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LARACHELUS MORLA, GEN. ET SP. NOV., A NEW MEMBER OF THE LITTLE-KNOWN EUROPEAN EARLY CRETACEOUS RECORD OF STEM CRYPTODIRAN TURTLES

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ABSTRACT—A relatively diverse record of European Early Cretaceous pan-cryptodiran turtles has been revealed from the analysis of new specimens and from a review of previously defined taxa. However, knowledge about many of these taxa remains relatively limited. We erect the new taxon, *Larachelus morla*, gen. et sp. nov., on the basis of a shell from the late Hauterivian–early Barremian of the Iberian Range (Spain). The comparative study of this taxon with the continental European Cretaceous pan-cryptodiran representatives and cladistic analyses reveal *L. morla* to be a member of the little-known European Early Cretaceous stem Cryptodira. Stem cryptodirans have been recognized from the Early Cretaceous of several continents. The study of *L. morla* not only confirms the presence of this group in the Early Cretaceous of Europe, it also provides new insights into the European evolution of Pan-Cryptodira. This finding reveals greater diversity in European Early Cretaceous continental pan-cryptodires, highlighting its Hauterivian–Aptian record. This diversity is particularly relevant in the Iberian Range, where several clades of turtles whose coexistence has not been recognized in the Lower Cretaceous of any other region are identified: paracryptodiran members, stem cryptodiran turtles, and representatives of several lineages of the crown group Cryptodira. This very high diversity of continental taxa shows a wide range of morphological diversity that could be related to adaptation to different ecological niches.

INTRODUCTION

Until recently, turtle diversity from the European Early Cretaceous was very poorly known (Lapparent de Broin, 2001). However, recent analyses show that it was high, being composed of several clades (Pérez-García et al., 2010, 2012). Most taxa found are members of Pan-Cryptodira. Limited knowledge of the western Laurasian early pan-cryptodires contrasts with that of their better-known Asian Early Cretaceous representatives (see Rabi et al., 2010; Tong et al., 2011).

Non-cryptodiran eucryptodires (sensu Joyce et al., 2004) are abundant and diverse in European Upper Jurassic formations, being represented by taxa that lived in coastal environments: Thalassemydidae, Plesiochelyidae, and Eurysternidae (Pérez-García et al., 2012). Recent studies have reviewed some Early Cretaceous taxa for which a phylogenetic position was controversial (e.g., *Chitraccephalus dumonii* Dollo, 1885, revised by Pérez-García, in press), studied taxa found several decades ago but not previously analyzed in detail and not named (e.g., *Sandownia harrisi* Meylan, Moody, Walker, and Chapman, 2000, and *Hoyasemys jimenezi* Pérez-García, de la Fuente, and Ortega, 2012), and defined new taxa by the study of unpublished material (e.g., *Galvechelone lopezmartinezae*, Pérez-García and Murelaga, in press). As a result of these studies, it is possible to identify several European Early Cretaceous pan-cryptodirans (Fig. 1A): members of Paracryptodira (*Pleurosternon bullockii* [Owen, 1842] and, probably, *Desmemys bertelsmanni* Wegner, 1911, “*Glyptops*” *typocardium* [Seeley, 1869], and *Dorsetochelys delairi* Evans and Kemp, 1976); non-paracryptodiran basal pan-cryptodirans (*Hylaeochelys belli* [Mantell, 1844] and *Brodiechelys brodiei* [Lydekker, 1889]);

and members of the crown group Cryptodira (*C. dumonii*, *H. jimenezi*, and *G. lopezmartinezae*, belonging to the clade that includes representatives of “Macrobaenidae,” “Sinemydidae,” and Pan-Chelonioidea; and *Peltochelys duchastelii* Dollo, 1885, and *Sandownia harrisi*, considered as potential representatives of the trionychian stem) (Meylan, 1988; Hirayama et al., 2000; Meylan et al., 2000; Lapparent de Broin, 2001; Pérez-García, 2011, in press; Pérez-García and Murelaga, in press; Pérez-García et al., 2012).

A specimen from the Early Cretaceous of the western Cameros Basin (Spain), recently recognized as a probable new eucryptodiran taxon (sensu Joyce et al., 2004) (Pérez-García and Murelaga, 2010; Pérez-García et al., 2012), is studied here. The Cameros Basin is the northwestern-most basin of the Iberian rift system. This basin is part of a group of northwest–southeast basins that originated via a rift system that initially developed during the breakup of Pangea (Salas et al., 2001). During the second rifting phase, related to the opening of the North Atlantic Ocean in the Upper Jurassic–Lower Cretaceous, non-marine deposits started to accumulate in that basin (Floquet, 1998). Alluvial fan, fluvial, and carbonate-precipitating lacustrine environments were generated in the western Cameros Basin, preserving fossils of various vertebrate groups. Studies have been focused almost exclusively on the dinosaur record, including spinosaurid and dromaeosaurid theropods, diplodocoid and titanosauriform sauropods, stegosaurian and ankylosaurian thyreophorans, basal euornithopods, dryosaurids, and basal iguanodontian ornithopods (see Torcida Fernández-Baldor, 2006; Pereda Suberbiola et al., 2011). However, the presence of several turtle taxa has recently been identified, corresponding to solemydids (stem Testudines sensu Joyce et al., 2011) and members of Pan-Cryptodira (Pérez-García et al., 2012). A partial skeleton of *C. dumonii*, and the specimen studied here, has been

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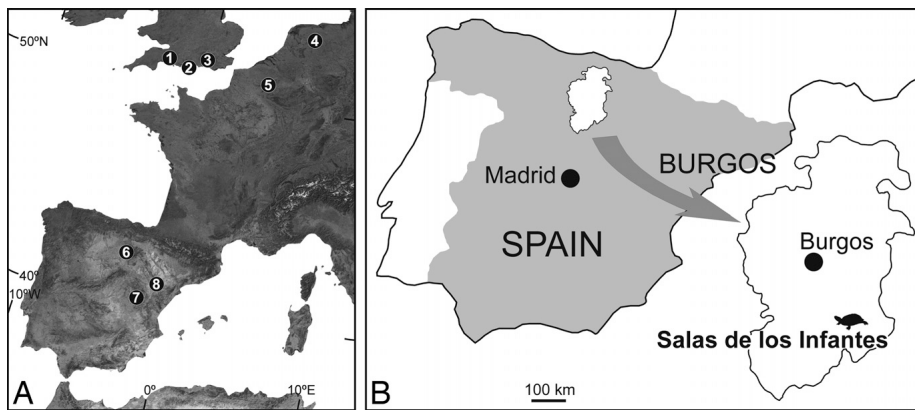


