurals separate completely the right costal plates from the left ones, with the interneural sutures continuing in line with the intercostal sutures, as in *O. leios*. The suprapyrgals are preserved in GM V3000-2, but the shell surface is damaged, so the suture is not clearly visible. It seems that two suprapyrgals are present and their shape and contacts are the

same as in *O. leios*. Eight costal plates are present. The first costal is sutured to the second and the third peripherals, while the second to seventh costals fit to the peripherals by pegs inserting in sockets of the peripherals. Eleven pairs of peripherals are present in GM V3000-2. The first peripheral is roughly triangular-shaped. It is sutured to the nuchal and does not reach the first costal plate in both GM V3000-1 and GM V3000-2. This condition is similar to that in *Dracochelys* (Brinkman, 2001), but differs from *Ordosemys leios* in which the first peripheral plate reaches the first costal plate. The second and third peripherals are roughly square while the fourth to ninth peripherals are longer than wide. The tenth and eleventh peripherals are mediolaterally expanded.

The scute sulci are deeply impressed on the carapace. As in *O. leios*, the cervical scute is very short and wide, and the vertebral scutes are all much wider than long, with a strongly angled lateral margin. The intervertebral sulcus crosses through the preneural and the third, the fifth, and the last neurals, respectively. The marginal scutes are restricted to peripheral plates. The ventral side of the carapace can be partly observed in GM V3001. The first costal plate bears a transverse and straight ridge from the first thoracic vertebrae to the axillary buttress.

PLASTRON (figs. 1, 5, 6): The complete plastron is preserved in GM V3000-2, but it is partly hidden by GM V3000-1 and is incomplete in GM V3000-1. The plastron is incomplete and crushed in GM V3001 with damaged anterior and posterior ends. The surface of the plastron is more decorated than the carapace, with widely spaced light vermiculated grooves. The midline suture in both GM V3000-1 and GM V3000-2 presents strong indentations throughout its length, and the right part is not tightly sutured to its counterpart but is separated from the left one by a narrow space. This indicates that these are not fully grown individuals. The strong indentations may remain in adult individuals, as in *Macrobaena* in which the midline suture between the hyoplastron is strongly sinusoidal (Tatarinov, 1959).

The plastron is loosely attached to the carapace by the series of pegs on the hyoplastron and hypoplastron that insert into the pits

on the peripherals. Some of the larger openings between the lateral processes of the plastron, including one on the hyoplastron and two in the hypoplastron (visible in GM V3001), may be for the musk ducts. These openings can also be seen on the right hypoplastron of GM V3000-2.

The anterior lobes of both GM V3000-1 and GM V3000-2 are a little damaged by crushing—the entoplastron is pushed inward in GM V3000-2 and outward in GM V3000-1; however, the general morphology can be made out. The anterior lobe is shorter than the bridge. At its base it is about as wide as that of the posterior lobe and the anterior margin is pointed. The anterior lobe of our specimens is wider than that in the reconstruction of *Ordosemys leios* by Brinkman and Peng (1993a), but it is more similar to that of *Macrobaena* (Tatarinov, 1959: fig. 10). The bridge is fan-shaped with a long contact with the carapace. The axillary and inguinal buttresses extend well anteriorly and posteriorly, as in *Ordosemys leios* (Brinkman and Peng, 1993a: figs. 2, 4). The bridge is longer than the anterior lobe and shorter than the posterior one. There is a semicircular lateral fontanelle between the hyoplastron, the hypoplastron, and the peripherals. It is different from that in *O. leios* in which the lateral fontanelle is narrow and anteroposteriorly elongated. A large and rounded medial fontanelle is present between the hyoplastron and hypoplastron. A second medial fontanelle is preserved in GM V3000-2 between the hypoplastron and the xiphiplastron. This is a diamond-shaped opening, wider than long and smaller than the more anterior one, as in *O. leios*. The posterior lobe is complete in GM V3000-2. The base of the posterior lobe is wide and the lateral margins converge gently posteriorly. As in *O. leios*, its posterior end does not reach the posterior margin of the carapace. The posterior lobe of the plastron of our specimens is different from *Sinemys* (Brinkman and Peng, 1993b) and *Manchurochelys* (Endo and Shikama, 1942). In the latter, the posterior lobe has a very narrow base and the posterior end of the plastron reaches the posterior margin of the carapace.

