Zootaxa 2534: 57–66 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A second specimen of *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 (Testudines: Eucryptodira) from the Early Cretaceous Yixian Formation of western Liaoning, China

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Abstract

Within the Early Cretaceous Jehol Biota of China, the turtle *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 was one of the first discovered tetrapod fossils, but no additional information on this enigmatic taxon has become available during the past half century since its discovery. Here, a new turtle skeleton from the Yixian Formation of western Liaoning Province is identified as referable to *M. manchoukuoensis* on the basis of an elongate oval shell, long and narrow second to fourth vertebral scutes, and two suprapygals, of which the second is much larger than the first. This specimen therefore represents the second specimen of *M. manchoukuoensis*, the holotype of which was probably lost during World War II. This discovery not only provides essential material that allows the validity of *M. manchoukuoensis* to be tested, but also substantially expands understanding of its bony anatomy, especially with regard to cranial morphology. Among other features, *M. manchoukuoensis* is characterized by a postorbital that does not contact the quadrate/squamosal and a deep temporal emargination, which support a close relationship with *Sinemys* spp. and distinguish it from the co-existing *Ordosemys liaoxiensis*. A cladistic analysis that includes *M. manchoukuoensis* further supports the hypothesis that Sinemydidae is a monophyletic group that includes *Sinemys* spp. and *Dracochelys bicuspis*.

Key words: Eucryptodira, Sinemydidae, *Manchurochelys manchoukuoensis*, Yixian Formation, western Liaoning, Jehol Biota

Introduction

Within the Early Cretaceous Jehol Biota of China, the turtle *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 was one of the first tetrapod fossils to be discovered, together with the choristodere *Manchurosuchus splendens* and the lizard *Yabeinosaurus tenuis*. Unfortunately, the type specimen of *M. manchoukuoensis* (a partial shell with a partial pelvic girdle and hindlimbs, collected from the Yixian Formation of Tsotzushan, Yixian, western Liaoning Province) was probably lost during World War II, together with many other valuable fossils including the type specimens of *M. splendens* and *Y. tenuis* (e.g. Ji 1995; Gao *et al*. 2000; Liu 2003). During the last two decades a great number of turtle fossils have been recovered from the Jehol Biota, and an additional species of *Manchurochelys* was erected: *M. liaoxiensis* Ji, 1995, from the Yixian Formation of western Liaoning. Since then, all additional turtle fossils from the Yixian Formation of western Liaoning have been assigned to *M. liaoxiensis* (e.g. Li & Liu 1999; Liu 2003; Tong *et al*. 2004), but that species has been referred to the genus *Ordosemys*, resulting in the combination *Ordosemys liaoxiensis*. Consequently, no new information on *M. manchoukuoensis* has become available over the course of the last half century.

A new turtle skeleton collected from the Yixian Formation of western Liaoning shows several characters, such as a shell that is longer than wide, and second to fourth vertebral scutes that are long and narrow. These characteristics are clearly distinct from the co-existing *Ordosemys liaoxiensis* but match those reported by Endo & Shikama (1942) in the original description of *Manchurochelys manchoukuoensis*. The new fossil is

Accepted by R. Butler: 25 Jun. 2010; published: 13 Jul. 2010

therefore identified as *M. manchoukuoensis*. As the second specimen of this taxon, it provides new insights into its osteology and its phylogenetic relationships among basal eucryptodiran turtles.

Material and methods

The new specimen, LPM-R00008, is housed at the Paleontological Museum of Liaoning (also referred to as Liaoning Paleontological Museum), Shenyang Normal University (Shenyang, Liaoning Province). The phylogenetic relationships of *Manchurochelys manchoukuoensis* with other eucryptodirans was analyzed by adding it to the data matrix of Vandermark *et al*. (2009), which in turn is based on the data matrix of Parham & Hutchison (2003). The final matrix consisted of 43 characters scored for 20 taxa, and was analyzed with PAUP* 4.0 beta 10 (Swofford 2002) using the branch-and-bound search option and ACCTRAN character state optimization. All characters were given equal weighting and multistate characters were treated as unordered.

Systematic Paleontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Eucryptodira Gaffney, 1975

Sinemydidae Ye, 1963

***Manchurochelys manchoukuoensis* Endo & Shikama, 1942**
(Figs 1–4)

Holotype: Registration No. 3898 (former Central National Museum of Manchoukuo) from Tsaotzushan, approximately 21km southwest of Yixian, western Liaoning, China. The whereabouts of the holotype are currently unknown, and it was probably lost during World War II.

Referred specimen: LPM-R00008 (Figs 1–4), an incomplete skeleton including the skull, shell, isolated cervicals, articulated caudal series, partial left forelimb, and the hind limbs. The specimen is from close to the type locality in Yixian County, western Liaoning (41° 32.142´ N; 121°01.614´E).

Type locality and horizon: Tsaotzushan, approximately 21km southwest of Yixian, western Liaoning Province; Jingangshan beds of the Early Cretaceous Yixian Formation (Barremian-Early Aptian: Chang et al. 2009).