FIGURE 1. A, type localities of the European Early Cretaceous pan-cryptodiran turtles. 1, Dorset (United Kingdom), type locality of *Pleurosternon bullockii*, “*Glyptops*” *typocardium* and *Dorsetochelys delairi*; 2, Isle of Wight (United Kingdom), type locality of *Brodiechelys brodiei* and *Sandownia harrisi*; 3, Sussex (United Kingdom), type locality of *Hylaeochelys belli*; 4, Gronau (Germany), type locality of *Desmemys bertelsmanni*; 5, Hainaut (Belgium), type locality of *Chitiracephalus dumonii* and *Peltochelys duchastelii*; 6, Burgos (Spain), type locality of *Larachelus morla*, gen. et sp. nov.; 7, Cuenca (Spain), type locality of *Hoyasemys jimenezi*; 8, Teruel (Spain), type locality of *Galvechelyone lopezmartinezae*. B, detailed geographical location of Salas de los Infantes (Burgos, Spain), the type locality of *Larachelus morla*.

identified from two outcrops near the town of Salas de los Infantes (province of Burgos, northern Spain), and Tenadas del Jabalí and Monte Puente Ballesta (Pérez-García, in press; Pérez-García et al., 2012) (Fig. 1B). Both outcrops are located in the Pinilla de los Moros Formation. On the basis of charophyte biozonation, this fluvial formation has been dated in the area of Salas de los Infantes as late Hauterivian–early Barremian (Martín-Closas and Alonso Millán, 1998).

The inclusion of the specimen from Monte Puente Ballesta in phylogenetic hypotheses allows its identification as a new representative of the stem group of Cryptodira, *Larachelus morla*, gen. et sp. nov. This provides new insights into the European evolution of this lineage, and increases the European Early Cretaceous diversity of Pan-Cryptodira.

Institutional Abbreviations—**CAMSM**, Sedgwick Museum, Department of Geology, University of Cambridge, Cambridge, United Kingdom; **DORCM**, Dorset County Museum, Dorchester, United Kingdom; **ICIPLR**, Centro de Interpretación Paleontológica de La Rioja, Igea, Spain; **IRSNB**, Institut Royal des Sciences Naturelles, Brussels, Belgium; **IWCMS**, Isle of Wight County Museum Service, Sandown, United Kingdom; **MCCM**,

Museo de las Ciencias de Castilla–La Mancha, Cuenca, Spain; **MDS**, Museo de Dinosaurios de Salas de los Infantes, Burgos, Spain; **MPG**, Museo Paleontológico de Galve, Teruel, Spain; **NHMUK**, The Natural History Museum, London, United Kingdom; **OXFUM**, Oxford University Museum of Natural History, Oxford, United Kingdom.

Anatomical Abbreviations—**Ab**, abdominal; **An**, anal; **C**, costal; **Egu**, extragular; **Ep**, epiplastron; **Fm**, femoral; **Gu**, gular; **Hp**, hypoplastron; **Hu**, humeral; **Hy**, hyoplastron; **Inf**, infra-marginal; **M**, marginal; **N**, neural; **P**, peripheral; **Pc**, pectoral; **Pl**, pleural; **Py**, pygal; **Spy**, suprapygal; **V**, vertebral; **Xi**, xiphiplastron.

MATERIALS AND METHODS

The specimen MDS-MPBS-6 is described herein and proposed as the holotype of a new taxon, *Larachelus morla*. It is compared with the relatively well-known European Early Cretaceous pan-cryptodiran members in which the shells have been preserved: *Pleurosternon bullockii*, *Hylaeochelys belli*, *Brodiechelys brodiei*, *Hoyasemys jimenezi*, *Chitiracephalus dumonii*,

TABLE 1. Comparison of shell characters of European Early Cretaceous pan-cryptodiran members.

Characters	<i>Larachelus morla</i>	<i>Pleurosternon bullockii</i>	<i>Hylaeochelys belli</i>
Shell height	High	Low	Low
Ornamentation	Absent	Present (pits)	Smooth to decorated (small striations)
Fontanelles	Absent	Absent	Central plastral fontanelle present to absent
Neurals-suprapygals contact	Absent	Present	Present to absent
Number of neurals	6	8 or 9	7–9
Number of suprapygals	1	2	2
Width of vertebral 5 in relation to 4	Wider	Narrower to equal	Considerably narrower
Neural that vertebral 3 posteriorly contacts	6	5	5
Overlap of vertebral 4 on suprapygals	Present	Present	Absent
Width of vertebral 5 in relation to posterior suprapygal	Equal	Considerably wider to equal	Considerably wider
Overlap of marginal 12 on posterior suprapygal	Present	Present	Absent
Carapace-plastron attachment	Partially ligamentous	Sutured	Sutured
Epiplastron-hyoplastron attachment	Ligamentous	Sutured	Sutured
Hypoplastron-xiphiplastron attachment	Ligamentous	Sutured	Sutured
Plastral sagittal sulcus	Straight	Straight	Slightly sinuous
Anal overlapping hypoplastron	Present	Absent	Absent

(Continued to next page)

TABLE 1. Comparison of shell characters of European Early Cretaceous pan-cryptodiran members. (Continued)

Characters	<i>Brodiechelys brodiei</i>	<i>Hoyasemys jimenezi</i>	<i>Chitracephalus dumonii</i>	<i>Galvechelone lopezmartinezae</i>	<i>Peltochelys duchastelii</i>
Shell height	Moderate	Low	Low	Low	Low
Ornamentation	Present (ridges)	Present (ridges)	Present (complex pattern)	Absent	Present (depressions)
Fontanelles	Absent	Dorsal and plastral fontanelles	Central plastral and xiphiplastral fontanelles	?	Absent
Neurals-suprapyrgals contact	Absent	?	Present	?	Present
Number of neurals	7–9	?	?	?	9
Number of suprapyrgals	2	2	?	?	2
Width of vertebral 5 in relation to 4	Narrower to equal	?	?	?	Wider
Neural that vertebral 3 posteriorly contacts	5 or 6	?	?	?	7
Overlap of vertebral 4 on suprapyrgals	Present to absent	Present	?	?	Present
Width of vertebral 5 in relation to posterior suprapyrgal	Slightly narrower to slightly wider	?	?	?	Considerably wider
Overlap of marginal 12 on posterior suprapyrgal	Absent	?	?	?	Absent
Carapace-plastron attachment	Sutured	Ligamentous	Ligamentous	?	Sutured
Epiplastra-hyoplastra attachment	Sutured	Ligamentous	Ligamentous	?	Sutured
Hypoplastra-xiphiplastra attachment	Sutured	Sutured	Sutured	?	Sutured
Plastral sagittal sulcus	Slightly sinuous	Straight	?	?	Markedly sinuous
Anal overlapping hypoplastra	Present	Absent	?	?	Absent

For explanations see online Supplementary Data 1.

