

## A Review of the Fossil Record of Turtles of the Clades *Platychelyidae* and *Dortokidae*

Edwin Cadena<sup>1</sup> and Walter G. Joyce<sup>2</sup>

<sup>1</sup> Alexander von Humboldt Foundation, Senckenberg Naturmuseum, 60325 Frankfurt am Main, Germany  
—email: cadenachelys@gmail.com

<sup>2</sup> Department of Geosciences, University of Fribourg, 1700 Fribourg, Switzerland  
—email: walter.joyce@unifr.ch

### ABSTRACT

The fossil record of platychelyid turtles expands from the Late Jurassic (Oxfordian) of Cuba to the Early Cretaceous (Valanginian) of Colombia. Platychelyids were adapted to freshwater to coastal environments. Current phylogenies confidently suggest that platychelyids are situated along the stem lineage of crown *Pleurodira*. A taxonomic review of the group concludes that of six named “platychelyid” taxa, four are valid and two are nomina nuda. Dortokids are a poorly understood group of freshwater aquatic turtles that are restricted to the Early Cretaceous (Barremian) to Eocene (Lutetian) of Europe. The phylogenetic position of the group is still under debate, but there is some evidence that these turtles are positioned along the stem lineage of crown *Pleurodira* as well. A taxonomic review of the group concludes that of four named dortokid taxa, two are valid, one is a nomen invalidum and one a nomen nudum.

### KEYWORDS

Phylogeny, biogeography, paleoecology, *Pan-Pleurodira*, *Platychelyidae*, *Dortokidae*

### Introduction

The informal term “stem-pleurodires” refers to the paraphyletic group of all pan-pleurodiran turtles (sensu Joyce et al. 2004) to the exclusion of crown *Pleurodira*. In contrast to the highly diverse fossil record of the cryptodiran stem, the pleurodiran stem is represented only by a small number of fossil specimens and taxa from a few localities worldwide. At present, there is strong evidence that the extinct clade *Platychelyidae* Bräm, 1965 (formally defined herein, redundant with *Platychelira* Gaffney et al., 2006) populates the stem lineage of *Pleurodira*. Although the evidence is less strong that the fossil clade *Dortokidae* Lapparent de Broin and Murelaga, 1996 (formally defined herein) may also be placed along the phylogenetic stem of *Pleurodira*, they are nevertheless discussed herein as well.

The first known platychelyid, *Platychelys oberndorferi* Wagner, 1853, was described from the Late Jurassic (Tithonian) of Kelheim, Ger-

many, based on a partial carapace. Two additional specimens, in particular a well-preserved carapace (Wagner 1861) and the anterior lobe of a plastron (Zittel 1877), were later described from the same locality. Rüttimeyer (1859a, 1859b) named another stem-pleurodire genus, *Helemys*, based on five specimens from the Late Jurassic (Kimmeridgian) of Solothurn, Switzerland, but he realized soon after that this taxon is synonymous with *Platychelys* (Rüttimeyer 1867, 1873). Almost a century after these discoveries, Bräm (1965) summarized all Swiss material of *P. oberndorferi* available to him, provided a schematic reconstruction and named the taxon *Platychelyidae*. A beautifully preserved, complete skeleton of a *P. oberndorferi* was reported by Karl and Tichy (2006) from the Late Jurassic (Tithonian) of Eichstätt, Germany, but this specimen remains in private hands and is therefore not explicitly discussed herein.

The first platychelyid found outside Europe is *Notoemys laticentralis* Cattoi and Freiberg, 1961, which is based on an almost complete cara-

pace and anterior plastral lobe that was found integrated into the patio of a private house, but that could be traced back to Late Jurassic (Tithonian) quarries in Neuquén Province, Argentina. The first comprehensive description of the type specimen was provided by Wood and Freiberg (1977), who concluded that this taxon is referable to the European clade Plesiochel[y]idae. However, de la Fuente and Fernández (1989), Fernández and de la Fuente (1993) and Gasparini et al. (2015) later presented two additional specimens from nearby localities in Neuquén Province, including a more complete, articulated shell with a partial skull, neck and postcranial bones, which clearly revealed the pleurodiran affinities of this taxon. The available material is extensively described in Wood and Freiberg (1977), Fernández and de la Fuente (1994) and Lapparent de Broin et al. (2007). de la Fuente (2007) referred a partial skeleton, including a damaged skull, to this taxon, but a description of this specimen is still outstanding.

The third known platychelyid also originates from the western hemisphere and constitutes the earliest record for this group of turtles. *Caribemys oxfordiensis* de la Fuente and Iturralde-Vinent, 2001, from the Late Jurassic (Oxfordian) of Cuba, is represented by a single, articulated, but poorly preserved shell and some associated postcranial elements. Given its close relationship with *N. laticentralis*, this taxon was referred to *Notoemys* by Cadena and Gaffney (2005) and we herein follow this assessment. No additional material has been found to date.

The most recently discovered and geologically youngest platychelyid is *Notoemys zapatocaensis* Cadena and Gaffney, 2005, which is based on a nearly complete shell from the Early Cretaceous (Valanginian) of Colombia. Two additional specimens were recently described from the type locality that provide important insights into the anatomy of this taxon (Cadena et al. 2013).

*Dortoka vasconica* Lapparent de Broin and Murelaga, 1996 and *Dortoka botanica* Lapparent de Broin in Gheerbrant et al., 1999 are based on plentiful, but fragmentary material from the Late Cretaceous (Campanian–Maastrichtian) of Spain (Lapparent de Broin and Murelaga 1996, 1999) and the Paleocene of Romania (Gheerbrant et al. 1999; Lapparent de Broin et al. 2004), respectively, and are therefore significantly younger than all

known platychelyids. These taxa share some unusual characteristics in the morphology of their shell and are therefore grouped in the taxon *Dortokidae* Lapparent de Broin and Murelaga, 1996 (e.g., Gheerbrant et al. 1999; Lapparent de Broin et al. 2004; Gaffney et al. 2006). Given the prevalence of redundant names, we herein place all valid dortokid species within *Dortoka*, but we retain *Dortokidae* as a potentially more inclusive, phylogenetically defined clade name. There is some evidence that *Dortokidae* may be situated along the phylogenetic stem of *Pleurodira*, but we agree that it is prudent to classify this taxon as *Pan-Pleurodira* indet. for the moment (Gaffney et al. 2006), because the currently available character evidence, which is derived from fragmentary specimens only, places this taxon within *Pan-Pleurodira*, but not necessarily within the crown group.

Mounting evidence indicates that the earliest known fossil turtle, *Proterochersis robusta* Fraas, 1913 from the Late Triassic of Germany, is not a stem-pleurodire (Fraas 1913; Gaffney 1975; Gaffney et al. 2007) but rather a stem turtle (Rougier et al. 1995; Joyce 2007; Joyce, Schoch et al. 2013). This taxon is therefore not discussed herein.

For institutional abbreviations see Appendix 1. Named platychelyid and dortokid genera are listed in Appendix 2.

## Skeletal Morphology

### Cranium

The only cranial material so far described for any potential stem-pleurodire belongs to *Notoemys laticentralis*. Only the posterior half of the skull is preserved, including most of the right otic chamber (quadrate, squamosal, prootic and opisthotic), basisphenoid, basioccipital, exoccipital, supraoccipital, the most posterior portion of the pterygoid and the most medial portions of the left prootic and the opisthotic. The skull is extensively described and figured in Fernández and de la Fuente (1994, fig. 2) and Lapparent de Broin et al. (2007, figs. 2, 4, pl. 1a–f). The most remarkable features of this skull are the ventrally widened prootic descending to the area articularis quadrati; the flattened, shortened and posteriorly rounded paroccipital process; the thickened medial portion of the columella; the ventral expo-

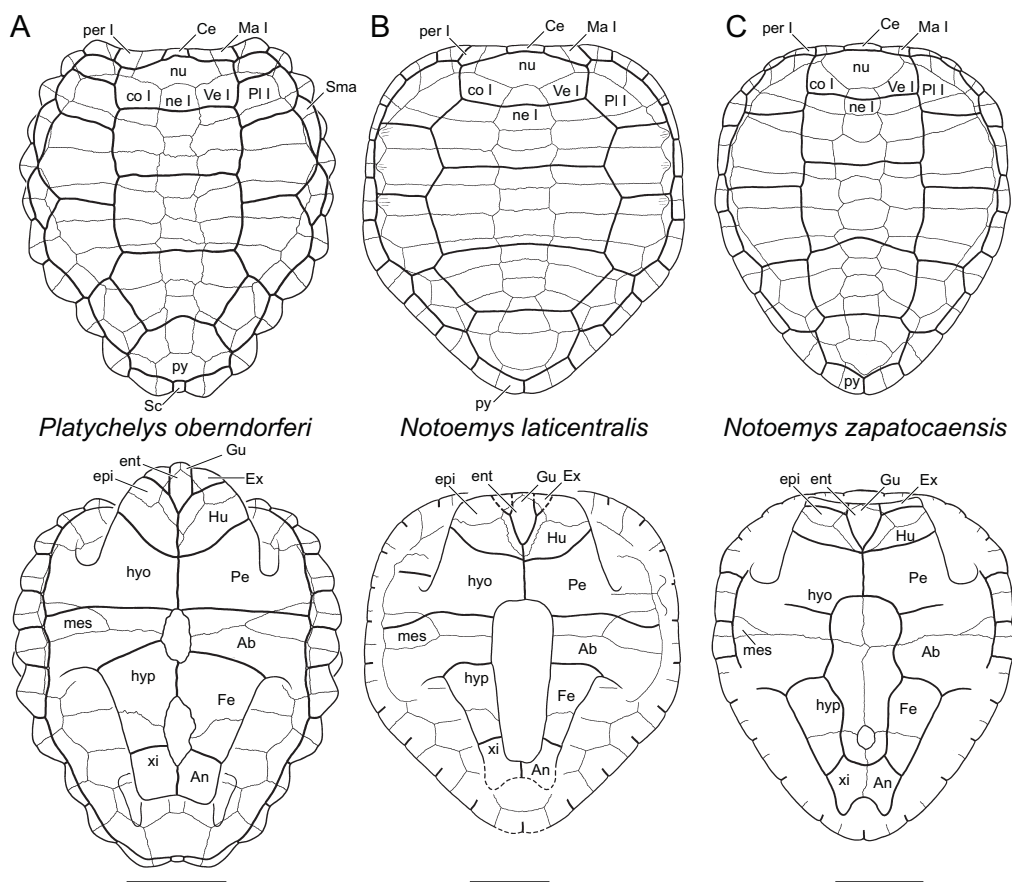


FIGURE 1. Shell morphology of *Platychelyidae* as exemplified by three species. **A**, *Platychelys oberndorferi* (modified from Lapparent de Broin 2001 with reference to NMS 8686). **B**, *Notoemys laticentralis* (modified from Fernández and de la Fuente 1994 with reference to MOZ P 2487). **C**, *Notoemys zapatoacaensis* IPN/MGJRG 150620061 (modified from Cadena et al. 2013). *Abbreviations*: Ab, abdominal scute; An, anal scute; Ce, cervical scute; co, costal; ent, entoplastron; epi, epiplastron; Ex, extragular scute; Fe, femoral scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; Ma, marginal scute; mes, mesoplastron; ne, neural; nu, nuchal; Pe, pectoral scute; per, peripheral; Pl, pleural scute; py, pygal; Sc, supracaudal; Sma, supramarginal scute; Ve, vertebral scute; xi, xiphiplastron. Scale bars approximate 5 cm.

