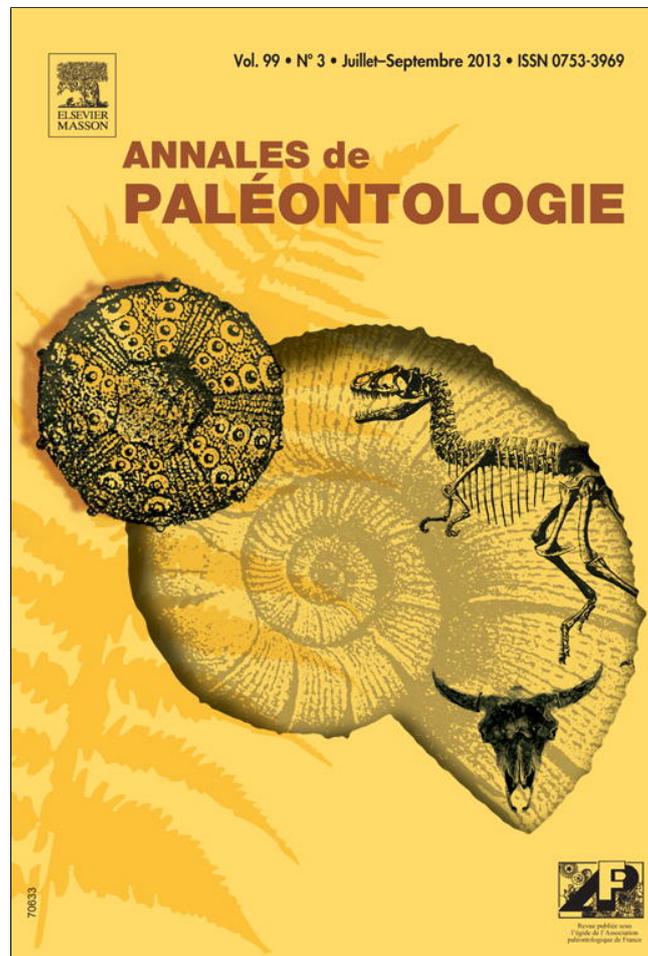


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Original article

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

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

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Abstract

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

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

Résumé

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

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carapace incomplète de la même localité est attribuée à Lindholmemydidae indet. *Glyptops* sp. provenant du Groupe de Wangshi, Jingangkou, Laiyang, Shandong est révisé et attribué à Lindholmemydidae.

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Mots clés : Testudines ; Lindholmemydidae ; Crétacé supérieur ; Province du Shandong ; Chine ; Systématique

1. Introduction

Lindholmemydidae Chkhikvazde in Shuvalov and Chkhikvazde, 1975 is a basal group of testudinoids known from the Cretaceous and Paleocene of Asia. Although their remains are abundant in some Late Cretaceous and Paleocene localities of Mongolia, the record of lindholmemydids in China is scarce (Sukhanov, 2000; Brinkman et al., 2008; Danilov and Sukhanov, 2013). Here we report on two specimens of Lindholmemydidae from the Late Cretaceous of Shandong, eastern China. The material is housed in Zhucheng Dinosaur Museum (ZCDM), Shandong, China. An isolated costal plate from the Late Cretaceous of Wangshi Group, Shandong, previously referred to *Glyptops* sp. (Chow, 1954) is revised and assigned to Lindholmemydidae.

The specimens ZCDM V0050 (field catalog number: KG-253) and ZCDM V0051 (field catalog number: KG-254) have been collected recently in the Upper Cretaceous Wangshi Group; Kugou locality, southeastern of Zhucheng City, in the eastern part of Shandong Province (Fig. 1 in Hone et al., 2011). Wangshi Group is divided, in ascending order, into Xingezhuang, Hongtuya and Jingangkou Formations. Abundant dinosaur remains discovered in the upper part of Xingezhuang Formation and lower part of the overlying Hongtuya Formation include hadrosaurid *Shandongosaurus*, the tyranosaurid theropod *Zhuchengtyranus magnus*, the ceratopsid *Sinoceratops zhuchengensis* and the leptoceratopsid *Zhuchengceratops inexpectus* (Xu et al., 2010a, 2010b; Hone et al., 2011). Turtle remains come from the fluvial conglomerates at the base of the Hongtuya Formation. Basalt within the upper part of Hongtuya Formation has been dated radiometrically to an age of 73.5 Ma (Campanian), which constrains the youngest age of the vertebrates bearing beds (Liu et al., 2010).

2. Systematic palaeontology

Order TESTUDINES Linnaeus, 1758

Suborder CRYPTODIRA Cope, 1868

Superfamily TESTUDINOIDEA Batsch, 1788

Family LINDHOLMEDYDIDAE Chkhikvazde in Shuvalov and Chkhikvazde, 1975

Genus *Shandongemys* n. gen.

Shandongemys dongwuica n. gen. and n. sp.

(Figs. 2 and 3)

Etymology. The genus name from Shandong Province; the species name from Dongwu, the ancient name of Zhucheng City where the specimen comes from.

Holotype. ZCDM V0050 (field catalog number: KG-253), a partial skeleton including incomplete skull, lower jaw, hyoid bones, incomplete shell with articulated carapace and plastron, disarticulated and incomplete fore and hind limbs. The relatively large size and absence of the