Galvechelone lopezmartinezae, and *Peltochelys duchastelii* (see Table 1 and Supplementary Data; Supplementary Data available online at www.tandfonline.com/UJVP). These comparisons are based on personal observation of the holotypes, as well as on other specimens assigned to some of them.

To establish the phylogenetic position of *L. morla*, we used a reduced version of the data matrix proposed by Sterli and de la Fuente (2011), from which all Pan-Pleurodira representatives were excluded (see Supplementary Data). We conducted a first analysis in which we included *L. morla*. Other taxa traditionally interpreted as basal eucryptodirans (sensu Joyce et al., 2004) were also included in a second analysis. These taxa are *Chengyuchelys baenoides*, from the Asian Middle Jurassic (we use the character coding proposed by Danilov and Parham, 2008); *Tholemys passmorei* and *Plesiochelys planiceps* from the European Upper Jurassic (based on personal observation of their holotypes, NHMUK R5871 and OXFUM J1582, respectively); and the European Early Cretaceous taxa *B. brodiei*, *H. belli*, and *C. dumonii* (based on observation of their holotypes, NHMUK R2643, NHMUK OR36529, and IRSNB R 11-12, respectively, and on the observation of other specimens attributed to these taxa, deposited in the NHMUK, CAMSM, DORCM, ICIPLR, IRSNB, IWCMS, MDS, and OXFUM).

The phylogenetic analyses were conducted using TNT v. 1.0 (Goloboff et al., 2008), with *Sphenodon punctatus* as the outgroup. The modifications on the processing of certain characters in *Pleurosternon bullockii*, *Dinochelys whitei*, and *Glyptops plicatulus* proposed by Pérez-García and Ortega (2011) have been included. The TNT analyses used here were run using the ‘New Technology Search’ option with ‘Sectional Search’ and ‘Tree Fusing’ checked (default settings). All characters were considered unordered and equally weighted.

The first phylogenetic analysis resulted in 94 most parsimonious trees (MPTs) of 407 steps (consistency index [CI] = 0.484, retention index [RI] = 0.849), and the second one resulted in 87 MPTs of 418 steps (CI = 0.471, RI = 0.841). Fifty-percent

majority rule consensus trees were generated from both sets of MPRs.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

PAN-CRYPTODIRA Joyce, Parham, and Gauthier, 2004

LARACHELUS MORLA, gen. et sp. nov.

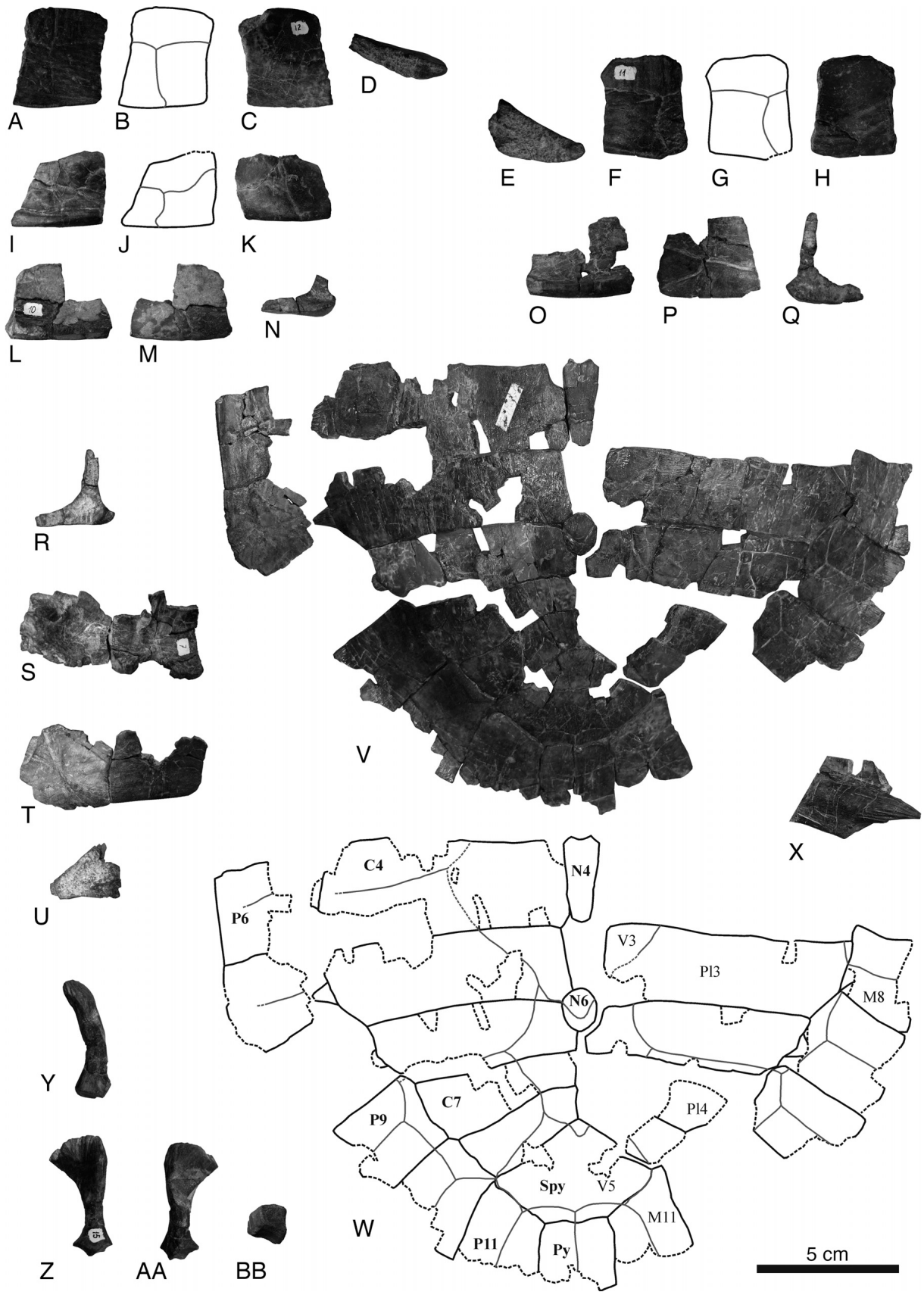
(Figs. 2–4)