sure of the stapedia canal and the absence of posterior closure of the recessus scalae tympani. A recent study focused on the basiptyergoid process of Mesozoic turtles confirms that the basiptyergoid process is already absent this early in panpleurodire evolution (Rabi, Zhou et al. 2013). A second, partial skull is mentioned in de la Fuente (2007) but still awaits description.

### Shell

Among platychelyids, Bräm (1965) provided descriptions for the shells of *Platychelys oberndorferi*, Fernández and de la Fuente (1994) and Lapparent de Broin et al. (2007) for *Notoemys*

*laticentralis*, de la Fuente and Iturralde-Vinent (2001) for *N. oxfordiensis* and Cadena et al. (2013) for *N. zapatoacaensis*. The shells of platychelyids are relatively small in size, with a maximum carapace length of approximately 30 cm (Figure 1). The carapace and plastron are proportional in size, and the anterior margin of the plastron typically protrudes beyond the anterior margin of the carapace. As in most crown pleurodires, the shells of platychelyids are characterized by the sutural articulation of the pelvis to the carapace and plastron, the well-developed anal notch varying from U- to V-shaped, one pair of laterally restricted mesoplasstra and a single gular scute. The carapace is

sculpted by one medial and two lateral lines of knobs, which correspond to the growth centers of the vertebral and pleural scutes, respectively. These knobs are extremely high in *P. oberndorferi*, with a marked pattern of radial bony striations. In contrast, representatives of *Notoemys* have only low knobs and lack radial striations, at least when preserved. The shell of platychelyid turtles can otherwise be distinguished from most other pleurodires by a marked costovertebral tunnel that is very wide through its entire length, an articulation tubercle on the anterior face of the first thoracic rib and reduction of neural II relative to the rest of the series, ventrally smooth and flat thoracic vertebrae with a hexagonal shape and centrolateral notch, and the presence of one or two plastral fontanelles, which may be affected by sexual dimorphism (Cadena et al. 2013).

*Dortoka botanica* is known from numerous fragmentary remains and an articulated, though heavily crushed shell (Lapparent de Broin et al. 2004). *Dortoka vasconica* is similarly known from partial shell material only, which provides unique insights to the internal anatomy of the shell but only a poor basis for rigorous reconstructions (Lapparent de Broin and Murelaga 1999; Pérez-García et al. 2012). We therefore do not provide a reconstruction for dortokids herein and highlight only the most notable morphological features of the group as reported in the literature.

The shell of dortokids generally resembles that of most crown pleurodires by having a short first thoracic rib, an articulated pelvis, a single gular scute and a large medial epiplastral contact, but differs in lacking mesoplastra. The bones of the shell are covered by microreticulations (sensu Lapparent de Broin and Murelaga 1999), and the carapace of dortokids, especially the neurals, is furthermore decorated by anteroposteriorly elongate tubercles and pits. The anterior portion of the carapace is enlarged by an elongated nuchal, but peripheral I is notably short and does not contact costal I posteriorly. The neural series consists of elongate elements with irregular, alternating shapes that fully separate the costals from one another. All five vertebrals are narrow, but pleural II laps at least partially onto costal I. The plastron is comparable in size to the carapace and has well-developed inguinal and axillary buttresses. The iliac scar is restricted to costals VII and VIII and is anteroposteriorly elongated.

### Postcranium

Little postcranial material is available for platychelyids and dortokids. Four cervical vertebrae are known for *Notoemys laticentralis* and are figured in Fernández and de la Fuente (1994, fig. 3) and Lapparent de Broin et al. (2007, pl. 1g–j). The preserved vertebrae include the atlas, the axis and cervicals III and IV. These cervicals are opisthocelous, low and have elongated centra and neural arches. Cervicals III and IV bear anteriorly oriented triangular transverse processes with a transverse anterior border. The prezygapophyses and postzygapophyses are widely separated from one another and are oriented along the horizontal plane. Neural spines are absent.

A partially preserved cervical VIII is known for *N. oxfordiensis* (de la Fuente and Iturralde-Vinent 2001, figs. 4, 5). It is posteriorly convex and has a low neural spine that is posteriorly continuous with the processes bearing the postzygapophyses. The posterior part of the ventral surface is smooth, slightly convex and lacks a keel. A badly preserved isolated caudal vertebra is also known for *N. oxfordiensis* (de la Fuente and Iturralde-Vinent 2001, figs. 4, 5) but lacks important anatomical details.

Bräm (1965, pl. 1.3, 4) reported two vertebral elements that had been found during acid preparation associated with a shell of *P. oberndorferi* and interpreted them as cervicals. As in *N. laticentralis* and *N. oxfordiensis*, the neural arches of these elements are low and the neural spines are reduced, but one element is biconcave whereas the other is biconvex, with large transverse processes. Lapparent de Broin (2000) and Gaffney et al. (2006) interpreted these vertebrae as cervical VII and VIII, respectively, but these elements still await more formal assessment.

Only a single cervical and up to 19 caudals have been referred to *Dortoka vasconica* (Lapparent de Broin and Murelaga 1999, figs. 5, 6). The cervical is highly fragmentary but can nevertheless be shown to be posteriorly convex. The caudal vertebrae are variously procoelous, amphicoelous and opisthocelous.

The available forelimb and hind limb elements of *Notoemys laticentralis* are described and figured in de la Fuente and Fernández (1989, fig. 3) and Fernández and de la Fuente (1994, figs. 6–9). These include the humeri, femora, the left radius, the ulnae, the left tibia, a partial left fibula

and parts of the carpus and pes. Important differences between the limb bones of *N. laticentralis* and crown pleurodirans are: (1) the head of the humerus is not truly hemispherical but anteroposteriorly wider than deep; (2) the proximal end of the ulna is more expanded; (3) the angle between the minor and major trochanters of the femur form an angle of approximately 60°, rather than 90°; (4) the tibial and fibular articular surfaces meet to form a variable ridge extension; and (5) the metacarpals are relatively short elements.

The femora, humeri and the right tibia and fibula are described and figured for *N. oxfordiensis* (de la Fuente and Iturralde-Vinent 2001, figs. 2, 3), but they are still attached to the shell and observations are limited. The femur of *N. oxfordiensis* is slightly longer than the humerus and both ends are slightly expanded. The femoral shaft is subcylindrical in cross section and arched dorsoventrally. The tibia is a massive bone expanded at both ends, and the shaft is unnaturally bent. The fibula is a slender element, more gracile than the tibia, with a rounded proximal articular surface.

No limb elements are known for *P. oberndorferi* or any dortokid.

### Phylogenetic Relationships

The stem lineage of pleurodires was long thought to be populated by the oldest known fossil turtle, *Proterochersis robusta*, and to therefore extend to the Triassic (Fraas 1913; Gaffney 1975; Lapparent de Broin et al. 2004; Gaffney et al. 2007), but new insights into the anatomy of this taxon combined with species-level cladistic analyses have thoroughly rejected that idea with increasing level of confidence (Rougier et al. 1995; Joyce 2007; Joyce, Schoch et al. 2013).

At present it is still difficult to resolve the phylogenetic relationships of various Jurassic turtles with confidence, as xinjiangchelyid, paracryptodiran and plesiochelyid turtles are variously placed inside the crown or outside the crown (e.g., Joyce 2007; Gaffney et al. 2007; Sterli and de la Fuente 2011; Anquetin 2012; Rabi, Zhou et al. 2013; Sterli et al. 2013). However, phylogenetic analyses universally retrieve all taxa herein referred to *Platycheilyidae* as stem-pleurodires and these can therefore be argued to be the oldest unambiguous crown turtles (Joyce, Parham et al. 2013).

*Platycheily oberndorferi* was originally referred to Emydidae (Wagner 1853; Rüttimeyer 1873) or Pleurosternidae (Lydekker 1889; Hay 1908; Kuhn 1964), but Bräm (1965) highlighted the pleurodiran affinities of this taxon, while noting differences with crown pleurodires, and created the new taxon *Platycheilyidae*. Starting with Gaffney et al. (1991), *P. oberndorferi* was included in most cladistic analyses of global turtle relationships and consistently retrieved as a stem-pleurodire (Figure 2).

Fernández and de la Fuente (1994) hypothesized with cladistic arguments that *Notoemys laticentralis* is more closely related to crown *Pleurodira* than to *P. oberndorferi*, a conclusion supported by the cladistic analysis of Lapparent de Broin and Murelaga (1999). Later, de la Fuente and Iturralde-Vinent (2001) expanded their sample to include *N. oxfordiensis* and confirmed in their cladistic analysis of 30 characters, of which 11 are parsimony uninformative, the derived position of *Notoemys* relative to *P. oberndorferi*.