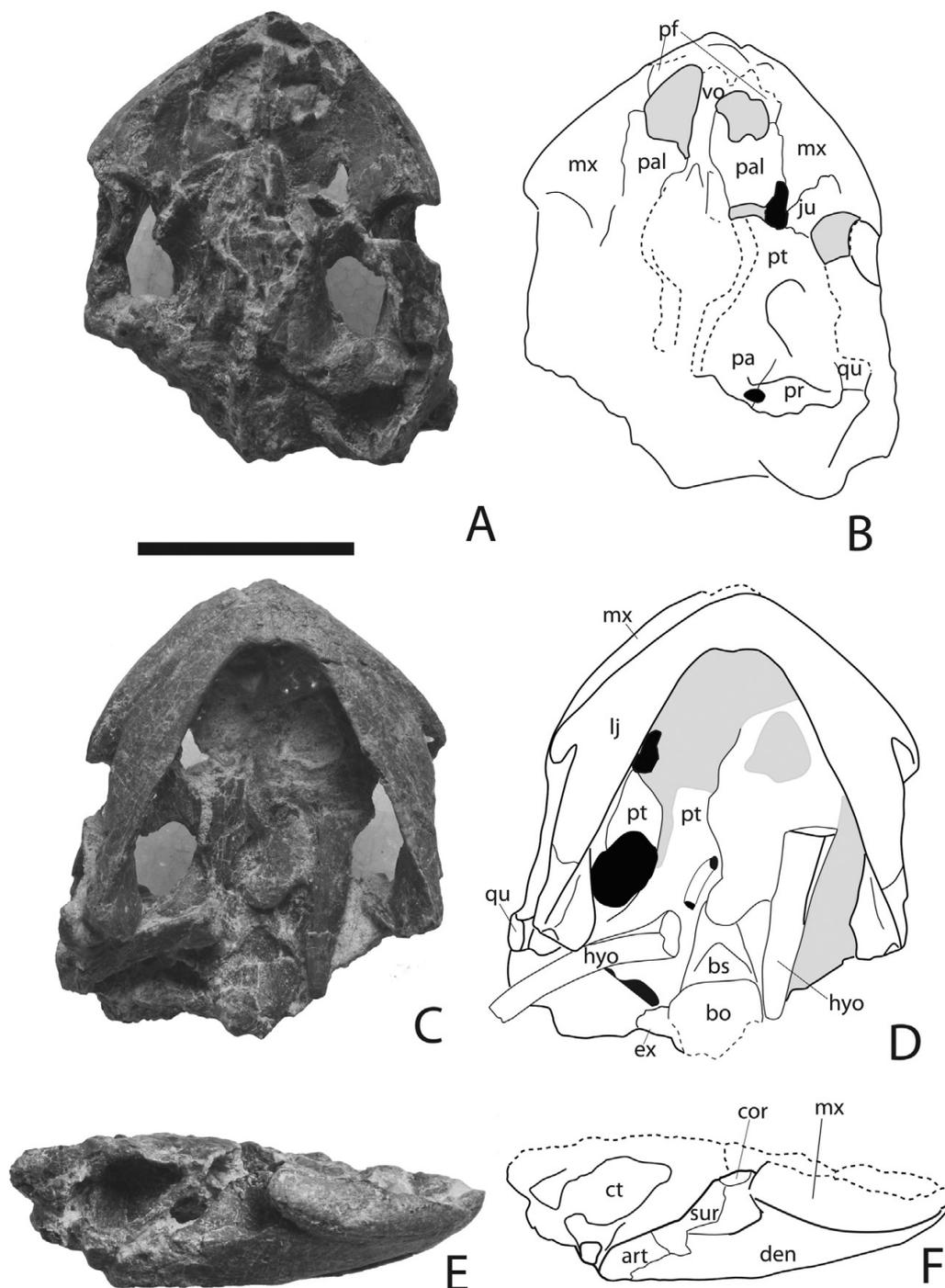


Fig. 1. *Shandongemys dongwuica* n. g. n. sp. from the Late Cretaceous of Kugou, Zhucheng, Shandong Province, China. Holotype (ZCDM V0050), skull in dorsal (A, B), ventral (C, D) and right lateral (E, F) views. Scale bar = 2 cm. art: articular; bo: basioccipital; bs: basisphenoid; cor: coronoid; ct: cavum tympani; den: dentary; ex: exoccipital; hyo: hyoid; ju: jugal; lj: lower jaw; mx: maxilla; pa: parietal; pal: palatine; pf: prefrontal; pr: prootic; pt: pterygoid; qu: quadrate; sur: surangular.

Shandongemys dongwuica n. g. n. sp. du Crétacé supérieur de Kugou, Zhucheng, province de Shandong, Chine. Holotype (ZCDM V0050), crâne en vues dorsale (A, B), ventrale (C, D) et latérale droite (E, F). Barre d'échelle = 2 cm. art : articulaire ; bo : basioccipital ; bs : basisphénoïde ; cor : coronoïde ; ct : cavum tympani ; den : dentaire ; ex : exoccipital ; hyo : hyoïde ; ju : jugal ; lj : mâchoire inférieure ; mx : maxillaire ; pa : pariétal ; pal : palatin ; pf : préfrontal ; pr : prootique ; pt : ptérygoïde ; qu : carré ; sur : surangulaire.

