A NEW PLATYCHELYID TURTLE (PAN-PLEURODIRA) FROM THE LATE JURASSIC (KIMMERIDGIAN) OF OAXACA, MEXICO

by OLIVER A. LÓPEZ-CONDE[1],[*], JULIANA STERLI[2],[*], JESUS ALVARADO-ORTEGA[3] *and* MARÍA L. CHAVARRÍA-ARELLANO[1]

[1]Posgrado en Ciencias Biológicas, Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación S/N, Ciudad Universitaria, Delegación Coyoacán, Distrito Federal 04510, México; vertebrate_palaeontology@comunidad.unam.mx, mariachavarra@outlook.com
[2]CONICET-Museo Paleontológico Egidio Feruglio, Av. Fontana 140, Trelew, Chubut 9100, Argentina; jsterli@mef.org.ar
[3]Universidad Nacional Autónoma de México, Circuito de la Investigación S/N, Ciudad Universitaria, Delegación Coyoacán, Distrito Federal 04510, México; alvarado@geologia.unam.mx
[*]Corresponding authors

Abstract: Until recently, the record of Mesozoic turtles in Mexico has been restricted to the Cretaceous. New discoveries in the Sabinal Formation (Tlaxiaco, Oaxaca) have extended the record into the Kimmeridgian (Late Jurassic). The Sabinal Formation is part of the Tlaxiaco Basin, which was a depocenter of continental and marine sediments dominated by transgressive-regressive marine conditions during the Jurassic–Cretaceous. The new turtle described here consists of an almost complete carapace associated with a plastron. Based on the unique combination of characters, this turtle is identified as a new species of Platychelyidae here named *Notoemys tlaxiacoensis*. Platychelyid characters in this specimen include the presence of the sulcus between vertebral 3 and 4 located on neural 6, the presence of a central plastral fontanelle, and a pair of reduced mesoplastra. The occurrence of Kimmeridgian platychelyids in Mexico confirms that the Hispanic Corridor acted as a connection between Tethyan and Palaeopacific faunas.

Key words: turtle, Late Jurassic, Sabinal Formation, Platychelyidae, Kimmeridgian, *Notoemys*.

PLATYCHELYIDAE is the sister clade of crown Pleurodira and includes the oldest members of Pan-Pleurodira. Until now, Platychelyidae has been represented by five species belonging to two genera: *Platychelys* and *Notoemys* (de la Fuente & Iturralde-Vinent 2001; Cadena & Gaffney 2005). Platychelyids are known from Europe, South and North America, and their fossil record spans from the Late Jurassic to the Early Cretaceous (Cadena & Joyce 2015).

The first described member of the Platychelyidae was *Platychelys oberndorferi* Wagner, 1853, now recognized in the Upper Jurassic (Kimmeridgian–Tithonian) of Germany and Switzerland (Karl & Tichy 2006). This was followed by the first platychelyid to be found outside Europe, *Notoemys laticentralis* Cattoi & Freiberg, 1961 (subsequently described by de la Fuente & Fernández 1989; Fernández & de la Fuente 1994; Lapparent de Broin *et al.* 2007). The oldest known platychelyid is *Notoemys oxfordiensis*, from the Upper Jurassic (Oxfordian) of Cuba (originally described as *Caribemys oxfordiensis* by de la Fuente & Iturralde-Vinent 2001). This species represents also the first platychelyid found in North America (de la Fuente & Iturralde-Vinent 2001). The Colombian *Notoemys zapatocaensis* is the only platychelyid known from the Lower Cretaceous (Valanginian) (Cadena & Gaffney 2005).

Previous cladistic analyses have recovered *N. laticentralis* as more closely related to Pleurodira than *P. oberndorferi* (Fernández & de la Fuente 1994), suggesting that platychelids are paraphyletic. This arrangement of panpleurodiran turtles was reinforced by the inclusion of the Late Jurassic taxon from Cuba (de la Fuente & Iturralde-Vinent 2001). With the subsequent discovery of *Notoemys zapatocaensis*, Cadena & Gaffney (2005) recovered all the mentioned species forming a monophyletic group in the stem of Pleurodira, named Platychelyidae. This hypothesis was followed by other authors (Cadena *et al.* 2013; Cadena & Joyce 2015).

The fossil record of Mesozoic turtles from Mexico is poorly known. Until recently, the only known record of Mesozoic turtles has been restricted to the Cretaceous (Reynoso 2006). However, recent discoveries have extended the fossil record to the Late Jurassic (Kimmeridgian) (Alvarado-Ortega *et al.* 2014). In this paper, we describe new material from the Sabinal Formation (Llano

Yosobé, Oaxaca, Mexico) and test its phylogenetic relationships.

GEOLOGICAL SETTING

The fossiliferous locality of Yosobé is located 3.5 km south-west of downtown Tlaxiaco, in the Mixteca region of Oaxaca, southern Mexico (Fig. 1). This site presents exposures almost 850 m long and 600 m wide, located in the bottom of a small valley in the south-eastern elevations of La Titana Hills. This valley is locally known as part of 'Llano Yosobé', and is located at between the coordinates 17°15′17.53.3″N 97°42′4.33″W and 17°14′45.71″N 97°42′20.24″W. The geological description of this site is based on its northern part since primary sedimentary structures are partially obliterated by a fault in the southern region. The fossiliferous sediments in the northern part of Yosobé are 60 m thick, at the base of which is a 30–40 cm thick marl layer containing trigonids, other bivalves and ammonites (Alvarado-Ortega et al. 2014; Barrientos-Lara et al. 2015, Alvarado-Ortega & Brito, 2016).

During the Jurassic, the Tlaxiaco Basin was active, receiving both continental and marine shelf sediments (Rueda-Gaxiola et al. 2007). López-Ticha (1985) named the Sabinal Formation comprising a sequence of marine bituminous shales exposed along the north-eastern of Oaxaca State. A marine bituminous shale, informally named the 'Sabinal formation' is exposed in the areas of Tezoatlán, Huajuapan de León, Chalcatongo, Huamuxtitlán and Tlaxiaco, into Oaxaca (Meneses-Rocha et al. 1994); as well as the marl-limestone strata described near Petlalcingo, Puebla (Pérez-Ibargüengoitia et al. 1965).

Meneses-Rocha et al. (1994) described the 'Sabinal formation' as a sequence of mudstone and wackestone clay, marl and dark grey to black bituminous shale strata with abundant calcareous concretions and ammonites, arranged in thin laminar layers of 5, 10 and 20 cm (Meneses-Rocha et al. 1994). López-Ticha (1969) estimated the age of the Sabinal formation based on its ammonite assemblage (see also Burckhardt 1930). The fossils of Yosobé were collected primarily from shale. Some of the fossils are preserved within nodules and others occur at the contacts between shale layers. The different types of preservation suggest different diagenetic processes. All the fossils preserved in nodules, including ostracodes and wood, are three-dimensional but most of the vertebrates and invertebrates preserved between layers of shale are severely flattened and commonly carbonized. Ostracodes are not preserved outside the nodules. These observations suggest that the nodules were formed relatively quickly after burial. The nodules commonly contain complete invertebrate carcasses, a process that seems to have facilitated three-dimensional preservation.