The phylogenetic analysis of Cadena and Gaffney (2005) was expanded to include *N. zapatocaensis* and 26 parsimony-informative characters, and concludes that *Notoemys* and *Platycheily* form a clade that is sister to crown *Pleurodira*. The vastly expanded analyses of Gaffney et al. (2006) and Cadena et al. (2013) also support this topology, but disagree in the exact interrelationship of the three species placed within *Notoemys*. We herein retain a polytomy within *Notoemys* to reflect the uncertain phylogenetic relationships within that taxon (see Figure 2).

The phylogenetic relationships of dortokids are still poorly resolved, mostly because of the fragmentary nature of all known taxa. Lapparent de Broin and Murelaga (1999) included *Dortoka vasconica* in an analysis of pan-pleurodires and concluded upon a placement along the stem of Pelomedusoides. Lapparent de Broin et al. (2004), in contrast, placed dortokids in a basal polytomy with Chelidae and Pelomedusoides. Gaffney et al. (2006) finally retrieved a placement of *D. vasconica* in an intermediate position between *Platycheilyidae* and crown *Pleurodira* along the phylogenetic stem of *Pleurodira*, but admitted little confidence in the result, because it was based on cervical and caudal vertebrae not associated with any shell material. We utilize this phylogenetic position herein but await more rigorous

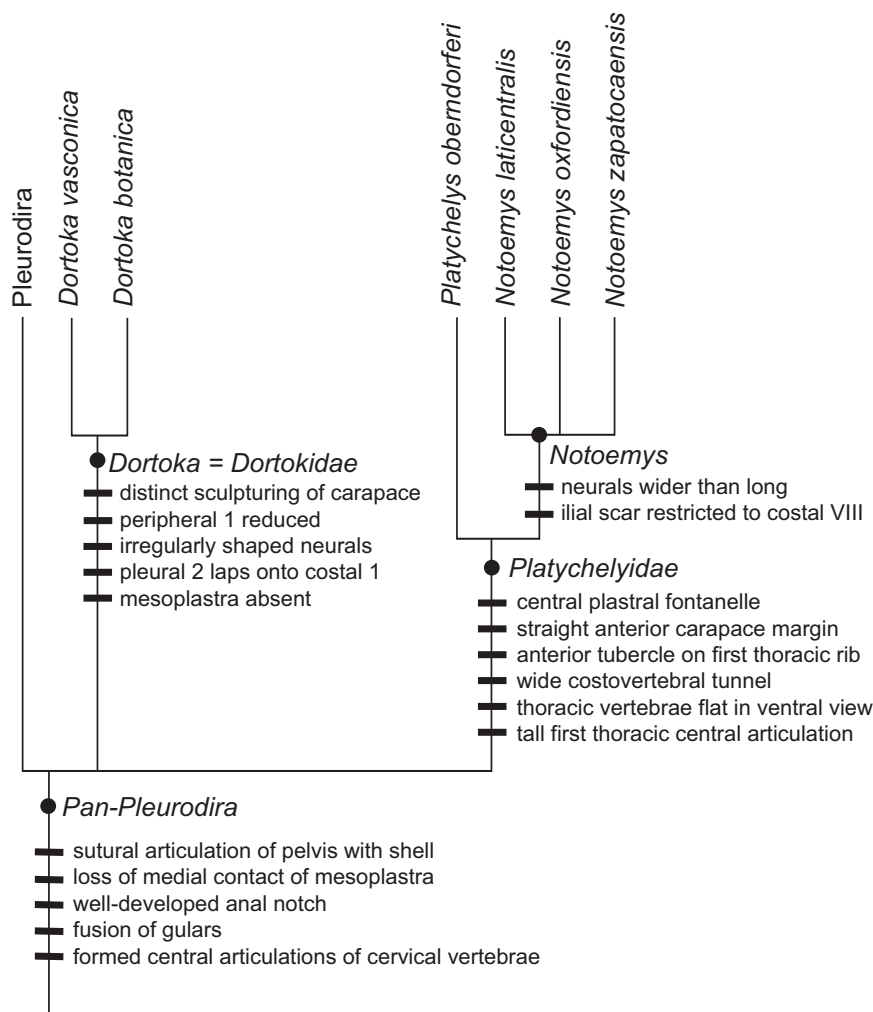


FIGURE 2. A phylogenetic hypothesis of *Pan-Pleurodira*, including all valid platychelyid and dortokid taxa, with diagnostic characters for the most important clades. The phylogenetic hypothesis is partially from Cadena et al. (2013), but characters were only included (or modified) if they support a clade within a global phylogenetic context (e.g., the loss of supramarginals unifies a clade more inclusive than *Pan-Pleurodira* and was therefore omitted).

analyses in the future using more complete specimens (see Figure 2). It is notable that dortokids are significantly younger than all known platychelyids and occur in concert with crown pleurodires (Figure 3).

### Paleoecology

All platychelyids come from marine or littoral stratigraphic sequences, with abundant invertebrates and marine reptiles, including plesiosaurs, pliosaurs, ichthyosaurs and metriorhynchid crocodilians (Bräm 1965; Fernández and de la Fuente

1994; de la Fuente and Iturralde-Vinent 2001; Cadena and Gaffney 2005). Almost all known specimens are known from articulated shells, and it is therefore apparent that they did not undergo substantial transport after death (Brand et al. 2003). However, it is also notable that most specimens were found in the vicinity of nearby islands or continents. Another particularity of platychelyid shells is the well-ossified carapace, but presence of central plastral fontanelles, in contrast to most marine turtles that exhibit a reduction in ossification in both the carapace and fontanelle. Furthermore, the preserved limbs of *N. laticen-*

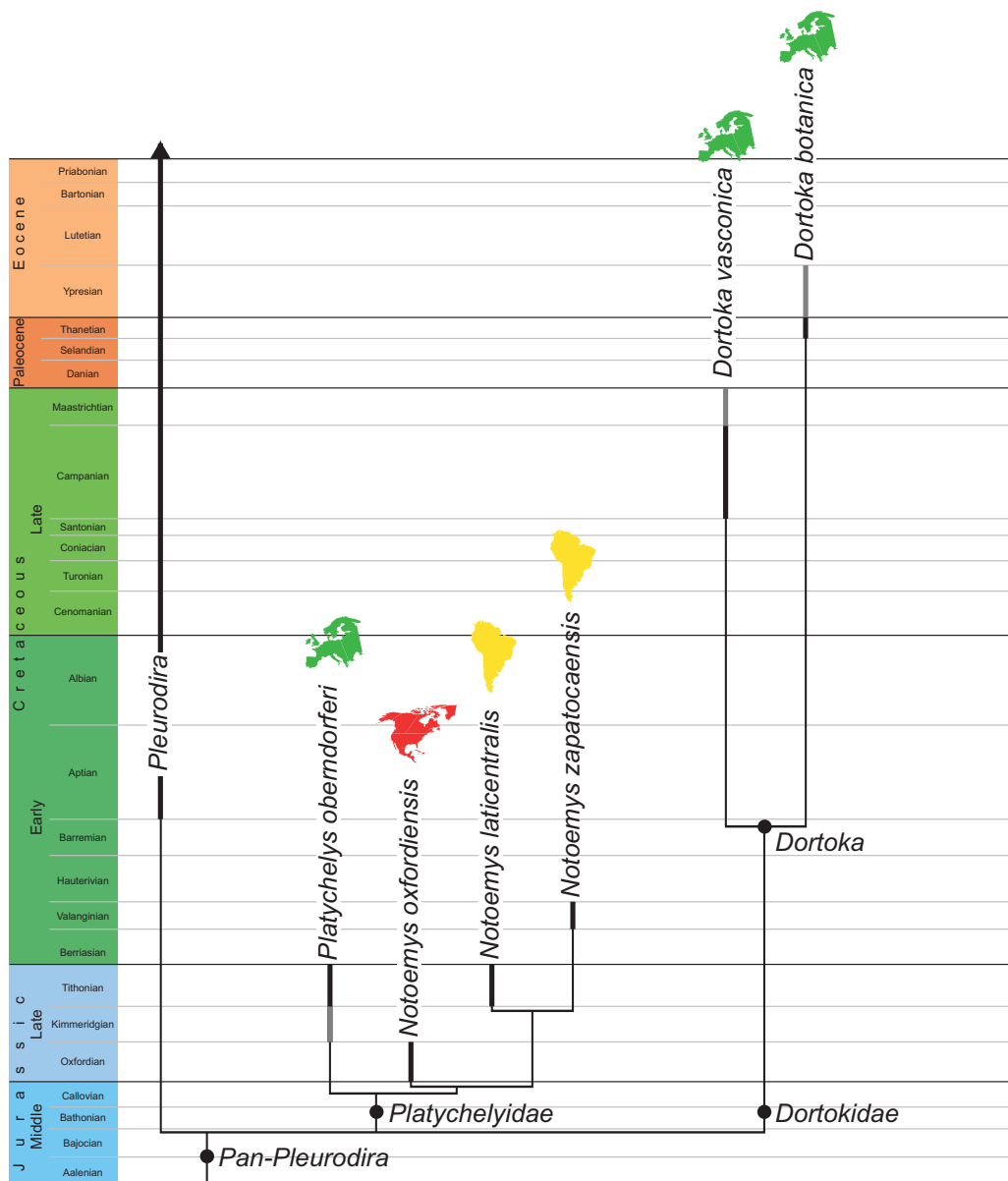


FIGURE 3. The stratigraphic and biogeographic distribution of valid platychelyid and dortokid taxa. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material.

*tralis* and *N. oxfordiensis* show that the femur was only slightly longer than the humerus and cylindrical in cross section, ratios typical for nonmarine turtles (Joyce and Gauthier 2004). There is therefore no evidence for the formation of a paddle, a conclusion informally supported by the complete skeleton of *P. oberndorferi* held in a private collection (Karl and Tichy 2006). The bone

microstructure of *P. oberndorferi* is typical for turtles with only moderate adaptations to aquatic environments (Scheyer 2009) and the large costovertebral tunnel, large hyoids (only visible in the privately held specimen) and shell decorations are reminiscent of the extant *Macrochelys temminckii* (alligator snapping turtle) and *Chelus fimbriata* (matamata turtle), which are gape and suction

feeders dependent on shallow waters, a resemblance already noted by Rüttimeyer (1873).