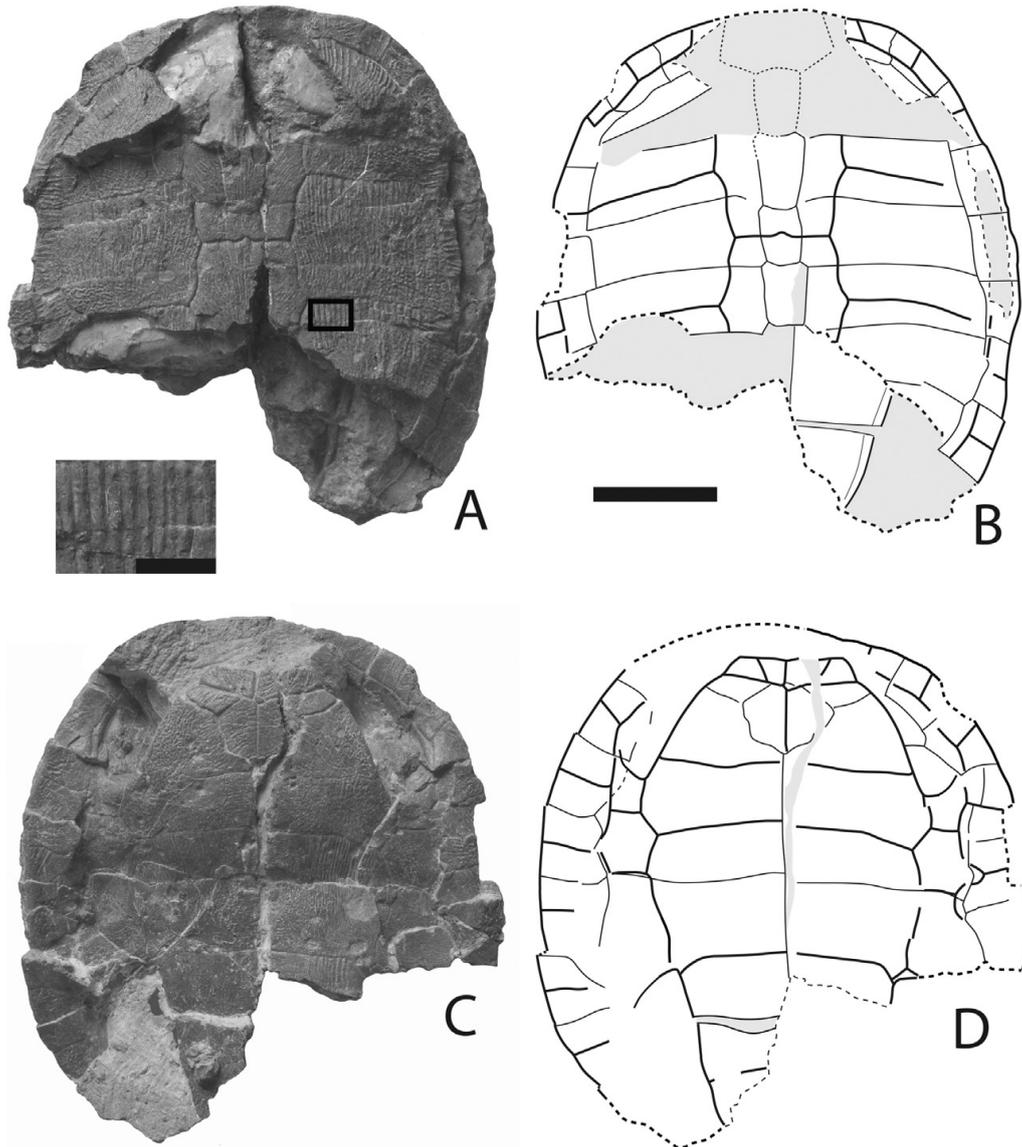


Fig. 2. *Shandongemys dongwuica* n. g. n. sp. from the Late Cretaceous of Kugou, Zhucheng, Shandong Province, China. Holotype (ZCDM V0050), shell in dorsal (A, B) and ventral (C, D) views and detail of ornamentation on carapace. Scale bar = 5 cm for A–D and 1 cm for ornamentation.

Shandongemys dongwuica n. g. n. sp. du Crétacé supérieur de Kugou, Zhucheng, province de Shandong, Chine. Holotype (ZCDM V0050), carapace en vues dorsale (A, B) et ventrale (C, D) et détails de l'ornementation. Barre d'échelle = 5 cm pour A–D et 1 cm pour l'ornementation.

fontanelles on the carapace and plastron indicate that the specimen belongs to an adult or sub-adult individual.

Type locality and horizon. Kugou, Zhucheng City, Shandong Province, China; Hongtuya Formation, Wangshi Group, Late Cretaceous.

Diagnosis. A genus of Lindholmemydidae, carapace low with a length of about 225 mm; similar to *Mongolemys*, but different from all other Lindholmemydidae in the presence of three wide inframarginals that are almost entirely included in the plastron; different from *Mongolemys* in the wider shell, carapace surface covered by strong ornamentation consisting of coarse parallel ridges and tubercles, vertebral 1/marginal 2 contact absent, wider plastron, shorter anterior lobe with a

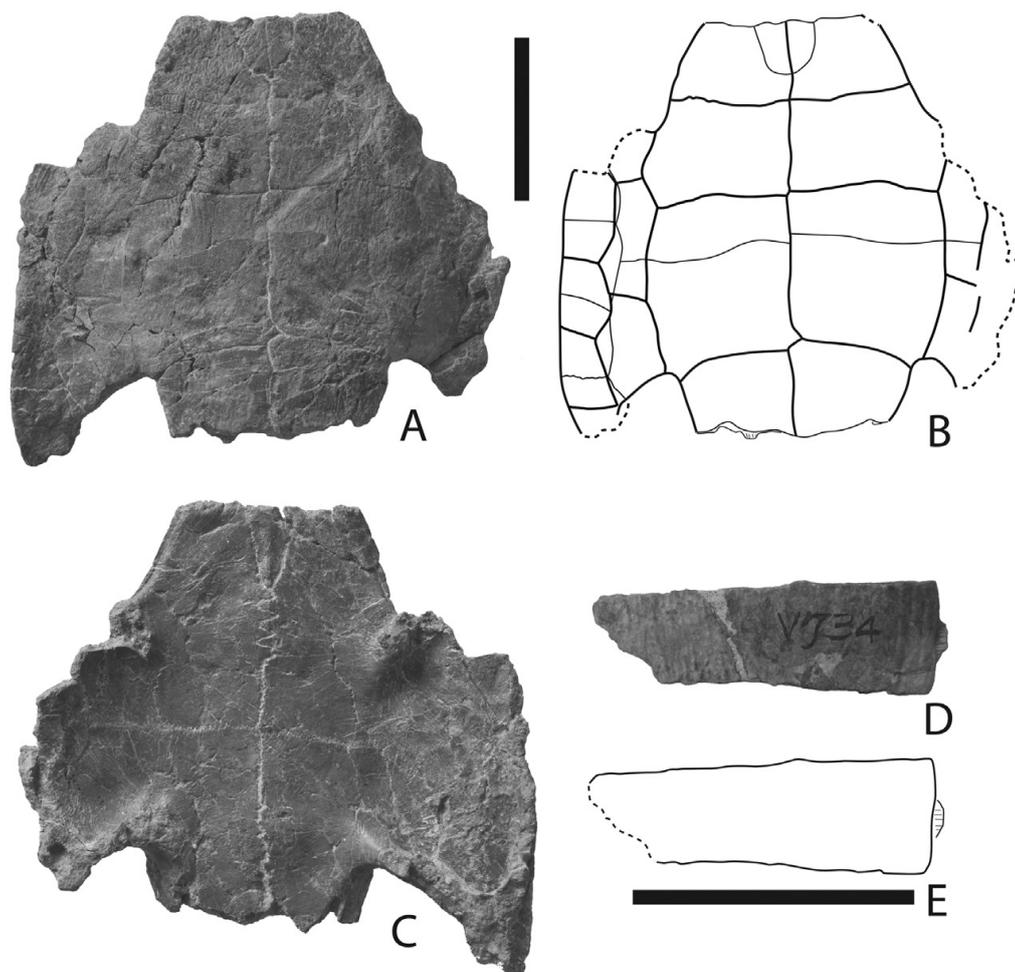


Fig. 3. Lindholmemydidae indet. from the Late Cretaceous of Shandong Province, China. Incomplete plastron and right bridge peripherals 4–7 (ZCDM V0051) from Kugou, Zhucheng in ventral (A, B) and dorsal (C) views. Isolated costal 3 from Jingankou, Laiyang in dorsal view (D, E). Scale bar = 5 cm (vertical scale bar for A–C and horizontal scale bar for D, E).