Although the large vertebrates in Yosobé are commonly disarticulated, complete or partially complete skeletons have been collected. The skeletal specimens are generally preserved by an incomplete process of nodule-formation, in which one or more adjacent nodules contains 3-D structures, but around them, the shale strata include strongly compressed structures of the same individual; therefore, it is very uncommon to obtain complete skeletons, especially when the nodules have been displaced from their original position, regardless the extent of the displacement. Vertebrate remains are generally black and relatively soft, but when weathered these can be white or red and are usually harder (Alvarado-Ortega et al. 2014).
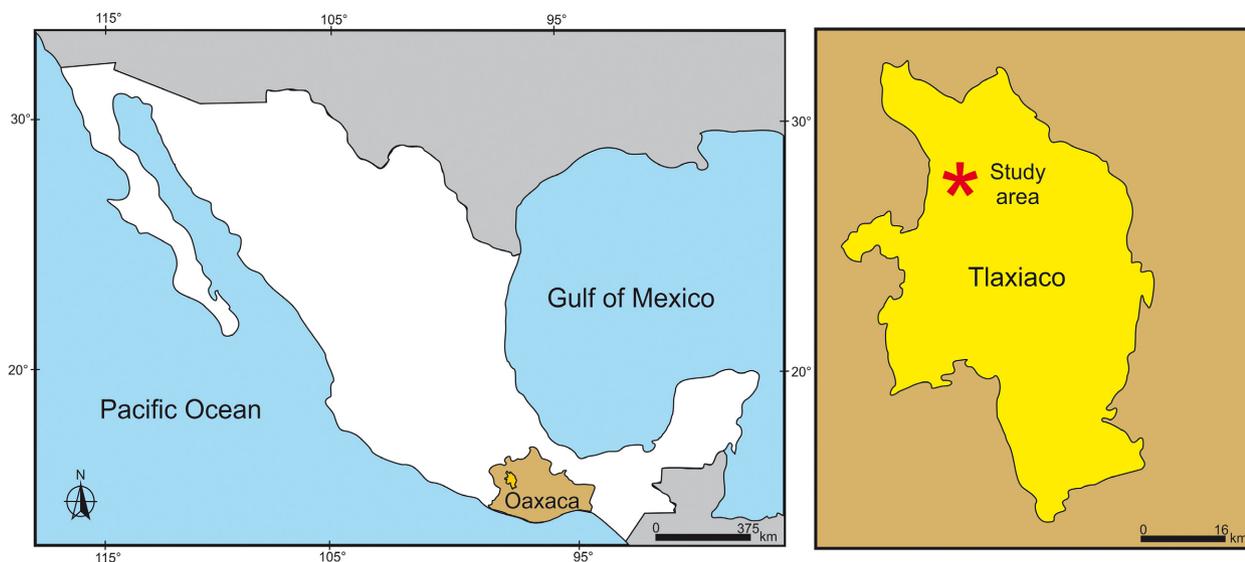

FIG. 1. Map of Mexico and Oaxaca State, southern Mexico, showing the location of Yosobé, where the new species described here, *Notoemys tlaxiacoensis*, was found. Colour online.

MATERIAL AND METHOD

The specimen described in this paper is deposited in the Colección Nacional de Paleontología of the Museo María del Carmen Perrilliat, Instituto de Geología UNAM (Universidad Nacional Autónoma de México), in Mexico City. The specimen consists of an almost complete carapace and several articulated plates of the plastron.

In order to establish the phylogenetic relationships of this specimen from Mexico, we added it to the dataset of Sterli *et al.* (2015). The matrix was built up in Mesquite (Maddison & Maddison 2011). Five new characters were added to the dataset to account for the morphology observed in the members of Platychelyidae. Four characters were modified from Cadena *et al.* (2013) and one character is new (Vertebral Scute D) (see López-Conde *et al.* 2016, appendix S1). We also modified two characters and omitted one character from Sterli *et al.* (2015) (see López-Conde *et al.* 2016, appendix S1). We also incorporated many of the changes suggested by Rabi *et al.* (2013, 2014), Zhou *et al.* (2014) and Zhou & Rabi (2015). A detailed list of the changes is provided in López-Conde *et al.* (2016, appendix S1). *Notoemys zapatocaensis* and the specimen from Mexico were added to this dataset; we re-scored all the platychelyids. Some changes to previous scorings can be found in López-Conde *et al.* 2016, appendix S1. The final dataset includes 100 taxa and 245 characters (López-Conde *et al.* 2016, appendices S2, S3). The phylogenetic analysis was performed in TNT program (Goloboff *et al.* 2008). Two rounds of Tree Bisection Reconnection (TBR) were run in order to find the most parsimonious trees (MPTs). In the first round 1000 replicates of Random Addition Sequences starting from a Wagner tree were run. In the second round, all the most parsimonious trees found in the first round were perturbated using TBR to find all the MPTs. Consistency and Retention indexes were calculated. Bremer support, Jackknife and Bootstrap resampling (with 1000 replicates) were performed to calculate the branch support. If more than one MPT was found, a strict consensus tree was calculated. We ran two analyses, one without any constraints and another with a molecular backbone constraint for the extant taxa. Constraints were applied following Guillon *et al.* (2012) (see López-Conde *et al.* 2016, appendix S4). To explore the nature of some polytomies on the strict consensus tree, we ran iterPCR script written by Pol & Escapa (2009). Later, a list of common synapomorphies to all the MPTs was calculated.

Institutional abbreviations. IGM, Colección Nacional de Paleontología 'María del Carmen Perrillat', Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico; MACN, Museo Argentino de Ciencias Naturales 'Bernadino Rivadavia', Buenos Aires, Argentina; MGJRG IPN-EAC, Museo Geológico Nacional 'José Royo y Gómez', Instituto Colombiano de Geología y Minería-Ingeominas, Bogotá, Colombia; MOZ, Museo Olsacher, Zapala, Argentina; NMB, Naturhistorisches Museum Basel, Basel, Switzerland; NMS, Naturmuseum Solothurn, Switzerland; QM, Queensland Museum, Queensland, Australia; USNM, United States National Museum (Smithsonian Institution), Washington DC, USA.

SYSTEMATIC PALAEONTOLOGY

TESTUDINES Batsch, 1788
PAN-PLEURODIRA Joyce *et al.*, 2004
PLATYCHELYIDAE Bräm, 1965

Genus NOTOEMYS Cattoi & Freiberg, 1961
Notoemys tlaxiacoensis sp. nov.
Figure 2

LSID. urn:lsid:zoobank.org:act:AF84A6BF-145A-43ED-A054-0D15FB712729

Derivation of name. The specific name refers to the city where this turtle was found (Tlaxiaco, Oaxaca, Mexico).

Holotype. IGM-4861; partially preserved shell, including both the partial carapace (Fig. 2A, B) and plastron (Fig. 2C, D).