The available taphonomic, paleoenvironmental, morphological and bone microstructural evidence therefore supports the conclusion that platychelyids were inhabitants of shallow waters with a certain tolerance or preference for brackish to salty waters. However, even those forms that preferred marine habitats were certainly restricted to lagoon areas, as the limbs of these relatively small turtles were only poorly adapted to open marine conditions. This tolerance of marine conditions, however, most certainly helped platychelyids to disperse along coastlines and among the continents during the early breakup of Pangaea.

All known dortokids originate from littoral or riverine sediments and are found associated with continental faunas (Lapparent de Broin and Murelaga 1996, 1999; Lapparent de Broin et al. 2004; Pérez-García et al. 2014). The shell histology and bone density of *D. vasconica* is comparable with that of freshwater forms (Pérez-García et al. 2012).

### Paleobiogeography

The oldest platychelyids are *Notoemys oxfordiensis* from the Late Jurassic (Oxfordian) of Cuba (de la Fuente and Iturralde-Vinent 2001) followed by *Platychelys oberndorferi* from the Late Jurassic (Kimmeridgian and Tithonian) of Germany and Switzerland (Wagner 1853; Rüttimeyer 1873) and *Notoemys laticentralis* from the Late Jurassic (Tithonian) of Argentina (Cattoi and Freiberg 1961; Figure 4). Fragmentary remains formerly referred to *Platychelys* from the Late Jurassic (Kimmeridgian–Tithonian) of Guimarota Mine, Portugal (Bräm 1973), have more recently been identified as indeterminate pleurosternids (Scheyer and Anquetin 2008), while the Early Jurassic taxon *Platychelys courrenti* Bergouinioux, 1935 is based on a nonfossiliferous concretion (Lapparent de Broin 2001). Considering that the vast majority of pan-pleurodire diversity occurred on the southern continents, the notable presence of the oldest unambiguous pan-pleurodires in the north requires special consideration.

During the Late Jurassic, Cuba was part of the recently formed Guaniguanico Terrane, which originated at the Caribbean borderland of the

Maya block (Yucatan Peninsula) (Iturralde-Vinent 1994) and which was narrowly separated from South America by the emerging proto-Caribbean from South America (Giunta and Orioli 2011). Western Europe was similarly separated from Africa by a narrow strait (Stampfli and Hochard 2009). Given the global presence of stem turtles throughout the Triassic and Jurassic, it is equally parsimonious to postulate an origination of the pleurodiran lineage in the north or in the south, but given that stem-pleurodires are notably absent in all other sedimentary environments of the northern continents throughout the Jurassic (Joyce, Parham et al. 2013), it is more plausible to postulate that *Pan-Pleurodira* indeed originated in the south and that platychelyids (and later dortokids) dispersed to neighboring land masses along the northern fringes of Pangaea. Independent of the geographical origin *Pan-Pleurodira*, it is evident that the split between *Notoemys* and *Platychelys* should have occurred prior to the Late Jurassic (see Figure 3).

The Early Cretaceous record of platychelyids is restricted to *N. zapatocaensis* from the Valanginian of Colombia (see Figure 4). The Early Cretaceous (Berriasian) taxon *Platychelys anglica* Lydekker, 1889 is now universally agreed to not represent a pan-pleurodire (Lapparent de Broin and Murelaga 1999; Lapparent de Broin 2001; Milner 2004; Joyce et al. 2011).

The fossil record of dortokids is currently restricted to Europe (Figure 5). The earliest record consists of fragments from the Barremian of Teruel Province, Spain (Murelaga Bereikua 1998), the Santonian Veszprém County, Hungary (Rabi, Vremir et al. 2013), and the Aptian Castellón Province, Spain (Pérez-García et al. 2014), all of which are herein considered to be undiagnostic of valid species. Considering that the early record is focused on Spain and that the Iberian Peninsula was closest to the southern continents during the Early Cretaceous (Stampfli and Hochard 2009), it is plausible that dortokids dispersed from Africa to Europe during the early Cretaceous via the Iberian Peninsula.

The Late Cretaceous record of dortokids includes remains from the Campanian of Lower Austria (Rabi, Vremir et al. 2013) and the Maastriichtian of nearby Alba and Hunedoara Counties, Romania (Rabi, Vremir et al. 2013). Rich, though fragmentary, remains are the basis of *Dor-*





FIGURE 4. The biogeographic distribution of figured platychelyid turtles. Stars mark the type locality of valid taxa. Locality numbers are cross-listed in Appendix 3. Abbreviations: CH, Switzerland; DE, Germany.

*toka vasconica* from Burgos Province, Spain (Lapparent de Broin and Murelaga 1996, 1999; Pérez-García et al. 2012). Fragmentary remains have also been reported from the Departments of

Bouches-du-Rhône, Charente-Maritime, Gard and Hérault, France (e.g., Lapparent de Broin et al. 2004; Vullo et al. 2010), of which only a purported partial pelvis is figured (Vullo et al. 2010).

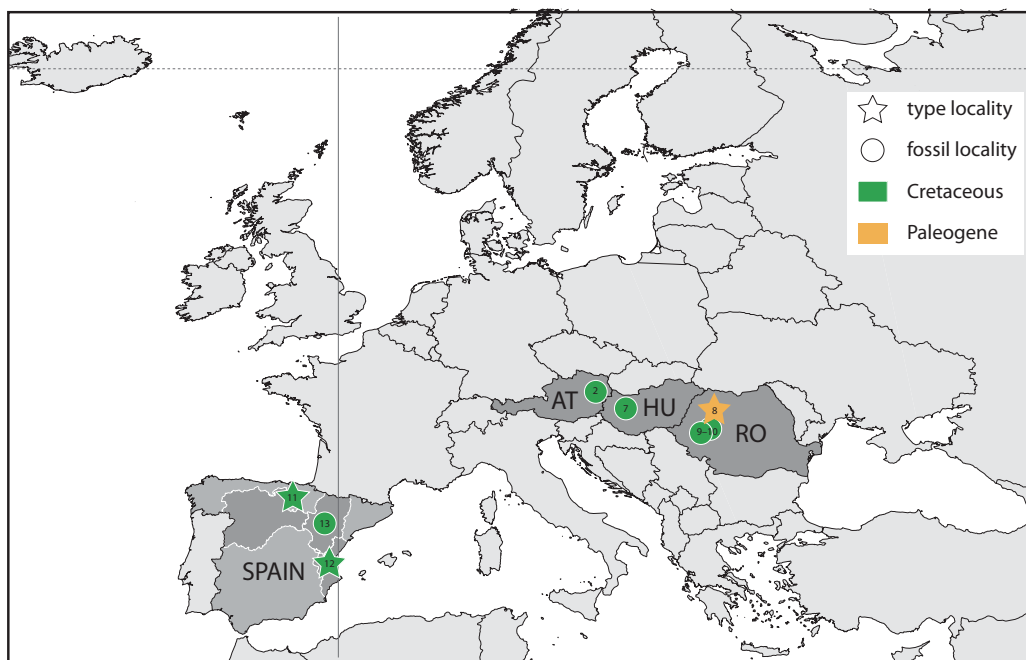


FIGURE 5. The biogeographic distribution of figured dortokid turtles. Stars mark the type locality of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: AT, Austria; HU, Hungary; RO, Romania. Note that France is not highlighted, because convincing material from that country has not yet been figured.

We therefore cannot rigorously verify the presence of this taxon in France.

The fossil record of dortokids ends with *Dortoka botanica* from the Thanetian–Ypresian of Sălaj County, Romania (Gheerbrant et al. 1999; Lapparent de Broin et al. 2004; Vremir 2013), which includes some of the best-preserved dortokid remains, including nearly complete shells. Younger remains are currently not known.

### Systematic Paleontology

#### Valid Taxa

See Appendix 4 for the hierarchical taxonomy of *Pan-Pleurodira* as described in this work.

#### *Pan-Pleurodira* Joyce et al., 2004

**Phylogenetic definition.** Following Joyce et al. (2004), the name *Pan-Pleurodira* is herein referred to the total-clade of *Pleurodira* (i.e., the clade deriving from the last common ancestor *Chelus fimbriatus* (Schneider, 1783), *Pelomedusa subrufa* (Bonnaterre, 1789) and *Podocnemis expansa* (Schweigger, 1812)).

**Diagnosis.** Representatives of *Pan-Pleurodira* are currently diagnosed relative to other turtles by the sutural articulation of the

pelvis with the shell, presence of a well-developed anal notch, a pair of mesoplastra lacking a medial contact, a single gular scute, central articulation in the cervical column and the loss of inframarginals. The clade is also diagnosed by a number of cranial characters, but these are not listed herein, because most platychelyids and dortokids are not known from cranial remains.

#### *Platychelyidae* Bräm, 1965

**Phylogenetic definition.** The name *Platychelyidae* is herein referred to the most inclusive clade that includes *Platychelys oberndorferi* Wagner, 1853, but no species of extant turtle.

**Diagnosis.** *Platychelyids* can be diagnosed as pan-pleurodires by the sutural articulation of the pelvis with the shell, presence of a well-developed anal notch, a pair of mesoplastra lacking a medial contact, a single gular scute, central articulation in the cervical column and the loss of inframarginals. *Platychelyids* are currently differentiated from other pan-pleurodires by the presence of central plastral fontanelles, wide vertebral scutes, a straight anterior carapace margin, development of an anterior tubercle along the anterior margin of the first thoracic rib, a wide costovertebral tunnel, flat thoracic vertebrae in ventral view and a first thoracic centrum that is wider than high.

**Comments.** The name *Platychelyidae* was originally coined by Bräm (1965), but its circumscription only included the type species, *Platychelys oberndorferi*. As we see no need for the proliferation of redundant names, we herein follow Cadena and

Gaffney (2005) by expanding *Platycheilyidae* to include all currently recognized species of *Notoemys*. Our phylogenetic definition of the name *Platycheilyidae* will allow the unambiguous application of the name in the future. The name *Platychelira* Gaffney et al., 2006 is herein ignored, because it is redundant with *Platycheilyidae*.

#### *Notoemys Cattoi* and Freiberg, 1961

Type species. *Notoemys laticentralis* Cattoi and Freiberg, 1961

Diagnosis. *Notoemys* can be diagnosed as a pan-pleurodire and platycheilyd by all of the apomorphies listed for these two clades above. *Notoemys* is currently differentiated from *P. oberndorferi* by plesiomorphically having a relatively smooth and flattened carapace and suprapygial elements, by lacking supra-marginals and by apomorphically exhibiting neurals that are consistently wider than long and an iliac scar that is restricted to costal VIII.