Lindholmemydidae indet. du Crétacé supérieur de la province de Shandong, Chine. Plastron incomplet et plaques périphériques droites 4–7 (ZCDM V0051) de Kugou, Zhucheng en vues ventrale (A, B) et dorsale (C). Costale 3 isolée de Jingankou, Laiyang en vue dorsale (D, E). Barre d'échelle = 5 cm (barres verticale pour A–C et horizontale pour D, E).

wide base, posterior lobe with backward convergent lateral margins, wider than long entoplastron and humeropectoral sulcus located close to the base of the anterior lobe.

Measurements (Table 1).

Description.

Skull: the skull is crushed dorsoventrally, lacking the skull roof (Fig. 1). The lower jaw is attached to the skull. Although deformed, the skull is likely low in origin. It has an oval outline and broad as in *Mongolemys* sp. (Sukhanov, 2000, Fig. 17.30). The skull length represents about one fifth of the carapace length. The temporal emargination is damaged, its extension is unknown. The check emargination, preserved on the right side, is relatively high with its upper edge above the lower margin of the orbit.

A fragment of ventral portion of the prefrontal is preserved between the vomer and the maxilla. It forms the anterior margin of the large foramen orbito-nasale and contacts the maxilla laterally. The descending process of the parietal is preserved on both sides, forming the lateral wall of the

Table 1

Measurements of lindholmemydids from the Late Cretaceous of Kugou, Zhucheng, Shandong Province, China (in mm).
Dimensions des lindholmémydides du Crétacé supérieur de Kugou, Zhucheng, province de Shandong, Chine (en mm).

<i>Shandongemys dongwuica</i> n. g. n. sp. (ZCDM V0050, holotype)	
Skull (length from the tip of the snout to occipital condyle/width)	
Preserved	(44)/36
Estimated	47/36
Carapace (length/width)	
Preserved	(200)/195
Estimated	225/195
Plastron (length/width)	180 × 146
Bridge length	73 (right), 71 (left)
Anterior lobe (length/width at the base)	50/102
Posterior lobe (length/width at the base)	61/83
<i>Lindholmemydidae</i> indet. (ZCDM V0051)	
Plastron (length/width, preserved)	(131)/117
Bridge length	78
Anterior lobe width at the base	91
Posterior lobe width at the base	78

braincase. As in *Mongolemys* sp., the parietal does not contribute to the processus trochlearis oticum. The medial process of the jugal is visible on the right side of the dorsal surface, posterior to the maxilla; it forms the anterior border of the fossa temporalis inferior. Both squamosals are absent.

Both premaxillae are preserved, but their ventral surface is hidden by the lower jaw and the dorsal surface is damaged. The maxilla is almost complete on both sides, but the ventral surface, including the triturating surface is not visible. The maxilla has a curved lateral surface. It forms the lower margin of the orbit and contacts the palatine medially, the prefrontal anteromedially and the jugal posteriorly on the dorsal surface. The vomer is an elongate element exposed dorsally between the palatines. The palatine is exposed only on dorsal surface. It forms the posterior margin of the foramen orbito-nasale and contacts the maxilla laterally and the vomer medially. There is also a short palatine/prefrontal contact preserved on the right side, lateral to the foramen orbito-nasale. The contact with the pterygoid posteriorly and the midline contact of the palatines are unclear because of the preservation. The foramen palatinum posterius is exposed on the right side with damaged margin and visible on dorsal and ventral views. It is an anteroposteriorly elongate large opening as in *Mongolemys* sp., surrounded by the maxilla, palatine and pterygoid in dorsal view.

The right quadrate is almost complete. The cavum tympani is triangular in lateral view and deep. There is a deep precolumellar fossa. The antrum postoticum is deep with the damaged bottom. If the incisura columellae auris is open or closed is unclear. The contact with the prootic medially is located lateral to the processus trochlearis oticum. The condylus mandibularis is wider than long with a concave facet. The right pterygoid is complete but crossed by a fissure, the left one is covered by a bone ventrally. In ventral view, the shape of the pterygoid agrees with that of *Mongolemys* sp., with a posteriorly directed processus pterygoideus externus. The pterygoid appears to have a long midline contact with its counterpart anterior to the basisphenoid, but the suture is covered by a bone. The right pterygoid/jugal contact is visible on the dorsal surface. On the ventral surface, the pterygoid contacts the quadrate posterolaterally, the basisphenoid posteromedially and the basioccipital posterior to the basisphenoid by a short suture. The canalis

caroticus internus is partly exposed ventrally as an open groove (sulcus caroticus internus), visible on the right pterygoid. The foramen posterius canalis carotici interni is located at the posterior edge of the pterygoid.

The incomplete right exoccipital is preserved. The basisphenoid is complete; its ventral surface is partly covered by a bone. In ventral view, the basisphenoid is an elongate triangle as in *Mongolemys* sp., separating the posterior portion of the pterygoids. It contacts the pterygoid anteriorly and the basioccipital posteriorly. A sharp ridge separates the basisphenoid into two parts, an anterior arrow shaped element and a posterior triangular part. The dorsal surface of the basisphenoid is exposed, but the structure and contacts are obscure. The basioccipital is incomplete, lacking the occipital condyle. It is a wider than long rectangle in ventral view with a concave ventral surface. It contacts the basisphenoid anteriorly, the exoccipital laterally and the pterygoid antero-laterally; the contact with the opisthotic is unclear. The prootic is better preserved on the right side. It forms the entire processus trochlearis oticum and contacts the parietal medially and the quadrate laterally. The processus trochlearis oticum is comparable in size to that of *Mongolemys* sp.