Revised diagnosis: A sinemydid turtle that is distinguished from *Sinemys lens* and *S. gamera* in having reduced frontals that are nearly excluded from the orbit, a cervical scute, a pygal, and eight neurals, and lacking a seventh peripheral process or spine. Distinguished from *Dracochelys bicuspis* by having separated prefrontals, a shallow nuchal emargination, a cervical scute, eight neurals, and a closed central plastral fontanelle.

Description. Skull. The skull is compressed dorsoventrally as a result of post-mortem crushing (Figs 1–3). The snout is poorly preserved, while the postorbital part of the skull is well preserved and in articulation. Dorsally, the skull has a length of 41 mm from the tip of the frontal to the posterior end of the crista supraoccipitalis and a width of 32 mm across the quadrates. The upper temporal emargination is well developed, resulting in complete exposure in dorsal view of the 'processus trochlearis oticum'. This differs from the condition in the co-existing *Ordosemys liaoxiensis*, in which the temporal emargination is much shallower (Tong *et al*. 2004). The crista supraoccipitalis is strongly elongated posteriorly beyond the main body of the occiput. The postorbital appears to be isolated from the quadrate/squamosal, similar to the

condition in *Sinemys lens* and *S. gamera*, but differing from the contact seen in *O. liaoxiensis*. Ventrally, the skull is partially exposed with the palatoquadrate and braincase floor visible (Fig. 3C, D). Near the anterior portion of the basisphenoid, a small foramen is present in the ptergoid, possibly representing the foramen basisphenoidale (= foramen carotico-pharyngeale), as in *Judithemys sukhanovi* (Parham & Hutchison 2003). In the posterolateral corner of the basisphenoid, there is a small opening for the foramen posterior canalis caroticus internus, which is partially enclosed by the pterygoid.

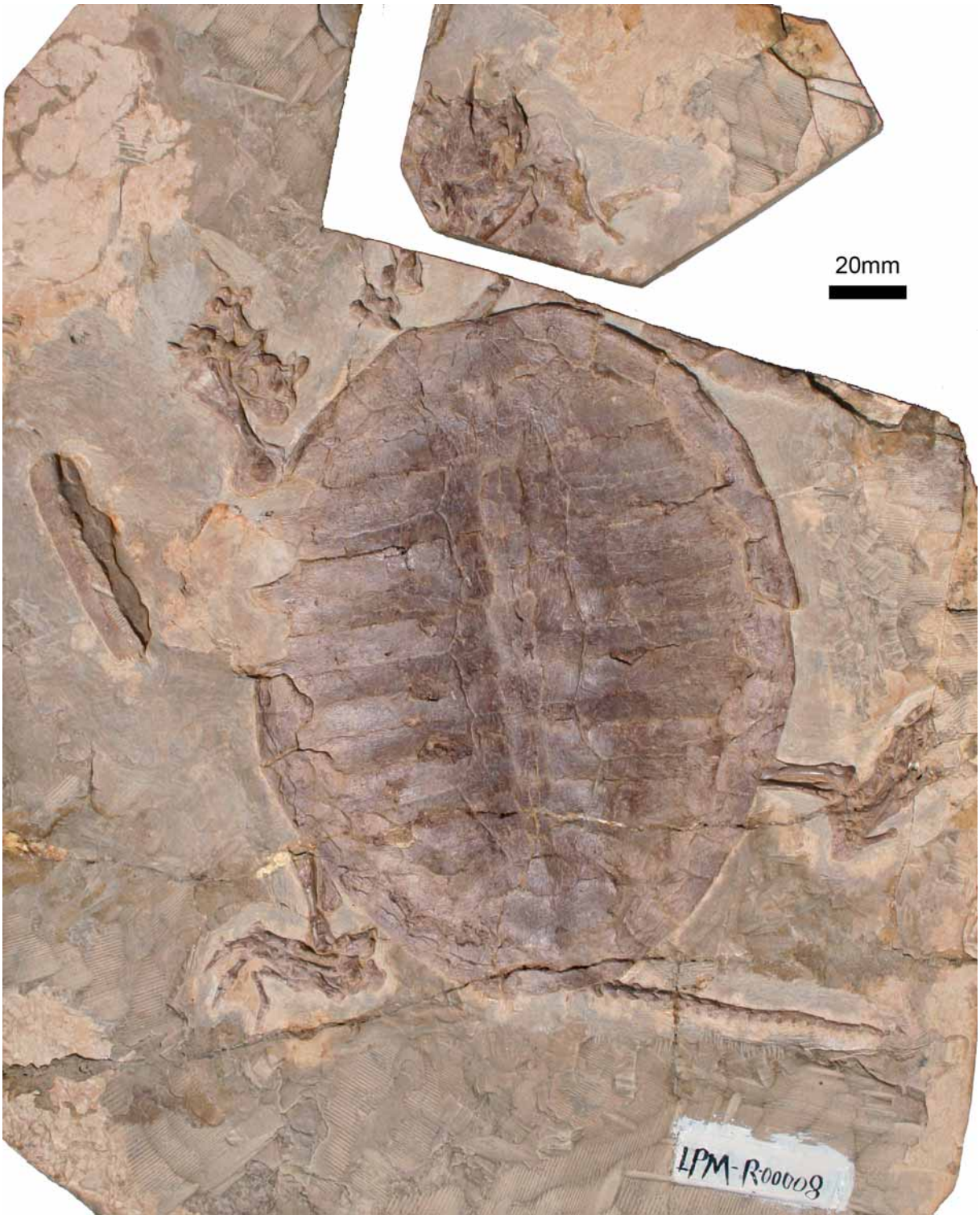

FIGURE 1. *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 (LPM-R00008), from the Early Cretaceous Yixian Formation of western Liaoning, China.

