THE FIRST SOFT-SHELLED TURTLE FROM THE JEHOL BIOTA OF CHINA

LU LI,1,2 WALTER G. JOYCE,3,* and JUN LIU1

1Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China, liului@ivpp.ac.cn; liujun@ivpp.ac.cn;
2University of Chinese Academy of Science, Beijing 100049, China; 3Department of Geosciences, University of Fribourg, 1700 Fribourg, Switzerland, walter.g.joyce@gmail.com

ABSTRACT—A new turtle from the Early Cretaceous (Aptian) Jehol Biota of western Liaoning, China, Perochelys lamadongensis, gen. et sp. nov., represents the first species of soft-shelled turtle from the Jehol Biota. The new taxon is diagnosed by the combination of the following characters: nuchal bone about five times wider than long; preneural absent; reversal of the orientation in the neural series at neural V; neural series fully separates costal series; costal VIIIIs reduced; plastral callosities poorly developed and poorly sculpted; postorbital bar narrow, around one-fourth of orbit diameter; jugal contacts squamosal; foramen jugulare posterius separated from fenestra postotica; neural spines weakly developed on anterior cervicals; and phalangeal formula for pes 2-3-3-4-?. High levels of homoplasy make the phylogenetic relationships of the new taxon difficult to assess, and the possibility therefore exists that Perochelys lamadongensis either represents a stem or a crown trionychid. This phylogenetic uncertainty confirms that the skeletal morphology of trionychids has remained virtually unchanged for the last 120 million years.

http://zoobank.org/urn:lsid:zoobank.org:pub:1FE50A16-5FE6-4DEE-B839-CE2A52038F55

INTRODUCTION

The Early Cretaceous (Aptian) Jehol Biota of China is famous for its great variety of exceptionally preserved fossils that provide important insights into a wide range of evolutionary, paleoecological, and phylogenetic questions (Chang et al., 2003; Zhou et al., 2003). Turtles were one of the earliest reported vertebrates (Chang et al., 2003; Zhou et al., 2010a), but the group has attracted significantly less attention relative to many other groups, although many well-preserved specimens are housed in public institutions. The first named turtle from the Jehol biota is Manchurochelys manchoukuoensis (Endo and Shimada, 1942; Zhou, 2010a). The second species, Manchurochelys liaoxiensis, was not named until 1995 (Ji, 1995). This species was soon after restudied and transferred to the genus Ordosemys (Li and Liu, 1999; Tong et al., 2004). Recently, a third species, Liaocheles jiangangensis, was reported from the Jiufotang Formation of Jianchang County, Liaoning Province (Zhou, 2010b). Here we report a new species of turtle from the same locality as L. jiangangensis that represents the first soft-shelled turtle from the Jehol Biota and that provides valuable information into the early evolution of the group.

Soft-shelled turtles (Trionychidae) are an ancient, morphologically unique, and highly specialized group of aquatic cryptodires (Meylan, 1987; Ernst and Barbour, 1989; Engstrom et al., 2004; Scheyer et al., 2007; Joyce et al., 2013). Although the monophyly of this group has never been questioned, the relationship of Trionychidae to other extant cryptodiran turtles has been controversial. Trionychidae plus Carettochelyidae form the clade Trionychia (Gaffney and Meylan, 1988; Meylan, 1988; Meylan and Gaffney, 1989; Shaffer et al., 1997; Joyce et al., 2004; Joyce, 2007). Molecular studies place this clade at the base of crown-group Cryptodira (Shaffer et al., 1997; Krenz et al., 2005; Parham et al., 2006; Shaffer, 2009; Barley et al., 2010; Lourenço et al., 2012), whereas unconstrained morphological studies support a more derived position within Cryptodira (Gaffney and Meylan, 1988; Joyce, 2007; Sterli, 2010; Anquetin, 2011; Sterli et al., 2013). The phylogenetic relationships among modern soft-shelled turtle species are still controversial, but it is generally accepted that Trionychidae consists of two clades, Cyclanorbinae and Trionychinae, and that Trionychinae includes some well-supported monophyletic clades (Meylan, 1987; Engstrom et al., 2004). The taxonomy and phylogenetic relationships of fossil trionychid species are far more controversial, and very little is known regarding the origin and early radiation of this group (Gardner et al., 1995; Joyce and Lyson, 2010, 2011; Vitek and Danilov, 2010, 2012; Danilov and Vitek, 2013; Joyce et al., 2013). The early record of soft-shelled turtles is poor, and most taxa are based either on fragmentary shells or skulls (Yeh, 1994; Hutchison, 2000; Sukhanov, 2000; Danilov and Vitek, 2013). More complete Mesozoic skull-shell-associated materials have been described only for trionychids from the Campanian and Maastrichtian of North America (Gardner et al., 1995; Brinkman, 2005; Joyce and Lyson, 2011; Vitek, 2012) or the Cenomanian–Santonian of Mongolia (Danilov et al., 2014). The new material described herein is a nearly complete skeleton and therefore represents the first complete Early Cretaceous skull-shell-associated trionychid worldwide.