Diagnosis. *Notoemys tlaxiacoensis* is a member of the Platychelyidae based on the sulcus between vertebral 3 and 4 located on neural 6 (character 143); central plastral fontanelle present (character 147) and a pair of reduced mesoplastra (character 162). It is a member of the genus *Notoemys* because they share the presence of two suprapygals (character 138) and the presence of the sulcus between vertebral 4 and 5 located on the suprapygal 1 (character 144). *Notoemys tlaxiacoensis* has the unique combination of the following characters that differentiate it from the other representatives of Platychelyidae: presence of a crest in the anteromedial part of vertebral scales 3 and 4 (absent in *N. laticentralis*, *N. zapatocaensis* and *P. oberndorferi*); neural 3 hexagonal (being slightly octagonal in *N. laticentralis* and *N. zapatocaensis* and rectangular in *P. oberndorferi* and *N. oxfordiensis*); neural 4 hexagonal (being rectangular in *P. oberndorferi*, *N. laticentralis*, *N. zapatocaensis* and *N. oxfordiensis*); neural 6 hexagonal (being octagonal in *P. oberndorferi*, rectangular in *N. laticentralis* and irregular in *N. zapatocaensis* and *N. oxfordiensis*); suprapygal 1 contacting posterolaterally the corner of peripheral 11 and also laterally the costal 8 (while in others representatives of platychelyids it only contacts the costal 8); peripheral 10 contacts only costal 7 and the limit 7–8, (in the platychelyids it also contacts costal 8); sulcus between pleural 4 and vertebral 5 is

FIG. 2. *Notoemys tlaxiacoensis* sp. nov. A, dorsal view of the carapace. B, drawing of the dorsal view of the carapace; arrows indicate the protuberance or crest in the vertebral scutes 3 and 4. C, ventral view of the plastron. D, drawing of the ventral view of the plastron. *Abbreviations*: AN, anal scute; AB, abdominal scute; c, costal; co, coracoid; FE, femoral scute; hyo, hyoplastron; hyp, hypoplastron; il, ilium; meso, mesoplastron; n, neural; p, peripheral; PE, pectoral scute; PL, pleural scute; sc, scapula; sp, suprapygal; V, vertebral scute; ul, ulna; xi, xiphiplastron. Thin lines, sutures; thick lines, scutes; dashed lines, broken borders; grey areas: sediment. Scale bar represents 5 cm. Colour online.

located on peripheral 11 (in others platychelyids it is on the costal 8); mesoplastron much wider than long.

Ocurrence. Llano Yosobé (17°15′17.53.3″N 97°42′4.33″W and 17°14′45.71″N–97°42′20.24″W), Yosobé site near Tlaxiaco town, Oaxaca State, Mexico (Fig. 1). Shale layer (Kimmerridgian in age) belonging to the Sabinal Formation.

DESCRIPTION

The specimen IGM-4861 consists of an almost complete shell, lacking all the rim of the carapace (Fig. 2A, B) and several plates from the plastron (Fig. 2C, D). In addition, there is postcranial material identified as

probable coracoid, ulna, ilium and scapula (Fig. 2B); the nature of their preservation prevents any further description.

Carapace bones

The preserved bony plates of the carapace are: the second (partial) to eighth neurals, suprapygal 1 and 2 (partial), eight pairs of costals (not all complete) and some peripherals (which distal ends are not known) (Fig. 2A, B).

Neurals. There are seven neurals preserved in *Notoemys tlaxiacoensis*; the first neural is missing. In general, the neurals are hexagonal. A fragment of the posterior part of neural 2 is preserved, whose margins diverge anteriorly. Laterally it contacts with the second costal (as in other members of Platychelyidae). The neural 3 is hexagonal in shape, longer than wide. It contacts laterally the third costal, anterolaterally has a short contact with the second costal and anteroposteriorly with the fourth costal. The shape of this neural is rectangular in *N. oxfordiensis* and octagonal in *N. laticentralis* and *N. zapatocaensis*. In *P. oberndorferi* the shape of this neural is variable, it is rectangular and longer than wide in specimens NMS 8685, 8686, and 8692, while it is hexagonal in NMB 596 and irregular in NMS 8691. The neural 4 is hexagonal in shape, longer than wide. Its anterior side is rounded and, laterally it contacts only the fourth costal (as in Platychelyidae). This neural is rectangular in *P. oberndorferi*, *N. laticentralis*, *N. zapatocaensis* and *N. oxfordiensis*. The neural 5 is hexagonal in shape, almost as long as wide. It is similar in shape to *N. oxfordiensis*, *N. laticentralis* and *N. zapatocaensis*. On the contrary in *P. oberndorferi* this neural is rectangular. Neural 5 in *N. tlaxiacoensis* laterally contacts the fourth and fifth costals (as in Platychelyidae). The neural 6 is hexagonal in shape, wider than long, while in *P. oberndorferi* it is octagonal, in *N. laticentralis* it is rectangular, and in *N. zapatocaensis* and *N. oxfordiensis*is irregular. In *N. tlaxiacoensis* neural 6 contacts laterally the fifth and sixth costals (as in other members of Platychelyidae). The neural 7 is hexagonal in shape (as in Platychelyidae) being wider than long; laterally it contacts the sixth and seventh costals. This arrangement is similar to *N. laticentralis* and *N. zapatocaensis* since in *P. oberndorferi* it contacts only the seventh costal. The neural 8 is hexagonal in shape, being wider than long. It has the same shape in *P. oberndorferi* and *N. laticentralis*, while in *N. zapatocaensis* it is irregular. Neural 8 contacts posteriorly the first suprapygal and laterally contacts the seventh and eighth costals as in *P. oberndorferi*, *N. laticentralis* and *N. zapatocaensis*.

Suprapygals. Suprapygal 1 is rectangular in shape and longer than wide. It is similar in shape to *P. oberndorferi* and *N. zapatocaensis*, whereas that of *N. laticentralis* is trapezoidal in shape. It contacts posteriorly the corner of the eleventh peripheral on the left side and laterally the eighth costal. Only the anterior part of suprapygal 2 is preserved and the lateral margins are posteriorly divergent.

Costals. Eight sets of costals are preserved, they are complete in the left side, but not on the right side.

Peripherals. The anteriormost peripherals and also the distal area of all of the preserved peripherals are missing. On the right side, the presence of the peripheral 2 and peripherals 7–11 are recognized, while on the left side, partial peripherals 4–11 are recognized. The only preserved contact of peripheral 2 is with costal 1. No limits of peripheral 4 are known and its only clear contact is with costal 2. The preserved contact of peripheral 5 is with the costal 3. Peripheral 6 contacts costals 3 and 4. Peripheral 7 contacts costals 4 and 5. Peripheral 8 contacts costals 5 and 6. Peripheral 9 contacts costals 6 and 7. In *Notoemys tlaxiacoensis* peripheral 10 contacts only costal 7, reaching the boundary between costals 7 and 8; in other representatives of Platychelyidae peripheral 10 also has an extensive contact with costal 8. The preserved contacts of peripheral 11 are anteriorly with costal 8 and medially with suprapygal 2.