Holotype—MDS-MPBS-6, a left ilium and a partial carapace preserving the fourth and sixth neural plates; the fourth to eighth left, fifth and sixth right, and the distal region of the seventh and eighth right costals; the suprapyrgal; the pygal; the second, fourth to seventh, and ninth to eleventh left peripherals; the second, fifth, seventh, eighth, ninth, and eleventh right peripherals; the right epiplastron; both hyoplastra; the right hypoplastron; and the left xiphiplastron (Figs. 2A–BB, 3A–P).

Paratypes—MDS-MPBS-18, right epiplastron (Fig. 3Q–T); MDS-MPBS-28, right xiphiplastron (Fig. 3U–Y).

Locality and Horizon—Monte Puente Ballesta site, Salas de los Infantes, Burgos, western Cameros Basin, Iberian Range, Spain. Pinilla de los Moros Formation, late Hauterivian–early Barremian (Martín-Closas and Alonso Millán, 1998; Pérez-García et al., 2012).

Etymology—The generic name refers to “Los siete infantes de Lara” (‘The Seven Infants of Lara’), a famous medieval Castilian romance from which is derived the name of the town of Salas de los Infantes, and ‘chelus’ (Greek for turtle). The specific name refers to ‘Morla,’ a fictional swamp turtle with a high carapace (the ‘Tortoise Shell Mountain’) from the fantasy novel ‘Die unendliche Geschichte’ (‘The Neverending Story’) by Michael Ende (1979).



Diagnosis—Pan-cryptodiran turtle belonging to the node that groups the common ancestor of *Xinjiangchelys latimarginalis* and Cryptodira, and all its descendants, sharing with the basal members of this node (node D in Fig. 5A–B): anal scutes anteromedially overlapping the hypoplastra. *Larachelus morla* has the following autapomorphies: partially ligamentous epiplastra-hyoplastra and hypoplastra-xiphiplastra contacts, with a linear ridge in the anterior margin of the hyoplastra and posterior margin of the hypoplastra that slots into a furrow in the posterior margin of the epiplastra and anterior margin of the xiphiplastra, respectively. It differs from other members of Pan-Cryptodira by the following character combination: high shell; broad plastral lobes; smooth outer surface; absence of fontanelles; six neurals; hexagonal and elongated fourth and fifth neurals (at least); subrounded last neural; medial contact of the last three pairs of costals; robust distal region of the dorsal ribs; single, large, and pentagonal suprapygal; slight thickening of the dorsolateral region of the anterior and middle peripherals; high bridge peripherals; long posterior peripherals and pygal; third vertebral scute significantly wider than the fourth and fifth ones; posterior margin of third and fourth vertebrae medially directed toward the posterior region; fifth vertebral as wide as the suprapygal; last pair of marginals overlapping onto the posterior region of the suprapygal; marginal scutes not contacting the costal plates except in those in the middle region of the peripheral series; epiplastra slightly wider than long, with much of their visceral surface depressed, and lacking dorsal processes; epiplastra-hyoplastra suture laterally directed to the anterior region; rhombic, relatively small, and longer than wide entoplastron; partially ligamentous carapace-plastron connection; absence of mesoplastra; hyoplastra and hypoplastra only in contact with peripherals; long bridge; laterally sinuous hypoplastra-xiphiplastra contact; absence of plastral kinesis; straight plastral sagittal sulcus; gular scutes superimposed onto the anterior area of the entoplastron; extragular-humeral sulcus laterally directed towards the anterior region; humeral-pectoral sulcus situated far behind the posterior margin on the entoplastron; numerous small inframarginal scutes; and anal scutes anteromedially overlapping the hypoplastra.

Larachelus morla differs from the basal members of Cryptodira by: medial contact of the last pairs of costals; presence of extragulars. It differs from *Brodiechelys brodiei* by: higher shell; smooth outer surface; fewer neurals; more costals with medial contact; single suprapygal; slight thickening of the dorsolateral region of the anterior and middle peripherals; fifth vertebral wider than the fourth one; fourth vertebral longer than wide; marginals overlapping the second suprapygal; partially ligamentous carapace-plastron connection; longer than wide entoplastron; straight plastral sagittal sulcus; and more than four pairs of inframarginals. It differs from *Siamochelys peninsularis* (sensu Tong et al., 2002) by: absence of mesoplastra; wider third vertebral scute; smooth outer surface; gulars overlapping onto the anterior area of the entoplastron; longer than wide entoplastron; and partially ligamentous carapace-plastron connection. It differs from the Asian taxa attributed to “Xinjiangchelyidae” (Tong et al., 2012) by: high shell; single suprapygal; dorsal process of epiplastron absent; posterior sulcus of gulars and extragulars not forming a straight line; gulars overlapping onto the anterior area of the

entoplastron; more than four pairs of inframarginals; and straight plastral sagittal sulcus.

DESCRIPTION

The posterior half of the carapace of *Larachelus morla* is subrounded. Its carapace is vaulted because the dorsal and ventral regions of its bridge peripherals define a right angle. The plastral bridge is not flat, the plastral lobes are broad, and the outer shell surface is smooth. However, lightly marked grooves corresponding to growth marks are preserved in some parts of the peripheral and costal plates (Figs. 2–4).