#### *Notoemys laticentralis* Cattoi and Freiberg, 1961

Taxonomic history. *Notoemys laticentralis* Cattoi and Freiberg, 1961 (new species).

Type material. MACN 18043 (holotype), a carapace and anterior plastral lobe (Wood and Freiberg 1977, fig. 1, pls. 1, 2; Lapparent de Broin et al. 2007, fig. 1g).

Type locality. Las Lajas locality, Picunches Department, Neuquén Province, Argentina (see Figure 4); Vaca Muerta Formation, Tithonian, Late Jurassic (Wood and Freiberg 1977).

Referred material and range. Late Jurassic (Tithonian), Zapala Department, Neuquén Province, Argentina (hypodigm of Fernández and de la Fuente 1993).

Diagnosis. *Notoemys laticentralis* can be diagnosed as a pan-pleurodire, platycheilyd and representative of *Notoemys* by the full list of apomorphies listed above. *Notoemys laticentralis* is currently differentiated from other *Notoemys* by an anteriorly constricted neural I that is in broad contact with costal II, posteriorly wider suprapygial I, vertebral scutes that are almost twice as wide as long, a well-developed posterolateral contact of marginal I with pleural I, and a large central plastral fontanelle that partially separates the xiphiplastral from one another. The skull of *N. laticentralis* can be distinguished from crown pleurodires by the ventrally widened prootic that contacts the area articularis quadrati, the flattened, shortened and posteriorly rounded paroccipital process, thickened medial portion of columella, ventral exposure of the stapedial canal and a posteriorly open recessus scalae tympani.

Comments. *Notoemys laticentralis* is typified based on a well-preserved carapace and partial plastron from the Late Jurassic of Neuquén Province, Argentina, but it has received a considerable amount of attention, because one of the two currently referred specimens, MOZ P 2487, provides the only known, though only partially preserved, skull of a stem-pleurodiran turtle in addition to a partial neck. This specimen was originally

reported by de la Fuente and Fernández (1989), described in detail by Fernández and de la Fuente (1994) and redescribed by Lapparent de Broin et al. (2007). The validity of this taxon is unproblematic.

#### *Notoemys oxfordiensis* (de la Fuente and Iturralde-Vinent, 2001)

Taxonomic history. *Caribemys oxfordiensis* de la Fuente and Iturralde-Vinent, 2001 (new species); *Notoemys oxfordiensis* Cadena and Gaffney, 2005 (new combination).

Type material. MNHNCu P 3209 (holotype), an articulated but extremely eroded shell, including proximal limb bone and an isolated cervical VIII (de la Fuente and Iturralde-Vinent 2001, figs. 2–5).

Type locality. Viñales locality, Pinar del Río Province, Cuba (see Figure 4); Jagua Vieja Member, Jagua Formation, Oxfordian, Late Jurassic (de la Fuente and Iturralde-Vinent 2001).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Notoemys oxfordiensis* can be diagnosed as a pan-pleurodire by the sutural articulation of the pelvis with the shell, a pair of mesoplastra lacking a medial contact, a single gular scute, central articulation in the cervical column and the loss of inframarginals; as a platycheilyd by presence of central plastral fontanelles and the straight anterior carapace margin; and as a representative of *Notoemys* by a smooth and flattened carapace and neurals than are consistently wider than long.

*Notoemys oxfordiensis* is currently differentiated from other *Notoemys* by the reduced central plastral fontanelle.

Comments. *Notoemys oxfordiensis* is based on a single, heavily eroded specimen from the Late Jurassic of Cuba. Much of the carapace has been stripped from the specimen, and only the visceral portions of part of the carapace remain. The specimen therefore does not document the external morphology of the carapace and should only be integrated into phylogenetic studies with caution. The species is primarily diagnosed based on the shape and size of the plastral fontanelles, a character known to vary through ontogeny (Joyce 2007). We nevertheless accept the validity of this taxon for the moment, because it is spatially and temporally separated from other species of *Notoemys*.

#### *Notoemys zapatocaensis* Cadena and Gaffney, 2005

Taxonomic history. *Notoemys zapatocaensis* Cadena and Gaffney, 2005 (new species).

Type material. IPN/MGJRG 140120031 (holotype), a carapace and the posterior part of a plastron (Cadena and Gaffney 2005, figs. 3–11).

**Type locality.** El Caucho farm locality, northeast of the town of Zapatoca, Department of Santander, Colombia (see Figure 4); Rosablanca Formation, Valanginian, Early Cretaceous (Cadena et al. 2013).

**Referred material and range.** Early Cretaceous (Valanginian) of Department of Santander, Colombia (referred material of Cadena et al. 2013 from type locality; see Figure 4).

**Diagnosis.** *Notoemys zapatocaensis* can be diagnosed as a panpleurodire, platychelyid and representative of *Notoemys* by the full list of shell apomorphies listed above. *Notoemys zapatocaensis* is currently differentiated from other *Notoemys* by a quadrangular neural I that lacks clear contact with costal II, a rectangular suprapyg I, relatively narrow vertebrals, an elongate gular that fully separates the humerals, the presence of a central plastral scute and a small and circular posterior plastral fontanelle.

**Comments.** *Notoemys zapatocaensis* is based on a relatively well-preserved shell from the Early Cretaceous of Colombia. Two additional specimens have since been referred to this taxon (Cadena et al. 2013), of which the better preserved was designated as the “paratype,” but this action has no nomenclatural significance, because paratypes are defined as all specimens in a type series beyond the holotype (ICZN 1999) and therefore cannot be designated beyond the type description. The validity of this taxon is uncontroversial.

*Notoemys zapatocaensis* has been reported to exhibit a large central plastral fontanelle (Cadena et al. 2013), but this is not correct as the hyo- and hypoplastral elements fully close up along the midline. Instead, this taxon exhibits an unusual supernumerary central scute that roughly covered the area of the fontanelle in other taxa, in particular *N. laticentralis*. The purported correlation of large central fontanelles with other male characteristics is therefore no longer apparent.

### *Platycheilus oberndorferi* Wagner, 1853

**Taxonomic history.** *Platycheilus oberndorferi* Wagner, 1853 (new species).

**Type material.** Type lost, a nearly complete carapace (Wagner 1853, pl. 1; Meyer 1860, pl. 18.4).

**Type locality.** Kelheim (formerly Kehlheim), Bavaria, Germany (Wagner 1853, see Figure 4); Solnhofen Formation, Tithonian, Late Jurassic (Schweigert 2007).

**Referred material and range.** Late Jurassic (Tithonian) of Kelheim, Germany (BSPG AS I 1438, almost complete carapace in dorsal view; Wagner 1861, pl. 1; Frickhinger 1994, fig. 506; NHMUK 50116, anterior portion of carapace, Lydekker 1889); Late Jurassic (Tithonian) of Zandt, Germany (a partial plastron described by Zittel 1877, pl. 28.3, and formerly held at BSPG, now lost); Late Jurassic (Kimmeridgian) of Solothurn, Switzerland (NMS 8685, shell fragment; NMS 8686–8690, almost complete shell and two cervical vertebrae, Bräm 1965, pl. 1.1–4, 6; NMS 8691, shell fragment; NMS 8692, left half of carapace, Bräm 1965, pl. 1.5; MH So 17, right half of carapace in visceral

view; MH sor.67.9, almost complete three-dimensional and entirely prepared shell with pelvic girdle) (hypodigm of Bräm 1965; see Figure 4).

**Diagnosis.** *Platycheilus oberndorferi* can be diagnosed as a panpleurodire and a platychelyid by the full list of apomorphies listed above. *Platycheilus oberndorferi* is currently differentiated from *Notoemys* by the presence of a strongly sculpted carapace with a serrated margin and high medial and lateral knobs with strong serrations, relatively narrow, rectangular vertebrals, supramarginals, a supracaudal scute, relatively narrow neurals, an iliac scar that extends onto the peripherals and pygals, by lacking apparent suprapygal elements.

**Comments.** The single most recognizable taxon from the Late Jurassic of Europe is *Platycheilus oberndorferi*. Similar to the recent alligator snapping turtle, *Macrochelys temminckii*, the shell of the holotype is highly sculptured and supernumerary scutes (inframarginals) are noticeable, too. In the type description, Wagner (1853, pl. 1) was not able to trace most sutures, but Meyer (1860, pl. 18.4) was able to do so later and published a much improved figure. Because the morphology of this taxon is so characteristic, its validity has never been questioned and specimens from other localities have been assigned to it without any sign of doubt. This material includes additional specimens from the type locality (Wagner 1861; Lydekker 1889), a specimen from Zandt near Eichstätt, Germany (Zittel 1877), and a larger number of specimens from Solothurn, Switzerland (Rütimeyer 1867, 1873; Bräm 1965), initially described under the name *Helemys* Rütimeyer 1859a, 1859b. Primarily due to the excellent preservation of the Solothurn material, *Platycheilus oberndorferi* most certainly is one of the best-studied turtles from the Late Jurassic of Europe, although it is unfortunate that much of the excellent material available has not been properly figured and described. A complete skeleton recently reported from the Late Jurassic (Tithonian) of Eichstätt provides enticing insights into the nonshell anatomy of this taxon (Karl and Tichy 2006) but unfortunately resides in private hands and therefore cannot be utilized for scientific studies.

According to Wagner (1853), the holotype of *Platycheilus oberndorferi* was part of the collection of Dr. Oberndorfer of Kelheim, Germany. This specimen was transferred to Munich in 1866 (Zittel 1877), where it was studied by Maack (1869), Rütimeyer (1873) and Oertel (1915). Currently, the holotype is not to be found at the Bayerische Staatssammlung für Paläontologie und Geologie. It likely was destroyed during a World War II air raid that effaced much of the collections of Bayerische Staatssammlung für Paläontologie und Geologie (Wellnhofer 1967). Although the holotype is now lost, it is well figured (Wagner 1853, pl. 1; Meyer 1860, pl. 18.4) and the application of the name *Platycheilus oberndorferi* is uncontroversial. We therefore see no need for the designation of a neotype.

