PALÆO VERTEBRATA

ARTICLE

Dortokid turtle remains from the Upper Cretaceous of Cruzy (Hérault, southern France) and phylogenetic implications

Haiyan TONG[a,b]*, Eric BUFFETAUT[c], Julien CLAUDE[d,e]

[a]*Palaeontological Research and Education Centre, Mahasarakham University, Kantarawichai, Maha Sarakham 44150, Thailand*
[b]*Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China*
[c]*CNRS (UMR 8538), Laboratoire de Géologie de l'Ecole Normale Supérieure, PSL Research University, 24 rue Lhomond, CEDEX 05, 75231 Paris, France*
[d]*Institut des Sciences de l'Evolution de Montpellier, CNRS/UM/IRD/EPHE, 2 Place Eugène Bataillon, cc64, CEDEX 05, 34095 Montpellier, France*
[e]*Faculty of Science, University of Chulalongkorn, 254 Phaya Thai Rd, Wang Mai, Pathum Wan, Bangkok 10330, Thailand*

**corresponding author: htong09@yahoo.fr*

Abstract: An isolated right costal 1 from the Late Cretaceous Massecaps locality (Cruzy, Hérault, southern France) is assigned to *Dortoka vasconica* (Dortokidae). This find adds a new element to the Late Cretaceous turtle fauna of Cruzy and further supports the hypothesis that two distinct lineages of Dortokidae were present in Europe during the Late Cretaceous-Paleogene due to geographical isolation.

Keywords: Turtle, *Dortoka vasconica*, Late Cretaceous, Cruzy, France

Submitted 31 March 2022, Accepted 18 October 2022
Published Online 14 November 2022, doi: 10.18563/pv.45.2.e3

INTRODUCTION

Dortokidae are a group of primitive pleurodiran turtles endemic to Europe (Cadena & Joyce, 2015). With a known stratigraphical distribution ranging from the Early Cretaceous to the Eocene, the family Dortokidae consists of *Dortoka vasconica* from the Campanian of Laño, Spain (Lapparent de Broin & Murelaga, 1999, 1996; Pérez-García *et al.*, 2012), *Ronella botanica* from the Thanetian of Rona and Jibou, Transylvania, Romania (Gheerbrant *et al.*, 1999; Lapparent de Broin *et al.*, 2004), *Eodortoka morellana* from the Aptian of Morella, Spain (Pérez-García *et al.*, 2014) and *Dortoka vremiri* from the Maastrichtian of the Haţeg Basin, Romania (Augustin *et al.*, 2021). Additional remains of that family have been reported from the Late Cretaceous of Spain and southern France as *Dortoka* sp. and from the Santonian of Iharkut, Hungary, the Campanian of Muthmannsdorf, Austria and the Maastrichtian of the Transylvanian and Haţeg basins, Romania as Dortokidae indet. (Lapparent de Broin *et al.*, 2004; Rabi *et al.*, 2013). Based on the surface ornamentation, some fragments of shell elements from the Hauterivian-Barremian of Teruel, Spain and the Eocene of the Şimleu Basin, Romania have also been referred to Dortokidae (Lapparent de Broin *et al.*, 2004; Pérez-García *et al.*, 2017; Vremir, 2013). In western Europe, abundant material of dortokids has been collected from the Campanian of Laño, Spain, whereas their remains are scarce in the Upper Cretaceous deposits of France (Lapparent de Broin & Murelaga, 1999). In this paper we report on an isolated costal 1 from the Late Cretaceous (Campanian) of Cruzy, Hérault, southern France. It is referred to *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996. The phylogenetic relationships within the family Dortokidae are discussed.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The Massecaps locality, where the specimen described below comes from, is situated about 1 km. NE of the village of Cruzy, Hérault, in southern France (Fig. 1). The fossil-bearing deposits consist of variegated claystones, sandstones and conglomerates, deposited during brief flood episodes in a braided river system, under a tropical climate, with alternating dry and wet seasons (Smektala *et al.*, 2014). On the basis of the vertebrate fauna, the vertebrate-bearing beds of Massecaps are dated as Late Campanian - Early Maastrichtian (Buffetaut *et al.*, 1999). The excavations since 1996 have unearthed thousands of fossils, mostly isolated bones. The vertebrate assemblage consists of bony fishes (lepisosteids and coelacanth *Axelrodichthys megadromos* (Cavin *et al.*, 2005, 2020)), amphibians (Buffetaut *et al.*, 1999), crocodiles (*Acynodon iberoccitanus*, *Allodaposuchus precedens* and Alligatoroidea indet. (Martin & Buffetaut, 2005; Martin, 2007)), turtles, pterosaurs (Buffetaut, 2008), birds (the enantiornithine *Martinavis cruzyensis* (Buffetaut, 1998; Walker *et al.*, 2007)), sauropod (titanosaurs (Díez Díaz *et al.*, 2013)), theropod (dromaeosaurid *Variraptor* and abelisaurids (Buffetaut *et al.*, 1999)) and ornithopod (*Rhabdodon* (Pincemaille-Quillevéré *et al.*, 2006)) dinosaurs and eutherian mammals (*Labes garimondi* (Martin *et al.*, 2015)), as well as egg-shell fragments. Turtle remains are by far the most abundant among the vertebrate remains, representing more than 70% of the fossils collected from the site. Most turtle remains belong to pleurodiran *Foxemys mechinorum* (Bothremydidae), a few shell fragments are referable to *Solemys* sp. (Helochelydridae) (Buffetaut *et al.*, 1999; Gaffney *et al.*, 2006), and a costal plate of Dortokidae is reported for the first time in the present study.