Age and Geological Context

The specimen described herein was excavated from the Xiaotaizi locality, Lamadong, Jianchang County, Huludao City, Liaoning Province, China. This locality is situated about 100 km west of Huludao City and 135 km southwest of the famous Sihe-tun locality. The holotype comes from the Xidian bed of the first member of the Jiufotang Formation (Duan et al., 2010). The basalt from the Jiufotang Formation was dated at 110.59 ± 0.52 Ma in Tebch, Inner Mongolia (Eberth et al., 1993). In Liaoning,
the lower Jiufotang Formation yielded an age of 120.3 ± 0.7 Ma (He et al., 2004). Recently, a tuff from the base of the Jiufotang Formation was reported an age of 122.1 ± 0.3 Ma (Chang et al., 2009). We therefore deduce that the fossil is approximately 120 Ma, or Aptian in age.

MATERIALS AND METHODS

We investigated the phylogenetic placement of the new trionychid taxon by integrating it into the only well-established character/taxon matrix (Meylan, 1987), as expanded by Joyce et al. (2009) and Joyce and Lyson (2010, 2011). This matrix has since been further expanded through the modification of characters and through the addition of taxa and characters (Vitek, 2011, 2012), but we purposefully use the matrix as published by Joyce and Lyson (2011), because all characters and taxa added by Vitek (2011, 2012) are focused on resolving the phylogenetic relationships of North American trionychids and are therefore not relevant to the specimen at hand. To better resolve the phylogenetic placement of the new taxon, we undertook a concerted search for additional characters, including in the relevant literature (Meylan, 1987, 1988; Meylan and Gaffney, 1989; Vitek, 2011, 2012), but we were unable to find any parsimony informative characters, which further highlights the small amounts of morphological variation that are apparent within the ingroup.

The new turtle could be scored for 45 of 83 cranial and postcranial characters from all major anatomical regions. The scoring for the new taxon is 4212412311 11?04?12?2 ?1?23????? ?????????? ??1?????? 1?1?121117 1?21?0000 00000002???? 000. To avoid the pitfalls associated with using a hypothetical ancestor (see Joyce and Lyson, 2010, for extensive discussion), polarity was created by using a molecular scaffold (Engstrom et al., 2004) and by assuming a monophyletic Trionychinae and Cyclanorbinae (Joyce et al., 2009; Joyce and Lyson, 2010, 2011). All characters were left unordered and unweighted, and the most parsimonious result was retrieved by running 1000 randomly seeded heuristic searches using PAUP 4.0b10 (Swofford, 2002).

SYSTEMIC PALEONTOLOGY

TESTUDINES Batsch, 1788
CRYPTODIRA Cope, 1868
TRIONYCHIA Hummel, 1929
PAN-TRIONYCHIDAE Joyce et al., 2004
PEROCHELYS LAMADONGENSIS, gen. et sp. nov. (Figs. 1–3)

Etymology—per-, continuous (Latin), in allusion to the continuous neural series that fully separates the costals; ‘chelys,’ turtle (Greek); ‘lamadong,’ in reference to the type locality.

Holotype—IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V 18048, a nearly complete skeleton.

Locality and Horizon—Xiaotaizi locality, Lamadong, Jianchuan County, Huludao City, Liaoning Province, China: 41°32.142′N, 121°04.042′E; Jiufotang Formation; Aptian, Lower Cretaceous.

