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A new turtle from the Xiagou Formation (Early Cretaceous) of Changma Basin, Gansu Province, P. R. China

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Abstract *Changmachelys bohlini* gen. et sp. nov., from the Lower Cretaceous Xiagou Formation, Changma Basin, north-western Gansu Province, adds to our understanding of the diversity and distribution of Early Cretaceous turtles in Asia. *Changmachelys bohlini* is similar to Early Cretaceous turtles from Asia included in "Macrobaenidae" in having a low domed carapace and a reduced, cruciform plastron with buttresses that do not extend onto the costals. With a carapace that exceeds 34 cm in length, it is one of the largest Early Cretaceous "macrobaenids". Despite the addition of this new taxon and new characters to previous phylogenetic analyses, the relationships of "macrobaenid" turtles remain poorly resolved. In addition to adding to the diversity of "macrobaenid" turtles in the Early Cretaceous of Asia, *Changmachelys bohlini* is of interest because each of the four available specimens documents a distinct stage of ontogenetic development of the shell. In the carapace, the dermal portions of the costals are unossified in the most juvenile specimen but peripherals are present. In contrast with the late ossification of the dermal bone of the carapace, the plastron ossifies relatively early.

Keywords Macrobaenidae · Early Cretaceous · Xiagou Formation · Gansu · China

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Introduction

Early Cretaceous turtles from Asia are of interest because they include basal members of extant crown-group cryptodires as well as more basal cryptodires (Sukhanov 2000; Hirayama et al. 2000). Representatives of crown group cryptodires in the Early Cretaceous include stem-testudinoids, stem-trionychids, and early carettochelyids (e.g. Danilov 1999; Hirayama et al. 2012; Tong et al. 2009). Basal cryptodires are represented by the enigmatic tortoise-like taxon *Sinochelys* (Hirayama et al. 2000). The most diverse group of turtles in the Early Cretaceous are basal eucryptodires characterised by having a low-domed carapace, a reduced, cruciform plastron loosely connected to the carapace, and procoelous cervical and caudal vertebrae. These have frequently been included in the Sinemydidae, although we follow Tong and Brinkman (2012) in restricting the Sinemydidae to the genus *Sinemys* and include the remaining turtles with this general morphology in "Macrobaenidae". Quotes are used around the family name to indicate that the group is likely paraphyletic.

Six genera of "macrobaenid" turtles are recognised from the Early Cretaceous of Asia. These are: *Manchurochelys* Endo and Shikama, 1942; *Kirgizemys* Nessov and Khozatsky, 1973 (including *Hangaiemys* Sukhanov and Narmandakh, 1974); *Ordosemys* Brinkman and Peng, 1993

(including *Asiachelys* Sukhanov et Narmandakh, 2006); *Dracochelys* Gaffney and Ye, 1992; *Liaochelys* Zhou, 2010b; and *Wuguia* Matzke et al., 2004. The most speciose of these is *Kirgizemys*, which includes five species: *K. exaratus* Nessov and Khozatsky, 1973; *K. dmitrievi* Nesov and Khozatskii, 1981; *K. kansuensis* (Bohlin, 1953); *K. hoburensis* (Sukhanov and Narmandakh, 1974); and *K. leptis* Sukhanov and Narmandakh, 2006. It is also the most widespread of the Early Cretaceous "macrobaenids", occurring in Kyrgyzstan, north-western China, Mongolia, and the Lake Baikal region of Buryatia, Russia. *Ordosemys* is represented by four species: *O. leios* Brinkman and Peng, 1993, *O. liaoxiensis* Tong et al., 2004; *O. perforata* (Sukhanov and Narmandakh, 2006), and *O. brinkmania* Danilov and Parham, 2007. It is widespread in northern China, occurring in Liaoning, Inner Mongolia, and the Junggar Basin of Xinjiang. *Wuguia* is represented by two species: *W. hutubeiensis* Matzke et al., 2004 and *W. efremovi* (Khosatzky, 1996), both from the Junggar Basin in Xinjiang. *Dracochelys*, from the Junggar basin of Xinjiang, plus *Liaochelys*, and *Manchurochelys*, both from Liaoning, are monospecific. In this paper, a new "macrobaenid" turtle from the Early Cretaceous Xiagou Formation of Gansu Province, China, is described as *Changmachelys bohlini* gen. et sp. nov. Like *Dracochelys*, *Liaochelys*, and *Manchurochelys*, it is monospecific and is geographically restricted to a single basin.

Turtles from the Early Cretaceous of Gansu were first described by Bohlin (1953), who recognised five genera. Two of these, *Peishanemys* Bohlin, 1953 and *Heishanemys* Bohlin, 1953, were synonymised with the basal eucryptodire *Sinochelys* Wiman 1930 by Brinkman et al. (2008). *Tsaotanemys* Bohlin, 1953 is similar to the early testudinoids *Mongolemys* Khosatsky and Młynarski 1971 and *Lindholmemys* Riabinin 1935, in having a broad plastron with a single pair of gular scutes and well-developed buttresses, so it is likely also a stem testudinoid. A series of isolated shell elements included in the genus *Osteopygis* Cope, 1868 by Bohlin (1953) were more recently included in the genus *Kirgizemys* as *K. kansuensis* by Danilov et al. (2006): *Osteopygis kansuensis* was first placed within *Hangaiemys* by Sukhanov and Narmandakh (1974), then to *Kirgizemys* by Nessov and Khosatzky (1981). Danilov et al. (2006) united *Kirgizemys* and *Hangaiemys* in one genus *Kirgizemys*. The remaining genus, *Yumenemys* Bohlin, 1953, is poorly known and remains enigmatic. Khosatzky (1996) considered it to be a synonym of *Mongolochelys*, while Brinkman et al. (2008) regarded it as a valid genus. The material described by Bohlin (1953) came from three localities, one west of Jiayuguan, one a short distance north of Jiayuguan, and one much farther north, in the area now referred to as Mazongshan. The locality west of Jiayuguan was revisited by the Sino-Japanese Silk Road

Dinosaur Project (Dong 1997), but no new material was collected. The exact locations of the remaining two sites are not known.

The only other report of a turtle from Early Cretaceous of Gansu is a single skeleton of *Sinemys* from eastern Gansu (Ye 1963). This specimen was recently redescribed by Tong and Brinkman (2012) as a new species of *Sinemys*, *S.* cf. *brevispinus*.

The turtle described here as *Changmachelys bohlini* gen. et sp. nov. is from exposures of the Xiagou Formation in the Changma Basin, a small basin in the Qilian Mountains south-west of New Yumen City and about 200 km from Bohlin's (1953) Jiayuguan localities (Fig. 1). The formation, which consists of finely laminated shales that were deposited in a lacustrine setting, has yielded an assemblage of vertebrates including two bird taxa, the ornithuraen *Gansus yumenensis* (Hou and Liu 1984; You et al. 2006), and the enantiornithen *Qiliania graffini* (Ji et al. 2011), an osteoglossomorph fish (Murray et al. 2010), and other unnamed taxa currently under study. The faunal assemblage is unusual in that birds are abundant and fishes are relatively rare. Turtles, often the most dominant vertebrate in the Early Cretaceous of western China, are also rare. Only four turtle specimens have been recovered compared to over a hundred birds. Although rare, the turtle specimens that have been recovered are well-preserved with each including articulated or closely associated cranial and postcranial remains. Also, the material is of interest because each specimen documents a distinct stage of development, making *Changmachelys* one of the first Early Cretaceous "macrobaenids" from Asia for which the post-hatchling ontogenetic development can be documented on the basis of a series of articulated skeletons.

Fig. 1 The Changma locality. *Shaded area* on *inset* of China is Gansu Province

Geology

The turtle fossils described here come from the Xiagou Formation, the lower unit of the Xinminpu Group (Bureau of Geology and Mineral Resources of Gansu Province 1989, 1997; Tang et al. 2001). The Xiagou Formation consists of finely laminated brownish−yellow mudstones and siltstones deposited in a lacustrine setting. Thus, environmentally, this locality is similar to the Yixian and Jiufotang formations of Liaoning. The age of the Xiagou Formation has been interpreted as Aptian on the basis of studies of stable carbon isotope chemostratigraphy (Suarez et al. 2008). This is generally equivalent to the Jiufotang Formation of Liaoning which has yielded the Jehol fauna including the turtles *Ordosemys* spp. and *Liaochelys jiangchangensis* (Zhou 2010a, b), and younger than the Yixian Formation, which has yielded the turtle *Manchurochelys manchoukuoensis* (Zhou 2010a, b). Its age relative to Early Cretaceous localities in Xinjiang and Mongolia is not known.

Materials and methods

The specimens are preserved as articulated or partially disarticulated skeletons and are prepared in relief, although in the case of the holotype specimen (CAGS IG-02-0902) the skull was removed and fully prepared.

Specimens are housed in the collections of the Chinese Academy of Geological Sciences (CAGS), Beijing, and Gansu Geological Museum (GSGM), Lanzhou, Gansu Province. The acronym CM refers to the Changma Basin. The acronym TMP refers to the Royal Tyrrell Museum of Palaeontology.