The epiplastra are preserved in both GM V3000-1 and GM V3000-2. The epiplastron

is a small plate located at the anterolateral margin of the plastron. When reconstructed in original position, they should meet one another at the midline anterior to the entoplastron, as in *Hangaemys* (Sukhanov and Narmadakh, 1974). The entoplastron is preserved in both GM V3000-1 and GM V3000-2. It is better preserved in GM V3000-2. It is an anteroposteriorly elongated plate, but the outline cannot be determined because of deformation. A low and sharp midline ridge can be seen on the anterior part of the dorsal side of the entoplastron of GM V3000-2. The hyoplastron and hypoplastron are large elements with a nearly symmetrical outline: the part forming the lateral process is nearly as large as the part forming the plastral lobes. These two parts are separated by the wide axillary or inguinal notch, as in *Ordosemys leios*, *Macrobaena*, and *Hangaemys*. The hyohyoplastral suture is nearly straight, while in *O. leios* it is slightly convex posteriorly. The xiphiplastra are well preserved in GM V3000-2. They are anteroposteriorly elongated plates that meet one another on the midline for nearly their full length. The hypoxiphiplastral sutures are strongly convex posteriorly, forming the posterior margin of the posterior medial fontanelle and with a strong indentation near the lateral end, as in *Ordosemys leios*. The posterior end of the plastron seems not to be completely ossified, which confirms the young age of the specimen. The posterior end of the plastron is nearly straight without an anal emargination.

The scute sulci are weak on the plastron in GM V3000-1 and GM V3000-2, while they are deeply printed in GM V3001. They are in good agreement with those of *Ordosemys leios*: the humeropectoral sulcus is convex posteriorly; the pectoroabdominal sulcus is roughly parallel to the hyohyoplastral suture, crossing the anterior part of the anterior medial fontanelle; the abdominofemoral sulcus is anteriorly convex, cutting the posterior part of the anterior medial fontanelle; the femoroanal sulcus is strongly convex anteriorly, cutting the posterior margin of the posterior medial fontanelle. The gular is not distinguishable, nor the inframarginal scutes on both GM V3000-1 and GM V3000-2. In GM V3001, very light sulci

are visible on the lateral margin of the hyoplastron and hypoplastron, which indicate that at least three inframarginal scutes were present.

VERTEBRAL COLUMN

CERVICAL VERTEBRAE: In GM V3001 (fig. 1), the series of eight cervicals is preserved but crushed; the first cervical (atlas) and the second cervical (axis) are detached from the series, whereas the other ones are in connection. Most of them are visible in left ventrolateral view except the first one, which is visible in dorsal view, and the second and eighth ones, which are visible in ventral view. The first to fourth cervicals are preserved in GM V3000-4: the first to third are nearly complete, with the ventral keel damaged, and the fourth one lacks its posterior part. The series of cervicals are preserved in GM V3000-1 and GM V3000-2, with both damaged and visible in dorsal view. Five anterior cervicals are preserved in GM V3000-3, visible in ventral view, with the fifth one lacking the posterior end.

The centrum of all cervicals is short and stout. All cervical vertebrae are keeled ventrally. The zygapophyses are widely spaced. The transverse process is stout and placed at the anterior half of the centrum, but near the midpoint. This is different from *Ordosemys leios* in which the transverse process is located near the anterior end (Brinkman and Peng, 1993a). The first cervical (atlas) is well visible in GM V3000-4 with a biconcave centrum. The second and third cervicals are opisthocoelous. The fourth cervical, in which the centrum is visible in GM V3000-3, appears to be biconvex, as in *Ordosemys leios*. The convexity of the following cervical centra cannot be determined because of the nature of preservation and crushing.