Dorsal Carapace Plates

The fourth neural plate of *L. morla* is hexagonal and elongated (Fig. 2V–W). Although the fifth neural is not preserved, its morphology can be inferred because all the plates surrounding it are present. This neural is similar to the previous one, but its posterior end is emarginated. The sixth neural is subrounded, slightly longer than wide. The posterior half of the sixth pair of costals, and the entire medial margin of the seventh and eighth pairs, make contact medially. The length and width of the preserved pairs of costals decrease toward the posterior region of the costal series. The transverse breadth of the seventh and eighth pairs of costals is similar to that of the peripherals with which they make contact. The proximal region of the dorsal ribs is relatively well developed; the distal region shows robust processes articulated with the peripherals (Fig. 2X). Therefore, although *L. morla* lacks fontanelles between the costal and peripheral plates, the sutures between them are weak. *Larachelus morla* has a single, large pentagonal suprapygal plate (Fig. 2V–W). This taxon has a slight dorsal thickening in the lateral edges in the anterior and middle peripherals (Fig. 2A–U). The angle defined by the dorsal and ventral surfaces of the peripherals of the bridge region is approximately a right angle (Fig. 2L–U). Their dorsal and ventral surfaces form an approximate right angle. The posterior peripherals and the pygal are long (Fig. 2V–W).

Dorsal Carapace Scutes

The third vertebral scute is significantly wider than the fourth one (Fig. 2V–W). The fifth vertebral is slightly wider than the fourth one. The length of each preserved scute decreases toward the posterior region of the vertebral series. The morphology of the known region of the third vertebral scute and that of the fourth are peculiar because the posterior margins of both scutes are not straight but medially directed toward the posterior region. Thus, the third vertebral reaches the posterior half of the sixth neural and the fourth vertebral overlaps the anterior area of the suprapygal plate. Anterolaterally, the fourth vertebral scute narrows, ending in an acute angle. Its lateral margins are not straight, but form an obtuse angle, the vertex of which coincides with the boundary between the third and fourth pairs of pleurals. Laterally, the fifth vertebral scute covers the entire suprapygal plate, with the width of the two elements being similar. The eleventh pair of marginals is not on the suprapygal. The limit of these scutes with the fifth vertebral is placed over the suture between

← FIGURE 2. Carapace and ilium of the holotype of *Larachelus morla*, gen. et sp. nov., MDS-MPBS-6. **A–D**, second left peripheral in **A–B**, dorsal, **C**, ventral, and **D**, anterior views; **E–H**, second right peripheral in **E**, posterior, **F–G**, dorsal, and **H**, ventral views; **I–K**, fourth left peripheral in **I–J**, dorsolateral and **K**, ventral views; **L–N**, fifth left peripheral in **L**, dorsomedial, **M**, ventral, and **N**, anterior views; **O–Q**, fifth right peripheral in **O**, dorsal, **P**, ventral, and **Q**, anterior views; **R–U**, articulated sixth and seventh left peripheral plates in **R**, anterior, **S**, medial, **T**, dorsal, and **U**, posterior views; **V–W**, posterior half of the carapace including the fourth and sixth neurals, the last five left costals, the fifth, sixth, and fragments of the seventh and eighth right costals, the suprapygal, the pygal, the sixth, seventh, ninth, tenth, and eleventh left peripherals, and the seventh, eighth, ninth, and eleventh right peripherals; **X**, distal area of the fifth left costal; **Y–BB**, left ilium in **Y**, posterior, **Z**, medial, **AA**, lateral, and **BB**, ventral views.