Carapace scutes

Vertebral scutes. Five vertebral scutes are preserved in *N. tlaxiacoensis*, some of them are partial. The second, third and fourth vertebral scutes are similar in shape to those of *N. laticentralis* (hexagonal) but they are wider than long. The anteromedial part of each vertebral scute has a protuberance or 'crest' (Fig. 2B) being different to the vertebral scutes observed in *P. oberndorferi*, *N. laticentralis* and *N. zapatocaensis*.

The anteromedial part of the vertebral 1 has not been preserved. The remaining part of the scute is rectangular in shape, being wider than long. Its lateral borders are convex as in *P. oberndorferi*, *N. laticentralis* and *N. zapatocaensis*. This vertebral partially covers the first costal and probably part of the nuchal and neural 1. The sulcus between the first and second vertebral is on the first costal. Vertebral 1 contacts laterally the first pleural. The anteromedial part of vertebral 2 has not been preserved. This vertebral is hexagonal in shape, wider than long. The shape of this scute is similar to that of *N. laticentralis* and *N. zapatocaensis* but differs from that of *P. oberndorferi*, which is rectangular in shape. The sulcus between second and third vertebrals is on the third neural and third costals. This scute covers the second neural, the anterior half part of the third neural and the proximal region of the first, second and third costals. It contacts laterally with the first and second pleurals. Vertebral 3 lacks a segment of the right anterior margin. It is hexagonal in shape, being wider than long. The shape of this scute is similar to that of *N. laticentralis*, while in *P. oberndorferi* and *N. zapatocaensis* it is rectangular in shape. This scute covers the posterior half of the third neural, the complete fourth and fifth neurals and the most anterior part of the sixth neural, in addition to the posteromedial region of the third, fourth, fifth and the most anterior region of sixth costals. The sulcus between third and fourth vertebrals is on the sixth neural, as in *P. oberndorferi*, *N. laticentralis* and *N. zapatocaensis*, and is considered to be a plesiomorphic character in Testudines. This state of the character is also observed in taxa as *Condorchelys antiqua* (Sterli 2008) and *Kayentachelys aprix* (Gaffney *et al.* 1987). In other turtles of the Late Jurassic, such as *Glyptops plicatulus* (Gaffney 1979), *Dinochelys whitei* (Gaffney 1979), *Plesiochelys etalloni* (Anquetin *et al.* 2014) and other members of the Plesiochelyidae (Anquetin *et al.* 2014) and

Pleurosternidae (Gaffney 1979), this sulcus is on the fifth neural. Vertebral 4 is hexagonal in shape and wider than long. The shape of this scute is similar to that of *N. zapatocaensis*, *P. oberndorferi* and *N. laticentralis*. The sulcus between fourth and fifth vertebrals is on first suprapygal, eighth costal and peripheral 11. This scute covers the most posterior part of the sixth neural and the complete seventh and eighth neurals, the anterior part of the first suprapygal, the medial area of the sixth, seventh and eighth costals, and small parts of the tenth and eleventh peripherals. Laterally, it contacts the third and fourth pleurals. Only the most anterior part of vertebral 5 is preserved, so its shape cannot be determined. This scute covers the posterior part of the first suprapygal, at least a part of the second suprapygal, most of the eighth costal and the anterolateral region of the eleventh peripheral. It contacts the fourth pleural laterally.

Pleural scutes. Four pleural scutes are visible on both sides of the carapace. They may be similar in shape to those of other members of Platychelyidae (i.e. first, second and third are pentagonal and the fourth is rectangular). The first pleural covers the distal part of the first and second costals. The sulcus between first and second pleurals is on the second costal. The second pleural covers the distal part of the second, third and fourth costals. The sulcus between second and third pleurals is on the fourth costal. The third pleural covers the distal part of the fourth, fifth and sixth costals and it seems seventh and eighth peripherals and the proximal part of the ninth. The sulcus between the third and fourth pleurals is on sixth costal. The fourth pleural covers the distal part of the sixth and seventh costals and also the ninth, tenth and part of the eleventh peripherals. The sulcus between the fourth and fifth pleurals is on the eleventh peripheral.

Plastral bones

Parts of the left hyoplastron, left mesoplastron, both hypoplastra and both xiphiplastra are present (Fig. 2C, D). Unfortunately, the anterior lobe is not preserved.

Hyoplastron. This contacts both the mesoplastron and the hypoplastron posteriorly.

Mesoplastron. This is triangular in shape, wider than long. In proportion, the mesoplastron of *N. tlaxiacoensis* is bigger than in other members of Platychelyidae. It contacts anteriorly the hyoplastron and posteriorly the hypoplastron. It lacks a midline contact with its counterpart.

Hypoplastron. The shape of the hypoplastron is similar to that of *P. oberndorferi*, *N. laticentralis* and *N. oxfordiensis*, but is proportionally bigger. The inguinal area is larger and more pronounced in relation to the right edge of the xiphiplastron. In Platychelyidae this area is narrower and less pronounced. The opening of the inguinal area is larger with some resemblance to that presented in *N. laticentralis*, *P. oberndorferi* and *N. oxfordiensis*. The arrangement of this area in *N. zapatocaensis* cannot be determined because it is broken.

Xiphiplastron. The suture of the xiphiplastron with the hypoplastron is close to the inguinal buttress, being very similar to that seen in *N. oxfordiensis*. This suture in *P. oberndorferi*, *N. zapatocaensis* and *N. laticentralis* is placed more distantly from the inguinal buttress. The posterior part of the xiphiplastron is not preserved.

Fontanelle. A central fontanelle is present in *N. tlaxiacoensis* and extends from the posteromedial part of the hyoplastron to the anteromedial portion of the hypoplastron. A fontanelle is also present in *P. oberndorferi* and *N. oxfordiensis*.

Plastral scutes

Pectoral. The pectoral scute lacks the anterior, medial and lateral parts. The sulcus between the pectoral and abdominal scutes is located on the posterior part of the hyoplastron and on the anterior part of the mesoplastron like in most members of Platychelyidae, except in *N. zapatocaensis* where this sulcus does not cross the mesoplastron. In contrast to *N. zapatocaensis*, this sulcus is slightly concave, as seen in *P. oberndorferi*, *N. oxfordiensis* and *N. laticentralis*.

Abdominal. The lateral margin of this scute cannot be recognized. The abdominal in *N. tlaxiacoensis* is wider than long. The bridge portion is similar to that of *N. oxfordiensis*, but it is more robust and longer than in *P. oberndorferi*, *N. laticentralis* and *N. zapatocaensis*. The sulcus between the abdominal and femoral scutes is located where the inguinal buttress starts and close of the suture of the hypoplastron with the xiphiplastron. This scute covers almost all the mesoplastron with the exception of its anterior area, and covers almost all the hypoplastron with the exception of its posterior area. It contacts the pectoral anteriorly and the femoral posteriorly.

Femoral. This is narrower and longer than in other members of Platychelyidae.

Anal. As only the anterolateral part of the anal scute is preserved, no further description of this element can be made.