Diagnosis—Perocheles lamadongensis can be diagnosed as a representative of Pan-Trionychidae by the presence of a ‘V’-shaped entoplastron and a ‘L’-shaped epiplastra and the absence of peripheral and pygal bones. Within Pan-Trionychidae, P. lamadongensis differs from cyclanorbines and plastomenids by reduced development of the bridge and all plastral elements. Among pan-trionychid taxa with a reduced plastron, P. lamadongensis differs from all by the combined absence of a preneural, presence of a wide nuchal, lack of a midline contact of any costal (otherwise only present in Dogania subplana), and the great reduction of costal VIII (absent in Dogania subplana).

DESCRIPTION

IVPP V 18048 is a nearly complete skeleton originally exposed in dorsal view (Fig. 1). The skull and shell, however, were also prepared in ventral view. The specimen includes a partial skull in occlusion with the mandible, the cervical series, the carapace and plastron, an articulated caudal series, the pectoral and pelvic girdles, and the fore- and hind limbs. At a certain distance, the specimens appear perfectly preserved; however, the specimen is heavily crushed and the surfaces of many bones, particularly in the skull, are damaged.

Skull and Mandibles

The skull is occluded with the mandibles (Fig. 2). They are dorsoventrally crushed, and the rostrum and much of the skull roof are damaged. The skull is lentoid in dorsal view. The distance from the broken rostrum to the posterior end of the crista supraoccipitalis is 54 mm, and the maximum width of the skull is 34 mm across the quadrates.

The premaxillae are not preserved. The left maxilla has lost its anterior end and dorsal process, whereas only a small ventral portion is preserved of the right one. The dorsal border of the posterior process of the maxilla forms the ventral margin of the orbit and posteriorly underlaps the jugal. Small nutrient foramina are distributed on the mid-ventral part of the maxilla in lateral view.

The orbit is oval and large, with a diameter about four times the width of postorbital bar (Fig. 2A). The orbit margin is formed by the maxilla ventrally, the frontal dorsally, and the postorbital and the jugal posteriorly. The interorbital bar is wider than the postorbital bar.

The prefrontals are not preserved except perhaps for the posterior tip on the left side (Fig. 2A). The left frontal is preserved, whereas the right one is missing. The frontal is a nearly triangular bone in dorsal view and forms most of the dorsal margin of the orbit. It has a narrow anterior margin contacting the prefrontal and a jagged posterior margin contacting the parietal posteriorly and the postorbital postlaterally. The postorbital is a small element between the parietal and the jugal. It is isolated from the temporal emargination as in most trionychids (Meylan, 1987). The paired parietals are quite long, extending posteriorly to approximately the level of the occipital condyle. The crista supraoccipitalis extends posteriorly, reaching the middle point of the second cervical.

The temporal emargination is elongate and very deep and the processus trochlearis oticum is exposed dorsally (Fig. 2A). The processus trochlearis oticum is trough-like, and dorsally concave. It is formed at least by the quadrate and the prootic; whether the parietal contributes to this processus is uncertain, but its contribution cannot have been large. The prootic is roughly trapezoidal and forms the major part of the processus trochlearis oticum. The large foramen stapedio-temporalis lies between the prootic and the quadrate but mainly in the former.

The jugal bifurcates into vertical and horizontal rami, but the base of the vertical ramus is lost. The vertical ramus extends dorsal-ly to contact the parietal, forming the major part of the postorbital bar; the thin, low horizontal ramus extends posteriorly to contact the squamosal and the region of the quadrate-jugal, forming almost all the temporal arch. The jugal forms the anterior limit of the cheek emargination, whose ventral margin is in line with the lower rim of the orbit. The quadrate-jugal cannot be identified due to the poor preservation of the portion between the jugal and quadrate.
FIGURE 1. IVPP V 18048, holotype, *Perochelys lamadongensis*, gen. et sp. nov., Early Cretaceous, Jiufotang Formation, Liaoning Province, China. Scale bar equals 50 mm.
The squamosal is quite long, forming the lateral wall of the temporal emargination. Its narrow anterior process is crushed ventrally, contacting the jugal and perhaps the quadratojugal. The squamosal is broadly articulated with the quadrate ventrally and medially, the opisthotic posteromedially. Its posterior crest is rather low and reaches almost as far posteriorly as the crista supraoccipitalis.