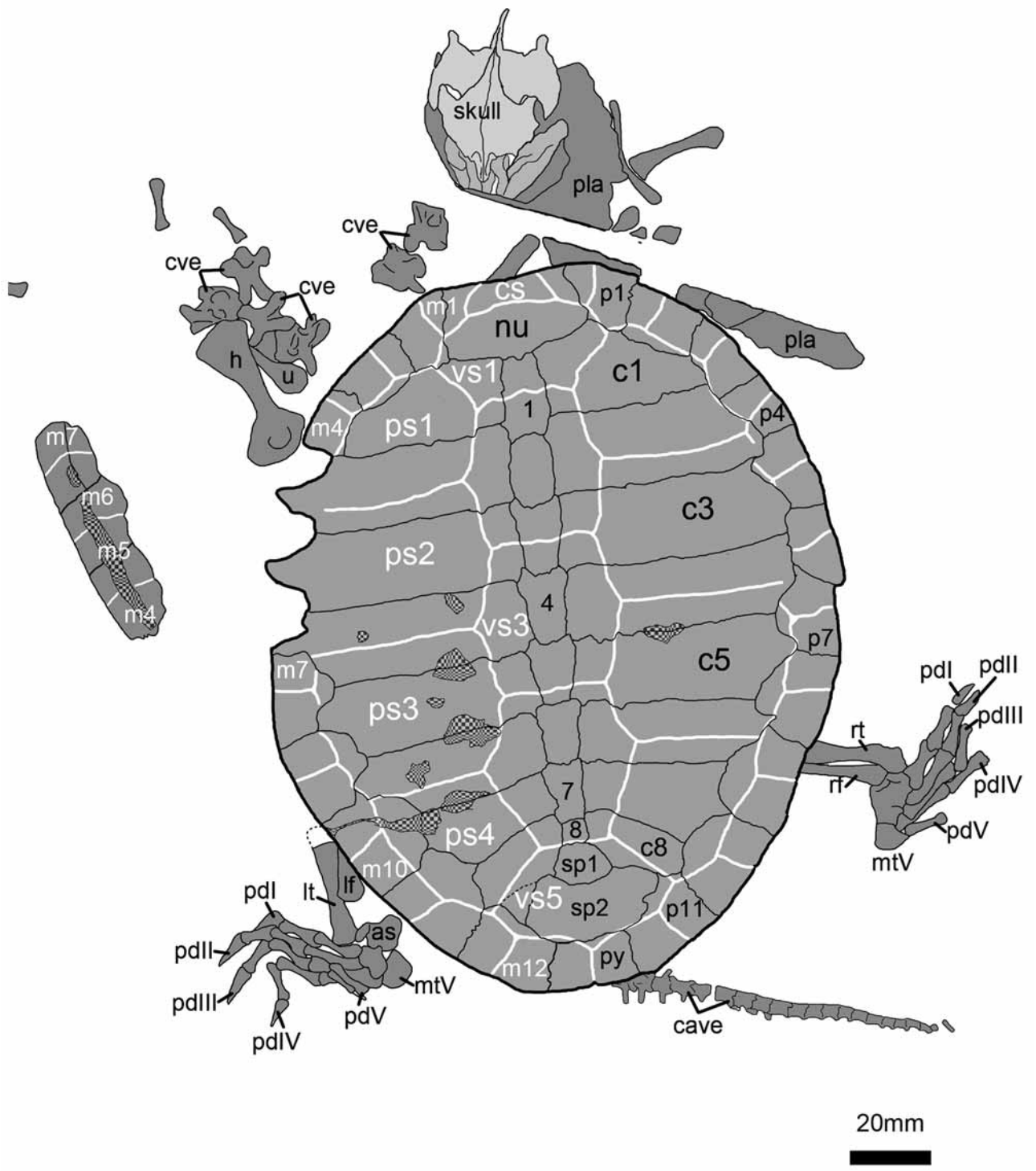

FIGURE 2. Line drawings of *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 (LPM-R00008), from the Early Cretaceous Yixian Formation of western Liaoning, China. Abbreviations: as, astragalocalcaneum; c1-c8, costal plates 1–8; cave, caudal vertebrae; cs, cervical scute; cve, cervical vertebrae; h, humerus; lf, left fibula; lt, left tibia; m1-m12, marginal scutes 1–12; mtV, metatarsal V; nu, nuchal; p1-p11, peripheral plates 1–11; pla, plastron; pdI-pdV, pedal digits I–V; ps1-ps4, pleural scutes 1–4; py, pygal; rf, right fibula; rt, right tibia; sp1-sp2, suprapygals 1–2; u, ulna; vs1-vs5, vertebral scutes 1–5; 1-8, neural plates 1–8.