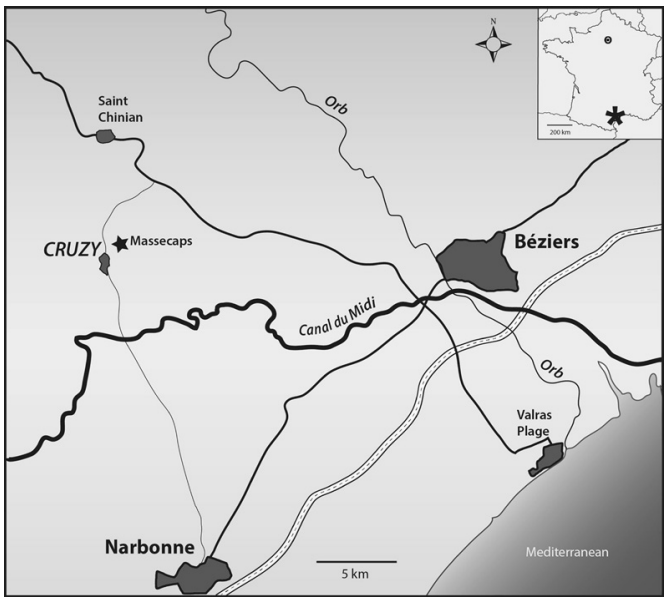

Figure 1. Map showing location of Massecaps, Cruzy, Herault, southern France (after Martin *et al.* 2015).