### *Dortokidae* Lapparent de Broin and Murelaga, 1996

**Phylogenetic definition.** The name *Dortokidae* is herein referred to the most inclusive clade that includes *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996, but no species of extant turtle.

Diagnosis. As for *Dortoka*.

Comments. The name Dortokidae was coined in concert with the naming of *Dortoka vasconica* (Lapparent de Broin and Murelaga 1996), because this taxon does not appear to be situated within previously named group of pleurodires. It is clear from current usage that Dortokidae is used to group all fossil turtles closely related to *D. vasconica*. We herein capture this meaning by use of a phylogenetic definition. *Dortokidae* and *Dortoka* are currently redundant in regards to their composition, but this may change in the future. A single diagnosis for both groups is nevertheless sufficient.

### *Dortoka* Lapparent de Broin and Murelaga, 1996

Type species. *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996.

Diagnosis. *Dortoka* can be diagnosed as a pan-pleurodire by the sutural articulation of the pelvis with the shell, presence of a well-developed anal notch, a single gular scute, central articulation in the cervical column and the loss of inframarginals. *Dortoka* is currently differentiated from other pan-pleurodires by the distinct microsculpturing of the shell consisting of a microreticulate pattern, and the distinct macrosculpturing of the carapace, particularly of the neurals, consisting of antero-posteriorly elongate pits and ridges, absence of contact between peripheral I and costal I, irregularly shaped neurals, a lapping of pleural II onto costal I and the absence of mesoplastra in some taxa.

### *Dortoka botanica* (Lapparent de Broin in Gheerbrant et al., 1999)

Taxonomic history. *Ronella botanica* Lapparent de Broin in Gheerbrant et al., 1999 (new species).

Type material. BBU JBB-21 (holotype), a partial plastron lacking the entoplastron, epiplastra and much of the bridge (Gheerbrant et al. 1999, fig. 14).

Type locality. Near village of Rona near Jibou, Sălaj County, Romania (see Figure 5); Jibou Formation, Thanetian, Paleocene (Gheerbrant et al. 1999; Lapparent de Broin et al. 2004).

Referred material and range. Paleogene, Sălaj County, Romania (referred material of Gheerbrant et al. 1999, Lapparent de Broin et al. 2004 from type locality and of Vremir 2013; see Figure 5).

Diagnosis. *Dortoka botanica* can be diagnosed as a pan-pleurodire by the sutural articulation of the pelvis with the shell, presence of a well-developed anal notch, a single gular scute and the loss of inframarginals; and as a representative of *Dortoka* by the distinct micro- and macrosculpturing of the carapace, absence of contact between peripheral I and costal I, a lapping of pleural II onto costal I and the absence of mesoplastra. *Dortoka botanica* is currently differentiated from other *Dortoka* by the restriction of the sculpturing to the neurals, the rectangular pleural II

that laps onto costal I along its entire width and the transverse humeropectoral sulcus.

Comments. *Dortoka botanica* is based on a partial plastron from the Paleogene of Romania (Gheerbrant et al. 1999), but relatively well-preserved specimens have since been retrieved from the type locality (Lapparent de Broin et al. 2004), including complete shells, that significantly expand the record for this taxon. The two valid species of dortokids are currently distinguished from one another on the basis of nuances in shell morphology, but are nevertheless assigned to different genera. Although we do not believe that it is possible to justify the naming of new genera using logical arguments, we nevertheless see no need for this redundant proliferation of names. We therefore transfer *botanica* from *Ronella* to *Dortoka*.

### *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996

Taxonomic history. *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996 (new species).

Type material. MCNA 6313, anterior half of a shell (Lapparent de Broin and Murelaga 1996, fig. 1a, b; Lapparent de Broin and Murelaga 1999, pl. 3.1).

Type locality. Laño Site, County of Treviño, Burgos Province, Castile and León, Spain (see Figure 5); Campanian, Late Cretaceous (Lapparent de Broin and Murelaga 1996).

Referred material and range. Late Cretaceous (Campanian–Maastrichtian) of Burgos Province (referred material of Lapparent de Broin and Murelaga 1996, 1999 and Pérez-García et al. 2012 from the type locality; see Figure 5).

Diagnosis. *Dortoka vasconica* can be diagnosed as a pan-pleurodire by the sutural articulation of the pelvis with the shell, presence of a well-developed anal notch, a single gular scute, central articulation in the cervical column and the loss of inframarginals; and as a representative of *Dortoka* by the distinct micro- and macrosculpturing of the carapace, absence of contact between peripheral I and costal I, irregularly shaped neurals, a lapping of pleural II onto costal I and the absence of mesoplastra. *Dortoka vasconica* is currently differentiated from other *Dortoka* by the presence of the sculpturing on the neurals and costals, the trapezoidal pleural II that distally laps onto costal I and V and the oblique humeropectoral sulcus.

Comments. *Dortoka vasconica* is based on a rather well-preserved anterior half of a shell from the Late Cretaceous of Spain, is the first “dortokid” to be named and represents the type species of *Dortoka*. Significant amounts of material from the type locality have been referred to this taxon and thereby provide additional insights into its anatomy, including the girdles and limb bones (Lapparent de Broin and Murelaga 1996, 1999; Pérez-García et al. 2012). Additional material that may be referable to this taxon was reported from the Late Cretaceous of southern France as well (Lapparent de Broin and Murelaga 1996, 1999; Lapparent de Broin et al. 2004; Vullo et al. 2010), but this claim was never supported with figured shell specimens.

## Problematic Taxa

### *Eodortoka morellana* Pérez-García et al., 2014 nomen dubium

Taxonomic history. *Eodortoka morellana* Pérez-García et al., 2014 (new species).

Type material. VM CMP MS3, a left partial hyoplastron lacking bridge region (Pérez-García et al. 2014, fig. 3a).

Type locality. Mas de la Parreta Quarry, Morella, Castellón Province, Valencia, Spain (see Figure 5); Arcillas de Morella Formation, Aptian, Early Cretaceous (Pérez-García et al. 2014).

Comments. *Eodortoka morellana* is based on a series of disassociated fragments from a single locality in Castellón Province, Spain, which combined were utilized to partially reconstruct the morphology of a shell (Pérez-García et al. 2014). We agree that at least some of the fragments can be diagnosed as being “dortokid” because they exhibit the characteristic microreticulations diagnostic of this taxon, but we do not see the utility of establishing a poorly diagnosed taxon based on fragmentary remains with questionable association. Although future finds may support the validity of this taxon, we herein consider it to be a nomen dubium.

### *Helemys serrata* Rüttimeyer, 1873 nomen nudum

Comments. Rüttimeyer (1859a, 1859b) reported on new turtle material from the Late Jurassic (late Kimmeridgian) turtle limestones of Solothurn, Switzerland, and noted the presence of two new species referable to the new taxon *Helemys*, but he provided neither a description nor a diagnosis for these taxa. Rüttimeyer (1867) soon after noticed that the Swiss material is referable to the German taxon *Platycheles oberndorferi* and that *Helemys* is therefore synonymous with *Platycheles*. In 1873, Rüttimeyer for the first time introduced the full species name *Helemys serrata* for the Swiss taxon (contra the claim of Anquetin et al. 2014), while at the same time noting that it is synonymous with *Platycheles oberndorferi*. All following authors similarly mention *H. serrata* only when listing synonyms for *P. oberndorferi*. Starting with the first usage by Rüttimeyer (1873), *H. serrata* has never been used as valid. The name therefore does not fulfill the requirements of the ICZN (1999) for availability and should be considered a nomen nudum.

### *Muehlbachia nopcsai* Vremir and Codrea, 2009 nomen nudum

Comments. The name “*Muehlbachia nopcsai*” was initially applied to fragmentary dortokid material from the Late Cretaceous (Maastrichtian) of Romania (Vremir and Codrea 2009) and has been used as valid in subsequent publications (e.g., Vremir 2010). However, given that the “type publication” was placed in an abstract volume, the name is not considered published and is therefore unavailable for nomenclatural considerations (ICZN 1999). Rabi, Vremir et al. (2013) already noted the

problematic status of this taxon name, but incorrectly concluded that it represents a nomen invalidum (i.e., a junior synonym). Instead, this name should be considered a nomen nudum until finally made available for nomenclatural consideration under the rules of the ICZN (1999).

### *Platycheles courantii* Bergounioux, 1935 nomen nudum

Comments. The name “*Platycheles courantii*” was coined by Bergounioux (1935) for a large object that was collected in the Department of Aude, France. Although the provenance of the specimen is unknown, Bergounioux (1935, 1936) provided a Late Jurassic age estimate. Highly schematic sketches of the specimen that resemble a highly irregular turtle carapace are provided in Bergounioux (1935, fig. 5; 1936), but photographs provided by Courrent (1936) clearly depict a large concretion, as already noted by Lapparent de Broin (2001). The specimen was formerly housed in the geological collections of the Scientific Society of the Department of Aude, but we were not able to clarify its current whereabouts. Given that a name must be based on remains of an actual organism to be considered available (ICZN 1999), we conclude that *Platycheles courantii* is a nomen nudum.

## Acknowledgments

We would like to thank Jérémy Anquetin, Márton Rabi and Juliana Sterli for helping improve the quality of this paper by carefully and thoughtfully scrutinizing the text and figures for inconsistencies.

Received 24 July 2014; revised and accepted 10 October 2014.