The palate is poorly preserved and provides little information (Fig. 2B). In the occiput, a foramen on the left side of the occipital condyle is identified as the foramen jugulare posterius. The posterior basicranial region is either crushed or covered by hyoid bones, but it appears that the foramen jugulare posterius is separated from the fenestra postotica, although it is unclear which bone or bones form this separation.

Both mandibular rami are preserved, although the anterior tip of the left one is missing (Fig. 2B). The two rami form an angle of about 50°. The processus coronoideus is prominently developed and has its greatest height in the middle of the lower jaw. The articularis mandibularis area is not well developed.

Hyoid Apparatus

Nine ossifications are recognized as elements of the hyoid apparatus (Fig. 2B). Their pattern is similar to that of the extant species Aspideretes hurum (Meylan, 1987). Five of them (or three pairs) form the corpus hyoidis. The posterior basibranchials are anteroposteriorly longer than the anterior pair of basibranchials, and the posterior basibranchials are split and displaced in ventral view laterally under the cornu branchiale I. The cornu branchiale I is bracket-shaped and longer than 30 mm. The cornu branchiale II likely consists of a single, narrow element.

Vertebrae and Ribs

At least five cervicals, 10 thoracics, two sacrals, and 17 caudals are present (Figs. 2, 3). Cervicals I through III are articulated with the skull and exposed in dorsal and ventral views. The remaining cervicals are covered by sediment. The atlas intercentrum was broken and split into two fragments that frame the basioccipital process. The centrum of the axis is slightly shifted to the right from the original position, whereas the atlas neural arches remain in situ. Cervicals II and III are quite long, opisthocoelous, and with a length four times their width. The ventral keel is thin and weak on the anterior half of the second centrum, unclear on the third. The neural spine is low and thin, and its height decreases towards the posterior on cervical II and III. Thoracics I through III are covered, whereas thoracics IV through X are exposed in ventral view. The thoracic centra are articulated with the ribs and with their neighbors. Two sacrals are exposed in both dorsal and ventral views. The first sacral rib is wider along its distal end than the second. The caudal centra decrease in size posteriorly, whereas the transverse processes decrease in width posteriorly.

Carapace and Plastron

The carapace is small, with a length of 123 mm and a maximum width of 136 mm (Figs. 1, 3A). It is subcircular, with a small notch at the posterior border as in the extant trionychid Dogania subplana. All costals and neurals are fully sculptured on the dorsal surface, but the nuchal only shows a hint of a callosity near its posteroomedial margin. The nuchal is bow-shaped and wide, with a width about five times its length, and the costiform processes are united. The nuchal does not have any sutural contacts with the remaining carapace. The suprascapular fontanelles are open and confluent. The neural series includes eight continuous

http://doc.rero.ch
neurals and lacks a preneural. Neural I is heptagonal and contacts two pairs of costals laterally. Neural V is tetragonal and only contacts (i.e., costal Vs) laterally. The remaining neurals are nearly hexagonal and contact two pairs of costals laterally. The anterior and posterior pairs of costal contacts are of unequal length: the shorter costal contact faces posteriorly in neurals I to IV and VIII, anteriorly in neurals VI and VII. The reversal of the orientation therefore occurs at neural V. There are eight pairs of costals, where costals III and IV are mediolaterally longer than all other costals. Costal VI is expanded along its lateral border. Costal VIIIIs do not meet along the midline and extend more posteriorly than neural VIII. The eighth costals are extremely short. Peripherals are absent.