DORSAL VERTEBRAE: The series of dorsal vertebrae is preserved in GM V3001, but most of them are hidden by the plastron. The first dorsal vertebra appears to have an anteriorly facing articulation surface. The posterior dorsal vertebrae are visible; they contact the strong and rounded rib head of the costal plate. The ventral surface is smoothly rounded without keel.

SACRAL VERTEBRAE: Three sacral vertebrae

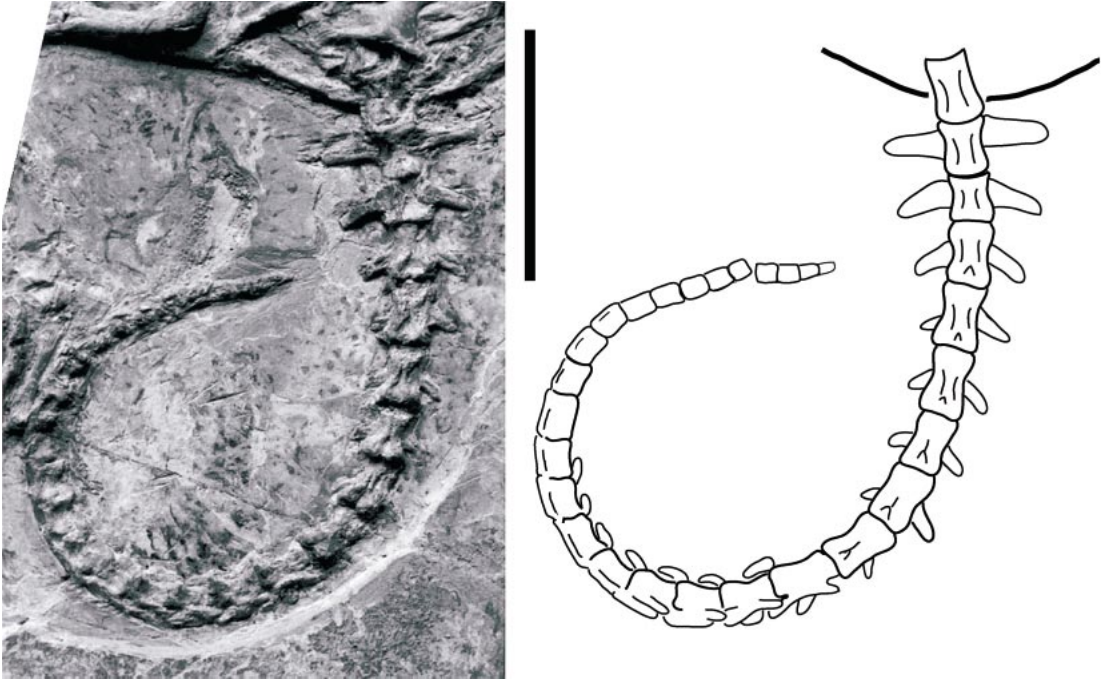


Fig. 8. *Ordosemys liaoxiensis* (Ji, 1995), GM V3001, Yixian Formation, Liaoning, China. Detail of tail. Scale bar = 50 mm.

are preserved but disarticulated. They are visible in ventral view. All have a low ventral keel which becomes sharper from the first to the third sacral vertebra, while the dorsal vertebrae which are placed just anteriorly have a smoothly rounded ventral surface. The first sacral has an amphicoelous centrum; the second one is procoelous and the third one has a condyle on its posterior end, while its anterior end is hidden by the left ischium.

CAUDAL VERTEBRAE: The complete series of 30 articulated caudals is preserved in GM V3001. An incomplete tail is preserved in GM V3000-2. In GM V3001, the first nine vertebrae are visible in ventral view and the remaining ones in right lateral view (fig. 8).