Systematic palaeontology

Testudines Batsch, 1788
Cryptodira Cope, 1868
Eucryptodira Gaffney, 1975
Centrocryptodira Gaffney and Meylan, 1988
"Macrobaenidae" Sukhanov, 1964

Changmachelys bohlini gen. et sp. nov.
(Figures 2, 3, 4, 5, 6, 7, 8, and 9)

Holotype: CAGS IG-02-0902, a partially disarticulated skeleton of a large individual, preserved in dorsal view (Fig. 2). The estimated shell length is 35 cm (Table 1). Elements on the left side are more disturbed than those on the right. The skull is complete, although crushed, and the hyoids and atlas/axis are preserved in place. The mandible is separate from the skull and largely intact. The carapace is nearly complete, although partially disarticulated. The nuchal is broken at the midline. All peripherals of the left side are preserved and all but the tenth and eleventh peripherals are preserved on the right side. The first peripheral of both sides remains in articulation with the nuchal. The second and third left peripherals are preserved as a unit but have shifted posteriorly relative to their costals. The fourth left peripheral is isolated and sitting on carapace. The fifth to seventh left peripherals have rotated so are visible on the lateral edge and anterior surface. The fourth to seventh right peripherals have been rotated so their inner surface is exposed dorsally. The first neural is displaced to the left of the carapace, the second to fifth are preserved as a unit and are sitting on the left costals, and the sixth to eighth are preserved in articulation with the costals. All costals are present. The first left costal has been displaced to the left and the first right has tilted forward. The second to fifth right costals are preserved as a unit, and the remaining costals, along with the sixth to eight neurals and the suprapygal, are preserved as a unit. The pygal and the last two peripheral elements of the right side are missing. The plastron is represented only by a fragment of the medial portion of a partial entoplastron and what appears to be a hyoplastron. The neck is represented by the atlas, axis and three isolated cervical vertebrae. The atlas and axis originally were preserved in articulation with the skull, although the atlas was removed and completely prepared. The three isolated cervicals are identified as the fifth, seventh, and eighth. The fifth is visible in ventral and ventro-lateral views, the seventh is visible in posterior view, and the eighth is visible in lateral view. The base of the tail is disarticulated, but the distal end of the tail is articulated and preserved in approximately the correct position relative to the carapace. The pectoral girdle is represented by a complete left shoulder girdle and a right scapula. The pelvic girdle is represented by an isolated ilium and ischium. Most of the limb elements are present, but widely scattered across the block. The left hand and foot are in approximately the correct position but the right hands and feet have been more strongly disturbed.
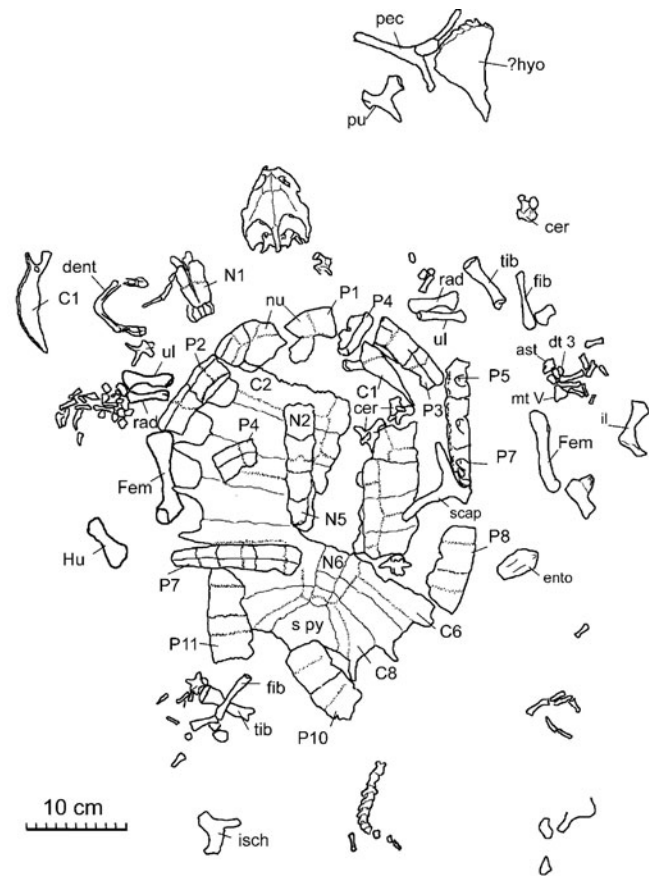
Type locality: From the Changma Basin, near the city of Changma, Gansu Province, north-western China.

Age: Xiagou Formation, Early Cretaceous, Aptian.

Etymology: The generic name is in reference to the Changma Basin, the only locality from which this turtle is currently known. The specific name is in honour of Birger Bohlin, who investigated the palaeontological record of Gansu as a part of the 1929–31 Sino-Swedish expedition led by Sven Hedin, and who described the first Early Cretaceous turtles from Gansu.

Fig. 2 Photograph and interpretive drawing of CSGM 05 IG-02-0902, the holotype specimen of *Changmachelys bohlini* gen. et sp. nov., seen in dorsal view. *ast* astragalocalcaneum, *C1* first costal, *C2* second costal, *C6* sixth peripheral *C8* eighth costal, *cer* cervical vertebra, *dent* dentary, *dt 3* third distal tarsal, *ento* entoplastron, *Fem* femur, *fib* fibula, *Hu* humerus, *?hyo* ?hyoplastron, *il* ilium, *isch* ischium, *mt V* metatarsal 5, *N1* first neural, *N2* second neural, *N5* fifth neural, *N6* sixth neural, *nu* nuchal, *P1* first peripheral, *P2* second peripheral, *P4* fourth peripheral, *P5* fifth peripheral, *P7* seventh peripheral, *P8* eighth peripheral, *P10* tenth peripheral, *P11* eleventh peripheral, *pec* pectoral girdle, *pu* pubis, *rad* radius, *s py* suprapygals, *scap* scapula, *tib* tibia, *ul* ulna

Paratypes: GSGM 05-CM-016 (Fig. 3), an articulated skeleton of an individual at an intermediate stage of development, visible in ventral view, complete except for the left forelimb, right hind limb, the posterior end of the carapace, and part of the right foot. The estimated shell length is 16 cm. The skull and lower jaw are covered by the hyoids and are crushed so individual bones cannot be identified. The

Table 1 Measurements of the lengths of major elements in the specimens of *Changmachelys bohlini* gen. et sp. nov; all measurements in cm

Element	CSGM 05 IG-02-0902	GSGM 05-CM-016	GSGM 05-CM-015	GSGM 07-CM-017
Carapace	35	16	–	4.7
Femur	8.4	3.5	2.2	1.1
Humerus	–	3.5	2.2	0.95
Ulna	4.6	2	1.3	0.6
Tibia	5	2.4	1.5	–

plastron is fully exposed in ventral view, although the epiplastra and entoplastron cannot be identified. The carapace is represented by the peripherals, which are articulated and form a narrow ring of bone encircling the shell, and portions of the costals, which are visible through fenestrae in the plastron. The rib heads are recognizable beneath the plastron, which has folded over the underlying bones. The suprapygal is exposed posterior to the xiphiplastron. The cervical series is complete although individual centra cannot be recognised. The dorsal centra are preserved in place. A complete pectoral girdle and right forelimb are seen in ventral view. The pelvis is represented by a complete right ilium. The proximal two thirds of the right hind limb is preserved.

GSGM 07-CM-017 (Fig. 4), an articulated skeleton of a very juvenile individual exposed in dorsal view. The estimated shell length is 4.7 cm (Table 1). The skull is in approximate position relative to the carapace, although the neck, nuchal, and anterior peripherals are missing. The skull
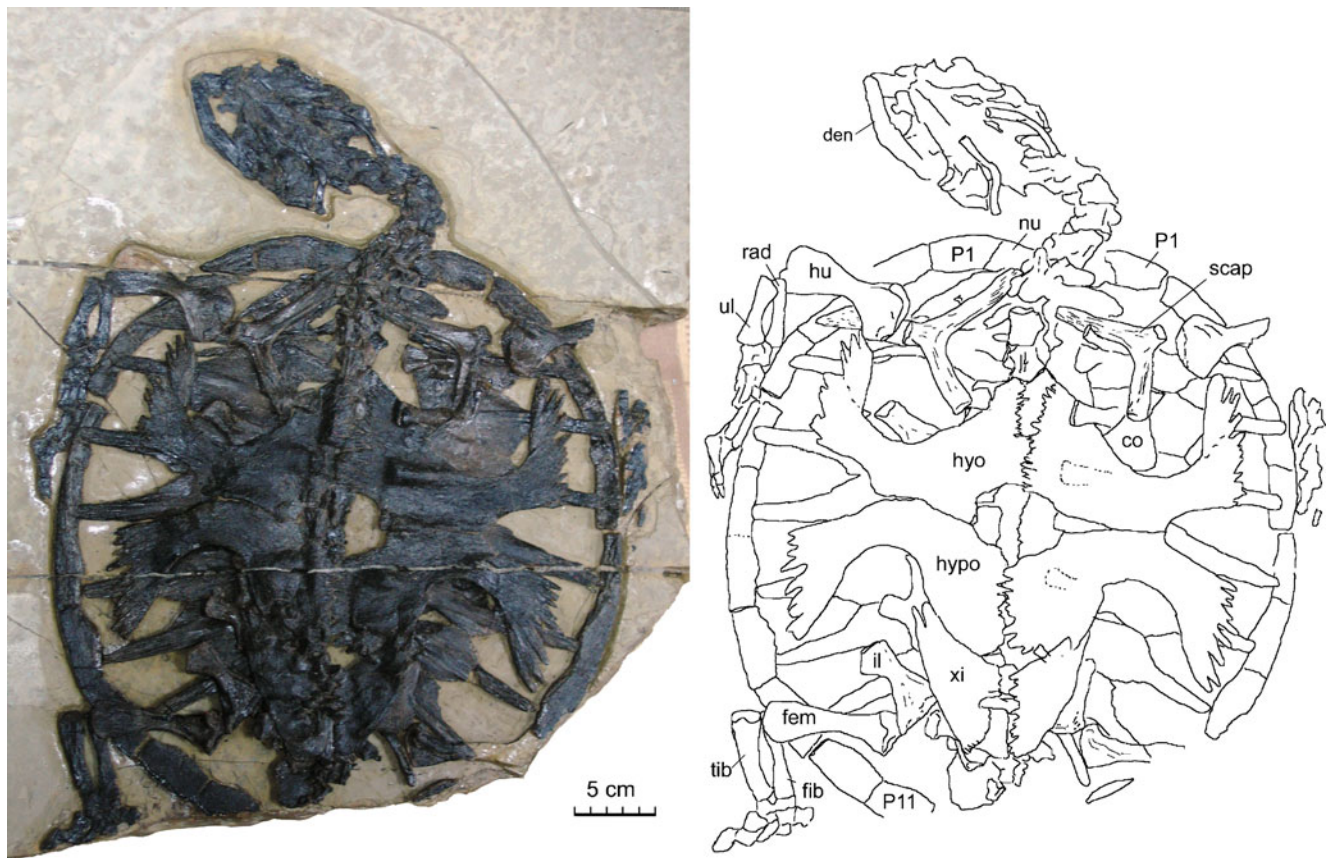
Fig. 3 Photograph and interpretive drawing of *Changmachelys bohlini* gen. et sp. nov. specimen GSGM 05-CM-016, seen in ventral view. *co* coracoid, *den* dentary, *fem* femur, *fib* fibula, *hu* humerus, *hyo* hyoplastron, *hypo* hypoplastron, *il* ilium, *nu* nuchal, *P1* first peripheral, *P11* eleventh peripheral, *rad* radius, *scap* scapula, *tib* tibia, *ul* ulna, *xi* xiphiplastron

