A Review of the Fossil Record of Turtles of the Clades

Platychelyidae and Dortokidae

Edwin Cadena¹ and Walter G. Joyce²

¹ Alexander von Humboldt Foundation, Senckenberg Naturmuseum, 60325 Frankfurt am Main, Germany
— email: cadenachelys@gmail.com
² 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, Germany, 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. Rütimeyer (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 (Rütimeyer 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 Plesiochelyidae. 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-
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Sure of the stapedial canal and the absence of posterior closure of the recessus scalae tympani. A recent study focused on the basipterygoid process of Mesozoic turtles confirms that the basipterygoid process is already absent this early in panteleurodire 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* and Cadena et al. (2013) for *N. zapatocaensis*. 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 mesoplastron and a single gular scute. The carapace is

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**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).  
*Abbreviations:* Ab, abdominal scute; An, anal scute; Ce, cervical scute; co, costal; ent, entoplastron; epi, epiplastron; Ex, extragular scute; Fe, femoral scute; Gu, gular 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.
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 Brion 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 Brion 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 Brion 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 Brion et al. (2007, pl. 1g–j). The preserved vertebrae include the atlas, the axis and cervicals III and IV. These cervicals are opisthocoelous, 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.

Brám (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 cervicalis. 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 Brion (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 Brion 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 opisthocoelous.

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 dorsolaterally. 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 *Platychelyidae* as stem-pleurodires and these can therefore be argued to be the oldest unambiguous crown turtles (Joyce, Parham et al. 2013).

*Platychelys oberndorferi* was originally referred to Emydidae (Wagner 1853; Rütimeyer 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 *Platychelyidae*. 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 *Platychelys* 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 *Platychelyidae* 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
analyses in the future using more complete specimens (see Figure 2). It is notable that dortokids are significantly younger than all known platy-
chelyids and occur in concert with crown pleurodires (Figure 3).

**Paleoecology**

All platycheleyids come from marine or littoral stratigraphic sequences, with abundant invertebrates and marine reptiles, including plesiosaurs, pliosaurs, ichthyosaurs and metriorhynchid cro-
odilians (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 spec-
imens were found in the vicinity of nearby islands or continents. Another particularity of platy-
chelyid 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 2. A phylogenetic hypothesis of Pan-Pleurodira, including all valid platycheleyid and dortokid taxa, with diag-
nostic 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).
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 Rütimeyer (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; Rütimeyer 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 (Brám 1973), have more recently been identified as indeterminate pleurosternids (Scheyer and Anquetin 2008), while the Early Jurassic taxon *Platychelys courrenti* Bergouinoux, 1935 is based on a nonfossiliferous concretion (Lapparent de Broin 2001). Considering that the vast majority of pan-pleurodires 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 Guaniguanoic 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 Maastrichtian of nearby Alba and Hunedoara Counties, Romania (Rabi, Vremir et al. 2013). Rich, though fragmentary, remains are the basis of *Dor-
*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).
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 Sâlaj 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 Platycheliria 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 platychelyid 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 suprapygal elements, by lacking supramarginals 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, platychelyid 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 suprapygal I, vertebral scutes that are almost twice as wide as long, a well-developed posterolateral contact of marginals and by apomorphically exhibiting neurals that partially separate 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*.

**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.** MNHN Cu 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 platychelyid 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 zapataocaensis**

Cadena and Gaffney, 2005

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

**Type material.** IPN/MGJR 140120031 (holotype), a carapace and the posterior part of a plastron (Cadena and Gaffney 2005, figs. 3–11).
Type locality. El Cauche farm locality, northeast of the town of Zapotoca, 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 zapatacoensis can be diagnosed as a panteleurodride, platychelyid and representative of Notoemys by the full list of shell apomorphies listed above. Notoemys zapatacoensis is currently differentiated from other Notoemys by a quadrangular neural I that lacks clear contact with costal II, a rectangular suprapygal I, relatively narrow vertebras, a supernumerary scute that roughly covered the area of the fontanelle in other taxa, in particular N. laticentralis (Wagner, 1853) and the apomorphy that extends onto the peripherals and pygals, by lacking apparent suprapygal elements.