## Appendix 1 Institutional Abbreviations

BBU	Babes-Bolyai University, Cluj-Napoca, Romania
NHMUK	Natural History Museum, London, United Kingdom
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
MACN	Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Buenos Aires, Argentina
MCNA	Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain
MH	Naturhistorisches Museum, Basel, Switzerland
NMS	Naturmuseum Solothurn, Solothurn, Switzerland
IPN/MGJRG	Museo Geológico José Royo y Gómez, Servicio Geológico de Colombia, Bogotá, Colombia

MNHNCu	Museo Nacional de Historia Natural, La Habana, Cuba
MOZ	Museo Provincial de Ciencias Naturales Prof. Dr. Juan A. Olsacher, Zapala, Argentina
VM	Valltorta Museum, Tírig, Spain

## Appendix 2 Named Platycheleid and Dortokid Genera

- Caribemys* de la Fuente and Iturralde-Vinent, 2001 (type species: *Caribemys oxfordiensis* de la Fuente and Iturralde-Vinent, 2001)
- Dortoka* Lapparent de Broin and Murelaga, 1996 (type species: *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996)
- Eodortoka* Pérez-García et al., 2014 (type species: *Eodortoka morellana* Pérez-García et al., 2014)
- Helemys* Rüttimeyer, 1859a, 1859b (no type species, a nomen nudum)
- Notoemys* Cattoi and Freiberg, 1961 (type species: *Notoemys laticentralis* Cattoi and Freiberg, 1961)
- Platycheleys* Wagner, 1853 (type species: *Platycheleys oberndorferi* Wagner, 1853)
- Ronella* Lapparent de Broin in Gheerbrant et al., 1999 (type species: *Ronella botanica* Lapparent de Broin in Gheerbrant et al., 1999)

## Appendix 3 Biogeographic Summary of Platycheleid and Dortokid Turtles

Numbers in brackets reference Figures 4 and 5.

### Argentina

- [1] Late Jurassic, lower to middle Tithonian; Neuquén Province; *Notoemys laticentralis* (Cattoi and Freiberg 1961; de la Fuente and Fernández 1989; Fernández and de la Fuente 1993)

### Austria

- [2] Late Cretaceous, Campanian; Muthmannsdorf Coal Mine, Lower Austria; *Dortokidae* indet. (Rabi, Vremir et al. 2013)

### Colombia

- [3] Early Cretaceous, late Valanginian; Zapatoca, Santander Department; *Notoemys zapatocaensis* (Cadena and Gaffney 2005; Cadena et al. 2013)

### Cuba

- [4] Late Jurassic, middle to late Oxfordian; Viñales, Pinar del Río Province; *Notoemys oxfordiensis* (de la Fuente and Iturralde-Vinent 2001)

### France

- Late Cretaceous, Campanian–Maastrichtian; Departments of Bouches-du-Rhône, Charente-Maritime, Gard and Hérault; *Dortokidae* indet. (not figured; Lapparent de Broin et al. 2004; Vullo et al. 2010)

### Germany

- [5] Late Jurassic, early Tithonian; Kelheim, Bavaria; *Platycheleys oberndorferi* (Wagner 1853, 1861)
- [6] Late Jurassic, early Tithonian; Zandt, Bavaria; *Platycheleys oberndorferi* (Zittel 1877)

### Hungary

- [7] Late Cretaceous, Santonian; Iharkút Bauxite Pit, Veszprém County; *Dortokidae* indet. (Rabi, Vremir et al. 2013)

### Romania

- [8] Paleogene, Thanetian–Ypresian; Rona near Jibou, Sălaj County; *Dortoka botanica* (Gheerbrant et al. 1999; Lapparent de Broin et al. 2004; Vremir 2013)
- [9] Late Cretaceous, Maastrichtian; Alba County; *Dortokidae* indet. (Rabi, Vremir et al. 2013)
- [10] Late Cretaceous, Maastrichtian; Hunedoara County; *Dortokidae* indet. (Rabi, Vremir et al. 2013)

### Spain

- [11] Late Cretaceous, Campanian; Laño Site, County de Treviño, Burgos Province, Castile and León; *Dortoka vasconica* (Lapparent de Broin and Murelaga 1996, 1999; Pérez-García et al. 2012)
- [12] Early Cretaceous, Aptian; Mas de la Parreta Quarry, Morella, Castellón Province, Valencia; *Dortokidae* indet. (Pérez-García et al. 2014)
- [13] Early Cretaceous, Barremian; Vallipón Site, Castellote, Teruel Province, Aragon; *Dortokidae* indet. (Murelaga Bereikua 1998)

### Switzerland

- [14] Late Jurassic, Kimmeridgian; Solothurn; *Platycheleys oberndorferi* (Rüttimeyer 1867, 1873; Bräm 1965)

## Appendix 4 Hierarchical Taxonomy of Platycheleid and Dortokid Turtles

- Pan-Pleurodira* Joyce et al., 2004
- Platycheleyidae* Bräm, 1965
- Platycheleys oberndorferi* Wagner, 1853
- Notoemys laticentralis* Cattoi and Freiberg, 1961
- Notoemys oxfordiensis* (Cadena and Gaffney, 2005)
- Notoemys zapatocaensis* Cadena and Gaffney, 2005
- Dortokidae* Lapparent de Broin and Murelaga, 1996
- Dortoka vasconica* Lapparent de Broin and Murelaga, 1996
- Dortoka botanica* (Lapparent de Broin in Gheerbrant et al., 1999)

## Literature Cited

- ANQUETIN, J. 2012. Reassessment of the phylogenetic interrelationships of basal turtles (Testudinata). *Journal of Systematic Paleontology* 10:3–45.
- ANQUETIN, J., C. PÜNTENER AND J.-P. BILLON-BRUYAT. 2014. A taxonomic review of the Late Jurassic eucryptodiran turtles from the Jura Mountains (Switzerland and France). *PeerJ* 2:e369.
- BERGOUNIOUX, F.-M. 1935. Contribution à l'étude paléontologique des chéloniens. *Mémoires de la Société géologique de France* 25:1–216.
- 1936. Jurassique supérieur de Saint-Jean de Barrou (Aude). *Bulletin de la Société d'Études scientifiques de l'Aude* 40:221–224.
- BONNATERRE, P.J. 1789. *Tableau encyclopédique et méthodique des trois règnes de la nature. Erpétologie*. Paris: Panckoucke. 72 pp.
- BRÄM, H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweizerische Paläontologische Abhandlungen* 83:1–190.
- 1973. Chelonia from the Upper Jurassic of Guimarota mine (Portugal). *Contribuição para o conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal)*. *Memórias dos Serviços geológicos de Portugal* 22:135–141.
- BRAND, L.R., M. HUSSEY AND J. TAYLOR. 2003. Taphonomy of freshwater turtles: decay and disarticulation in controlled experiments. *Journal of Taphonomy* 1:233–245.
- CADENA, E.A. AND E.S. GAFFNEY. 2005. *Notoemys zapatoensis*, a new side-necked turtle (Pleurodira: Platycheilyidae) from the Early Cretaceous of Colombia. *American Museum Novitates* 3470:1–19.
- CADENA, E.A., C.A. JARAMILLO AND J.I. BLOCH. 2013. New material of the platycheilyid turtle *Notoemys zapatoensis* from the Early Cretaceous of Colombia; implications for understanding Pleurodira evolution. In: D.B. Brinkman, P.A. Holroyd and J.D. Gardner, eds. *Morphology and Evolution of Turtles*. Dordrecht, Netherlands: Springer. pp. 105–120.
- CATTOL, N. AND M.A. FREIBERG. 1961. Nuevo hallazgo de Chelonia extinguidos en la Republica Argentina. *Physica* 22:202.
- COURRENT. 1936. La tortue géante de Saint-Jean de Barrou. *Bulletin de la Société d'Études scientifiques de l'Aude* 40:217–220.
- DE LA FUENTE, M.S. 2007. Testudines. In: Z. Gasparini, L. Salgado and R. Coria, eds. *Patagonian Mesozoic Reptiles*. Bloomington, IN: Indiana University Press. pp. 50–86.
- DE LA FUENTE, M.S. AND M.S. FERNÁNDEZ. 1989. *Notoemys lat-centralis* Cattoi & Freiberg, 1961 from the Upper Jurassic of Argentina: a member of the infraorder Pleurodira (Cope, 1868). *Studia Paleochelonologica* 3(2):25–32.
- DE LA FUENTE, M.S. AND M. ITURRALDE-VINENT. 2001. A new pleurodiran turtle from the Jagua formation (Oxfordian) of western Cuba. *Journal of Paleontology* 75:860–869.
- FERNÁNDEZ, M.S. AND M.S. DE LA FUENTE. 1993. Las tortugas casiquelidias de las calizas litográficas titonianas del área Los Catutos, Neuquén, Argentina. *Ameghiniana* 30:283–295.
- 1994. Redescription and phylogenetic position of *Notoemys*: the oldest Gondwanian pleurodiran turtle. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 193:81–105.
- FRAAS, E. 1913. *Proterochersis*, eine pleurodire Schildkröte aus dem Keuper. *Jahreshefte der Gesellschaft für Naturkunde in Württemberg* 69:13–90.
- FRICKHINGER, K.A. 1994. *Die Fossilien von Solnhofen*. Stuttgart: Goldschneck-Verlag Korb. 336 pp.
- GAFFNEY, E.S. 1975. A phylogeny and classification of the higher categories of turtles. *Bulletin of the American Museum of Natural History* 155:389–436.
- GAFFNEY, E.S., P.A. MEYLAN AND A.R. WYSS. 1991. A computer assisted analysis of the relationships of the higher categories of turtles. *Cladistics* 7:313–335.
- GAFFNEY, E.S., T.H. RICH, P. VICKERS-RICH, A. CONSTANTINE, P. VACCA AND L. KOOL. 2007. *Chubutemys*, a new eucryptodiran turtle from the early cretaceous of Argentina, and the relationships of the Meiolaniidae. *American Museum Novitates* 3599:1–35.
- GAFFNEY, E.S., H. TONG AND P.A. MEYLAN. 2006. Evolution of the side-necked turtles: the families Bothremyidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History* 300:1–698.
- GASPARINI, Z., M.S. FERNÁNDEZ, M. DE LA FUENTE, Y. HERRERA, L. CODORNIÚ AND A. GARRIDO. 2015. Reptiles from lithographic limestones of the Los Catutos Member (middle–upper Tithonian), Neuquén Province, Argentina: An essay on its taxonomic position and preservation in an environmental and geographic context. *Ameghiniana* 52:1–28.
- GHEERBRANT, E., V. CODREA, A. HOSU, S. SEN, C. GUERNET, F. LAPPARENT BROIN AND J. RIVELINE. 1999. Découverte de vertébrés dans les Calcaires de Rona (Thanétien ou Sparnacien), Transylvanie, Roumanie: les plus anciens mammifères cénozoïques d'Europe Orientale. *Eclogae Geologicae Helveticae* 92:517–535.
- GIUNTA, G. AND S. ORIOLI. 2011. The Caribbean plate evolution: trying to resolve a very complicated tectonic puzzle. In: E. Sharkov, ed. *New Frontiers in Tectonic Research—General Problems, Sedimentary Basins and Island Arcs*. Rijeka, Croatia: InTech. pp. 221–248.
- HAY, O.P. 1908. *The Fossil Turtles of North America*. Washington, DC: Carnegie Institution of Washington. (Publications 75.) 568 pp.
- [ICZN] INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1999. *International Code of Zoological Nomenclature*, 4th ed. London: International Trust for Zoological Nomenclature. 306 pp.
- ITURRALDE-VINENT, M. 1994. Cuban geology: a new plate tectonic synthesis. *Journal of Petroleum Geology* 17:39–70.
- JOYCE, W.G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48:1–102.
- JOYCE, W.G., S.D. CHAPMAN, R.T.J. MOODY AND C.A. WALKER. 2011. The skull of the solemydid turtle *Helochelydra nopscai* from the Early Cretaceous (Barremian) of the Isle of Wight (UK) and a review of Solemydidae. *Special Papers in Paleontology* 86:75–97.
- JOYCE, W.G. AND J.A. GAUTHIER. 2004. Paleogeology of Triassic stem turtles sheds new light on turtle origins. *Proceedings of the Royal Society of London B* 271:1–5.
- JOYCE, W.G., J.F. PARHAM AND J.A. GAUTHIER. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology* 78:989–1013.