The anterior end of the snout is damaged. A pair of premaxillae is partially exposed in palatal view. The maxilla medially contacts the palatine. An isolated element possibly represents a small nasal. The prefrontals are missing, but the articular facets on the frontals indicate that the prefrontals were completely separated

along the midline. The frontals are about 11 mm long, and firmly contact one another along the dorsal midline. Posteriorly, the frontals contact the parietals along an anteriorly concave suture. The parietal is sub-triangular, and represents the largest element of the skull roof. Posteriorly, the parietal forms a notable crest that is confluent with the crista supraoccipitalis. Laterally, the postorbital is well developed, and together with the prefrontal strongly limits the contribution of the frontal to the orbital rim. Posteriorly, the postorbital is separated from the squamosal, as in *Sinemys* spp. A crescentic element is well preserved at the anterior corner of the quadrate, and is interpreted as a possible quadratojugal. Together with the prootic and the possible quadratojugal, the quadrate forms medially the 'processus trochlearis oticum', a thickening of the anterior wall of the otic capsule. Laterally, the quadrate is constricted to form the cavum typmpani and encloses completely the incisura columellae auris. The squamosal bears posteriorly a rounded crest that is curved laterally towards its end. The supraoccipital forms an elongate supraoccipital crest. The prootic, opisthotic, supraoccipital and exoccipital are dorsally well exposed within the upper temporal fossa (Fig. 3A,B). A large foramen is situated between the prootic and the quadrate for the dorsal exit of the canalis stapedio-temporalis.

The palatoquadrate elements are exposed in ventral view. The quadrate forms the anterolateral wall of the middle ear, the condylus mandibularis, and the cavum tympani. The anterior portion of the large pterygoid firmly contacts the opposing pterygoid along the midline but the posterior portion is separated from the opposing element by the basisphenoid. Near the rostral tip of the basisphenoid, a cleft-like opening is present on the pterygoid-basisphenoid suture that is interpreted here as the foramen caroticum laterale, as in *Dracochelys bicuspis*. On each side, small foramina penetrate the pterygoid, possibly representing the foramen basisphenoidale (= foramen carotico-pharyngeale), as in *Judithemys sukhanovi* (Parham & Hutchison 2003). As in other eucryptodirans, the pterygoid forms posteriorly the floor of the middle ear, and more laterally contacts the quadrate.

The braincase is well exposed in ventral view, except for where it is partially overlapped by the hyoid on the left side. The basisphenoid is triangular and as long as wide, in contrast to the elongated basisphenoid of *Sinemys gamera* (Brinkman & Peng 1993a). A pair of blind pits is present on the middle portion of the basisphenoid. Posteriorly, the basisphenoid has a nearly straight suture with the basioccipital. More laterally, there is a small opening, the foramen posterior canalis caroticus internus, which is enclosed by the pterygoid and basisphenoid. As in *Dracochelys bicuspis*, *Sinemys* spp., and *Ordosemys* spp., the canal seems not to be completely enclosed between the foramen posterior canalis caroticus internus and the foramen basisphenoidal. The basioccipital is a massive element and forms the occipital condyle posteriorly.

Shell: The elongate oval shell of *Manchurochelys manchoukuoensis* (LPM-R00008) is well exposed in dorsal view (Figs 1–2), with a length of 170 mm and a width of 140 mm, slightly larger than the holotype, which has a width of 125 mm. The carapace is low and slightly sculptured by small and numerous pits and grooves. A shallow midline depression is present along the neural region on the carapace, as in *Ordosemys liaoxiensis*. Costal-peripheral fenestrae are absent, as in the holotype specimen.

The cervical scute is small and trapezoid. Its maximum width of 22 mm is approximately 3.7 times its minimum length of 6 mm. The vertebral scutes are sub-hexagonal and oriented along the midline of the shell. The first and fifth scutes are distinctly wider than long, while the second to fourth scutes are much longer than wide. This differs from the co-existing *Ordosemys liaoxiensis*, in which the vertebral scutes are much wider than long (Ji 1995; Li & Liu 1999; Tong *et al*. 2004).

Twelve pairs of marginal scutes are present. The first pair is small and subtriangular and the second is enlarged and strongly convex medially. By contrast, the remaining peripherals are subrectangular and slightly elongated posteriorly along the shell margin. The last pair of peripherals meet one another along the midline, and are the largest in size with a marginal length of 25 mm. In contrast, the last pair of peripherals is strongly reduced in the holotype of *M. manchoukuoensis*.