Lower jaw: the lower jaw is almost complete, with only the posterior end of the left ramus damaged (Fig. 1). It is relatively high, with a small symphyseal beak and fused symphysis. There is no retroarticular process, as in *Mongolemys* sp. The coronoid process, a little damaged on the left side and not exposed on the right, is low. A depression is present below the coronoid process for the M. adductor mandibulae externus pars superficialis (Gaffney, 1979). The triturating surface is not visible. The structure and contacts on the lingual surface of the lower jaw are obscure.

Hyoid bones: both right and left cornu brachial I are incompletely preserved, lacking the distal end (Fig. 1). It is a rod-like bone with a sub-rectangular cross-section on its proximal portion. The bone narrows distally, with a sub-rounded cross-section.

Shell: the shell is incomplete, lacking the posterior portion of both carapace and plastron (Fig. 2).

Surface ornamentation: the carapace and plastron are covered with strong ornamentation, consisting of raised ridges and tubercles. The ridges are thin and in a radiating pattern on the vertebral area (on neurals and the medial end of the costals). The coarse anteroposteriorly directed and parallel ridges cover the middle portion of the costals. The anterior half of the costal 2 and the lateral portion of other costals are covered with raised tubercles. On the lateral end of the costals and medial part of the peripherals, the parallel ridges are perpendicular to the suture. The random tubercles and ridges cover the lateral portion of the peripherals. On the plastron, the raised vermiculated tubercles cover the anterior lobe, the xiphiplastron and the medial part of the hyoplastron and hypoplastron. The anteroposteriorly directed parallel ridges are located medial to the inframarginals.

The carapace is low with an oval outline, smooth margin and without any keel. The width of the carapace is about 87% of its length. The nuchal is missing, but the front margin of the carapace is preserved as imprint, which shows that the anterior margin of the carapace is convex forward, without a cervical notch.

The nuchal is not preserved, but the outline is partly distinguishable on the imprint. It is trapezoid and wider than long. The neural 2–4 are preserved. The neural 1, preserved as imprint, is rectangular. The neural 2–4 are hexagonal with short anterolateral sides. As indicated by the medial margin of the costals 4, the neural 5 has also short anterolateral sides. The neural formula of the first five neurals is thus of $4 > 6 > 6 > 6 > 6$. The suprapyrgals and pygal are missing. The costal 1, damaged on both sides, is slightly longer than the costal 2. It contacts the peripheral 1 through 3. The complete costals 2–3 and the right costal 4; and incomplete left costal 4 and right

costal 5–6 are preserved. The costal 2–5 are similar in size and shape. The peripheral series is incompletely preserved on both sides. The peripheral 1 is wider than long, with a long contact with the costal 1. The peripheral 2 and 7–8 are all wider than long.

As preserved on the right side, the vertebral 1 does not contact the marginal 2, in contrast to *Mongolemys elegans* (Cadena et al., 2013). The vertebral 2–3 are roughly as long as wide. The pleural 2–3 are clearly wider than the corresponding vertebrae, with the interpleural sulci running posterolaterally. All preserved marginals are restricted in the peripherals. The marginals 1–2 and 7–8 are clearly shorter than the corresponding peripherals.

The plastron lacks part of the posterior lobe. It is sutured to the carapace. The slightly concave anterior rim of the plastron is located posterior to the anterior margin of the carapace. The anterior lobe is short and wide, which is shorter than the bridge; and its base is wider than that of the posterior lobe. The bridge is relatively short and narrow, with its minimal length representing 50% of plastron width. The posterior lobe has the straight lateral margins that are convergent backward. The axillary buttress is relatively strong, extending at least to half width of the costal 1. The contact of the inguinal buttress with the costal is not visible. The musk ducts are absent.

The epiplastron has a short contact with its counterpart, which represents about one third length of the entoplastron. The entoplastron is diamond-shaped and wider than long. The hyoplastron is shorter than the hypoplastron on the midline, but its contribution to the bridge is similar to the latter. The xiphiplastron is longer than wide.

There are one pair of gulars and one pair of intergulars, the latter overlapping slightly the entoplastron. The intergular/gular limit is marked as a light groove on the left side but as a fold on the right side. The humeropectoral sulcus is located slightly posterior to the entoplastron, and close to the base of the anterior lobe. The pectoral is short, with its length less than half of that of the abdominal. The femoroanal sulcus is located far posterior to the hypoplastron/xiphiplastron suture. There is a complete row of three large inframarginals which is almost entirely restricted in the bridge; only the lateral tip of the inframarginal 2 extends onto the peripheral 5. The inframarginals increase in size from the front to the back; inframarginal 3 being much larger than inframarginal 2. On the visceral surface, the skin-scutal sulci are located close to the margin of the posterior lobe.

Limb bones: the right radius is complete, with expanded distal end. The incomplete manus and pes are disarticulated. The metapods, phalanges and the claws are slender as in fresh water turtles.

Comparisons and discussion. ZCDM V0050 is a testudinoid because the plastral buttresses contact the costal plates (Gaffney and Meylan, 1988). It is assigned to Lindholmemydidae based on the continuous row of inframarginal scutes (Hirayama et al., 2000; Sukhanov, 2000). The presence of a pair of intergulars is unusual among Lindholmemydidae, since most members of the family lack intergulars. Although it can be considered as a primitive character, considering that the lateral limits of these scutes are different from other sulci on the shell, the presence of a pair of intergulars in ZCDM V0050 is likely an anomaly of development.