- JOYCE, W.G., J.F. PARHAM, T.R. LYSON, R.C.M. WARNOCK AND P.C.J. DONOGHUE. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. *Journal of Paleontology* 87:612–634.
- JOYCE, W.G., R.R. SCHOCH AND T.R. LYSON. 2013. The girdles of the oldest fossil turtle, *Proterochersis robusta*, and the age of the turtle crown. *BMC Evolutionary Biology* 13:266.
- KARL, H.-V. AND G. TICHY. 2006. Altmühltal: neue Schildkrötenfunde im Plattenkalk. *Biologie in unserer Zeit* 4:18–19.
- KUHN, O. 1964. *Fossilium Catalogus, Volume 1: Animalia, Part 107, Testudines*. The Hague: Ysel Press. 299 pp.
- LAPPARENT DE BROIN, F. DE. 2000. The oldest pre-Podocnemidid turtle (Chelonii, Pleurodira), from the early Cretaceous, Ceará state, Brasil, and its environment. *Treballs del Museu de Geologia de Barcelona* 9:43–95.
- 2001. The European turtle fauna from the Triassic to the Present. *Dumerilia* 4:155–217.
- LAPPARENT DE BROIN, F. DE, M.S. DE LA FUENTE AND M.S. FERNÁNDEZ. 2007. *Notoemys laticentralis* (Chelonii, Pleurodira), Late Jurassic of Argentina: new examination of the anatomical structures and comparisons. *Revue de Paléobiologie* 26:99–136.
- LAPPARENT DE BROIN, F. DE AND X. MURELAGA. 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. *Comptes Rendus de l'Académie des Sciences de Paris* 323:729–735.
- 1999. Turtles from the Upper Cretaceous of Lanõ (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Álava* 14:135–211.
- LAPPARENT DE BROIN, F. DE, X. MURELAGA BEREIKUA AND V. CODREA. 2004. Presence of Dortokidae (Chelonii, Pleurodira) in the earliest Tertiary of the Jibou Formation, Romania: paleobiogeographical implications. *Acta Palaeontologica Romaniaae* 4:203–221.
- LYDEKKER, R. 1889. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*. Part 3, Chelonia. London: Longmans. 239 pp.
- MAACK, G.A. 1869. Die bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kehlheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. *Palaeontographica* 18:193–336.
- MEYER, H. VON. 1860. *Zur Fauna der Vorwelt. Reptilien aus dem lithographischen Schiefer des Jura in Deutschland und Frankreich*. Frankfurt am Main: Heinrich Keller Verlag. 142 pp.
- MILNER, A.R. 2004. The turtles of the Purbeck Limestone Group of Dorset, southern England. *Palaeontology* 47:1441–1467.
- MURELAGA BEREIKUA, X. 1998. Primeros restos de tortugas del Cretácico Inferior (Barremiense superior) de Vallipón (Castellote, Teruel). *Mas de las Matas* 17:189–200.
- OERTEL, W. 1915. Beiträge zur Kenntnis der oberjurassischen Schildkrötenegattung *Hydropelta*. *Centralblatt für Mineralogie, Geologie und Paläontologie* 1915:336–348.
- PÉREZ-GARCÍA, A., J.M. GASULLA AND F. ORTEGA. 2014. *Eodortoka morellana* gen. et sp. nov., the first pan-pleurodiran turtle (Dortokidae) defined in the Lower Cretaceous of Europe. *Cretaceous Research* 48:130–138.
- PÉREZ-GARCÍA, A., T.M. SCHEYER AND X. MURELAGA. 2012. New interpretations of *Dortoka vasconica* Lapparent de Broin and Murelaga, a freshwater turtle with an unusual carapace. *Cretaceous Research* 36:151–161.
- RABI, M., M. VREMIR AND H. TONG. 2013. Preliminary overview of Late Cretaceous turtle diversity in eastern Central Europe (Austria, Hungary, and Romania). In: D.B. Brinkman, P.A. Holroyd and J.D. Gardner, eds. *Morphology and Evolution of Turtles*. Dordrecht, Netherlands: Springer. pp. 307–336.
- RABI, M., C.-F. ZHOU, O. WINGS, S. GE AND W.G. JOYCE. 2013. A new xinjiangchelyid turtle from the Middle Jurassic of Xinjiang, China and the evolution of the basiptyergoid process in Mesozoic turtles. *BMC Evolutionary Biology* 13:203.
- ROUGIER, G.W., M.S. DE LA FUENTE AND A.B. ARCUCCI. 1995. Late Triassic turtles from South America. *Science* 268:855–858.
- RÜTIMEYER, L. 1859a. Notiz über Schildkröten von Solothurn. *Verhandlungen der schweizerischen naturforschenden Gesellschaft* 43:57–59.
- 1859b. Die Schildkröten im Portland-Kalk von Solothurn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* 1859:366–367.
- 1867. Die Schildkröten. In: F. Lang and L. Rüttimeyer. *Die fossilen Schildkröten von Solothurn*. Zürich: Allgemeine schweizerische Gesellschaft für die gesammten Naturwissenschaften. pp. 1–47. (Neue Denkschrift Der Allg. Schweizer Gesellschaft Für Die Gesammten Naturwissenschaften 22.)
- 1873. Die fossilen Schildkröten von Solothurn und der übrigen Juraformation, mit Beiträgen zur Kenntniss von Bau und Geschichte der Schildkröten im Allgemeinen. Zürich: Allgemeine schweizerische Gesellschaft für die gesammten Naturwissenschaften. 185 pp. (Neue Denkschriften der Allgemeinen schweizerischen Gesellschaft für die gesammten Naturwissenschaften 25.)
- SCHEYER, T.M. 2009. Conserved bone microstructure in the shells of long-necked and short-necked chelid turtles (Testudinata, Pleurodira). *Fossil Record* 12:47–57.
- SCHEYER, T.M. AND J. ANQUETIN. 2008. Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. *Lethaia* 41:85–96.
- SCHNEIDER, J.G. 1783. *Allgemeine Naturgeschichte der Schildkröten, nebst einem systematischen Verzeichnisse der einzelnen Arten und zwey Kupfern*. Leipzig: Johann Gottfried Müllersche Buchhandlung. 364 pp.
- SCHWEIGERT, G. 2007. Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany—first results and open questions. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 245:117–125.
- SCHWEIGGER, A.F. 1812. *Prodromus monographiae cheloniorum, part 1. Königsberger Archiv für Naturwissenschaft und Mathematik* 1812:271–458.
- STAMPFLI, G.M. AND C. HOCHARD. 2009. Plate tectonics of the Alpine realm. *Geological Society Special Publications* 327:89–111.
- STERLI, J. AND M.S. DE LA FUENTE. 2011. A new turtle from the La Colonia formation (Campanian-Maastrichtian), Patagonia, Argentina, with remarks on the evolution of the vertebral column in turtles. *Palaeontology* 54:63–78.
- STERLI, J., D. POL AND M. LAURIN. 2013. Incorporating phylogenetic uncertainty on phylogeny-based palaeontological dating and the timing of turtle diversification. *Cladistics* 29:233–246.

- VREMIR, M. 2010. New faunal elements from the late Cretaceous (Maastrichtian) continental deposits of Sebes area (Transylvania). *Acta Musei Sabesiensis* 2:635–684.
- 2013. An early Eocene freshwater turtle assemblage from the Simleu Basin (NW Romania): paleobiogeographic significance. *Acta Musei Sabesiensis* 5:597–625.
- VREMIR, M. AND V. CODREA. 2009. Late Cretaceous turtle diversity in Transylvanian and Hateg Basins (Romania). In: Abstract volume of the 7th Romanian Symposium on Paleontology; 2009 Oct 22–24; Cluj-Napoca, Romania. pp. 122–124.
- VULLO, R., F. LAPPARENT DE BROIN, D. NÉRAUDEAU AND N. DURRIEU. 2010. Turtles from the Early Cenomanian paralic deposits (Late Cretaceous) of Charentes, France. *Oryctos* 9:37–48.
- WAGNER, A. 1853. Beschreibung einer fossilen Schildkröten und etlicher anderer Reptilien-Überreste aus den lithographischen Schiefen und dem grünen Sandsteine von Kehlheim. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klasse* 7:241–264.
- 1861. Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers. 2: Schildkröten und Saurier. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klasse* 9:67–124.
- WELNHOFER, P. 1967. Ein Schildkrötenrest (Thalassemydidae) aus den Solnhofener Plattenkalken. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 7:181–192.
- WOOD, R.C. AND M.A. FREIBERG. 1977. Redescription of *Notomys laticentralis* the oldest fossil turtle from South America. *Acta Geológica Lilloana* 13:187–204.
- ZITTEL, K.A. 1877. Bemerkungen über die Schildkröten des lithographischen Schiefers in Bayern. *Palaeontographica* 24:75–184.