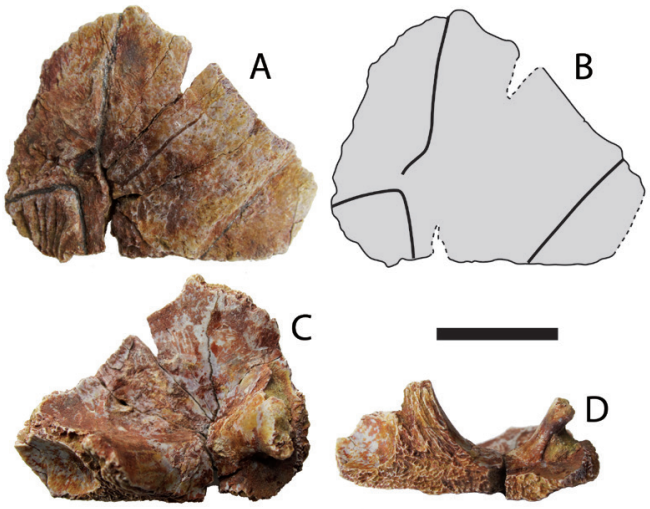

Figure 2. *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996 from the Late Cretaceous of Massecaps locality (MC M1127), Cruzy, southern France. Costal 1 in dorsal (**A-B**), ventral (**C**) and posterior (**D**) views. Scale bar = 2 cm.

SYSTEMATIC PALEONTOLOGY

Dortokidae Lapparent de Broin & Murelaga, 1996

Dortoka Lapparent de Broin & Murelaga, 1996

Dortoka vasconica Lapparent de Broin & Murelaga, 1996

Referred material: a right costal 1 (MC M1127, Musée de Cruzy) from the Massecaps locality, Cruzy, Hérault, southern France; Late Cretaceous (Late Campanian-Early Maastrichtian).

Description and comparisons:

The right costal 1 (Fig. 2) is nearly complete, lacking the lateral tip. The plate is relatively long, as preserved, it measures 3.6 cm. in length and 4.5 cm. in width, with a length/width ratio of about 66 %. As in *Dortoka vasconica* from Laño, the outer surface is covered with a clear microreticulate ornamentation, and strong anteroposteriorly directed ridges are present on the posteromedial corner, corresponding to the area covered by vertebral 2 (Lapparent de Broin & Murelaga, 1999). The plate is relatively stout, with a thick sutural border with the nuchal anteromedially, the peripherals 2-4 anterolaterally, the neural 2 posteromedially and the costal 2 posteriorly. The medial border (the contact with the neural 1 or the left costal 1) which is intact, is thin and smooth. This suggests that the costal 1 was not sutured to its counterpart (or to the neural 1). This seems to be comparable to the condition in *Dortoka vasconica* from Laño, which lacks a neural 1 (holotype, MCNA 6313) or has a reduced neural 1 (MCNA 7404); both have the anterior part of the right and left costals 1 meeting one another along the midline (Pérez-García, Scheyer & Murelaga, 2012, Fig. 1, A and C). The anteromedial contact with the nuchal is relatively short and oblique, comparable to that seen in *Dortora vasconica* from Laño, whereas this suture is longer and less oblique in *Eodortoka morellana*, *Ronella botanica* and *Dortoka vremiri* (Augustin *et al.*, 2021; Lapparent de Broin & Murelaga, 1999; Pérez-García *et al.*, 2014, 2012).

The scute sulci are clearly imprinted. Vertebral 1 is narrow, with the lateral sulcus directed slightly anterolaterally, extending onto the nuchal as in *Dortoka vasconica*, whereas in *Ronella botanica*, *Dortoka vremiri* and *Dortoka* sp. from the Campanian of Champ-Garimond, Gard, France, vertebral 1 is wider than the nuchal. Vertebral 2 is narrow too, with its anterolateral sulcus directed posterolaterally. The pleural 1 extends partially to the costal 2, and the pleural 2 covers the posterolateral part of the costal 1 as in *Dortoka vasconica*. In comparison, in *Ronella botanica* and *Dortoka vremiri*, the pleural 1 is restricted to the costal 1 and pleural 2 covers the posterior part of the costal 1, excluding the pleural 1 from the costal 2. In *Eodortoka morellana*, the pleural 2 does not extend onto the costal 1 (Pérez-García *et al.*, 2014).