The centra are long and robust with their size decreasing posteriorly, with the last ones being very small and short. The first two caudals are procoelous. The third one is amphicoelous and the remaining ones are opisthocelous. The anterior caudals have long transverse processes. From the second caudal to the eighth, the transverse processes decrease in length. There are two ventral processes

placed at the posterior part of the centrum on the anterior caudals. These ventral processes become closer posteriorly. The well-developed hemal spines are visible from the 10th to 16th caudal.

In comparison to *O. leios*, GM V3001 seems to have a longer tail, although *O. leios* has only 13 caudals preserved, forming an incomplete caudal series. The structure of the caudals of GM V3001 is similar to that of *O. leios*, including the first two procoelous caudals, the amphicoelous third one and the opisthocelous remaining ones, and the ventral processes and well-developed hemal spines.

APPENDICULAR SKELETON

PECTORAL GIRDLE: The pectoral girdle is preserved in GM V3001 (fig. 1). Both scapula and coracoid are preserved on both sides, but disarticulated.

Both scapula and coracoid are rather short and stout as in *Ordosemys leios*. The scapula has a glenoid neck, like in most primitive turtles (Gaffaney and Meylan, 1988). The dorsal process of the scapula has a roughly

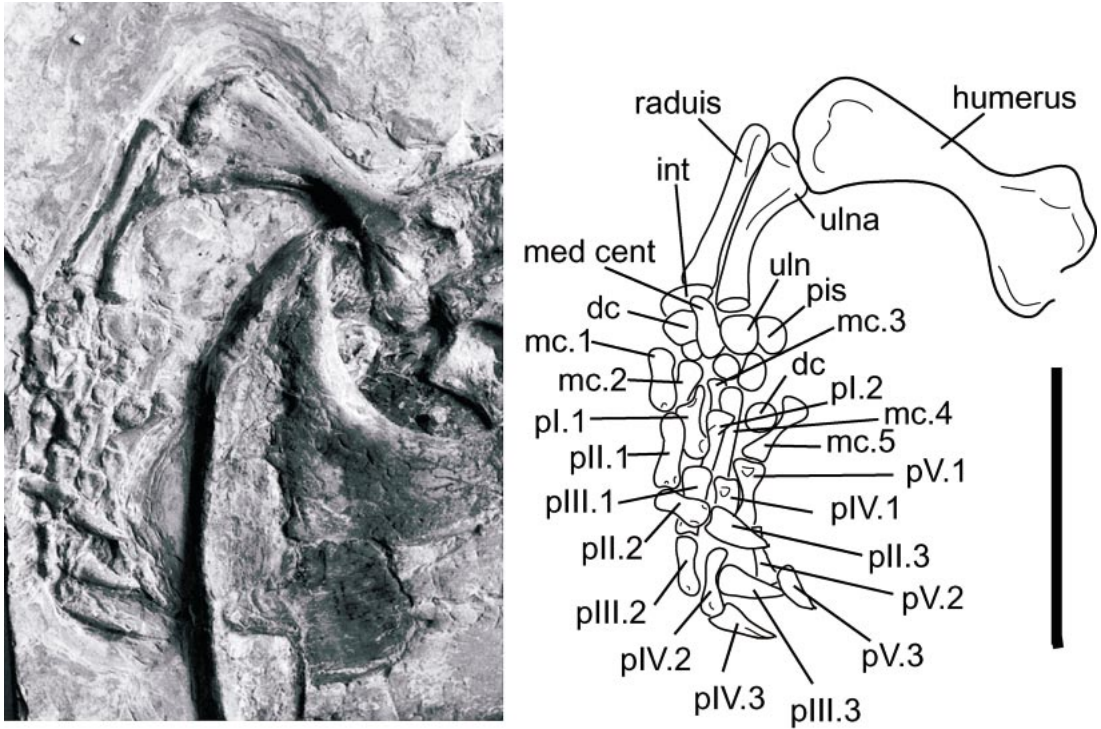


Fig. 9. *Ordosemys liaoxiensis* (Ji, 1995), GM V3001, Yixian Formation, Liaoning, China. Detail of forelimb. Scale bar = 50 mm. Abbreviations: **dc**, distal central; **int**, intermedium; **mc**, metacarpal; **med cent**, medial central; **p**, phalanx; **pis**, pisiform; **uln**, ulnare.

oval cross section. The acromion process has its medial end hidden by the plastron on both sides. The angle formed by these two processes is about 90° ; this can be confirmed in GM V3000-2 in which the scapula is visible.