Lindholmemydidae is a paraphyletic group of basal Testudinoids from Asia (Danilov and Sukhanov, 2013). The family includes about a dozen species, ranging in age from the late Early Cretaceous to Paleocene (Sukhanov, 2000). The skull of lindholmemydids is poorly known due to very limited cranial material available. Khosatzky and Młynarski (1971) briefly described and illustrated a skull of *M. elegans* from the Late Cretaceous of Gobi Desert, Mongolia. Sukhanov (2000) provided the description and illustration of the skull of *Mongolemys* sp. from the Nemegt

Formation of Mongolia. Additional skull remains of *M. elegans* have been described recently (Cadena et al., 2013). Nessonov (1986) has reported an isolated skull of *Lindholmemyss elegans* from the type locality of the species (Dzharakhuduk, Central Kizylkum, Uzbekistan); but according to the recent review, this skull is referable to trionychoid Adocidae (Danilov and Parham, 2005). As preserved, the skull of ZCDM V0050 is comparable to that of *Mongolemys* sp. in general shape and proportion (Sukhanov, 2000). The skull is low and broad with a relatively large foramen palatinum posterius. The foramen posterius canalis carotici interni is located at the posterior end of the pterygoid and the internal carotid is partly exposed ventrally. The skull of ZCDM V0050 appears to be more primitive than that of *M. sp.* and *M. elegans* (Cadena et al., 2013) in the more exposed internal carotid, implying a longer sulcus caroticus internus on the ventral surface of the skull. In addition, the processus trochlearis oticum is almost entirely formed by prootic. In *M. sp.* and *M. elegans*, the internal carotid is more closed. The processus trochlearis oticum is formed by prootic and quadrate in *M. sp.*

Based on the shell morphology, Danilov et al. (2012) recognized a group among lindholmemydids which includes *Elkemys australis* (Ye, 1974) and *Hokouchelys chenshuensis* Ye, 1974 from the Paleocene of Guangdong, southern China and *Gravemys* spp. (*G. barsboldi* from the Late Cretaceous Nemegt Formation of Tansaltai Gobi, Mongolia and *G. hutchisoni* Danilov, 2003 from the Subashi Formation of Turfan, Xijiang, China) (Ye, 1974a, 1974b; Danilov, 2003; Brinkman et al., 2008; Danilov et al., 2012). This group is characterized by the presence of 4–5 wide inframarginals that extend strongly onto the peripherals, a large cervical notch, large anal notch and relatively narrow vertebral scutes 2–3.

Two additional groups are recognized here among the remaining members of Lindholmemydidae mainly on the basis of the inframarginal morphology. The first is composed of *L. elegans* Riabinin, 1935 from the Late Cretaceous of Bissekty Formation, Dzharakhuduk, Central Kizylkum, Uzbekistan; *Hongilemys* spp. (*H. kurzanovi* Sukhanov and Narmandakh, 2006 from the Barungoyot Formation of Mongolia and *H. martinsoni* Chkhikvadze, 1975 from the Bayn Shire Formation of Transaltai Gobi, Mongolia); '*Mongolemys*' *tatarinovi* Sukhanov and Narmandakh, 1976 (restricted to the holotype according to the recent work of Danilov and Sukhanov, 2013) from the Paleocene of Mongolia; '*M.*' *trufanensis* Ye, 1974 from the Paleocene of Shanshan, Xinjiang, China, *Amuremys planicostata* (Riabinin, 1930) from the Yuliangzi Formation, Amur River Region, *Tsaotanemys rugosus* Bohlin, 1953 from the Cretaceous of Jiayuguan, Gansu, China, *Paragravemys erratica* Sukhanov, Danilov and Narmandakh, 1999 from the Late Cretaceous Bayn Shire Formation of Mongolia and *Paramongolemys khosatzkyi* Danilov and Sukhanov, 2013 from the Late Paleocene of Mongolia (Riabinin, 1930, 1935; Bohlin, 1953; Ye, 1963, 1974b; Sukhanov and Narmandakh, 1976; Ye, 1994; Sukhanov et al., 1999; Sukhanov, 2000; Danilov and Sukhanov, 2001, 2013; Danilov et al., 2002; Brinkman et al., 2008). Following Danilov (pers. com., 16/10/2012), *Khodzhakulemys occidentalis* (Nessonov, 1984) from the mid-Cretaceous of Uzbekistan is considered here as a member of *Lindholmemyss* (Nessonov and Krassovskaya, 1984; Danilov, 1999). This group is characterized by the presence of three or four narrow inframarginals which are mostly restricted in the plastron, a small or absence of cervical notch, small anal notch and relatively wide vertebrals 2–3.

ZCDM V0050 and *M. elegans* Khosatzky and Młynarski, 1971 from the latest Cretaceous Nemegt Formation, Transaltai Gobi, Mongolia constitute the last group. This group is characterized by three wide inframarginals entirely or almost entirely included in the plastron, absence of a cervical notch, small anal notch (not preserved in ZCDM V0050), short bridge and relatively wide vertebrals 2–3 (Khosatzky and Młynarski, 1971; Sukhanov, 2000; Danilov et al., 2012; Cadena et al., 2013). ZCDM V0050 differs from *M. elegans* in the shell surface ornamentation,

the general shape of the carapace and plastron, and the proportion of different plastral elements. The carapace of ZCDM V0050 is wide, with the width represents 87% of its length; and it is not widened posteriorly. The shell of *M. elegans* is narrower and slightly widened posteriorly, with a width/length ratio about 75% (Danilov et al., 2012). ZCDM V0050 has the shell surface strongly sculptured, with coarse ridges and tubercles. The shell surface of *M. elegans* is almost smooth, bearing only a net of thin branching sulci, though some specimens have a well-developed sculpture consisting of small tubercles and crests, which are however much less pronounced than in ZCDM V0050 (Sukhanov, 2000; Danilov et al., 2012; Cadena et al., 2013). The sculptured specimens of *M. elegans* probably belong to a separate species (Sukhanov, 2000). The vertebral 1 in ZCDM V0050 does not contact the marginal 2; while this scute is wider in *M. elegans* which reaches the marginal 2. The plastron of ZCDM V0050 is wide, the anterior lobe is short with a wide base, and the posterior lobe has backward convergent lateral margins. In *M. elegans*, the plastron is narrow, the anterior lobe is long which is not much widened at the base, and the posterior lobe is narrow with nearly parallel lateral margins. In addition, ZCDM V0050 has a wider entoplastron, which is wider than long; and the humeropectoral sulcus is located posteriorly, close to the base of the anterior lobe. In *M. elegans*, the entoplastron is longer than wide or as long as wide; and the humeropectoral sulcus is located far anterior to the base of the anterior lobe.