The nuchal plate is large and rectangular, covered dorsally by the cervical scute, the first marginal scute, and the first vertebral scute. There are eight neural plates present along the midline. They are slender and long and have an irregular, sub-rectangular shape. The eighth neural is greatly reduced, less than half of the size of the other neurals. The suture of the eighth neural and the first suprapygal is almost overlapped by the fourth intervertebral sulcus. Two suprapygals are present. The first suprapygal is much smaller than the second one,

as in *Sinemys lens*, but different from *Ordosemys* spp., in which two suprapygals are comparable to each other in size (Brinkman & Peng 1993b; Tong *et al*. 2004). The pygal is rectangular. Eleven pairs of peripheral plates are present in LPM-R00008. The first pair is small and roughly triangular. The next five pairs of peripherals appear to be rectangular and longer than wide, with exception of the fifth peripherals, which have a small medial process. The medial process is accentuated in the last five pairs of peripherals. These peripherals are much larger than the first six pairs of peripherals.

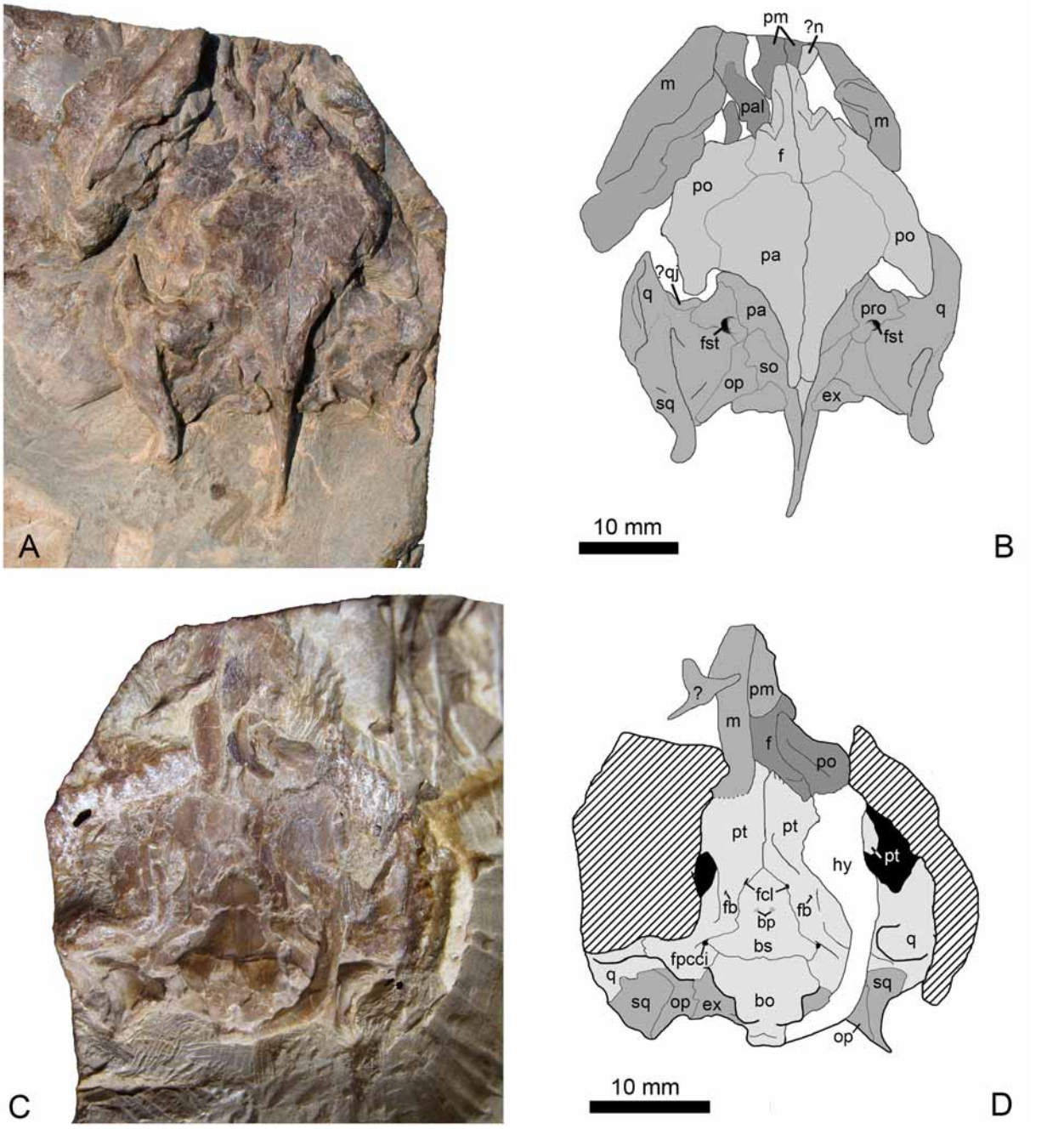

FIGURE 3. Skull of *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 (LPM-R00008) from the Early Cretaceous Yixian Formation of western Liaoning, China, in dorsal (A, B) and ventral (C, D) views. Abbreviations: bo, basiocciptial; bp, blind pits; bs, basisphenoid; ex, exoccipital; f, frontal; fb, foramen basisphenoidale; fcl, foramen caroticum laterale; fpcci, foramen posterior canalis caroticus internus; fst, foramen stapedio-temporale; hy, hyoid; m, maxilla; ?n, possible nasal; op, opisthotic; pa, parietal; pal, palatine; pm, premaxilla; po, postorbital; pro, prootic; pt, pterygoid; q, quadrate; ?qj, possible quadratojugal; so, supraoccipital; sq, squamosal; ?, unknown bone.