The distal part of the coracoid is not visible on either side, but is hidden by the plastron, so the whole shape and the length of this bone are not determinable. The right coracoid is more visible, presenting an anteriorly concave anterior margin and a nearly straight posterior margin.

FORELIMB: Both forelimbs are preserved in GM V3001 (figs. 1, 9); only the right one is preserved in GM V3000-1. In GM V3001, both humeri are preserved and visible in ventral view. They are not articulated to the pectoral girdle. The radius and ulna, as well as the manus, are preserved on both sides, but they are crushed and partly disarticulated; the left manus is partly hidden by the shell.

The humerus is similar to that of *O. leios*, with a slight S-shaped curve. The proximal

end is very enlarged. The medial process is larger and taller than the lateral one, and they are separated by a wide and shallow median fossa. The distal end is wide with the articular surface facing ventrally. The radius and ulna are nearly equal in length.

The carpus is preserved but disturbed. The tentative interpretation is shown in figure 9. The pisiform is a rather large and oval-shaped bone which is only slightly smaller than the ulnare. Medial to it is the roughly square ulnare. The series of five distal carpals is preserved on the right manus of GM V3001. The metacarpals and phalanges are relatively long and robust with well-formed articulating surfaces and five claw-bearing digits. The claws are dorsoventrally flattened as in other turtles. The phalangeal formula is 2-3-3-3-3.

PELVIC GIRDLE: The complete pelvic girdle is preserved in GM V3001, but it is crushed and disarticulated. The left ilium is visible in lateral view. It has a strong posteriorly di-

rected blade with slight rugosities on its dorsal edge. The right one is partly hidden by the ischium. The pubes are not visible completely on either side, but the right one is more exposed. The pubis has a roughly triangular ventral plate. The pectineal process is broken off on the right pubis. The thyroid fenestra is large. Both ischia are preserved. They are hourglass-shaped. The lateral portion forms the acetabulum, and the metichial process is strong; between them is the rodlike ventral plate.

HIND LIMB: Both hind limbs are preserved in GM V3001, more or less in connection but very crushed. Both femora are complete or nearly so. The right one is visible in anteroventral view while the left one is visible in dorsal view. The femur is slightly longer than the humerus. The femoral head is oval in shape. There is a longitudinal crest on the dorsal surface from the head to about half the length of the shaft. The trochanter major is taller and larger than the trochanter minor, but it is lower than the femoral head. The trochanters are separated from each other by a wide and open intertrochanteric fossa. The shaft is slender. The distal end is expanded with the tibial condyle larger than the fibular condyle. A sharp crest is present along the posteroventral margin of the femur. Both tibia and fibula are complete and visible in ventral view. They are similar to those of *Ordosemys leios*. The tibia is longer than the radius (radial/tibial ratio = 0.76) and its length is about 68% of that of femur. It has an expanded head and a wide distal end. The fibula has an expanded and triangular distal end.

The feet are not complete on either side; they are crushed and have been restored. The tarsus is disarticulated. Distal to the tibia and fibula is the large astragalocalcaneum. The distal tarsals are not complete, but the fourth distal tarsal appears to be the largest. The metatarsals and phalanges are long and stout with well-defined articular condyles. They are longer than those of the manus. The phalangeal formula is 2-3-3-3-3. The first to fourth digits bear claws.

DISCUSSION

All the material studied in this paper is assigned to the same species. The slight dif-

ferences in shell outline between GM V3001 and GM V3000-1 and GM V3000-2 are mainly due to postmortem deformation. The different size of the fontanelles on the carapace and the plastron may be due to age or individual variation.