On the inner surface, the first thoracic rib is not preserved, the preserved attachment site suggests that this rib was reduced and sutured to the medial 1/4 of the thoracic rib 2. The head of the thoracic rib 2 is raised, strong and laterally flattened. A blunt ridge extends from this rib head laterally then rises and becomes larger, extending onto the costal 2 at about half width of the plate to form a robust process against the axillary buttress. Thus the lateral half of the contact between the costals 1 and 2 is extremely thick (Fig. 2D). The axillary buttress attachment scar is located on both costals 1 and 2. In *Dortoka vasconica*, the morphology of the axillary attachment site is variable, being on both costals 1-2 or restricted to costal 1, but the supporting process from the costal extends onto the costal 2 (Lapparent de Broin & Murelaga, 1999; Pérez-García *et al.*, 2012). Thus in this respect, the costal 1 from Massecaps falls within the variation of *Dortoka vasconica*. In *Eodortoka morellana*, *Ronella botanica* and *Dortoka vremiri*, both the axillary buttress attachment and the supporting process are restricted to costal 1 (Augustin *et al.*, 2021; Lapparent de Broin *et al.*, 2004; Lapparent de Broin & Murelaga, 1999; Pérez-García *et al.*, 2012, 2014).

PALAEOBIOGEOGRAPHY, INTERRELATIONSHIPS WITHIN DORTOKIDAE AND THE REDEFINITION OF *DORTOKA* AND *RONELLA*

Eodortoka morellana from the Aptian of Spain is considered as the basalmost Dortokidae and sister group of a more advanced clade composed of *Dortoka vasconica*, *Ronella botanica* and *Dortoka vremiri* (Augustin *et al.*, 2021; Pérez-García *et*

al., 2014). This taxon presents a series of primitive features including the presence of mesoplastra, the pleural 2 excluded from costal 1, the axillary buttress inserting on the costal 1, the pubis scar restricted in the xiphiplastron and the humeropectoral sulcus located posterior to the entoplastron.

On the basis of the phylogenetic analyses, Augustin *et al.* (2021) recognised two lineages within Dortokidae during the Late Cretaceous to Paleogene: a western lineage consisting of *Dortoka vasconica* from the Late Cretaceous of Spain and an eastern lineage that includes *Ronella botanica* from the Paleocene of Romania and *Dortoka vremiri* from the Maastrichtian of Romania. The clade *Ronella botanica* + *Dortoka vremiri* is supported by two synapomorphies: first pleural scute restricted to the first costal and pectorals partially covering the entoplastron. These authors have noticed also that Dortokidae indet. from the Santonian of Iharkut, Hungary, and the Campanian of Muthmannsdorf, Austria share with *Ronella botanica* and *Dortoka vremiri* the first pleural scute restricted to the costal 1 (Augustin *et al.*, 2021). According to this phylogenetic hypothesis, the genus *Dortoka* is paraphyletic and understanding its palaeogeographical evolution is thus made difficult.

The costal 1 from Cruzy referred to *Dortoka vasconica* shows that this species extended to southern France during the Late Cretaceous. The comparisons with available material from western and eastern Europe (Fig. 3, Table 1) provide additional evidence that further supports the phylogenetic hypothesis of Augustin *et al.* (2021). Having undergone a vicariant evolution, these two lineages present distinct combinations of derived and primitive features. The synapomorphies observed on costal 1 shared by the members of the western lineage (*Dortoka vasconica* from Laño and Cruzy) include the pleural 1 extending partially onto the costal 2 and the pleural 2 covering the posterolateral part of the costal 1, the axillary buttress and its supporting process located on both costals 1-2 and the relatively short and oblique costal 1/nuchal contact. An additional synapomorphy of this lineage is observed on the plastron, the more anteriorly placed pubic scar, located on both xiphiplastron and hypoplastron. *Dortoka vasconica* retains the humeropectoral sulcus located posterior to the entoplastron, a primitive feature that is shared with *Eodortoka morellana*. The western lineage likely also includes *Dortoka* sp. from the Campanian of Champ-Garimond, Gard, and Villeveyrac and Quarante, Hérault. A nuchal from Champ-Garimond figured in Lapparent de Broin & Murelaga (1999, Pl.3, fig.19) and again in Lapparent de Broin *et al.* (2004, Pl.3, fig.7) shows a relatively short and oblique contact with the costal 1, similar to that seen in *Dortoka vasconica* from Laño and Cruzy. However, the specimen from Champ-Garimond has the vertebral 1 wider than the nuchal, contrary to dortokids from Laño and Cruzy in which the vertebral 1 does not completely cover the nuchal laterally. The hypoplastra from Champ-Garimond, Villeveyrac and Quarante show the pubic scar extending on that plate as in *Dortoka vasconica* (Lapparent de Broin & Murelaga, 1999, Pl. 3, fig. 17-18, 20). Based on the weaker ornamentation and smaller overlapping of the pubis scar on the hypoplastron, Lapparent de Broin & Murelaga (1999) suggested that these remains from southern France may represent different species of *Dortoka*.