retains a three-dimensional aspect and is visible in dorsal and right lateral view. The carapace is articulated and visible in dorsal view. Except for the missing anterior elements in the series, the peripherals are articulated and form a narrow ring of bone. The dorsal vertebrae form a solid row down the centre of the carapace but individual centra cannot be identified. Costals are preserved in articulation with the dorsal centra. The plastron, articulated except for the left hyoplastron, is partially visible in internal view between the costals. The left hyoplastron is present anterior to the carapace. The right forelimb is fully articulated and preserved in place. The left humerus and radius-ulna are present but disarticulated. The left pelvis is visible in internal view beneath the seventh and eight costals, and both femora are present, although slightly displaced.

GSGM 05-CM-015 (Fig. 5) is a disarticulated skeleton of an individual at an intermediate stage of development visible in dorsal view. Measurements of limb elements indicate it is intermediate in size between GSGM 05-CM-016 and GSGM 05-CM-017 (Table 1). The skull is disarticulated and partially scattered, the bones of the face forming a group in the correct approximate position relative to the plastron, and the skull

roof and supraoccipital have shifted posteriorly to overlie the plastron. The carapace is disarticulated with some costals exposed in dorsal view and some in ventral. The peripherals are rod-like blocks of bone that are widely scattered across the specimen. The plastron is partially visible in internal view. Two cervical vertebrae can be identified adjacent to the left humerus. One of these includes both the neural arch and centrum, which are sutured to one another. The second is an isolated neural arch that has a tall, elongate neural spine, and is tentatively identified as the eighth cervical. Much of the tail is present. The base of the tail is disarticulated, but the distal end is articulated and is in approximately correct position relative to the shell. An isolated coracoid is present near the base of the tail. The left humerus is seen in dorsal view. Both forearms and hands are articulated. The left hind limb is fully articulated, including a metacarpus and foot visible in dorsal view. Most of the elements of the right hind limb are present, but partially disarticulated.

Diagnosis: A "macrobaenid" differing from all other Early Cretaceous "macrobaenids" from Asia in being round in
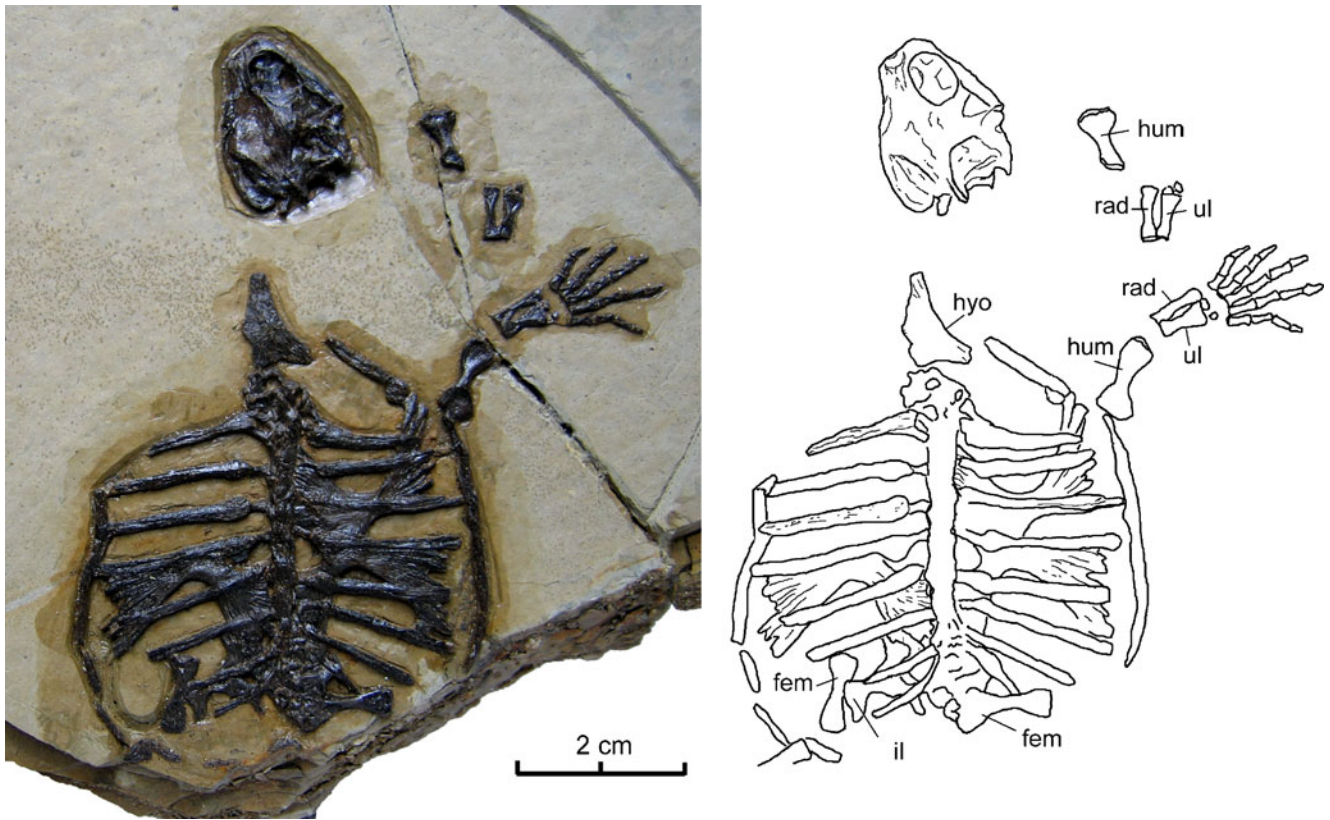
Fig. 4 Photograph and interpretive drawing of *Changmachelys bohlini* gen. et sp. nov. specimen GSGM 07-CM- 017, seen in dorsal view. *fem* femur, *hum* humerus, *hyo* hyoplastron, *il* ilium, *rad* radius, *ul* ulna

outline and in retaining well-developed costal-peripheral fenestrae in individuals of large size. Similar to *Liaochelys*, *Manchurochelys*, *Ordosemys*, and *Dracochelys* and differing from *Kirgizemys* and *Wuguia* in that surface of carapace is smooth, without plications extending posterior