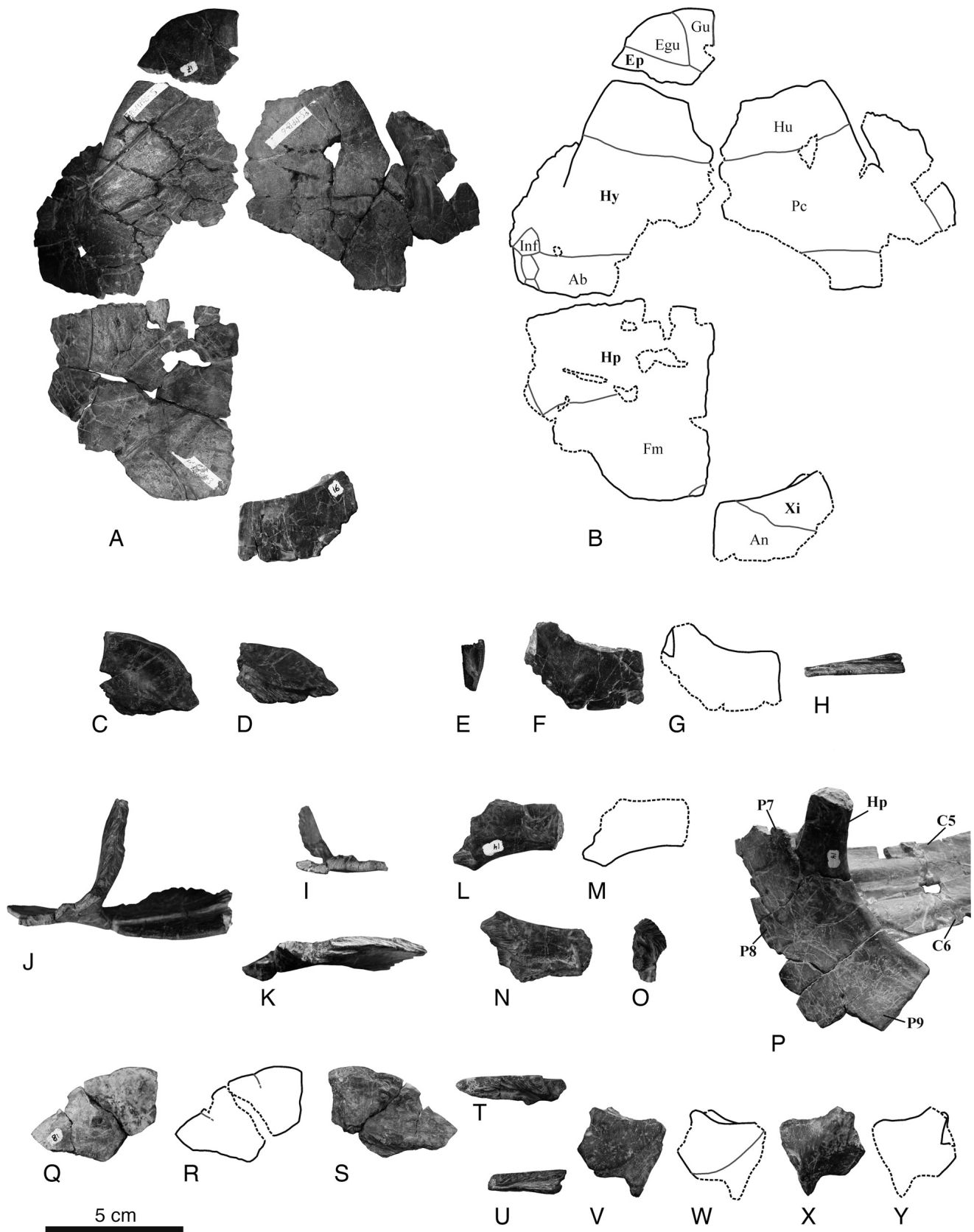


FIGURE 3. Plastron of *Larachelus morla*, gen. et sp. nov. **A–P**, MDS-MPBS-6, holotype of the taxon. **A–B**, plastron in ventral view, including the right epiplastron, both hyoplastra, the right hypoplastron, and the left xiphiplastron; **C–D**, right epiplastron in **C**, dorsal and **D**, posterodorsal views; **E–H**, left xiphiplastron in **E**, lateral, **F–G**, dorsal, and **H**, anterior views; **I–J**, right hyoplastron in **J**, anterolateral and **I**, anteromedial views; **K**, right hypoplastron in posterior view; **L–O**, process of the right hypoplastron in **L–M**, ventral, **N**, dorsal, and **O**, lateral views; **P**, area of contact of the hypoplastron and the peripheral series. **Q–T**, MDS-MPBS-18, right epiplastron in **Q–R**, ventral, **S**, dorsal, and **T**, posterior views. **U–Y**, MDS-MPBS-28, right xiphiplastron in **U**, anterior, **V–W**, ventral, and **X–Y**, dorsal views.

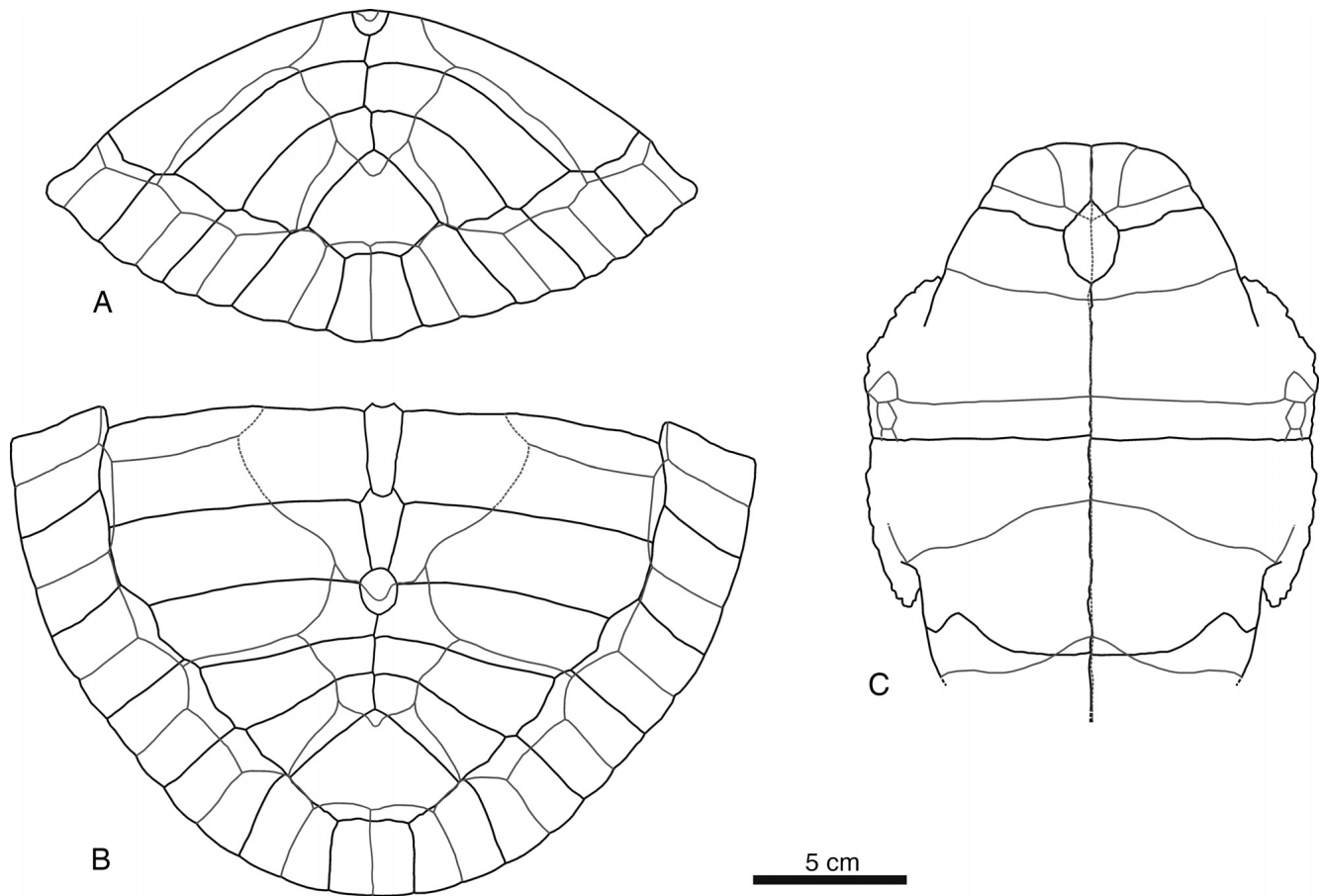


FIGURE 4. Reconstruction of shell of *Larachelus morla*, gen. et sp. nov., in **A**, posterodorsal, **B**, dorsal, and **C**, ventral views.

the suprapygal and the last pair of peripherals. However, the last pair of marginals covers the posterior region of the suprapygal plate. The seventh pair of marginal scutes laterally overlaps the fourth and fifth pairs of costal plates. The marginal scutes do not overlap or make contact with the costal plates from the posterior half of the eighth pair of marginals to the anterior area of the eleventh pair. The first pairs of marginal scutes do not make contact with the costal plates (Fig. 2A–Q).