In addition of *Ronella botanica* and *Dortoka vremiri*, the eastern lineage probably also includes Dortokidae indet. from the Santonian of Iharkut, Hungary and the Campanian of Muthmannsdorf, Austria. The members of this lineage share synapomorphic characters such as the pleural 1 restricted to costal 1, the pleural 2 covering the posterior part of the costal 1 and the humeropectoral sulcus cutting the entoplastron; whereas the axillary buttress attachment scar and the supporting process located entirely on costal 1, the longer and less oblique costal 1/ nuchal contact and the pubic scar restricted to the xiphiplastron are primitive features shared with *Eodortoka morellana*. According to the description, some figured specimens and reconstructions, the material from the Maastrichtian of the Transylvanian and Haţeg basins, Romania, which have been referred to *Muehlbachia nopcsai* (Vremir & Codrea, 2009) (considered as a *nomen nudum* by Cadena and Joyce (2015)) also exhibits the same characters (Rabi *et al.*, 2013; Vremir, 2010).

The presence of two lineages of dortokid turtles is the result of geographical isolation as suggested by Augustin *et al.* (2021). During the Late Cretaceous, Europe was an archipelago. The western part, including Spain and France, belonged to the Ibero-Armorican landmass and the eastern part, including Hungary, Austria and Romania, were part of the Austroalpine and Tisia-Dacia blocks. These two regions were separated one from another by extensive seaways (Csiki-Sava *et al.*, 2015). The faunal separation between the western and the eastern