Comments. Notoemys zapatacoensis 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 uncontrover
ciable. Notoemys zapatacoensis 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 supormermary 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

Diagnosis. Platychelys oberndorferi can be diagnosed as a panteleurodride and a platychelyid by the full list of apomorphies listed above. Platychelys 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 vertebras, supramarginals, a suprapygal scute, relatively narrow neurons, 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 Platychelys 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 (Rütimayer 1867, 1873; Bräm 1965), initially described under the name Helymys Rütimayer 1859a, 1859b. Primarily due to the excellent preservation of the Solothurn material, Platychelys 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 Platychelys 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), Rütimayer (1873) and Oertel (1915). Currently, the holotype is not to be found at the Bayerische Staatsammlung für Paläontologie und Geologie. It likely was destroyed during a World War II air raid that effaced much of the collections of Bayernische Staatsammlung 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 Platychelys oberndorferi is uncontrover
cial. 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 suture 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 anterior half of a shell from the Late Cretaceous of Spain, referred material and range.

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, Sâlaj County, Romania (see Figure 5); Jibou Formation, Thanetian, Paleocene (Gheerbrant et al. 1999, Lapparent de Broin and Murelaga 2004).

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

Diagnosis. Dortoka botanica can be diagnosed as a pan-pleurodire by the suture 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, 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 botanica 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-Garcia 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 hypoplastron 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 Rütimeyer, 1873 nomen nudum

Comments. Rütimeyer (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. Rütimeyer (1867) soon after noticed that the Swiss material is referable to the German taxon Platychelys oberndorferi and that Helemys is therefore synonymous with Platychelys. In 1873, Rütimeyer 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 Platychelys oberndorferi. All following authors similarly mention Helemys serrata only when listing synonyms for P. oberndorferi. Starting with the first usage by Rütimeyer (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).

Platychelys courrenti Bergounioux, 1935 nomen nudum

Comments. The name “Platychelys courrenti” 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 Platychelys courrenti is a nomen nudum.

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Appendix 1

Institutional Abbreviations

<table>
<thead>
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<th>Abbreviation</th>
<th>Institution</th>
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<tr>
<td>BBU</td>
<td>Babes-Bolyai University, Cluj-Napoca, Romania</td>
</tr>
<tr>
<td>NHMUK</td>
<td>Natural History Museum, London, United Kingdom</td>
</tr>
<tr>
<td>BSPG</td>
<td>Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany</td>
</tr>
<tr>
<td>MACN</td>
<td>Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Buenos Aires, Argentina</td>
</tr>
<tr>
<td>MCNA</td>
<td>Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain</td>
</tr>
<tr>
<td>MH</td>
<td>Naturhistorisches Museum, Basel, Switzerland</td>
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<tr>
<td>NMS</td>
<td>Naturmuseum Solothurn, Solothurn, Switzerland</td>
</tr>
<tr>
<td>IPN/MGJRG</td>
<td>Museo Geológico José Royo y Gómez, Servicio Geológico de Colombia, Bogotá, Colombia</td>
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Appendix 2
Named Platychelyid 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)

Eodorotoka Pérez-García et al., 2014 (type species: Eodorotoka morellana Pérez-García et al., 2014)

Helemys Rütimeyer, 1859a, 1859b (no type species, a nomen nudum)


Platychelys Wagner, 1853 (type species: Platychelys 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 Platychelyid 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 zapotocaensis (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; Platychelys oberndorferi (Wagner 1853, 1861)
[6] Late Jurassic, early Tithonian; Zandt, Bavaria; Platychelys 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)

Switzerland
[14] Late Jurassic, Kimmeridgian; Solothurn; Platychelys oberndorferi (Rütimeyer 1867, 1873; Bräm 1965)

Appendix 4
Hierarchical Taxonomy of Platychelyid and Dortokid Turtles

Pan-Pleurodira Joyce et al., 2004
Platychelyidae Bräm, 1965
Platychelys oberndorferi Wagner, 1853
Notoemys laticentralis Cattoi and Freiberg, 1961
Notoemys oxfordiensis (Cadena and Gaffney, 2005)
Notoemys zapotocaensis 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)
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LAPPARENT DE BROIN, F. DE. 2000. The oldest pre-Podocnemidid turtle (Cheloniidae, Pleurodira), from the early Cretaceous, Ceará state, Brazil, and its environment. Treballs del Museu de Geologia de Barcelona 9:43–95.


Editor’s note: This article is intended to be included with others in a forthcoming book being coordinated by Walter G. Joyce to elucidate the fossil record of turtles. The individual articles that will form the components of this book are being published separately in the next several volumes of the Bulletin of the Peabody Museum of Natural History.