The plastron consists of nine elements, and these elements do not form a solid plate (Fig. 3B). The general shape and interrelationships of the nine bones are very similar to those of *Pelodiscus sinensis*. Weak sculpturing is only present on the middle part of the hypopleura, hypopleura, and xiphiplastron. Although the callosities are poorly developed on the hypopleura, hypopleura, and xiphiplastron, we nevertheless score them as being present. The epiplastra are ‘J’-shaped, with an anterior extension of intermediate length. The entoplastron is boomerang-shaped, but the angle between the two rami is unclear, because the entoplastron is broken along the midline and the elements appear shifted. The hypoplastra are sutured but not fused with the hypoplastra. The hypoplastra and
hypoplastra do not meet their counterparts at the midline.
The bridge is short, less than one-fifth of the hypoplastron
width. The hypoplastron has at least three medially directed
processes, and its lateral lobe is shorter than the medial lobe.
The medial margin of the hypoplastron is poorly preserved,
but the medial hypoplastral processes seem clustered rather
than divided. The xiphiplastron meet along the midline via
their anterior and posterior medial processes; between them
lies a relatively large fenestra. The anterior xiphiplastral pro-
cesses are positioned on either side of the most lateral of the
posterior hypoplastral processes.

Girdles and Appendages

Both the pectoral and pelvic girdles are preserved (Fig. 3B).
Their shape is essentially the same as that of Pelodiscus sinensis.
The triradiate pectoral girdle is broken, and the coracoid is dislo-
cated from the scapula. The coracoid is well exposed except for
its distal end, which is hidden by the plastron. Its articular facet
for the scapula is concave. The dorsal end of the main body of
the scapula is exposed dorsal to the nuchal. This dorsal projec-
tion is rather long, longer than the acromion process. The ilium
was lost during preparation, but it was observed that the dorsal
process is curved posteriorly. The pubes are partially covered by
the plastron ventrally. The anterolaterally extended pectinal
process is wide, at least as wide as the length of interpubic
contact. The two pectinal processes lie in a single plane with the
interpubic symphysis, and they broadly contact the xiphiplastron.
The thyroid fenestra is a large, confluent opening between the
pubes and ischia, and the ischiom does not send a process into
the thyroid fenestra. The ischium produces a distinct posterolat-
eral directed process, the metischiial process.

Nearly all appendicular elements are preserved, but the pha-
langes of the hand are partially disarticulated, and it is therefore
not possible to deduce the manual formula (Fig. 1). The ecte-
condylar foramen is open. The elements of the hind limb are lon-
ger and more robust than the corresponding elements of the
forelimb. Three small phalanges that are much smaller than
most other phalanges remain articulated on the left hand. Given
that the smallest element of this series is an distal phalanx that
lacks a claw, that all elements are shorter than most other pha-
langes, and that P. lamadongensis likely had three claws
on its first three digits, we conclude that digit IV or V had a series
of at least four phalanges (Delfino et al., 2010). The observed
phalangeal series of the posterior part of the pes is 1-4-3, and the last phalanx of
digits II and III is claw-shaped, but there should be a claw on the
first digit and the formula should be 2-3-3-4 for digits I-IV.

COMPARISON AND DISCUSSION

Alpha Taxonomic Considerations

In comparison with recent trionychids, P. lamadongensis is similar to Dogania subplana, Pelodiscus sinensis, and Apalone mutica in its shell morphology. In particular, these taxa have a nuchal that has a width greater than four times its length and lack a preneural. Among recent trionychines, only members of Aspideretes have preneurals, but this character is rather common among fossils (Hay, 1908; Joyce et al., 2009). None of the costals meet along the midline in P. lamadongensis. Among recent trionychids, this condition is recognized only in Dogania subplana and unambiguously interpreted as a highly derived autapomorphy (Meylan, 1987; Engstrom et al., 2004). The costal VIIIs of P. lamadongensis are reduced, as in Apalone spp. and Rafetus spp. P. lamadongensis resembles Pelodiscus sinensis in cranial morphology: the jugal contacts the squamosal posteriorly and the parietal dorsally, the foramen jugulare posterior is separated from the fenestra postotica, the postorbital bar is moderate relative to the orbit, and the processus troclear is formed by the prootic, with less than a third being contributed from the quadrate (Meylan, 1987).

Among fossil taxa, the Late Cretaceous 'Aspideretes' maortuen-
sis has been reported to have a complete neural series (Yeh, 1965; Karl, 1999) and may therefore resemble P. lamadongensis in this regard (Table 1). However, examination of the holotype of 'Aspideretes' maortuenensis clearly reveals that this taxon has a short, diamond-shaped neural VIII that does not contribute to the carapacial rim. Both taxa nevertheless resemble one another greatly in the poor development of plastral callousities. P. lamadong-
ensis resembles the Late Cretaceous Apalone latus in having a reversal at neural V and reduced costal VIIIs. However, the lateral margin of costal V is more expanded than that of costal VI and costal VIIIs meet at the midline in the latter (Gardner et al., 1995).