The complete row of broad inframarginals of *M. elegans* and ZCDM V0050 that prevent the contact between the plastral scutes and marginal scutes are more primitive than the reduced inframarginals of *Pseudochrysemys gobiensis* Sukhanov and Narmandakh, 1976 from the Paleocene of Mongolia, in which the abdominal scutes contact the marginal scutes. In addition, although ZCDM V0050 shares with *P. gobiensis* absence of vertebral 1/marginal 2 contact and relatively broad vertebrales 2–3; it differs from the latter in the absence of a cervical notch, the slightly notched anterior rim of the plastron which is posterior to the anterior margin of the carapace, narrower posterior plastral lobe and gulars only slightly extending onto entoplastron. In *P. gobiensis*, there is a shallow cervical notch, the anterior rim of the plastron is straight and reaches the level of the anterior margin of the carapace, the posterior plastral lobe is wider and gular scutes extend deeply onto entoplastron (Sukhanov and Narmandakh, 1976; Danilov et al., 2012). The detailed comparisons between ZCDM V0050 and other lindholmemydids are summarized in Table 2. Based on these comparisons, ZCDM V0050 appears to be distinct from other known lindholmemydids; a new genus and species are erected: *Shandongemys dongwuica* n. g. n. sp.

Of the three groups of Lindholmemydidae, the *Elkemys/Gravemys/Hokouchelys* group is the geologically youngest, ranging in age from the latest Cretaceous (Maastrichtian) to Paleocene; and has a wide geographical distribution (Mongolia, North and South China). It is supposed to be a natural group and the members are considered as possible close relatives of geoemydids and testudinids since they share the apomorphic features such as a large anal notch and relatively narrow vertebral scutes 2–3; though the retention of four inframarginals in this group is considered as primitive (Danilov et al., 2012). The two other groups appear to be more primitive since they share some plesiomorphic features such as the relatively wide vertebral scutes and small anal notch. The group consisting of *Shandongemys* and *M. elegans* is known from the late Late Cretaceous (Campanian-Maastrichtian); while the *Lindholmemyd* group has a wider geological range and morphologically more heterogeneous. The inclusion of '*M. tatarinovi*' and '*M. trufanensis*' in the latter group is in agreement with the opinion of Sukhanov (2000), Danilov (2003) and Danilov and Sukhanov (2013) that these species should be excluded from the genus *Mongolemys*.

Lindholmemydidae indet.

Fig. 3

Table 2

Comparisons between *Shandongemys dongwuica* n. g. n. sp. and other lindholmemydid taxa.
Comparaisons entre Shandongemys dongwuica n. g. n. sp. et d'autres lindholmémydés.

Character/Taxon	<i>Shandongemys dongwuica</i>	<i>Mongolemys elegans</i>	<i>Elkemys australis</i>	<i>Gravemys barsboldi</i>	<i>Hokouchelys chenshuensis</i>
Carapace length	225 mm	250–350 mm	About 250 mm	280 mm	350 mm
Shell height	Low	Moderate	Moderate	Moderate	High
Carapace shape	Oval, not expanded posteriorly	Oval, expanded posteriorly	Oval, not expanded posteriorly	Oval, narrowed posteriorly	Oval, not expanded posteriorly
Carapace surface ornamentation	Present and strong, coarse ridges and tubercles	Smooth or with sculpturing of tubercles and ridges	Smooth	With sculpturing of tubercles and ridges	Smooth
Shell thickness	Thick	Thin	Thin	Moderate	Thick
Cervical notch	Absent	Absent	Large	Large	Large
Vertebral 1/marginal 2 contact	Absent	Present	Absent	Absent	Absent
Axillary buttresses	Moderate	Weak	Weak to moderate	Moderate to strong	Strong
Vertebral 3 shape	As wide as long	As wide as long	Longer than wide	Longer than wide	Longer than wide
Length of anterior lobe	About 27% of plastron length	About 30% of plastron length	About 25% of plastron length	About 22–24% of plastron length	About 20% of plastron length
Shape of anterior lobe	Short and wide	Relatively long and narrow	Short and wide	Short and wide	Short and wide
Bridge length (minimal length of bridge/plastron width)	Short (50%)	Short (50–57%)	Long (60–70%)	Long (60–72%)	Long (about 73%)

Table 2 (Continued)

Character/Taxon	<i>Shandongemys dongwuica</i>	<i>Mongolemys elegans</i>	<i>Elkemys australis</i>	<i>Gravemys barsboldi</i>	<i>Hokouchelys chenshuensis</i>
Contribution of hyoplastron and hypoplastron to the minimal length of bridge	Approximately equal	Approximately equal	Greater in hyoplastron	Greater in hyoplastron	Greater in hyoplastron
Shape of posterior lobe	Relatively wide at the base with straight backward convergent margins	Narrow at the base with straight nearly parallel lateral margins	Wide at the base with convex lateral margins in femoral	Wide at the base with straight backward convergent lateral margins	Relatively wide at the base with lateral margins slightly convergent backward
Anal notch	Shallow?	Shallow	Large	Large	Large
Entoplastron	Wider than long	Longer than wide or as wide as long	Wider than long	Wider than long	Wider than long
Humeropectoral sulcus	Anterior to the base of anterior lobe	Far anterior to the base of anterior lobe	Anterior to the base of anterior lobe	At the base of anterior lobe	Anterior to the base of anterior lobe
Pectoral overlapping entoplastron	No	No	Yes	No	No
Inframarginals (number)	Wide (3)	Wide (3)	Wide (4–5)	Wide (4)	Wide (4)
Inframarginals extending onto peripherals	No	No	Yes, strongly	Yes, strongly	Yes, strongly
Character/Taxon	<i>Lindholmemyx elegans</i>	<i>Amuremys planicostata</i>	<i>Tsaotanyx rugosus</i>	<i>Hongilemys kurzanovi</i>	<i>Paramongolemys khosatzkyi</i>
Carapace length	250 mm	200–300 mm	About 130 mm	250 mm	290 mm
Shell height	High	?	High	Moderate	Moderate
Carapace shape	Oval, expanded posteriorly	Oval	Oval, not expanded posteriorly	Oval	Oval, expanded posteriorly