to the sulci. Similar to *Manchurochelys*, *Kirgizemys*, *Wuguia*, and *Dracochelys* and differing from *Liaochelys and Ordosemys* in that the vertebral scutes 2–4 are narrow. Skull similar to *Dracochelys*, *Liaochelys*, and *Kirgizemys* and differing from *Manchurochelys* and *Ordosemys* in that
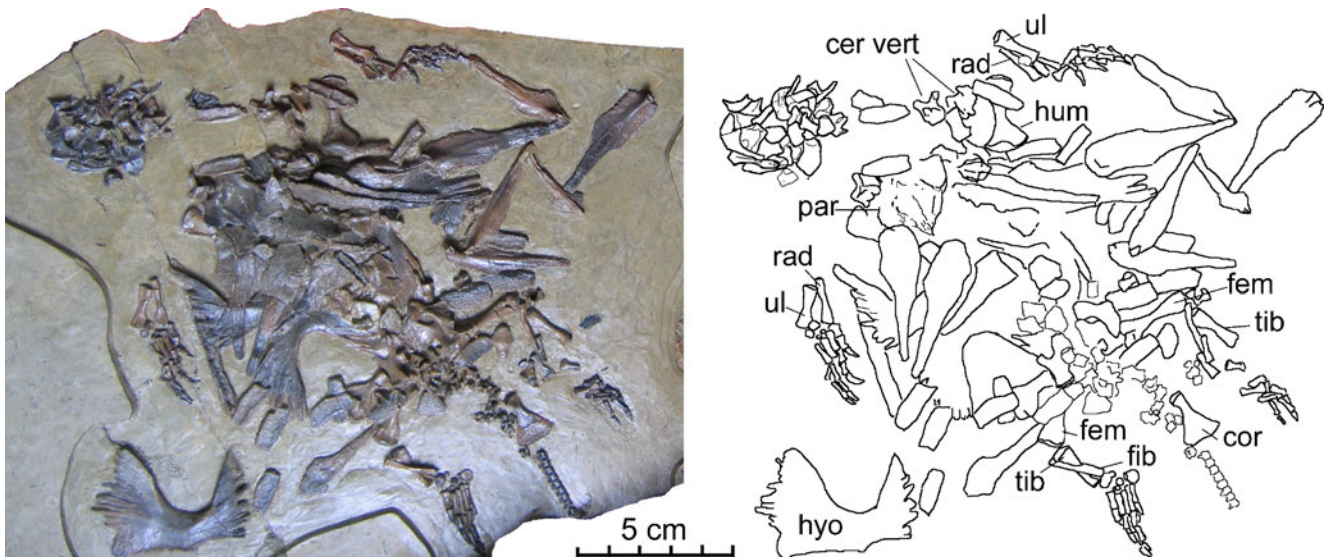

Fig. 5 Photograph and interpretive drawing of *Changmachelys bohlini* gen. et sp. nov. specimen GSGM 05-CM-015, seen in dorsal view. *cer vert* cervical vertebra, *cor* coracoid, *fem* femur, *fib* fibula, *hum* humerus, *hyo* hyoplastron, *par* parietal, *rad* radius, *tib* tibia, *ul* ulna

prefrontals contact one another at the mid-line. Differing from *Dracochelys* in that carapace does not have a tapered posterior end.

Description: *Changmachelys* is large-bodied "macrobaenid" with a smooth shell that is round in outline and has large costal-peripheral fenestrae. A round shell is frequently encountered in Jurassic xinjiangchelyids (Brinkman et al. 2012) and is present in the Late Cretaceous "macrobaenid" *Aurorachelys gaffneyi* (Vandermark et al. 2009), but is not otherwise seen in Early Cretaceous "macrobaenids". Rather, in these turtles, the shell is typically elongate and is oval or has a tapering posterior end in outline. *Ordosemys* is an exception to this pattern because its shell is about as wide as long, but it is more sub-rectangular in dorsal outline. Although the size of costal-peripheral fenestrae is generally

an unreliable taxonomic character because they close with growth, their presence in *Changmachelys bohlini* is considered to be significant because the large size of the holotype specimen indicates that it is an adult. Indeed, with an estimated shell length of 34 cm, it is one of the largest Early Cretaceous "macrobaenid" currently known. Together, these features clearly distinguish *Changmachelys bohlini* from all other early Cretaceous "macrobaenids".

Skull: The skull is similar to that of *Kirgizemys hoburensis* as described by Sukhanov and Narmandakh (1974) in being relatively long, and in having sub-parallel cheek regions and a triangular face (Fig. 6). The narial opening is large. The orbits are located far forward and are separated from the external narial opening by a narrow bar formed by the maxilla and prefrontal. The temporal emargination is well
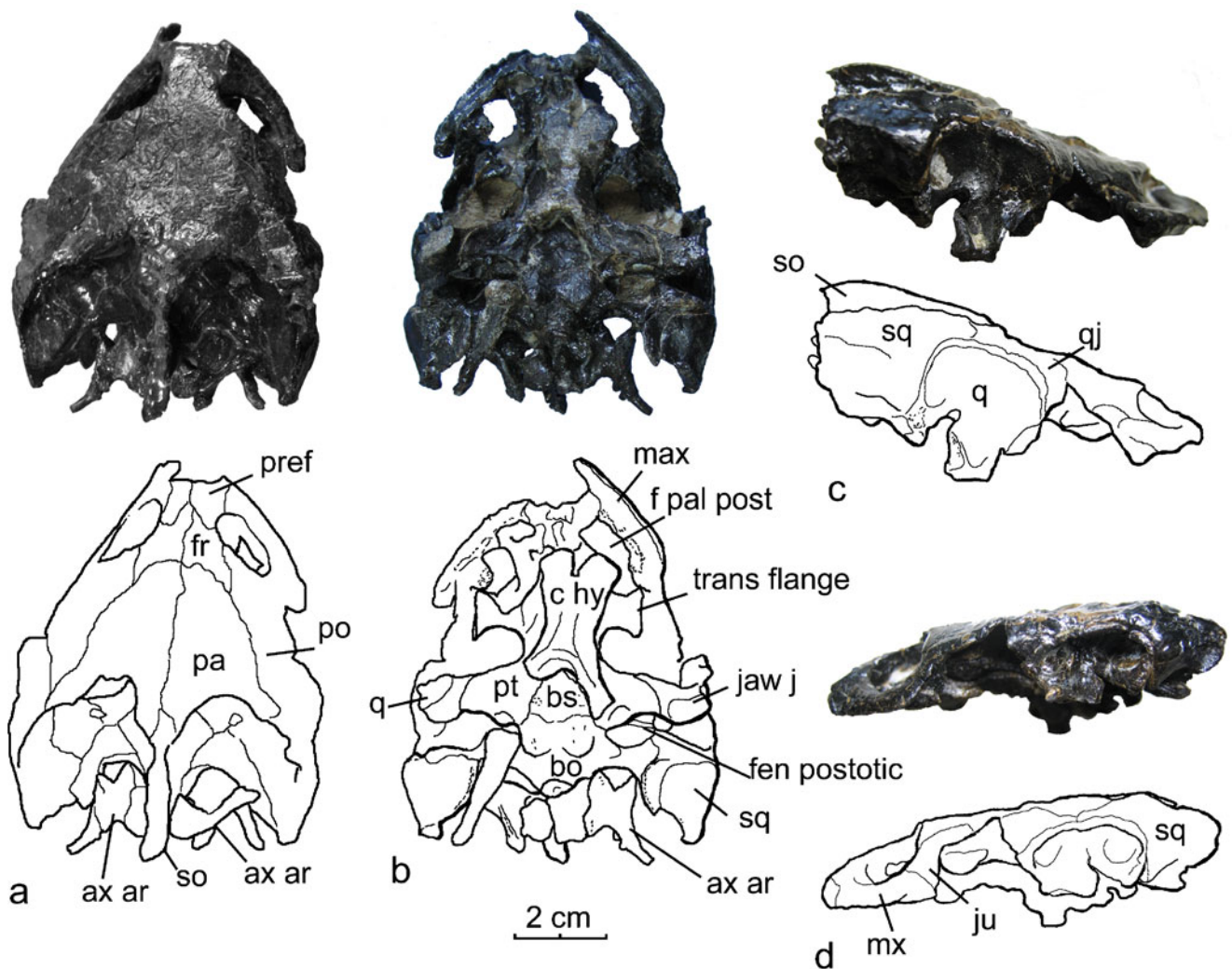

Fig. 6 Photographs and interpretive drawings of *Changmachelys bohlini* gen. et sp. nov. skull, from holotype specimen CAGS IG-02-0902 in: **a** dorsal, **b** ventral, **c** right lateral, **d** left lateral views. *ax ar* axis arch, *bo* basioccipital, *bs* basisphenoid, *c hy* corpus hyoideus, *f pal post* foramen palatinum posterius, *fen postotic* fenestra postotica, *fr* frontal, *jaw j* jaw joint, *ju* jugal, *max* maxilla, *pa* parietal, *po* postorbital, *pref* prefrontal, *pt* pterygoid, *q* quadrate, *qj* quadratojugal, *so* supraoccipital, *sq* squamosal, *trans flange* transverse flange of pterygoid. All to same scale

developed, extending to the anterior edge of the otic capsule. However, because the otic capsule is short and the skull is elongate, the anterior end of the emargination is well separated from the orbits, the distance between the orbits and the anterior end of the temporal emargination being equal to the depth of the emargination (Fig. 6a). The supraoccipital crest, visible in both the holotype specimen and GSGM 07-CM-017, is long and narrow and extends just posterior to the squamosals (Figs. 4, 6a).

Sutures are generally distinct in the holotype specimen, allowing most bones of the skull roof to be identified. The prefrontals meet at the midline. There is no evidence for nasals in front of the prefrontals. The length of the frontals is about equal to the length of the orbit. The frontals form part of the orbital margin, separating the prefrontal and postorbital. The contact between the frontal and the postorbital is moderately long and parallel to the midline. The parietals, which are the largest bones of the skull roof, extend from the posterior edge of the orbits to the base of the narrow portion of the supraoccipital crest. Posterolaterally, the parietal meets the squamosal. The squamosal is broadly exposed dorsally, but is not strongly extended in a sharp point posteriorly.

As seen in dorsal view (Fig. 6a), the otic capsule is relatively short antero-posteriorly and slopes posteriorly. The stapedial foramen is large and is bordered by the quadrate and prootic. The supraoccipital forms the long supraoccipital process.