P. lamadongensis is different from Aspideretoides spp. from the Late Cretaceous and Paleogene in lacking a preneural and in lacking a postorbital contribution to the upper temporal emargination (Gardner et al., 1995). The Late Cretaceous 'Trionyx' kansaensis is larger and possesses a strong nuchal emar-
gination (Vitek and Danilov, 2010). The new species is similar to the Late Cretaceous 'Trionyx' kyrgyzensis in having poorly devel-
oped plastral callousities, but differs in having an anteroposteriorly
shorter nuchal and shorter xiphiplast (Nessov, 1995). P. lamadong-
ensis is different from the Late Cretaceous Aesxenmys spp. by its small size, by lack of a preneural, and in the type of sculpt-
turing (Vitek, 2012). The comparisons between P. lamadongensis
and other Cretaceous trionychids are summarized in Table 1. The
cumulative differences fully justify recognizing it as a new species of fossil pan-trionychid.

Phylogenetic Considerations

Our phylogenetic analysis reveals that 10 most parsimonious sol-
cutions can be retrieved with 264 steps that differ only in the place-
ment of P. lamadongensis (Fig. 4). The new fossil turtle is
placed equally well as sister to the extant trionychids Nilssonia for-
mosa, Dogania subplana, or Pelodiscus sinensis, or as sister to the clades Apalonina or Gigantaestuarochelys (sensu Engstrom et al., 2004), or along the stem of Trionychinae, Cyclorinuridae, or even Trionychidae. The only portion of the tree from which P. la-
madongensis is notably absent is Cyclorinuridae and Plastomenidae.
This poor result is surprising, given that P. lamadongensis is known from a complete skeleton and could be scored for more than half
(54%) of characters. High levels of homoplasy have long been
known to make it difficult to retrieve solid phylogenetic result
within Trionychidae (Meylan, 1987) and high levels of homoplasy
(consistency index [CI] = 0.31) are clearly to blame here as well.
The observation that P. lamadongensis can be placed equally well
within the tips of the tree as well as at the base is nevertheless
revealing, because it demonstrates that it is currently still not possi-
bile to even partially unravel the morphological evolution at the
base of Trionychidae. The possible placement of P. lamadongensis
as sister to crown Trionychidae forces us to conservatively classify
the new fossil as a representative of the total group of crown Trio-
nychidae (Pan-Trionychidae sensu Joyce et al., 2004) and hints at
the possibility that the poorly ossified trionychine morphotype
seen in P. lamadongensis may be the basal condition for Trionychi-
da (see Joyce and Lyson, 2010). The frustrating lack of character
that would allow us to resolve the basal evolution of crown Triony-
chidae, by contrast, supports the notion that soft-shelled turtles
quite rapidly acquired the substantial list of characteristic traits
that distinguish them so clearly from all other turtles (Meylan,
1987), likely during the Early Cretaceous, but did not change sig-
ificantly over the course of their Late Cretaceous to Recent evo-
lution, at least as currently preserved.

The uncertainty regarding the phylogenetic placement of P. lamadongensis is highly unfortunate, because this taxon cannot
help inform the debate regarding the age of the trionychid crown. A recent molecular divergence dating analysis using highly conservative, fossil-based priors calculated the divergence of Trionychidae to range from 86 (Coniacian) to 126 (Aptian) Ma, with a mean at 105 Ma (Albian) (Joyce et al., 2013). These dates are broadly consistent with the conclusion that the Aptian P. lamadongensis might be a stem or crown trionychid. However, unless extremely high rates of morphological evolution are proposed at the base of the trionychine stem lineage, the great age of P. lamadongensis makes it more likely that the trionychine morphotype indeed represents the basal morphology of the trionychid crown group.