PHYLOGENETIC ANALYSIS

Two phylogenetic analyses were performed: one unconstrained and the other using molecular constraints. We used the unconstrained analysis to perform all the subsequent analyses because the trees that we obtained were optimal and for the clade we are interested in this study, both analyses resulted in identical results.

Unconstrained phylogenetic analysis

A total of 4800 most parsimonious trees of 893 steps were found after two rounds of TBR in TNT program (López-

Conde *et al.* 2016, appendix S5). The consistency and retention indexes were 0.345 and 0.772, respectively. A strict consensus was calculated (López-Conde *et al.* 2016, appendix S6). *Notoemys tlaxiacoensis* was recovered inside the clade *Notoemys*. *Platychelys oberndorferi* is the sister group of *Notoemys*. An abbreviated strict consensus tree is shown in Figure 3.

The clade Platychelyidae is supported by nine synapomorphies present in all the trees and has a Bremer support value of 4. These characters are: carapace pentagonal in shape with a straight anterior margin and posterior margin tapering medially (character 126, Carapace F; not known for *N. tlaxiacoensis*); neurals irregular in shape, wider than long (character 131, Neural B); sulcus between vertebral 3 and 4 located on neural 6 (character 143, Vertebral C); central plastral fontanelle present (character 147, Plastron B); a pair of reduced mesoplastra (character 162, Mesoplastron A); extragulars reaching the entoplastron (character 173, Extragular D; not known for *N. tlaxiacoensis*); articulation tubercle on the anterior face of the first thoracic rib (character 205, Dorsal rib D; not known for *N. tlaxiacoensis*); thoracic vertebrae smooth and flat ventrally, hexagonal in shape (character 207, Dorsal vertebra B; not known for *N. tlaxiacoensis*); and costovertebral tunnel wide all along the entire length of the thoracic vertebrae (character 208, Dorsal vertebrae C; not known for *N. tlaxiacoensis*). A list of common synapomorphies for all the clades and taxa is provided in López-Conde *et al.* (2016, appendix S7).

The clade *Notoemys* has a Bremer support value of 2. When all the species of *Notoemys* are included in the cladistic analysis, there are no synapomorphies common to all the trees, but there are four synapomorphies common to some trees. These characters are: absence of musk ducts (character 133); presence of two suprapygals (character 138); sulcus between vertebrals 4 and 5 located on suprapygal 1 (character 144); and inguinal buttress not contacting the costals (character 163). The lack of synapomorphies common to all trees is due to the incomplete nature of two species, *N. oxfordiensis* and *N. tlaxiacoensis*. Characters 133 (absence of musk ducts) and 163 (inguinal buttress contacting peripherals only) are potential synapomorphies for the *Notoemys* clade because they have an ambiguous optimization due to the unknown condition for *N. tlaxiacoensis* (López-Conde *et al.* 2016, appendix S8). The coding of those characters for *N. tlaxiacoensis* will determine whether these characters are synapomorphies for *Notoemys* or synapomorphies of a more exclusive clade. The same happens with characters 138 and 144. They are potential synapomorphies for *Notoemys* clade because they have an ambiguous optimization due to the unknown condition in *N. oxfordiensis* (López-Conde *et al.* 2016, appendix S8).

To explore the behaviour of *N. oxfordiensis* and *N. tlaxiacoensis* in the cladistic analysis and their impact in the recovery of synapomorphies in the clade *Notoemys*, we ran different analyses excluding one or both species at a time. If *N. oxfordiensis* and *N. tlaxiacoensis* are excluded from the analysis, 4800 MPTs of 891 steps are recovered and the clade *Notoemys* is supported by four synapomorphies (characters 133, 138, 144 and 163; Fig. 3B). When only *N. tlaxiacoensis* is excluded from the analysis, 4800 MPTs of 893 steps are recovered and synapomorphic characters 133 and 163 support the clade *Notoemys* (Fig. 3C). On the other hand, when only *N. oxfordiensis* is excluded from the analysis, 4800 MPTs of 891 steps are recovered and synapomorphic characters 138 and 143 support the clade *Notoemys* (Fig. 3D). As we stated above the behaviour of these taxa in the phylogenetic analysis is due to the nature of the specimens where some characters cannot be codified. The script iterPCR of Pol & Escapa (2009) (López-Conde *et al.* 2016, appendix S9) suggests that characters 138 and 144 might help to solve the phylogenetic position of *N. oxfordiensis*, while characters 133, 163 and 164 might help to solve the position of *N. tlaxiacoensis*.

The phylogenetic relationships within *Notoemys* cannot be assessed because no discrete and informative characters were found to be included in a cladistic context. The inclusion of geometric morphometric data in the future may help to solve their interrelationships.

Molecularly constrained phylogenetic analysis

The constrained analysis resulted in 10 000 trees (maximum number of trees set in memory) of 916 steps (López-Conde *et al.* 2016, appendix S10), 23 steps longer than the most parsimonious trees found in the unconstrained analysis. A strict consensus was calculated (López-Conde *et al.* 2016, appendix S11). The main differences between these trees and the unconstrained trees pertain to the relationships among extant taxa, an unsurprising outcome. The clades of interest for this work (e.g. Platychelyidae, *Notoemys*) are recovered in the same position, composed by the same taxa, and supported by the same characters. A list of common synapomorphies is provided in López-Conde *et al.* (2016, appendix S12).

DISCUSSION

Comparisons with previous cladistic analyses

The first cladistic analysis to recover *Notoemys* as the sister clade to *Platychelys* was carried out by Cadena & Gaffney (2005). Since then, these two genera have been