Plastral Plates

The epiplastra of *L. morla* are slightly wider than long (Fig. 3A–D, Q–T). Much of the visceral surface of these plates is depressed. These plates lack dorsal processes. The lateral contact surface of the epiplastra with the hyoplastra is directed anteriorly. This contact is not sutured but partially ligamentous. In that area, the epiplastra have a furrow into which slots a projection extending along the anterior margin of the hyoplastra (Fig. 3C–D, I–J, S–T). A similar relationship is observed between the hypoplastra and xiphiplastra, where the furrow is on the xiphiplastra (Fig. 3E–H, K, U–Y). In contrast, the contact of the two epiplastra with each other, as well as that of the entoplastron with the epiplastra and with the hyoplastra, is sutured (Fig. 3A–D, Q–T). *Larachelus morla* lacked plastral kinesis despite the partially ligamentous contact between epiplastra and hypoplastra, and between hypoplastra and xiphiplastra. The sutured union between epiplastra and entoplastron, which penetrates between this pair of plates, and the sinuous morphology of the hypoplastra-xiphiplastra suture do not allow movement

between these elements. Furthermore, these sutures do not coincide in position or morphology with the boundaries between plastral scutes. By contrast, the peculiar structure with furrows and slots generates very robust joints, and is unique to this taxon. Although the entoplastron is not preserved, its morphology can be inferred from all the preserved adjacent plates (Figs. 3A–B, 4C). The entoplastron is inferred to have been relatively small, rhombic, and longer than it is wide. The hyoplastra and the xiphiplastra have similar lengths, being slightly longer than that of the hypoplastra (Figs. 3A–B, 4C), and the two plates are sutured to each other. However, the plastron has a partially ligamentous connection with the carapace. The plastral processes only make contact with the peripheral plates. The bridge is long and extends from the rear end of the second peripheral plate to the anterior region of the eighth peripheral (Fig. 2A–W). The anterior ends of the hyoplastral processes and the posterior hypoplastral processes are robust, fitting into deep cavities in the peripheral plates (Fig. 3L–P). The contact line between hypoplastra and xiphiplastra zigzags slightly because laterally the hypoplastra protrude further into the xiphiplastra (Figs. 3A–B, 4C).

Plastral Scutes

The sagittal sulcus of *L. morla* is straight. This taxon has a pair of gular scutes (sensu Hutchison and Bramble, 1981; Joyce, 2007) (Figs. 3A–B, 4C) that are superimposed on the anterior area of the entoplastron. The plastral area covered by the extragular scutes is slightly higher than that covered by the gulars. The extragular-humeral groove is not perpendicular to the

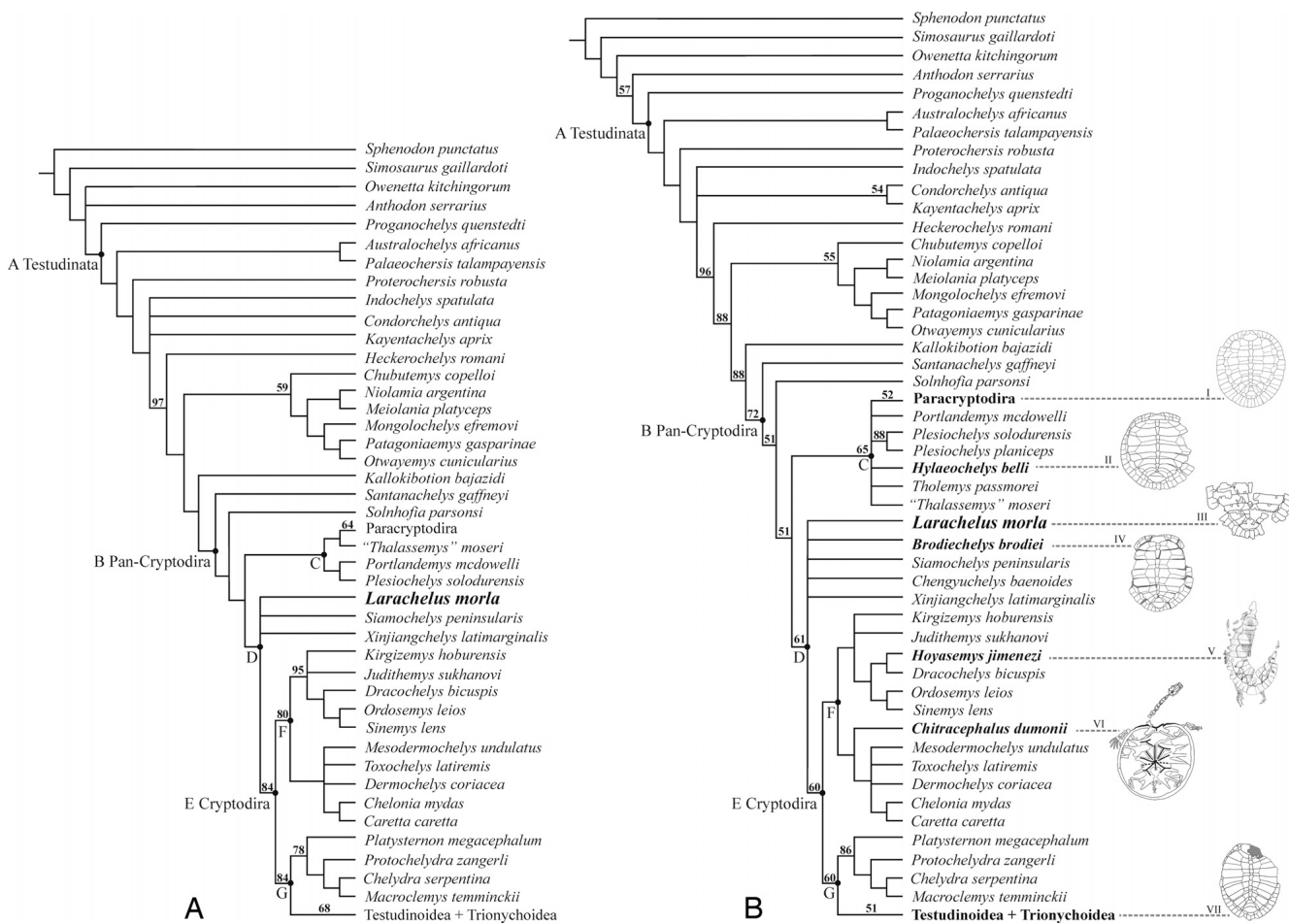


FIGURE 5. Phylogenetic relationships of *Larachelus morla*, gen. et sp. nov., within Pan-Cryptodira, based on **A**, a reduced version of the data matrix proposed by Sterli and de la Fuente (2011), and **B**, an augmented data set from the original matrix. Values refer to percentages under 100% obtained in the majority rule consensus. Taxa in bold in **B** correspond to pan-cryptodirans recorded in the European Early Cretaceous. Figures (based on our direct study of these specimens): **I**, *Pleurosternon bullockii* (CAMSM J5327); **II**, *Hylaeochelys belli* (OXFUM J13796); **III**, *Larachelus morla* (MDS-MPBS-6); **IV**, *Brodiechelys brodiei* (NHMUK R11147); **V**, *Hoyasemys jimenezi* (MCCM-LH 84); **VI**, *Chitraccephalus dumonii* (IRSNB R 11-12); **VII**, *Peltochelys duchastelii* (IRSNB Ct. R. 16).

medial axis, but is anterolaterally directed. The humeral-pectoral sulcus is situated far behind the posterior margin on the entoplastron. *Larachelus morla* has several small inframarginal scutes. Their number cannot be determined. Anteromedially, the anal scutes overlap the hypoplastra.