### Temporal Considerations

Sinaspideretes wimani was thought to be the oldest known member of Trionychidae (Young and Chow, 1953), but this view is no longer tenable (Meylan and Gaffney, 1992) and the material is now thought to represent an adocusian (Tong et al., 2014). The oldest diagnosable pan-trionychid material was therefore thought to be ‘Aspideretes’ maortuensis and ‘A’. alashanensis from Maortu, Jilantai, Alxa (Albian or Aptian), and ‘Trionyx’ kyrgyzensis from the upper part of the Alamyshik Formation of Kyrgyzstan (lower-middle Albian) (Yeh, 1965; Nessov, 1995). The Maortu turtles have since been shown to be Late Cretaceous in age (Brinkman et al., 2008). Fragmentary shell remains have recently been described from the Hauterivian to Albian of Japan under the name Kappachelys okurai that show the incipient shell microstructure of extant trionychids and therefore represent the basal stem lineage of the group (Hirayama, 2005; Nakajima et al., 2009; Hirayama et al., 2013). Although the results of our analysis are disappointing in that the phylogenetic placement of Perochelys lamadongensis is unclear, it is nevertheless apparent that this taxon is among the first turtles with modern trionychid characteristics.

### ACKNOWLEDGMENTS

We thank X.-L. Wang and Z.-H. Zhou (Institute of Vertebrate Paleontology and Paleoanthropology) for help during the collection of the specimen, R. Hirayama (Teikyo Heisei University), D. Brinkman (Royal Tyrrell Museum of Palaeontology), and C.-F. Zhou (Shenyang Normal University) for references. D. Brinkman, I. Danilov, P. Meylan, H. Tong, and N. Vitek are thanked for numerous comments that significantly helped improve the quality of the manuscript. Funding for this work was provided by National Natural Science Foundation of China Grant 41172017 and National Basic Research Program of China (973 Program) Grant 2012CB821902.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Nuchal emargination</td>
<td>Absent</td>
<td>Weak</td>
<td>Absent</td>
<td>?</td>
<td>Absent</td>
<td>?</td>
<td>Absent</td>
</tr>
<tr>
<td>Times of nuchal width to length</td>
<td>6</td>
<td>4–6</td>
<td>5</td>
<td>5–6</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Prenueal</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
<td>?</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Number of neurals</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Neural reversal</td>
<td>5 or adjacent</td>
<td>5 or 6</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Costal VIIIs reduced</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Plastral sculpturing</td>
<td>Developed</td>
<td>Developed</td>
<td>Developed</td>
<td>No</td>
<td>Developed</td>
<td>Poorly developed</td>
<td>Poor developed</td>
</tr>
<tr>
<td>Lateral hypoplastron lobe</td>
<td>Shorter</td>
<td>Shorter</td>
<td>Shorter</td>
<td>Longer</td>
<td>Longer</td>
<td>Longer</td>
<td>Shorter</td>
</tr>
<tr>
<td>Ratio of minimal bridge length to maximal hypoplastral length</td>
<td>About 50%</td>
<td>About 50%</td>
<td>About 50%</td>
<td>About 50%</td>
<td>About 50%</td>
<td>About 50%</td>
<td>About 50%</td>
</tr>
<tr>
<td>Medial hypoplastral processes</td>
<td>Divided</td>
<td>Divided</td>
<td>Divided</td>
<td>Clustered</td>
<td>Clustered</td>
<td>Clustered</td>
<td>Clustered</td>
</tr>
</tbody>
</table>

FIGURE 4. Ten equally parsimonious placements of Perochelys lamadongensis, gen. et sp. nov. (indicated in gray), within a topology imposed by a molecular scaffold. The new taxon is found throughout the tree but is notably absent only from Cyclanorbinae and Plastomenidae.
LITERATURE CITED


Scheyer, T. M., P. M. Sander, W. G. Joyce, W. Böhme, and U. Witzel. 2007. A plywood structure in the shell of fossil and living soft-
shelled turtles (Trionychidae) and its evolutionary implications. Organisms Diversity and Evolution 7:135–144.


Submitted January 15, 2014; revisions received March 17, 2014; accepted March 24, 2014. Handling editor: Juliana Sterli.

Citation for this article: Li, L., W. G. Joyce, and J. Liu. 2015. The first soft-shelled turtle from the Jehol Biota of China. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2014.909450.