considered to be a monophyletic group named Platy-chelyidae. In different cladistic analyses, Platychelyidae has been diagnosed by disparate characters. The cladistic analysis presented here includes a broader taxonomic sampling than previous studies, thus testing the mono-phyly of Platychelyidae on a broader scale. There are
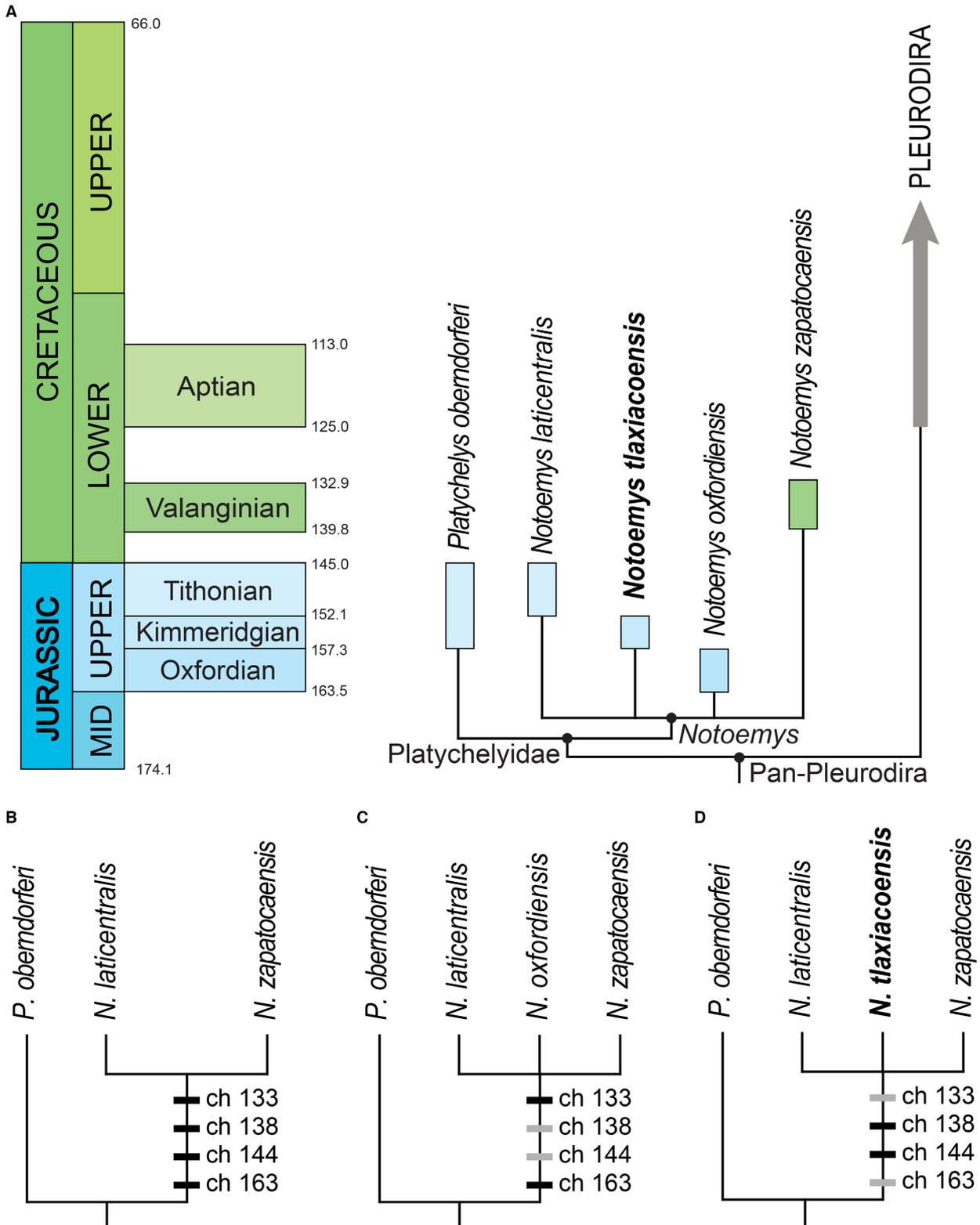
some characters that have been identified as synapomorphies in previous analyses. These characters are: central plastral fontanelle (Cadena & Joyce 2015); anterior tubercle on first thoracic rib (Cadena & Gaffney 2005, character 12; Cadena *et al.* 2013, character 66; Cadena & Joyce 2015); wide costovertebral tunnel (Cadena & Gaffney 2005, character 13; Cadena *et al.* 2013; Cadena & Joyce 2015); thoracic vertebrae flat in ventral view (Cadena & Gaffney 2005, character 14; Cadena *et al.* 2013, character 67; Cadena & Joyce 2015); and carapace with posterior sides tapering medially (Cadena & Gaffney 2005, character 6; Cadena *et al.* 2013, character 65). Other characters are equivocal. The character 'straight anterior carapace margin' (Cadena & Gaffney 2005, character 5; Cadena & Joyce 2015) is included in the present analysis in the definition of the character about the shape of the carapace (character 126, Carapace F); consequently, it has been recovered as a synapomorphy of Platychelyidae. The character 'first thoracic rib nearly as long as second thoracic rib' of Cadena & Gaffney (2005) is included in this analysis in the character Dorsal rib A. The character 'carapace with dorsal protuberances located on the posterior region of the pleural and vertebral scales' (Cadena *et al.* 2013) has not been included in the present analysis because the carapace of several members of the clade does not show those protuberances. For instance the carapace is smooth in the holotype (MACN-PV 18043) and referred specimens (MOZ-PV 2487 and 4040) of *N. laticentralis*, and it is unknown for both *N. oxfordiensis* and *N. tlaxiacoensis*. The character 'second neural smaller than the remaining neural series' (Cadena *et al.* 2013) is present in *P. oberndorferi*, in *N. laticentralis*, and could be present in *N. oxfordiensis*. However this is not the case for specimen MGJRG IPN 15-EAC 150620061, *N. zapatocaensis*. In *N. tlaxiacoensis* this character is unknown. Cadena & Gaffney (2005) proposed that the character 'thoracic ribs 9, 10 and 11 forming sacrum and attaching to ilium' characterizes Platychelyidae. However, based on the specimens of platychelyids listed in López-Conde *et al.* 2016, appendix S1), our interpretation is that thoracic ribs 9 and 10 are sutured to the ilium and what Cadena & Gaffney (2005) identified as thoracic rib 11 is the first sacral rib (sutured with sacral vertebra 1) and the sacral 1 is the sacral rib 2. In *N. laticentralis* thoracic ribs 9 and 10 contact the ilium, as sacral ribs 1 and 2 (Fernández & de la Fuente 1994). In *P. oberndorferi* thoracic ribs 9 and 10

also contact the ilium, but among the available specimens, only one (NMB 596) preserves sacral rib and sacral vertebra 1. This character is not known for *N. tlaxiacoensis* and *N. oxfordiensis*. The character 'neural alternating in size' (Cadena & Gaffney 2005) was incorporated in the character 'irregular, alternating in shape' of Cadena & Joyce (2015; E. A. Cadena pers. comm. 2016) and this character is included in the present matrix as well (character 131). The characters 'first thoracic central articulation concave, wider than high' (Cadena & Gaffney 2005, p. 11) and 'tall first thoracic central articulation' (Cadena & Joyce 2015) represent the same character which was not included because it is highly variable in our matrix and usually not reported for extinct taxa.

As for the clade Platychelyidae, there have been several characters proposed as synapomorphies for the clade *Notoemys*. The character 'neurals wider than long' (Cadena & Joyce 2015) has been recovered here as synapomorphy of the clade Platychelyidae and not of *Notoemys* (see López-Conde *et al.* 2016, appendix S7). In the phylogenetic context of this paper, several characters previously considered as synapomorphies of *Notoemys* are actually autapomorphies for *P. oberndorferi* (see López-Conde *et al.* 2016, appendix S7). These characters are: extension of iliac scar in the costals, suprapygal and peripherals (Cadena *et al.* 2013, character 82; Cadena & Joyce 2015) and supramarginal scales not continuous (Cadena & Gaffney 2005, character 2; Cadena *et al.* 2013, character 64). The character 'smooth and relatively flatter shell with lower dorsal protuberances lacking radial striation' (Cadena & Gaffney 2005; Cadena *et al.* 2013) is also a symplesiomorphy for Pan-Pleurodira. The character 'neural 3 in posterolateral contact with costal 4' (Cadena *et al.* 2013, character 62) has been obtained as a synapomorphy of *Notoemys* clade, however specimens NMS 8685 and 8686 of *P. oberndorferi* show that this contact is present in this species too. Two characters that could be useful to differentiate *P. oberndorferi* and *Notoemys* clade are: the shape of cervical scale (Cadena & Gaffney 2005; Cadena *et al.* 2013, character 61) and the size of the space between the first and the second thoracic ribs (Cadena *et al.* 2013). Both characters are difficult to score because of continue morphological variation among the taxa. The second character is only known for *N. laticentralis* and *N. zapatocaensis*. Another character proposed as a synapomorphy of *Notoemys* is the larger size of suprapygal 1