Ilium

The left ilium of MDS-MPBS-6 is preserved (Fig. 2Y-BB). The region near the contact area with the carapace is highly fluted. This corresponds to a ligamentous junction, a characteristic of pan-cryptodiran members. This region is relatively short and straight.

PHYLOGENETIC ANALYSIS

The resulting tree topology of the two phylogenetic analyses carried out here basically coincides with that proposed by Sterli and de la Fuente (2011) (Fig. 5). Eucryptodira cannot be recognized in any of them. *Santanachelys gaffneyi* and *Solnhofia parsonsi* are obtained as the two basal-most pan-cryptodiran taxa. The other pan-cryptodirans are grouped into two lineages (Fig. 5A-B, nodes C and D). Both clades are represented in the

European Lower Cretaceous record (Fig. 5B). In the first analysis, clade C groups *Portlandemys mcdowellii*, *Plesiochelys solodurensis*, “*Thalassemys*” *moseri*, and the Paracryptodira members (Fig. 5A, node C). In the second analysis, *Plesiochelys planiceps*, *Hylaeochelys belli*, and *Tholemys passmorei* are also included in this clade (Fig. 5B, node C). In both analyses, clade C is diagnosed by: osseous connection between carapace and plastron (character 89 of Sterli and de la Fuente, 2011); axillary buttresses contact peripherals and first costal (character 98); and inguinal buttresses contact peripherals and costal V (character 100). Its sister group is a monophyletic group (Fig. 5A-B, node D) composed of a polytomy including several Asian taxa which are not grouped together (*Siamochelys peninsularis*, and two turtles traditionally attributed to ‘Xinjiangchelyidae’: *Xinjiangchelys latimarginalis* and *Chengyuchelys baenoides*), the European taxa *B. brodiei* and *L. morla*, and the clade Cryptodira. In the first analysis (Fig. 5A), clade D is diagnosed by two synapomorphies: vertebrals II-IV as narrow as, or narrower than, the pleurals (character 87), and first dorsal rib extends less than halfway across first costal (character 127). In the second analysis (Fig. 5B), clade D is diagnosed by the first of these characters and by anal scutes anteromedially overlapping the hypoplastra (character 113). In both analyses, Cryptodira (node E) is diagnosed by:

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absence of extragulars (character 106); posterior cervical vertebrae with strongly developed ventral keels (character 117); eighth cervical centrum significantly shorter than the seventh (character 118); cervical central articulations (character 119); and absence of cleithra (character 136). In both analyses, *Larachelus morla* is diagnosed by medial contact of the last pairs of costals (character 82).

The position of *L. morla* in other turtle global phylogenetic analyses, such as those proposed by Hirayama et al. (2000), and by Gaffney et al. (2007) (more limited both in characters and in taxa), is consistent with that obtained by the phylogenetic analyses performed here (see Supplementary Data).

DISCUSSION

Morphological Diversity and Paleoecological Implications

Although the European Upper Jurassic turtle record includes several coastal groups, all of the Early Cretaceous pancryptodiran taxa are continental. Most of these turtles are known from the shell only. Comparisons between shells among these taxa are very limited, and their intraspecific variability has been poorly analyzed. Comparisons of the shell of *L. morla* to those of other European taxa allows us to characterize it in detail (see Table 1 and Supplementary Data).

Due to the limited and generally poor record for most Early Cretaceous pancryptodirans, their lifestyles have hardly been analyzed. However, the high diversity in shell morphologies observed here could be related to adaptations to different ecological niches (Benson et al., 2011). In addition, although the cranial material of this group is very limited, much morphological and structural variability is observed, probably also related to adaptations for different lifestyles. The skull of *Sandownia harrisi*, for example, has one of the most extensive secondary palates known in turtle taxa, which could be related to a trophic modification associated with the development of a broad crushing surface (Meylan et al., 2000). The short, wide, and high morphology of the skull of this taxon contrasts with the very elongate, depressed skull of *C. dumonii*, which necessarily involves different trophic habits (Pérez-García, in press).

Systematic and Biogeographic Implications

The results of our cladistic analyses identify *Larachelus morla* as a new member of the little-known European Early Cretaceous stem Cryptodira. During the Early Cretaceous, Pancryptodira was a very diverse group in Europe. In fact, *L. morla* is not the first member of Pancryptodira identified from the Iberian Range (Spain). This study, as well as other recent ones (Pérez-García, in press; Pérez-García and Murelaga, in press; Pérez-García et al., 2010, 2011, 2012), indicates that the Hauterivian–Aptian interval recorded a wide diversity of pancryptodirans, higher than in any other area of the European Lower Cretaceous. Members of clade C (probable pleurosternid representatives), the new stem cryptodiran *L. morla*, members of cryptodiran clade F (*Ho. jimemezi*, *C. dumonii*, *G. lopez-martinezae*), and members of cryptodiran clade G (a new taxon, tentatively assigned to the trionychian stem lineage) have been collected there (Fig. 5B).

The greatest diversity for clade C (Fig. 5A–B) is recorded in the Upper Jurassic of Europe. The distribution of Pleurosternidae (Paracryptodira) included Europe, as well as North America. Moreover, Europe was also home to taxa traditionally assigned to Thalassemydidae and Plesiochelyidae. These coastal groups were unique to this continent. Eurysternidae, obtained here as a basal member of Pancryptodira, also had a European distribution. Continental members of clade D have been identified from the Asian Middle Jurassic (Hirayama et al., 2000). This clade is identified in Europe from the Early Cretaceous. How-

ever, these turtles are not recorded in North America until the Late Cretaceous (Pérez-García, in press). The coexistence of continental members of clades C and D during the Early Cretaceous is exclusive to Europe.

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