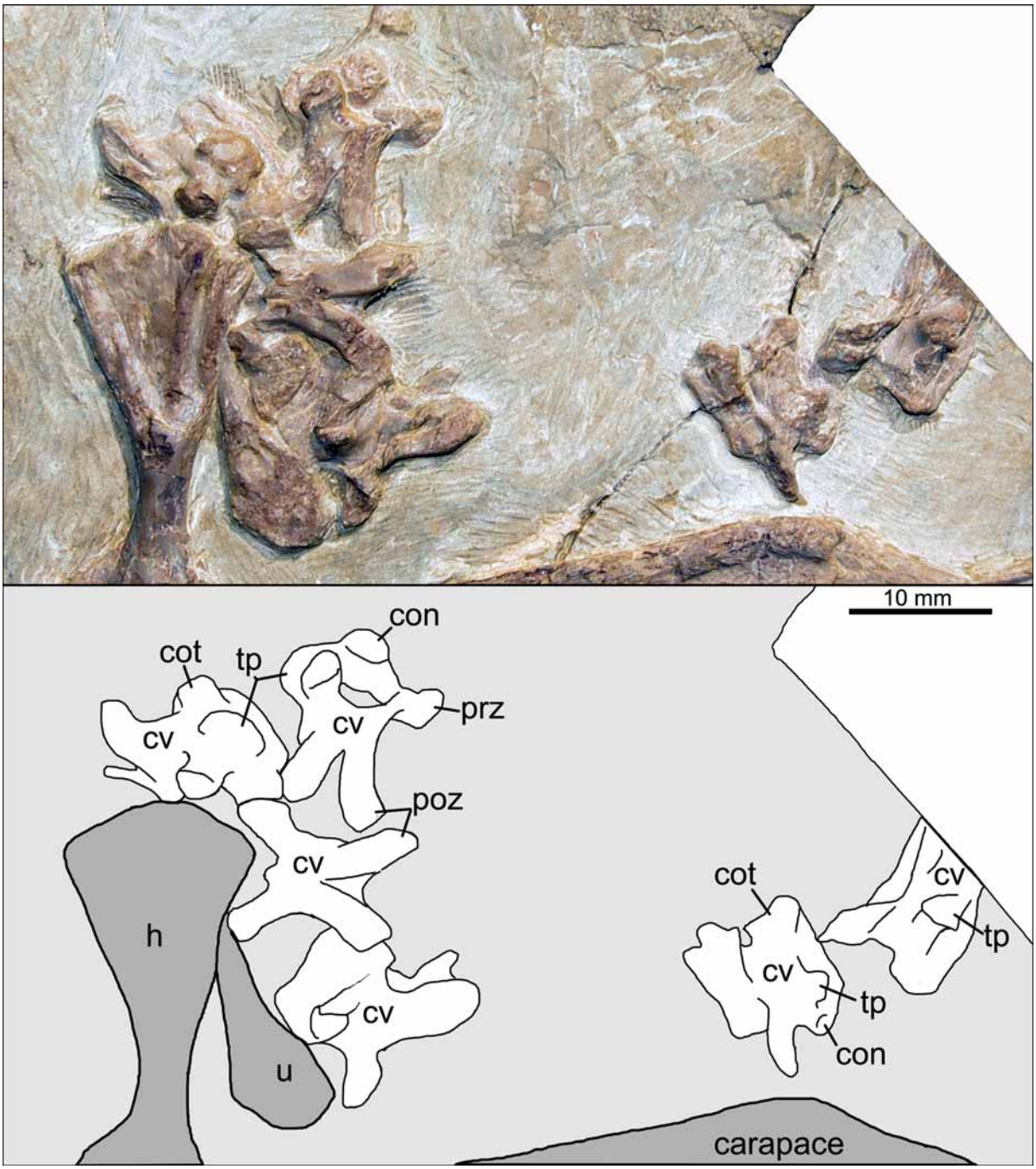

FIGURE 4. Cervical vertebrae of *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 (LPM-R00008) from the Early Cretaceous Yixian Formation of western Liaoning, China. Abbreviations: con, condyle; cot, cotyle; cv, cervical vertebra; h, humerus; prz, prezygapophysis; poz, postzygapophysis; tp, transverse process; u, ulna.