The right and left lateral sides of the skull of the holotype specimen are compressed differently, with the facial region being relatively undistorted in left lateral view, and the temporal region being relatively undistorted in right lateral view (Fig. 6c, d). Thus, together they document the major features of the lateral surface of the skull. The jugal (Fig. 6d) is reduced to a narrow bar extending from the maxilla to the postorbital. The suborbital portion of the face is narrow. The quadrate has a nearly circular tympanic cavity (Fig. 6c). The incussura columella auris is narrow, but short, and opens up just posterior to the quadrate articular surface.

In ventral view (Fig 6b), much of the palate is obscured by the hyoids in all available specimens, although in the holotype specimen the corneal branch has been removed to expose the lateral portion of the palate. The triturating surface of the maxilla is narrow. The foramen palatinum posterior is very large and includes the maxilla in its border. The right pterygoid is nearly completely exposed ventrally. The transverse flange of the pterygoid is large and projects well posteriorly, as is also the case in *Dracochelys bicuspis* and *Kirgizemys* spp. (Danilov et al. 2006; Gaffney and Ye 1992; Sukhanov and Narmandakh 1974). Between the transverse flange and the quadrate, the pterygoid forms the border of the short, nearly circular sub-temporal fossa. The foramina posterior canalis caroticus internus is a large opening located within the pterygoid just lateral to the basioccipital. The more anterior

portions of the canal are covered by the hyoids, so it is uncertain whether or not this canal was exposed ventrally as in other Early Cretaceous "macrobaenids".

Only the posterior end of the basisphenoid is visible. The lateral edges of this element taper strongly towards the midline, indicating that in ventral view the basisphenoid is triangular. A pair of shallow depressions is present on its ventral surface near the posterior end of the bone. This differs from *Ordosemys*, where distinct pits are present (Brinkman and Wu 1999). It is uncertain whether or not basioccipital tubercula are present ventrally because that area is covered by the hyoids.

The basioccipital is long and narrow in ventral view and has antero-posteriorly oriented basioccipital tuberculae. No strong change in elevation is present between the ventral surface of the basisphenoid and the occipital condyle. The suture between the basioccipital and the basisphenoid is located at the posterior edge of the pterygoid with the pterygoid contacting only the antero-lateral corner of the basioccipital. Thus, the main body of the basioccipital is located posterior to the quadrates.

A striking feature of the skull is the anterior position of the jaw joint relative to the posterior edge of the skull. The fenestra postotica faces ventrally posterior to the pterygoid and lateral to the basioccipital and is barely visible in posterior view. This fenestra is bordered posteriorly by the exoccipital, which extends laterally to meet the quadrate. The left stapes is preserved in place and is visible through the fenestra postotica. The ventral surface of the squamosal is exposed in ventral view posterior to the quadrate. A ventrally-facing fenestrae postotica is widespread in "macrobaenids" from Asia, but is absent in *Dracochelys bicuspis*, where the jaw joint is located near the posterior edge of the skull and the fenestrae postotica is visible in posterior view, as in extant cryptodires generally.

Lower jaw: The lower jaw, visible in occlusal view in the holotype specimen (Fig. 2) and ventral view in GSGM 07-CM-016 (Fig. 3), is short and wide compared to the skull, reflecting the anterior position of the quadrates relative to the posterior edge of the skull. The dentaries form about half the length of the lower jaw. These elements form an angle of approximately 90° relative to one another. The triturating surfaces are narrow. The posterior end of the triturating surface extends onto the base of the tall coronoid process. A low lingual ridge is present along the posterior portion of this surface. This ridge becomes weaker anteriorly and does not reach the symphysis. The length of the post-dentary region is slightly less than the length of the dentary. In contrast to the strongly diverging dentaries, the post-dentary portions of the lower jaw are parallel to one another. Thus, they form a distinct angle with the dentary.

Hyoids: In both GSGM 05-CM-016 and the holotype specimen, the hyoids are preserved in place (Figs. 3, 6b). The corpus hyoideus is massive and a single pair of branchial horns, the cornu branchiale II, extends posterior to the skull. The size of the hyoid suggests that *Changmachelys bohlini* was an efficient suction feeder.

Carapace: As reconstructed, the carapace in adult individuals is round in dorsal outline, with a distinct nuchal emargination (Fig. 7). The length of the carapace of the holotype specimen, approximately 34 cm, is subequal to its width. The juvenile specimens, GSGM 05-CM-016 and GSGM 07-CM- 017, also have a round carapace with length subequal to width (Figs. 3, 4). The antero-lateral edge of the carapace is raised from the first peripheral to about the seventh. Costo-peripheral fenestrae are well developed from at least the second costal to the suprapygal. The carapace is evenly convex, lacking the mid-dorsal depression present in *Ordosemys* and some of the "macrobaenids". The surface of the carapace is smooth, lacking the plications extending posteriorly from the sulci such as are present in *Kirgizemys* and *Wuguia* (Matzke et al. 2004; Sukhanov and Narmandakh 1974).

The neurals, only recognizable as distinct elements in the holotype specimen, are relatively short and wide and are rectangular to weakly hexagonal in shape. Distinct neurals

cannot be identified in any of the subadult specimens. If ossified, they do not extend lateral to the dorsal vertebrae.

The first costal is relatively narrow anteroposteriorly. The curvature of the right first costal, seen in edge view in the holotype, shows that the shell was moderately domed (Fig. 2). The proximal rib heads of the first costals are long. The second to fourth costals are parallel sided and are directly laterally. The fifth to eighth costals slope increasingly strongly posteriorly. A dominant feature of all the costals is the presence of long rib ends. Because the peripherals are narrow, only the tips of these would have contacted the peripherals resulting in the extensive costal-peripheral fenestrae.

The carapace of the most juvenile specimen, GSGM 07-CM-017, is notable for the greatly reduced ossification of the dermal portion of the costals (Fig. 4). The dermal portion of the costals is represented by slight swellings near the proximal end of the second, third and fourth costals. These swellings are absent on the fifth to eighth costals. In GSGM 05-CM-016 (Fig. 3) and GSGM 05-CM-015 (Fig. 5), the free end of the ribs forms about half the length of the costals so the costal-peripheral fenestrae of these individuals would have been relatively larger than in the holotype specimen.

The peripheral series of the holotype specimen is disarticulated, although all elements are represented on at least one side (Fig. 2). The first peripheral is a subrectangular element, slightly wider posteriorly, that contacts the nuchal and first costal. The second to sixth peripherals are narrow, rectangular elements. The seventh and eighth become wide and the ninth to eleventh are nearly square. The third peripheral has a notch on its medial edge marking the site of articulation with the rib. On the fourth to seventh peripherals, which are seen in medial view, pits for the distal ends of the ribs are well developed but a pit for the hypoplastron is only present on the seventh peripheral. Thus, the contact between the inguinal buttress and the carapace would have been restricted to the seventh and eighth peripherals. It is likely that the axial buttress had a similar restricted area of contact, although the anterior peripherals are only seen in dorsal view so the articular surface for the hypoplastron cannot be seen.

As reconstructed, the eighth costal articulates with the eleventh, rather than the tenth, peripheral (Fig. 7). The presence of this contact is a result of the greater posterior slope of the eighth costal rib. However, the increased slope of the costal could be the result of a slight deformation of the seventh or eighth costals, resulting in a reorientation of the lateral rib of the eighth costal. Thus, it is uncertain if the articulation of the eighth costal and the eleventh peripheral is a natural feature of the taxon, so it is not included in the diagnosis.

The juvenile specimens differ from the adult individual in that the peripherals are less well ossified. The peripheral series of GSGM 07-CM-017, the smallest available individual, is represented by a narrow band of bone that varies little in
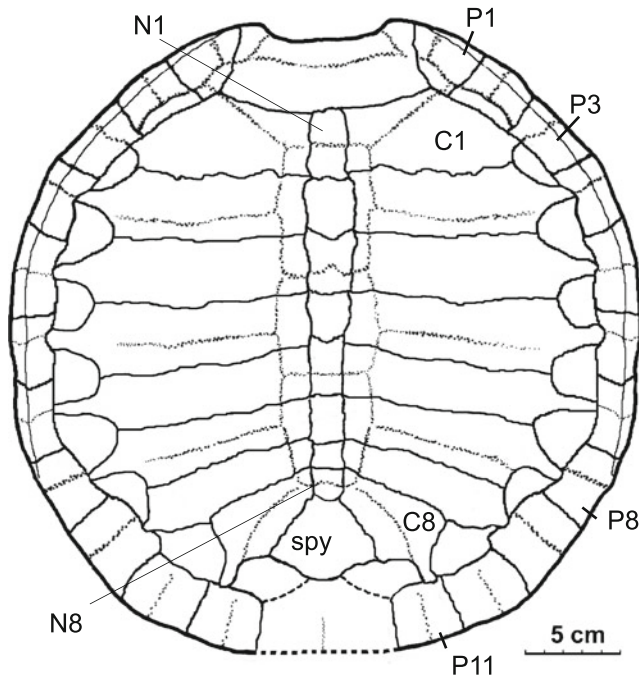

Fig. 7 Reconstruction of carapace of *Changmachelys bohlini*, gen. et sp. nov. based on CAGS IG-02-0902. Sutures are *solid lines*, sulci *dotted lines*, inferred sutures *dashed lines*. *C1* first costal, *C8* eighth costal, *N1* first neural, *N8* eighth neural, *P1* first peripheral, *P3* third peripheral, *P8* eighth peripheral, *P11* eleventh peripheral, *spy* suprapygal series

thickness though its entire length (Fig. 4). In GSGM 05-CM-016, which is intermediate in size, the posterior peripherals are only slightly wider than the anterior and lateral peripherals (Fig. 3).