Table 2 (Continued)

Character/Taxon	<i>Lindholmemyx elegans</i>	<i>Amuremys planicostata</i>	<i>Tsaotanemyx rugosus</i>	<i>Hongilemys kurzanovi</i>	<i>Paramongolemys khosatzkyi</i>
Carapace surface ornamentation	Smooth or with sculpturing of tubercles and ridges	Pronounced tubercles and ridges	Parallel ridges or small warts arranged into rows or fused to small irregular branching ridges	Smooth?	Smooth
Shell thickness	Thick or thin	Thick	Thick	Thick	?
Cervical notch	Weak	Weak	Weak	Weak	
Vertebral 1/marginal 2 contact	Absent	Absent	Present	Absent	Present
Axillary buttresses	Strong	Moderate	?	?	Weak
Vertebral 3 shape	As wide as long	As wide as long	As wide as long	As wide as long	Longer than wide
Length of anterior lobe	About 25% of plastron length	?	About 20% of plastron length	?	About 26% of plastron length
Shape of anterior lobe	Short and wide	?	Short and wide	Relatively long and wide	Relatively long and narrow
Bridge length (minimal length of bridge/plastron width)	Long (about 65%)	?	Short (about 53%)	Long (about 65%)	Moderate (57%)
Contribution of hypoplastron and hypoplastron to the minimal length of bridge	Approximately equal	?	Approximately equal	Approximately equal	Approximately equal
Shape of posterior lobe	Relatively wide at the base with convex margins in femoral	?	Relatively wide at the base with slightly convex lateral margins convergent backward	Relatively wide at the base with lateral margins convergent backward	Relatively wide at the base with straight backward convergent margins
Anal notch	Shallow	?	Large	?	Shallow

Table 2 (Continued)

Character/Taxon	<i>Lindholmemyx elegans</i>	<i>Amuremyx planicostata</i>	<i>Tsaotanemyx rugosus</i>	<i>Hongilemyx kurzanovi</i>	<i>Paramongolemyx khosatzkyi</i>
Entoplastron	Longer than wide or wider than long	As wide as long	As wide as long	As wide as long	Slightly longer than wide
Humeropectoral sulcus	Close to the base of anterior lobe	Far anterior to the base of anterior lobe	Posterior to the base of anterior lobe	Far anterior to the base of anterior lobe	Anterior to the base of anterior lobe
Pectoral overlapping entoplastron	No	No	No	No	No
Inframarginals (number)	Narrow (3)	Narrow (?)	Narrow (4)	Narrow (3)	Narrow (3)
Inframarginals extending onto peripherals	Yes, slightly	No	No?	Yes, slightly	No

Referred material. ZCDM V0051 (field catalog number: KG-254), right bridge peripherals 4–7 articulated with an incomplete plastron which lacks the epiplastra and xiphiplastra; Kugou, Zhucheng City, Shandong Province, China; Hongtuya Formation, Wangshi Group, Late Cretaceous; IVPP V734, an isolated costal 3 from Jinshankou, Laiyang, Shandong Province, Wangshi Group, Late Cretaceous.

ZCDM V0051 (Fig. 3A–C; Table 1).

Description. The size of ZCDM V0051 is slightly smaller than that of ZCDM V0050. The lateral margins of the peripherals are divergent backward, indicating that the shell is expanded posteriorly. The dorsal and ventral sheets of the peripherals form a wide angle of about 80°, which would indicate, if the specimen is not deformed, that this turtle has a rather high domed shell.

The surface of the plastron is worn, but some anteroposteriorly directed parallel ridges are visible. The plastron is thick; the thickness at the posterior margin close to the midline is of 8 mm. The axillary and inguinal buttresses, though incomplete, are strong. The inguinal notch is wider than the axillary notch. The entoplastron is narrow and longer than wide in ventral view. In visceral view, this plate bears a long posterior process. The epi-hyoplastral suture is transverse. The hyoplastron and hypoplastron have the similar bridge length. On the visceral surface, the skin-scutel sulci are located close to the margin of the plastron.

The humeropectoral sulcus is straight and located anterior to the axillary notch. The pectoral scute is relatively long, with its length representing more than half length of the abdominal scute. There are three inframarginals, they are narrow and extend slightly onto the peripherals.

Comparisons and discussion. ZCDM V0051 is a lindholmemydid, based on the strong axillary and inguinal buttresses and presence of a complete row of inframarginals. It differs from *S. dongwuica* from the same locality in the high domed shell which is expanded posteriorly; the entoplastron that is longer than wide, a longer pectoral scute and narrower inframarginal scutes. ZCDM V0051 is reminiscent of *L. elegans* and *Hongilemys kurzanovi* in having three narrow inframarginals that extend slightly onto the peripherals, relatively long pectoral scute and relatively high domed shell. More complete material is needed for a precise systematic assignment.

IVPP V734 (Fig. 3D–E)

Description. The plate is an isolated costal 3 with the medial end damaged. It measures 5.7 cm in width, 2 cm in length at the lateral end and 0.4 cm thick. The shell surface, although worn, is covered with clear ornamentation consisting of low anteroposteriorly directed ridges on the lateral portion and rows of isolated or coalesced pustules on the medial part. The plate is slightly convex dorsally and expanded laterally. The anterior and posterior suture margins are intact. The lateral border is smooth with a free rib end, showing the presence of a carapacial fontanelle. The outer surface of the plate is devoid of any sulci, indicating that vertebral scutes are narrow. On the inner surface, the light rib swelling becomes more prominent laterally.

Comparisons and discussion. IVPP C734 was originally described as a right costal 4 and tentatively assigned to paracryptidiran? *Glyptops* sp., based on the general morphology of the plate, size and the ornamentation (Chow, 1954). This specimen is referred here to Lindholmemydidae on the basis of the ornamentation pattern of the shell surface which is reminiscent of that of some members of that family, but distinct from vermiculated ridges of *Glyptops* and large celled pattern of nanhsiungchelyids. However, the ornamentation in IVPP V734 is somewhat different from that of *S. dongwuica*. It belongs to a juvenile because of the presence of the carapacial fontanelle.

Disclosure of interest

The authors have not supplied their declaration of conflict of interest.

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