Vertebral column: Six cervical vertebrae are preserved, but are displaced from their original position, representing most of the cervical series of eight vertebrae. They are subrectangular in dorsal view, and comparable to each other in size (Fig. 4). The neural spine is strongly reduced. The centra are keeled ventrally. The development and orientation of the articular surfaces of the centra cannot be determined in most cases because of poor preservation, but some nevertheless appear to be opisthocoelous. The undivided transverse processes are positioned anteriorly near the proximal end of the centrum. The dorsal vertebrae are not exposed. In contrast, the caudal vertebrae are well preserved. The proximal five caudals are exposed in ventral view and in articulation with remaining column, while a distal caudal series is exposed in lateral view, comprising 14 articulated caudals and two slightly displaced caudals. The transverse processes are slender and

long in the proximal caudals, but strongly decrease in length posteriorly. The transverse processes disappear in the distal caudal series. Chevrons appear to be present on nearly all caudals.

Appendicular skeleton: The hind limbs are well preserved in articulation, but the forelimbs are only partially preserved on the left side with a humerus, ulna, and several isolated phalanges. The humerus is remarkable with two well expanded ends. The humeral head is dorsally positioned on the proximal end.

The hindlimbs are exposed in dorsal view and consist of both tibiae and fibulae and pedes. The tibia and fibula are subequal in length. Of these, the fibula is more slender. The tarsus is somewhat displaced from its original position. The largest tarsal is the astragalocalcaneum, and is situated adjacent to the distal ends of the tibia and fibula. The fifth metatarsal is large and subcircular. The phalanges are well preserved on the left side, with a phalangeal formula of 2-3-3-3-3. The unguals are slightly shorter than the penultimate phalanx.

Discussion

In the Jehol Biota, two turtle taxa have been erected so far: *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 and *Ordosemys liaoxiensis* (Ji, 1995). Although both are from the Yixian Formation, *M. manchoukuoensis* and *O. liaoxiensis* are distinct from each other in their carapace morphology. In particular, in *M. manchoukuoensis*, the shell is an elongate oval, the second to fourth vertebral scutes are long and narrow, and of the two suprapygals the second is much larger than the first (Endo & Shikama 1942). By contrast, in *O. liaoxiensis*, the shell is nearly as wide as long, the vertebral scutes are short and wide, and the two suprapygals are comparable in size (Ji 1995; Tong *et al*. 2004). The new specimen described here (LPM-R00008) can be confidently assigned to *M. manchoukuoensis* based on the presence of the above characters.

Cladistic analysis recovered 20 most parsimonious trees (MPTs) with a length of 89 steps (CI = 0.52, RI = 0.77, RC = 0.40). A 50% majority rule consensus tree places *Sinemys* spp., *Ordosemys* spp., and *Dracochelys bicuspis* more basely than macrobaenids, as in the previous studies of Gaffney *et al*. (1998), Parham & Hutchison (2003), Gaffney *et al*. (2007) and Vandermark *et al*. (2009), although this topology is supported by only 60% of the MPTs. *Sinemys* spp., *D. bicuspis*, and *M. manchoukuoensis* form a distinct basal eucryptodiran clade, which is supported by three characters: absence of postorbital-squamosal contact; opisthocoelous fourth cervical; and low neural spines in cervical vertebrae. However, the presence of an opisthocoelous fourth cervical is uncertain in *M. manchoukuoensis*. Although this hypothesis needs to be tested by discovery of additional material, this phylogenetic result supports the widely accepted hypothesis that *M. manchoukuoensis* falls into a monophyletic Sinemydidae (Gaffney & Ye 1992; Brinkman & Peng 1993a, b; Gaffney *et al*. 1998). Furthermore, *Dracochelys bicuspis* shows a close relationship with *Sinemys* spp. and *M. manchoukuoensis* as was previously hypothesized by Gaffney *et al*. (1998) and Brinkman (2001). However, *Ordosemys* spp. are excluded from the sinemydid clade, differing from the hypothesis of Gaffney *et al*. (1998), and placed as sister group to the clade consisting of sinemydids, macrobaenids and crown cryptodires, as in the previous studies of Brinkman & Wu (1999) and Tong *et al*. (2004).

The skull structure of *M. manchoukuoensis* (LPM-R00008) is similar to that of *Sinemys* spp. and significantly different from *Ordosemys liaoxiensis*. For example: 1) the parietal is well separated from the squamosal in *Sinemys* spp. and LPM-R00008, while a parietal-squamosal contact is present in *O. liaoxiensis*; 2) the postorbital is distally separated from the quadrate/squamosal in *M. manchoukuoensis* (LPM-R00008) and *Sinemys* spp., while a postorbital-squamosal contact is well present in *O. liaoxiensis*; 3) the temporal emargination of *M. manchoukuoensis* (LPM-R00008) is well developed as in *Sinemys* spp., but different from the shallow emargination in *O. liaoxiensis*; 4) in *M. manchoukuoensis* (LPM-R00008), the crista supraoccipitalis is elongated far beyond the bilateral squamosal crests, as in *Sinemys gamera*, but different from that of *Sinemys lens*, in which these crests are comparable in length to each other (Brinkman & Peng 1993a), while the crista supraoccipitalis of *O. liaoxiensis* is much shorter than the squamosal crests (Tong *et al*. 2004). However, these features are uncertain in *Dracochelys bicuspis* because of poor preservation of the cranial roof. In addition, these taxa are similar in several features, such as that the floor of the canalis caroticus internus is thin or absent in the four taxa, which is also present in many macrobaenids; prefrontals are well