The suprapygal series of the holotype specimen is preserved in articulation, but sutures are difficult to identify so the number and shape of these elements are uncertain. The posterior suprapygal has a posterior extension at the mid-line, presumably to contact the pygals and to separate costal-peripheral fenestrae between the eighth costal and the suprapygal. In GSGM 05-CM-016, the suprapygal is a plate-like element of subequal width and length (Fig. 3).

The pygal is not preserved on any of the available specimens.

Sulci on the carapace are only visible on the holotype specimen. These are broad, shallow grooves that are generally distinct. The nuchal scute is wide. The first vertebral scute is wide anteriorly, but narrows posteriorly. Its contact with the second vertebral is located near the posterior end of the first costal. Vertebrals two and three are narrow scutes with nearly straight lateral edges. The width of the anterior half of vertebral four is similar to that of vertebral three. The posterior half of vertebral four tapers inward so the contact with the anterior edge of the fifth vertebral is much narrower. The fifth vertebral is fan-shaped, widening posteriorly so its posterior end is more than double the width of its anterior end. The pleurals are wide, rectangular scutes. The pleural-marginal sulcus between the first pleural and the peripherals is located on the first and second peripherals. A strong change in elevation is present across this sulcus, with the marginal being elevated relative to the pleural. Farther posteriorly, the sulcus is located on the unossified area between the peripherals and costals.

Plastron: The plastron is preserved only in the subadult specimens. As is generally the case in Early Cretaceous eucryptodires from Asia, the plastron is much smaller than the carapace and is generally cruciform in shape. The bridge is narrow and the lateral edge of the plastron expands to give a long contact with the peripherals, extending from the third peripheral anteriorly to the eighth posteriorly. Large fenestrae are present medially between the hyo- and hypoplastron and between the plastron and the peripherals, and a smaller fenestra is present between the hypoplastron and the xiphiplastron. Because the plastron of the holotype specimen is not preserved, it is not known if these fenestrae are retained in adults. In specimen GSGM 05-CM-016, as preserved, the axillary buttress extends to the third peripheral and the inguinal buttress extends to the seventh and eight peripherals (Fig. 3). The position of the axillary buttress in this specimen differs from the typical "macrobaenid" condition since it usually extends to the second peripheral, and the possibility that this is a result of displacement of the

hyoplastron or distortion of the carapace must be considered. However, the second peripheral in GSGM 05-CM-016 is partially covered by the humerus, so it is not possible to determine whether or not a contact was present with that bone.

Epiplastra are not preserved on any of the available specimens. The entoplastron, present in the holotype specimen, has the long, narrow shape typical of "macrobaenids". The hypoplastra bear a series of long pegs on their medial edges that would have provided a strongly interdigitating midline suture. Xiphiplastra have a rounded posterior end.

Sulci cannot be identified on the plastron of any of the available specimens.

Vertebrae: The neck, completely preserved in GSGM 05-CM-016, is short, about equal to the skull in length (Fig. 3). A strong bend in the neck indicates that it was highly flexible in the horizontal plane. Individual centra cannot be recognised in GSGM 05-CM-016, but the atlas, axis, and three isolated cervical centra are present in the holotype specimen (Figs. 6a, b, 8). The axis is opisthocoelous. Both the posterior cotyle and the anterior condyle are taller than wide. Transverse processes are long and located at the anterior end of the centrum. Post-zygapophyses are flat and narrower than the transverse processes. A strong crest on the neural arch extends the length of the neural arch. A mid-ventral keel ends in a pair of tubercles on the posterior edge of the centrum below the posterior cotyle. The three more posterior cervicals are all procoelous, indicating that a biconvex centrum must have been present in the middle of the neck. The ventral keel, visible on the more anterior of these centra, is more strongly developed than on the atlas.

The first and second dorsal vertebrae are visible in the holotype specimen and in GSGM 05-CM-016. In the holotype specimen, these remain attached to the first neural. A
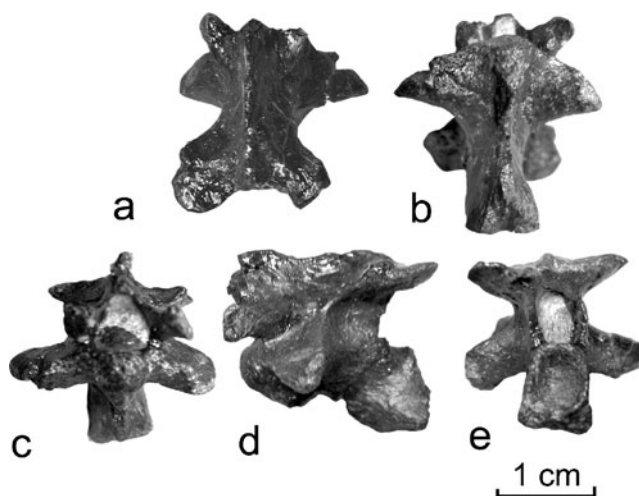

Fig. 8 Axis of *Changmachelys bohlini* gen. et sp. nov., from type specimen CAGS IG-02-0902, in **a** dorsal, **b** ventral, **c** anterior, **d** left lateral, and **e** posterior views

longitudinal break in the first neural exposes the tall, narrow neural spines of these centra. A slender element attached to the transverse process is interpreted as the first dorsal rib. In GSGM 05-CM-016, the first and second dorsal vertebrae are visible in ventral view anterior to the hyoplastron. The centra are short and have a low mid-ventral keel.

The sacrum is represented in the holotype specimen by an isolated vertebra that is relatively short and has large articular surfaces for the sacral rib. The posterior end of the centrum is flat.

Much of the tail is preserved in both the holotype specimen and GSGM 05-CM-015 (Figs. 2, 5). In both specimens, the base of the tail is disarticulated, but the distal end is articulated and is in the approximately correct position relative to the shell. All caudal centra are short. The transverse processes of the most anterior caudals of the holotype specimen are approximately equal to the length of the centrum and are directed strongly laterally. These become shorter and more posteriorly oriented and are lost mid-way along the tail. The haemal spines of the more posterior caudal vertebrae of the holotype specimen appear oversized relative to the size of the centra, but are normally developed in GSGM 05-CM-015.

Appendicular skeleton: The scapula has a long dorsal process and a short acromion process. These processes form an angle of approximately 90° with each other. A distinct neck is present supporting the glenoid. The coracoid is a flattened, fan-shaped element intermediate in length between the scapular and acromion processes. The glenoid is oval in shape, longer than high.

The forelimb is present in all specimens, and is fully articulated in CAGS 07-CM-017 (Fig. 4) and CSGM 05-CM-015 (Figs. 5, 9a). In the holotype specimen, the proximal and distal ends of the humerus are not fully preserved so the length of the element is uncertain. The ulna is slightly longer than the radius and is more robust. In the juvenile specimens, the humerus is nearly straight, with only a slight curvature of the proximal and distal edges. The proximal end is enlarged so that the width of the proximal end is about three times the diameter of the humerus. The medial process is larger than the lateral and the intertrochanter fossa is broad. The distal end is about twice as wide as the diameter of the humerus. The radius and ulna are both relatively straight elements that are about two-thirds the length of the humerus. In GSGM 07-CM-017, the smallest of the available specimens, a large gap is present between the humerus and the radius/ulna, reflecting the extensive development of cartilage on the ends of these limb bones.

The elements of the carpus in the holotype specimen are well ossified and have distinct articular surfaces, indicating that they would have been closely articulated. In GSGM 05-

CM-015 (Fig. 9a), four poorly ossified, round carpal elements are present. The two larger elements are tentatively identified as the ulnare and intermedium, and the two smaller elements as the second and third distal carpals. In GSGM 07-CM-017, only two carpal elements are ossified (Fig. 4).

All five metacarpals are preserved in GSGM 07-CM-017 (Fig. 4). The first is a short, broad element. The remaining four are subequal in length but differ in thickness, the fourth and fifth being progressively more slender compared to the third.

The phalanges of the holotype specimen are disarticulated, but a fully articulated hand is present in GSGM 05-CM-015 (Fig. 5) and GSGM 07-CM-017 (Fig. 4). The length of the hand measured from the centre of the carpus is about twice that of the ulna, proportions that are indicative of a strongly aquatic mode of life (Joyce and Gauthier 2004). The phalangeal formula is 2, 3, 3, 3, 3, with the third toe being the longest. The unguals are long and strongly curved. In contrast to the more proximal joints, little space is present between the individual phalanges despite the immature stage of development of these specimens.