FIG. 3. Simplified strict consensus tree obtained in this study. A, simplified strict consensus trees calibrated in time showing the relationships within Platychelyidae. B, phylogenetic relationships within Platychelyidae considering only two species of *Notoemys*, *N. laticentralis* and *N. zapatocaensis*; when *N. tlaxiacoensis* and *N. oxfordiensis* are excluded from the analysis, the node *Notoemys* is supported by four synapomorphies (characters 133, 138, 144, 163). C, phylogenetic analysis excluding *N. tlaxiacoensis*; when this taxon is excluded, the clade *Notoemys* is supported by two unambiguous synapomorphies (characters 133 and 163) and two ambiguous ones (characters 138 and 144). D, phylogenetic analysis excluding *N. oxfordiensis*; when this taxon is excluded, the clade *Notoemys* is supported by two unambiguous synapomorphies (characters 138 and 144) and two ambiguous ones (characters 133 and 163). Colour online.

(Cadena & Gaffney 2005, character 8; Cadena *et al.* 2013, p. 69). This character is problematic at the moment and the revision of *P. oberndorferi* (P. Sullivan & W. Joyce, pers. comm. 2016) will help to elucidate the form of the pygal and suprapygal regions in this taxon.

The analysis of de la Fuente & Iturralde-Vinent (2001) did not recover *P. oberndorferi*, *N. oxfordiensis* and *N. laticentralis* as a monophyletic group, but as successive outgroups of Pan-Pleurodira. The clade formed by *N. oxfordiensis*, *N. laticentralis* and Pleurodira was supported by two characters (iliac scar not reaching the peripherals and supramarginals absent). In the present analysis, both characters (iliac scar reaching the peripherals and supramarginals present) are recovered as autapomorphies of *P. oberndorferi* (see López-Conde *et al.* 2016, appendix S7). Moreover, de la Fuente & Iturralde-Vinent (2001) recovered *N. laticentralis* as the sister group of Pleurodira based on the following characters: quadrate with ventral process extending medially to contact braincase below cranioquadrate space (character 3), hyomandibular branch of facial nerve lies within its own canal (character 4), iliac scar ovaloid (character 12), sacral rib reduced (character 13) and posterior entoplastral process reduced (character 26). Characters 3, 4 and 26 are included in the present cladistic analysis as characters Quadrate A (character 49), Hyomandibular nerve A (character 88) and Entoplastron B (character 152), respectively. Characters 49 and 88 are only known for the extant species of Pleurodira and character 49 is also known for *N. laticentralis* (the only platychelyid with a preserved skull). Character 152 is scored as reduced for all the members of platychelyid and Pleurodira in this analysis. The common mapping of these characters here shows that characters 49 and 152 are symplesiomorphies for Pan-Pleurodira and that character 88 is ambiguous for Platychelyidae because it is unknown for all the members of the clade (López-Conde *et al.* 2016, appendix S13). Character 12 (shape of iliac scar) of de la Fuente & Iturralde-Vinent (2001) was not included in the present analysis as explained above. Character 13 (size of sacral rib) has not been incorporated in this analysis but, as discussed above, the morphology of the sacral region in *P. oberndorferi*, *N. zapatocaensis* and *N. laticentralis* is similar. In extant pleurodires in general, thoracic ribs 9 and 10 contact the ilium (e.g. *Chelus fimbriatus*, USNM 117455) while in *Elseya dentata* (QM J 59279) only thoracic rib 10 contacts the ilium. In extant pleurodires it is common that the sacral ribs are reduced and in some cases they do not contact the ilium. This character needs further exploration. Consequently, the characters proposed by de la Fuente & Iturralde-Vinent (2001) as synapomorphies of *N. laticentralis* and Pleurodira are considered here to be simplesiomorphies of Pan-Pleurodira or Platychelyidae or their optimization is ambiguous in this phylogenetic context.

Time calibrated tree

Although the interrelationships among the different species of *Notoemys* are not resolved by this cladistic analysis, temporal calibration of the phylogeny shows that the divergence between *Platychelys* and *Notoemys* clades must have occurred at least by the end of the Middle Jurassic (Fig. 3A). This minimum age is provided by the oldest member of the clade, *N. oxfordiensis*, from the Oxfordian of Cuba. The location of *P. oberndorferi* (Kimmeridgian–Tithonian of Europe) as the sister group of *Notoemys*, generates a ghost lineage leading to *P. oberndorferi*, at least, from the Oxfordian to the Kimmeridgian (11.4 Ma). The lack of resolution within *Notoemys* produces several ghost lineages within the clade, all from the end of the Middle Jurassic (Callovian) to the Kimmeridgian (c. 7 Ma) for *N. tlaxiacoensis*, to the Tithonian (c. 12 Ma) for *N. laticentralis* and to the Valanginian (c. 24 Ma) for *N. zapatocaensis*. New discoveries and/or the addition of more characters to the cladistic analysis might allow us to better adjust the phylogeny of stem-Pleurodira to the stratigraphic record. Previous to the discovery of *N. tlaxiacoensis*, the genus *Notoemys* was known from two (Oxfordian and Tithonian) of the three stages of the Upper Jurassic and from the Valanginian (Lower Cretaceous). That fossil record shows two gaps, one in the Kimmeridgian (Upper Jurassic) and another in the Berriasian (Lower Cretaceous). The new record from Mexico, *N. tlaxiacoensis*, fills the gap in the Jurassic and represents the first record from the western Caribbean.

Palaeogeography of the Caribbean and the connection of Europe, the Caribbean and western South America