separated medially by frontals in *Sinemys* spp., *M. manchoukuoensis* and *Ordosemys* spp., but a different condition is apparent in *D. bicuspis*, in which the prefrontals contact another along the midline (Gaffney & Ye 1992; Brinkman & Peng 1993a, b; Tong *et al*. 2004). As suggested by the previous studies of Brinkman & Wu (1999) and Tong *et al*. (2004), the cranial morphology of *Ordosemys* spp. appears to be more primitive than that of the Sinemydidae by having a postorbital-squamosal contact, a parietal-squamosal contact, and a relatively small foramen palatinum posterius, all of which are confirmed by the results of the phylogenetic analysis. However, within the family Sinemydidae, resolution of the relationship of *D. bicuspis* with *Sinemys* spp. and *M. manchoukuoensis* will require additional material.

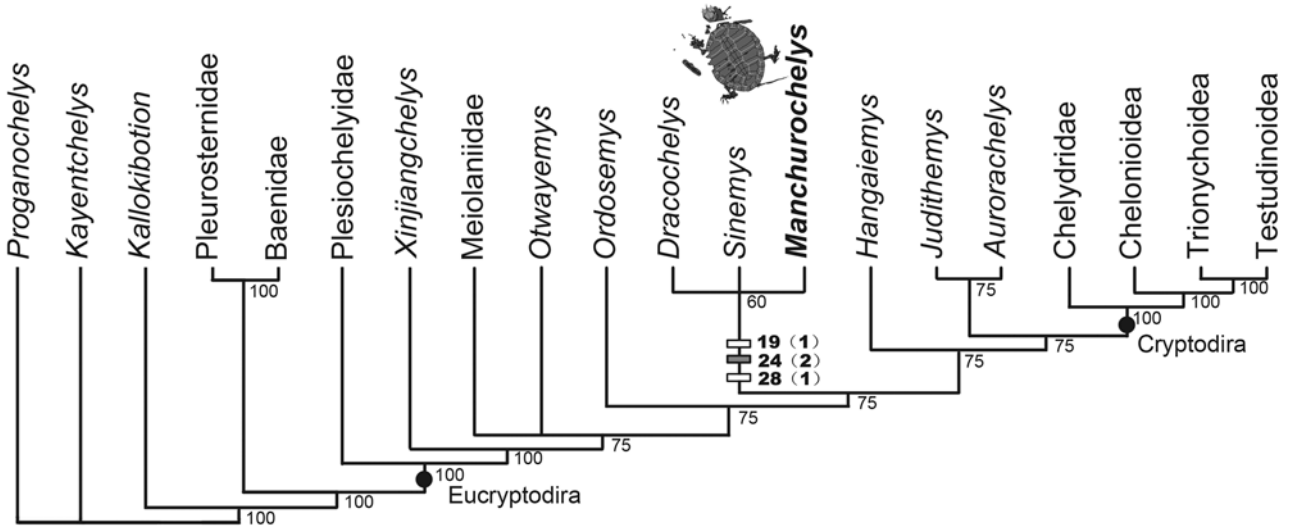

FIGURE 5. A cladogram showing the phylogenetic position of *Manchurochelys manchoukuoensis*. Data matrix including 20 taxa and 43 characters is modified from Vandermark *et al*. (2009), which in turn is based upon the data matrix of Parham & Hutchison (2003). A 50% majority-rule consensus tree was derived from 20 most parsimonious trees with tree length of 89 (CI = 0.52, RI = 0.77, RC = 0.40). The scoring of *Manchurochelys manchoukuoensis* was as follows: 00?0?11110 ?0?1?11111 11????1101 0??111???? 000.

Conclusions

(1) A second specimen of *Manchurochelys manchoukuoensis* Endo & Shikama, 1942 (LPM-R00008) from the Early Cretaceous Yixian Formation of western Liaoning Province confirms the validity of this taxon.

(2) The cranial morphology of *M. manchoukuoensis* (LPM-R00008), such as the postorbital separated from the quadrate/squamosal and the deep upper temporal emarginations, support a close relationship of this taxon with *Sinemys* spp., and clearly differentiate it from the co-existing taxon *Ordosemys liaoxiensis*.

(3) A phylogenetic analysis supports the monophyly of a sinemydid clade consisting of *Sinemys* spp., *Dracochelys bicuspis* and *M. manchoukuoensis*.

Acknowledgements

The author would like to thank the director of Paleontological Institute, Shenyang Normal University, Prof. Ge Sun for his encouragement, and Qiang Yang for his skilful preparation. I want to thank Dr. Walter Joyce (University of Tübingen, Tübingen) and Dr. Jérémy Anquetin (Muséum National d'Histoire Naturelle, Paris, France) for numerous helpful suggestions and corrections that have greatly improved the quality of the manuscript. Supported by the National Natural Science Foundation of China (NSFC Grant No. 40802007) and the Ph.D. Start-up Foundation of Shenyang Normal University.

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