The turtle collection of the IVPP studied by Li and Liu (1999) includes five specimens (IVPP V11554–V11558); only IVPP V11554 has been prepared and described in detail. The reexamination of these specimens confirms that this collection and the GM collection studied in the present paper belong to the same species. These turtle remains are clearly different from *Manchurochelys manchoukuoensis* (Endo and Shikama, 1942) in the wider shell, the vertebral scutes that are wider than long, the presence of two medial fontanelles and the single lateral fontanelle on the plastron, and the posterior lobe of the plastron that is wider at its base; consequently, they are excluded from *Manchurochelys*.

The Liaoning specimens are referred to the genus *Ordosemys* on the basis of the very similar skull structure. The prefrontals not meeting in the midline are different from *Hangaemys* and *Macrobaena*. The postero-lateral process of the parietal contacts the squamosal in our specimens and IVPP V11554, such a process is present in *Ordosemys* sp. (Brinkman and Wu, 1999), but the posterior tip of the process and the squamosal are not preserved in the latter. It is very likely that the parietal/squamosal contact is present also in *Ordosemys* sp. The parietal/squamosal contact, present also in *Hangaemys* and most cheloniids, is considered as a primitive feature since it is widespread in primitive tetrapods and amniotes and present in *Proganochelys* (Gaffney, 1990, 1996). The medium-sized foramen palatinum posterius of our specimens, found also in *Ordosemys* sp., is different from the very large one in *Sinemys*, *Dracochelys*, and *Hangaemys*. Although the large foramen palatinum posterius is considered as a derived character, the primitive state is mentioned as a small or absent foramen (Gaffney, 1996). Thus, the medium sized foramen can be considered as an intermediate state. The opened incisura colomellae auris with a small tubercle at the posteroinferior margin can be observed in

both GM V3000-4 and *Ordosemys* sp., different from the closed incisura in *Sinemys*.

The shells from Liaoning present the autapomorphic features of *Ordosemys* among the "macrobaenid group" pointed out by Brinkman and Peng (1993a): the presence of a preneural and the presence of a fenestra between the hypoplastron and xiphiplastron. Both have a rounded or nearly rounded shell outline and vertebral scutes wider than long with strongly angled lateral margin. Besides the fact that the size of *O. liaoxiensis* is smaller than that of *O. leios*, the differences between the Liaoning turtles and *O. leios* are mainly on shell features: the shell surface is slightly decorated with small vermiculated grooves in *O. liaoxiensis*, different from the smooth shell surface of *O. leios*; both have a small triangular-shaped first peripheral, but this plate does not reach or barely reaches the first pleural plate in *O. liaoxiensis*, while the contact between the first peripheral and the first costal is present and more important in *O. leios*; and the lateral plastral fontanelle is semicircular in *O. liaoxiensis* instead of anteroposteriorly elongated and narrow in *O. leios*. Few differences can be observed on the skull: in the Liaoning specimens, the skull is narrower; the pterygoid is wider, and the basisphenoid has a longer posterior part with the pair of pits more anteriorly located and the foramen basisphenoidale placed more posteriorly, within or near the pits. The bones surrounding the foramen palatinum posterius are variable; in GM V3001, the pterygoid takes part in its formation, while in GM V3000-4, it does not seem to do so. These differences justify the erection of the species *Ordosemys liaoxiensis*.

The cladistic analysis by Li and Liu (1999) led to consider *O. liaoxiensis* to be most closely related to *Dracochelys/Hangaichelys*, but this consideration is based on some mistaken characters (prefrontals meeting on the midline) of IVPP V11554. The plesiomorphic characters observed in *Ordosemys* (prefrontals not meeting on the midline, parietal/squamosal contact and incisura columellae auris open) are more primitive than those of Sinemydidae and support the basal position of *Ordosemys* among Centrocryptodira suggested by Brinkman and Wu (1999).

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