As mentioned in the introduction, platychelyid turtles have been found in the Oxfordian of Cuba (*N. oxfordiensis*) (Fig. 4A), in the Kimmeridgian of Mexico (*N. tlaxiacoensis*) (Fig. 4B), in the Kimmeridgian–Tithonian of Europe (*P. oberndorferi*), in the Tithonian of western Argentina (*N. laticentralis*) (Fig 4C) and in the Valanginian of Colombia (*N. zapatocaensis*) (Fig. 4D). This distribution of closely related taxa in the Jurassic of Europe, the Caribbean and western South America has been also observed in several groups of invertebrates (e.g. pelecipods, ammonites, brachiopods, ostracods) and vertebrates (e.g. crocodiliforms, plesiosauroids, ichtyosaurians, pliosauroids) (Gasparini 1978, 1992; Hillebrandt 1981; Westermann 1981, 1992; Imlay 1984; Bartok *et al.* 1985; Sandoval & Westermann 1986; Hillebrandt *et al.* 1992; Gasparini & Fernández 1996; Damborenea 2000; Aberhan 2001). The link between the Tethys and the Pacific Ocean started in the Early Jurassic when Pangea began to break up, separating the northern landmass (Laurasia) from the
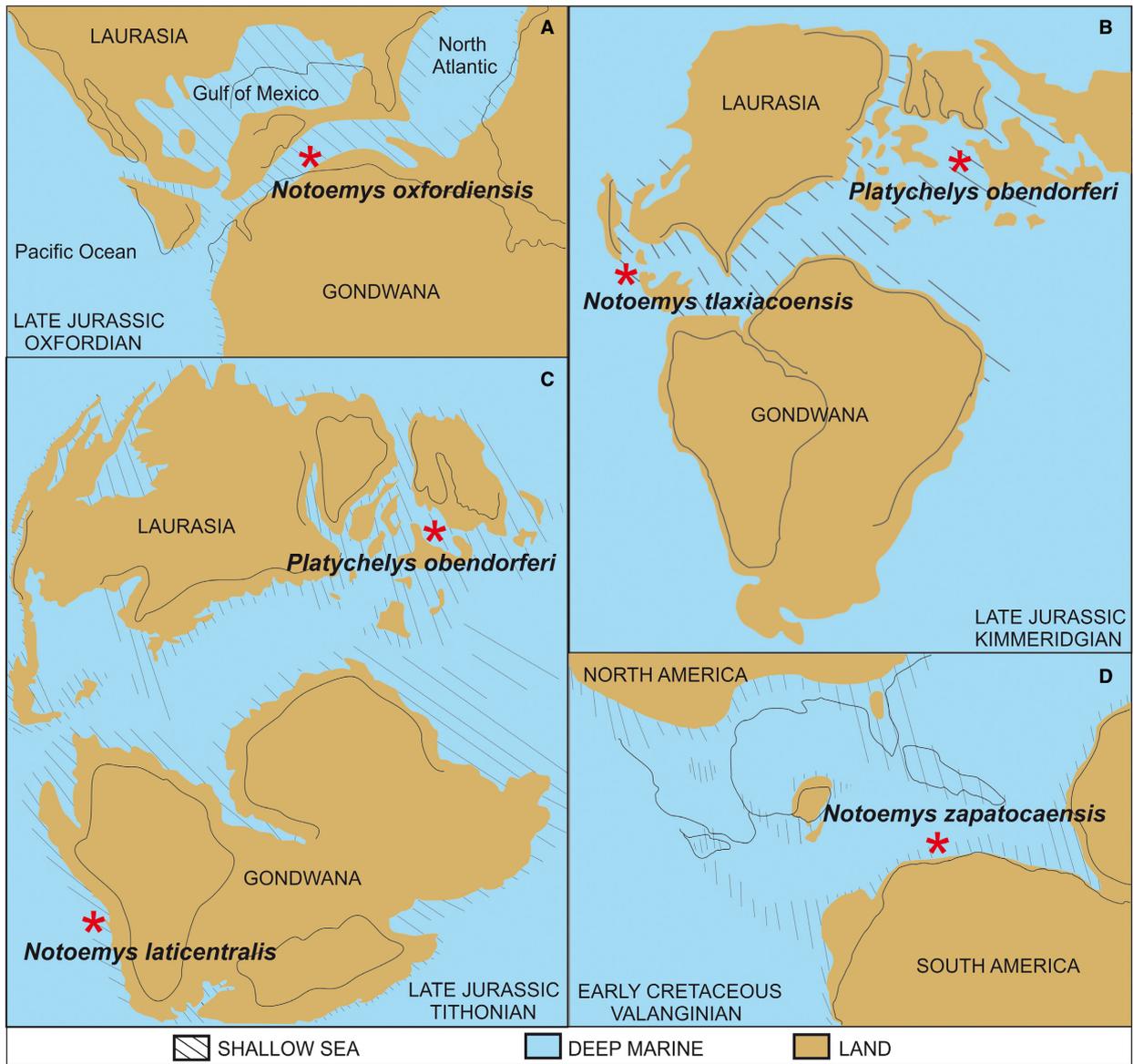
FIG. 4. Distribution of Platychelyidae during the Late Jurassic and Early Cretaceous. A, *Notoemys oxfordiensis* (based on Iturralde-Vinent 2004–2005). B, *Notoemys tlaxiacoensis* and *Platychelys obendorferi* (based on Golonka & Krobicki 2001). C, *Notoemys laticentralis* and *Platychelys obendorferi* (based on Cadena & Joyce 2015). D, *Notoemys zapatocaensis* (based on Iturralde-Vinent 2004–2005). Colour online.

southern landmass (Gondwana). The connection incipiently started in the Bathonian (or even earlier in the Hettangian or Pleinsbachian following Smith 1982), but it was in the Oxfordian when this connection and the Circumtropical Current were established (Frakes *et al.* 1992; Parrish 1992; Iturralde-Vinent 2003). The presence of a similar fauna in the Tethys, Caribbean and western South America led Smith (1982) to propose the presence of the 'Hispanic Corridor' along the Caribbean, communicating both oceans. This 'Hispanic Corridor' was well established in the Oxfordian; before then it was more of a filter than an actual corridor (Iturralde-Vinent 2004–2005).

CONCLUSIONS

The fossil record of turtles in Mexico is poorly studied. Here we describe the oldest turtle from Mexico found near Tlaxiaco (Oaxaca) in outcrops of the Sabinal Formation (Kimmeridgian). Our new cladistic analysis shows that the oldest turtle from Mexico belongs to the clade Platychelyidae, and more specifically to the genus *Notoemys*. Furthermore, the unique combination of characters shown by the only known specimen allows us to recognize it as a new species of *Notoemys*, here named *N. tlaxiacoensis*. Currently, the greatest diversity of Platychelyidae

is found in the Americas, while only *Platychelys oberndorferi* has been identified in Europe. The fossil record of platychelyids on both continents during the Late Jurassic and Early Cretaceous reinforces the proposed connection between the Tethys and the Palaeopacific through the Hispanic Corridor.

DATA ARCHIVING STATEMENT

The following data files for this study are available in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.508g5):

Appendix S1. Changes to Sterli *et al.* (2015)'s data set.
Appendix S2. Phylogenetic data set in Nexus format.
Appendix S3. Phylogenetic data set in TNT format.
Appendix S4. Constraints used in the constrained analysis.
Appendix S5. Unconstrained analysis: Most parsimonious trees in CTF format.
Appendix S6. Unconstrained analysis: Strict consensus tree.
Appendix S7. Unconstrained analysis: List of synapomorphies common to the three MPTs.
Appendix S8. Common mapping of characters 133, 138, 144 and 163.
Appendix S9. Results of iterPCR script.
Appendix S10. Constrained analysis: most parsimonious trees in CTF format.
Appendix S11. Constrained analysis: strict consensus tree.
Appendix S12. Constrained analysis: list of synapomorphies common to all the trees.
Appendix S13. Common mapping of characters 49, 88 and 152.

This published work and the nomenclatural act it contains, have been registered in ZooBank: http://zoobank.org/References/DBB99A4F-AF62-4735-96DC-977802BA2969.

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