The pelvic girdle is well ossified in all specimens. The ilium has a tall, robust shaft with a straight anterior edge and a slender posterior process. These proportions vary little with development. The pubis and ischium are subequal in size. The pectineal process of the pubis is robust and is only
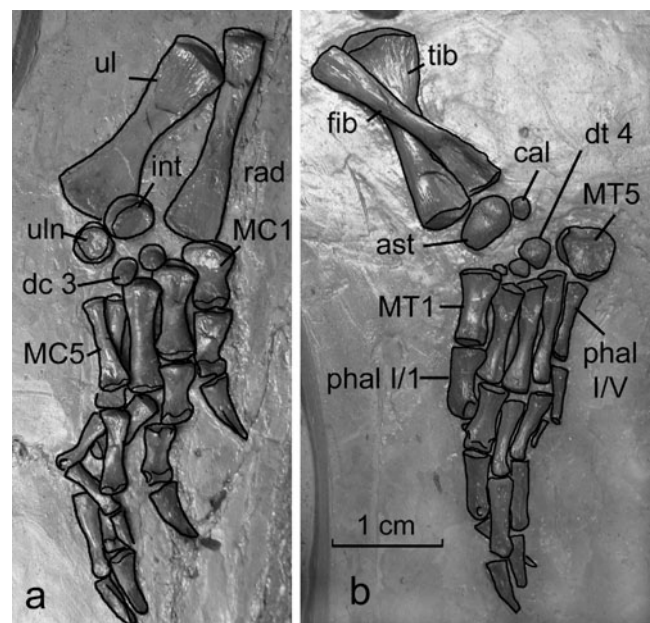

Fig. 9 *Changmachelys bohlini* gen. et sp. nov., articulated hand and foot of specimen GSGM 05-CM-015. **a** right hand, **b** right foot. *ast* astragalus, *cal* calcaneum, *dc 3* distal carpal 3, *dt 4* distal tarsal 4, *fib* fibula, *int* intermedium, *MC1* metacarpal 1, *MC5* metacarpal 5, *MT1* metatarsal 1, *MT5* metatarsal 5, *phal 1/I* first phalanx of first digit, *phal 1/V* first phalanx of fifth digit, *rad* radius, *tib* tibia, *ul* ulna, *uln* ulnare

slightly smaller than the medial process. The posterior process of the ischium is long and slender.

The femur is elongate and relatively straight and has an oval-shaped proximal articular surface. Tibia and fibula are 70 % the length of the femur and about 25 % longer than the radius and ulna. The tibia is slightly longer than the fibula.

The hind foot of the holotype specimen is represented by an astragalocalcaneum, three distal tarsals, the third to fifth metatarsals preserved in articulation, plus disarticulated and scattered phalanges. The astragalus and calcaneum are fully fused and the distal tarsals are fully ossified so they are closely articulated with one another. The distal tarsals are subequal in size. As with the carpus, the tarsus of juvenile individuals is less fully ossified. In GSGM 05-CM-015, the tarsus includes five elements: the astragalus, calcaneum, and the second to fourth distal tarsals (Fig. 9b). The astragalus is the larger of the two proximal tarsal bones and is located distal to the tibia and fibula. The calcaneum is a much smaller element lateral to the astragalus and distal to the fibula. The distal tarsals are rounded blocks of bone that decrease in size from the fourth to the second.

The metatarsals and phalanges are articulated in GSGM 05-CM-015. These are well ossified with little space between them (Fig. 9b). The first metatarsal is relatively short and robust. The second to fourth metatarsals are subequal in length. A plate-like fifth metatarsal is in position adjacent to the fourth distal tarsal.

Discussion

With the presence of a low domed carapace with a reduced, cruciform plastron that has poorly developed buttresses not extending onto the costals, *Changmachelys bohlini* is similar to Early Cretaceous turtles from Asia that are generally included in the "Macrobaenidae". To evaluate the relationships of *C. bohlini* to these "macrobaenids", a cladistic analysis was undertaken. The data matrix used by Zhou (2010a, b), which was based on that of Parham and Hutchison (2003) and Vandermark et al. (2009), was the basis for our analysis. Because the goal of this study was to interpret the interrelationships of "macrobaenids" from Asia, the taxa included were those generally considered to be "macrobaenids" and/or sinemydids, and taxa that have been thought to be related to them, with *Proganochelys quenstedti* and *Kayentachelys aprix* included as outgroups. In addition to *C. bohlini*, two other Asian taxa were added: *Annemys*, using data presented in Sukhanov (2000) and Brinkman et al. (2012), and *Wuguia*, using data presented in Matzke et al. (2004), Matzke and Maisch (2004), and Danilov and Sukhanov (2006). Also, two characters were

added: character 44, vertebral scute width (wide vs. narrow), and character 45, surface texture of the carapace (vertebral and pleural scutes smooth or with plications extending posteriorly from sulci). Following Knauss et al. (2011), kinosternoids are included within Chelydroidea. The resulting data matrix included 21 taxa and 45 characters (Appendix 1). This data matrix was analysed with PAUP*4.0 beta 10 (Swofford 2002) using the Branch-and-Bound search options. All characters were given equal weight and multistate characters were treated as unordered. The search recovered 122 most parsimonious trees with a consistency index (excluding uninformative characters) of 0.4536, a homoplasy index of 0.5464, and a retention index of 0.6882. As in the analysis of Zhou (2010a, b), the strict consensus tree fails to resolve the relationships of the Early Cretaceous and Jurassic eucryptodires from Asia (Fig. 10a). However, it differs in that the Late Cretaceous "macrobaenids" *Judithemys* and *Aurorachelys* form a monophyletic group that is a sister taxon to the crown-group cryptodires. More resolution of relationships is apparent in the 50 % majority rule consensus tree (Fig. 10b). In this tree, *Changmachelys bohlini* is a sister taxon to *Kirgizemys* spp., and the *Changmachelys bohlini* + *Kirgizemys* spp. clade is the sister group to the Late Cretaceous "macrobaenid" plus crown group cryptodires. In other aspects, the tree is similar to the consensus tree obtained by Zhou (2010b). Thus, the addition of the new species and new characters to previous phylogenetic analyses does not resolve the interrelationships among Early Cretaceous eucryptodires from Asia, but it does suggest that *Changmachelys* and *Kirgizemys* are relatively closer to crown-group cryptodires.

Patterns of ontogenetic development

The presence of a series of articulated specimens of three distinct sizes provides an exceptional record of the post-hatchling ontogenetic development of this taxon. Because the holotype specimen is one of the largest known Early Cretaceous "macrobaenids", it can be considered to be a fully mature adult despite the presence of well-developed costal-peripheral fenestrae, a feature that is generally considered typical of juveniles. Specimens GSGM 05-CM-015 and GSGM 05-CM-016 are from individuals with a carapace slightly less than half the length of the carapace of the holotype specimen. The smallest individual, specimen GSGM 07-CM-017, which has a carapace of 4.7 cm in length, is 12 % of the length of the holotype specimen.

Differences in the skull of the smallest and largest individuals differ in that the orbits are relatively large in the juvenile compared to the adult and the size of the skull relative to the carapace in the juvenile individual is greater than in the adult. In the presence of a deep cheek

Fig. 10 Results of PAUP
analysis. **a** Strict consensus
cladogram of 122 most
parsimonious trees (TL=100
steps, CI=0.4700, HI=0.5300,
RI=0.6882, RC=0.3235); **b**
50 % majority rule consensus
cladogram. The *numbers* refer
to bootstrap values
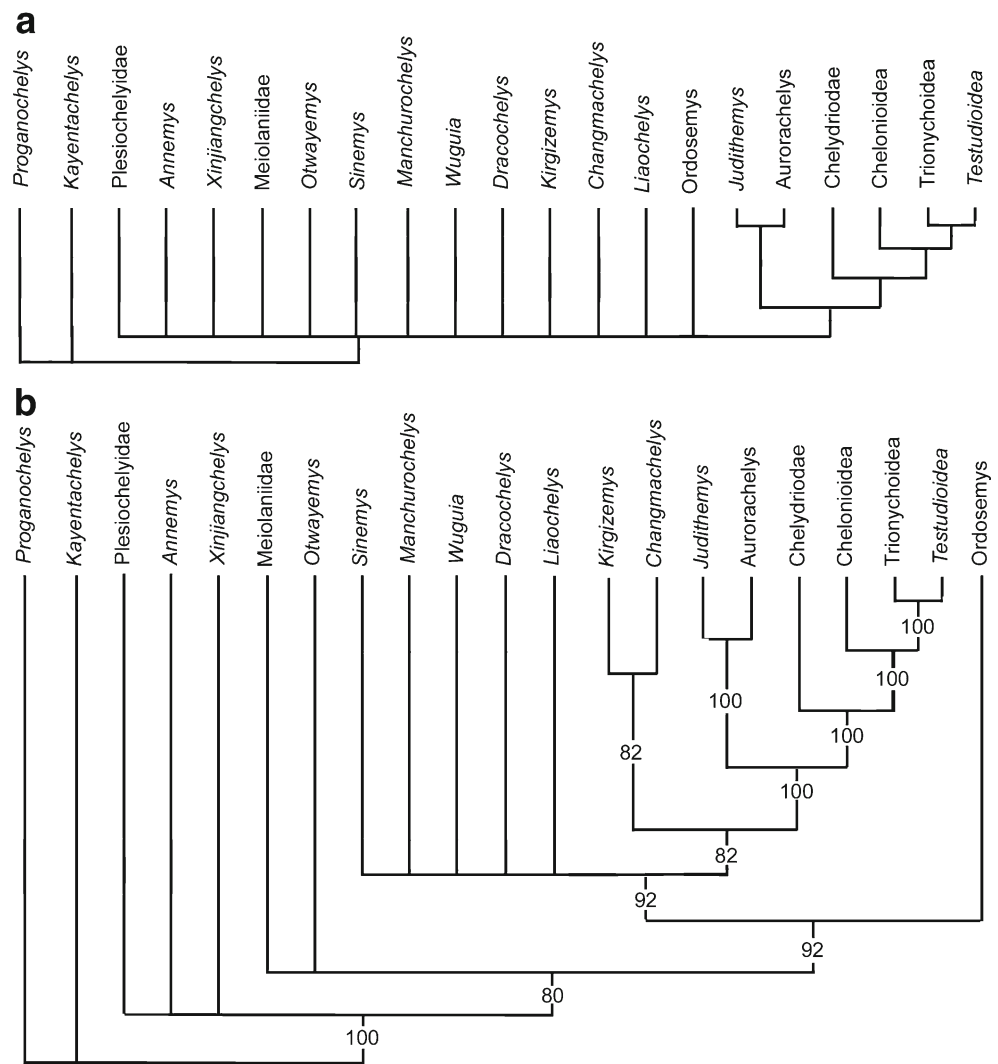
emargination, long, narrow supraoccipital crest, contact of
the prefrontals at the midline, and position of the jaw joint
relative to the posterior end of the skull, the subadult skulls
agrees with that of the adult.

The shell undergoes significant change in the degree of
ossification during development. Ossification of the costals
is delayed compared to extant turtles, such as *Chelydra
serpentina*. In the most juvenile of the available specimens
of *Changmachelys bohlini*, none of the ribs show the devel-
opment of dermal bone. In contrast, in a juvenile specimen
of *Chelydra serpentina* that has a carapace 5 cm long
(specimen TMP 1990.7.435), all the costals have dermal
bone along the proximal quarter of their length.

The ossification of the peripherals precedes that of
the dermal portion of the costals based on the observa-
tion that the most juvenile carapace that is available has
a nearly full ring of peripherals. It is unclear whether or
not the missing peripherals on that specimen are lost or
unossified. The former is considered more likely be-
cause cervical vertebrae are also missing.

In contrast with the late ossification of the carapace,
the plastron ossifies relatively early. Among the three
sub-adult individuals, very little difference is present in
degree of ossification of the plastron of the most juve-
nile and the most mature individuals.

This pattern of early ossification of the plastron relative
to the carapace is common for turtles and is seen in a
number of basal eucryptodires from Asia. In *Yaxartemys
longicaudata*, which is represented by a juvenile skeleton,
plastron elements are distinct whereas the costals show little
or no development of dermal bone (Riabinin 1948). No
peripherals are evident, so it is possible that in *Y. long-
icaudata* development of the peripherals is even more
delayed than in *C. bohlini*. *Changisaurus microrhinus* from
the Jurassic of southern China, originally described as a
lizard by Young (1959) and reinterpreted as a turtle by
Baird (1948), is of equally small size but does have
peripherals.

The presence of a poorly ossified carapace but well-
ossified plastron in the most subadult individuals of these

early eucryptodires mirrors the pattern of ossification of the shell in the earliest turtle, *Odontochelys semitestacea*, which has a well-developed plastron but poorly ossified carapace (Li et al. 2008). However, *Odontochelys semitestacea* does not have ossified peripherals. Because these generally appear early in the ontogenetic development of basal eucryptodires, it is likely that the lack of an ossified carapace in *Odontochelys semitestacea* is primitive, rather than a secondary feature associated with the development of an aquatic mode of life as suggested by Reisz and Head (2008).

Biogeographic patterns

Distinct biogeographic patterns of distribution of fossil fish in the Early Cretaceous of Asia have been recognised by Chang and Miao (2004). Because turtles are widely distributed in this area and are of high diversity, they provide an independent test of the extent to which these patterns are common to aquatic vertebrates. With the fish, one of the most striking patterns is the presence of an assemblage of teleosts dominated by osteoglossomorphs in Gansu and localities to the east, and an assemblage of more basal teleosts in Xinjiang to the west. A similar east–west division of turtles is suggested by the presence of *Sinemys* and *Sinochelys* in Gansu and Shandong but not Xinjiang (Tong and Brinkman 2012). Because *Changmachelys* occurs only in the Changma Basin, it does not contribute to the definition of regional biogeographic patterns. Rather, its restricted distribution suggests that the presence of basins with internal drainage in China during the Cretaceous had a significant effect on turtle evolution in the Cretaceous of China, with basins tending to develop endemic taxa.

Appendix 1

Data matrix used to evaluate the relationships of *Changmachelys bohlini* gen et sp. nov.

1. Nasals 0: present; 1: absent.
2. Prefrontals meet 0: not on midline; 1: on midline,
3. Prefrontal-vomer contact 0: no; 1: yes.
4. Processus pterygoideus externus 0: no flange; 1: with vertical flange.
5. Foramen palatinum posterius 0: small or moderate; 1: very large.
6. Interpterygoid vacuity 0: open; 1: closed.
7. Processus trochlearis oticum 0: absent; 1: present.
8. Middle ear with 0: nothing 1: pterygoid floor.
9. Canalis caroticus internus 0: not formed by pterygoid; 1: partially or entirely by pterygoid.
10. Canalis caroticus internus 0: formed partially by pterygoid; 1: formed entirely by pterygoid.
11. Split between palatine artery and internal carotid artery 0: outside skull; 1: embedded in bone.
12. Floor of canalis caroticus internus 0: thin or absent; 1: thick.
13. Palatine artery 0: palatine equal to or greater than carotid; 1: palatine less than carotid.
14. Foramen posterius canalis carotici interni formed by 0: BS or PT; 1: BS and PT as in baenids.
15. Fenestra perilymphatica 0: large (normal); 1: small.
16. Blind pits on BS 0: no; 1: yes.
17. Posterior temporal emargination 0: not developed; 1: at least partially developed.
18. PA-SQ contact 0: present; 1: absent.
19. PO-SQ contact 0: present; 1: absent.
20. Vertebral articulations 0: platycoelous or amphicoelous; 1: formed: concavo-convex.
21. Transverse process of cervicals 0: on middle of centrum; 1: on anterior of centrum.
22. Posterior cervicals with 0: no ventral process; 1: ventral process.
23. Cervical ribs 0: present; 1: absent.
24. Cervical 4 0: amphicoelous 1: biconvex; 2: opisthocoelous.
25. Cervical 8 0 amphicoelous; 1 procoelous; 2; biconvex; 3: opisthocoelous.
26. Double articulation between cervicals 7 and 8 0: no; 1: yes.
27. Transverse processes on cervicals 0: double; 1: single.
28. Spine on cervical 8 0: high; 1: low.
29. Biconcave caudal 0: absent; 1: present.
30. Caudal centra 0: amphicoelous or opisthocoelous; I: procoelous.
31. Chevrons 0: well developed; 1: small or absent.
32. First thoracic rib 0: extends to peripherals; 1: fails to reach peripherals.
33. First thoracic centrum, 0: faces anteriorly; 1: faces strongly anteroventrally.
34. Mesoplastra 0: present; 1: absent.
35. Ligamentous carapace-plastron attachment 0: no, sutured; 1: yes.
36. Supramarginal scales 0: present; 1: absent.
37. Dorsal process on epiplastron 0: present; 1: absent.

38. Entop1astron separating epiplastron 0: yes; 1: no, epi-plastra broadly contact.
39. Epiplastron 0: broad; 1: narrow.
40. Gular (extragular) scales 0: present, full set; 1: absent, one set.
41. Carapace greater than 30 cm long 0: no; 1: yes.
42. Neural shape 0: rectangular; 1: hexagonal.
43. Distance between antero-lateral tip of hyoplastron and postero-lateral tip of hypoplastron 0: much greater than bridge; 1: much shorter than bridge 2: subequal to the length of the bridge.
44. Vertebral scutes 0: wider than long; 1: narrow.
45. Surface texture, plications extending posteriorly from sulci 0: absent; 1: present.

Data matrix

Proganochelys	00000 00000 00?00 00000 00000 00000 00000 00000 00000
Kayentachelys	00110 01000 00?00 00000 00000 00?00 00000 10000 00200
Plesiochelyidae	01110 11111 00000 01000 00100 01?00 00010 11100 01200
Xinjiangchelys	??1?? ??111 0000? ?1??0 10000 000?? ?1011 11100 10000
Annemys	01111 01110 00000 01000 00?00 0110? ???01 0? 10? 01010
Meiolaniidae	00110 11111 01?00 00001 00011 00000 00011 10100 1?200
Otwayemys	????? ????? ????? ???01 00?12 000?0 00011 11100 0?000
Sinemys	00111 11111 00000 11111 10022 01?11 00011 11111 00010
Dracochelys	?1111 11111 00?0? 111?1 00022 0?0?? ?0011 11111 00000
Kirgizemys	01111 11111 1100? 11001 11111 010?? ?1011 11111 00011
Ordosemys	00110 11111 0000? 11101 10012 00011 00011 101?? 00000
Liaochelys	01??0 ?1??? ????? ?1101 110?? ?1??? 1??11 1???? 00000
Manchurochelys	00?0? 11110 ?0?1? 11111 11??? ?1101 0??11 1???? 00010
Wuguia	????? ????? ????? ????? ????? ????? ?0?01 1?11? 00011
Changmachelys	11?11 11111 ???0? 01001 11111 ?1??1 0?011 1???? 10010
Judithemys	?1?10 11111 1100? 11??1 11111 01011 11011 11111 11000
Aurorachelys	????? ????? ????? ????? ????? ????? ????? ????? 11010
Chelydroidea	11110 11111 11100 01101 11111 01111 01111 11111 01111
Chelonioidea	01110 11111 11000 01101 11111 11101 11111 11111 11110
Trionychoidea	11110 11111 11000 01111 11111 11101 11110 11100 01210
Testudinoidea	11110 11111 11100 01111 11112 11101 11110 11101 01210

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