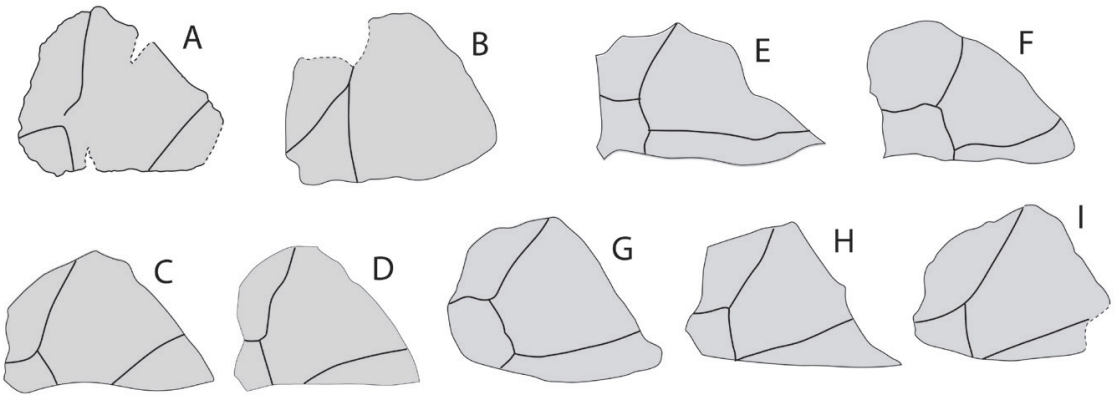

Figure 3. Comparisons of costal 1 of Dortokidae. **A and C-D**, *Dortoka vasconica* from the Campanian of, Massecaps locality, Cruzy, Herault, France (A) and Laño, Spain (C-D, after Pérez-García *et al.* (2012)); **B**, *Eodortoka morellana* from the Aptian of Morella, Spain (after Pérez-García *et al.* (2014)); **E**, *Ronella botanica* from the Late Paleocene of Romania (after Lapparent de Broin *et al.* (2004)); **F**, *Ronella vremiri* from the Maastrichtian of Haţeg Basin, Romania (after Augustin *et al.* (2021)) ; **G-I**, Dortokidae indet. from the Santonian of Iharkut, Hungary (G), Maastrichtian of Transylvanian Basin, Romania (H) and Campanian of Muthmannsdorf, Austria (I) (after Rabi *et al.* (2013)). Left costals 1 are switched for convenience. Not to scale.

Table 1. Comparisons between different taxa of Dortokidae.

	Dortoka vasconica		*Eodortoka morellana*	*Ronella botanica*	*Ronella vremiri*	Dortokidae indet.		Dortokidae gen. et sp. nov.
	Laño	Cruzy				Iharkut	Muthmannsdorf	Transylvanian Basin
Carapace length	18-19 cm	-	13 cm	25 cm	19 cm	-	-	20 cm
Costal 1/nuchal contact	Short and oblique	Short and oblique	Long and more horizontal	Long and more horizontal	Long and more horizontal	Long and more horizontal	Long and more horizontal	Long and more horizontal
Pleural 1 extending on costal 2	Partially	Partially	Fully	No	No	No	No	No
Pleural 2 covers costal 1	Posterolaterally	Posterolaterally	No	Posteriorly	Posteriorly	Posteriorly	Posteriorly	Posteriorly
Vertebral 1 overlapping lateroposterior corners of nuchal	No	No	No	Yes	Yes	No	No	No
Axillary buttress Scar and supporting process	On costals 1-2	On costals 1-2	On costal 1	On costal 1	?	On costal 1	On costal 1	On costal 1
Gulars	Small	?	?	Large	Small	?	?	Small
Humeropectoral cutting entoplastron	No	?	No	Yes	Yes	Yes	-	Yes
Pubic scar extending onto hypoplastron	Yes	?	No	No	No	No	?	No
References	Lapparent de Broin & Murelaga (1999); Pérez-García *et al.* (2012)	This study	Pérez-García *et al.* (2014)	Lapparent de Broin *et al.* (2004)	Augustin *et al.* (2021)	Rabi *et al.* (2013)		Rabi *et al.* (2013); Vremir (2010)

areas has previously been recognised for other vertebrate groups, including turtles. Helochelydrid turtles and eutherian mammals are recorded from the Ibero-Armorican area; whereas the turtle *Kallokibotion* and kogaionid multituberculates are known from the Austroalpine and Tisia-Dacia areas (Csiki-Sava *et al.*, 2015; Gheerbrant & Astibia, 2012; Gheerbrant & Teodori, 2021; Joyce, 2017; Martin *et al.*, 2015; Rabi *et al.*, 2013). The rhabdodontid ornithopod dinosaurs also show a west-east differentiation similar to that of dortokid turtles (Csiki-Sava *et al.*, 2015; Ösi *et al.*, 2012). The earliest member of the eastern lineage, represented by the Hungarian dortokids from the Santonian, suggests that the split between the western and eastern lineages of Dortokidae occurred no later than Santonian.

The presence of two distinct lineages of Dortokidae raises the problem of the currently used taxonomy for that family. In a review of the family Dortokidae, Cadena & Joyce (2015) synonymized the genus *Ronella* with *Dortoka*. Subsequently, Augustin *et al.* (2021) assigned their new species from the Late Cretaceous of Haţeg Basin to *Dortoka*, as *D. vremiri*. Since *Dortoka vremiri* is closer to *Ronella botanica* than to *Dortoka vasconica* and the genus *Dortoka* is probably represented by

more than one species in western Europe, in respect of the monophyly of the taxa, we suggest referring the members of the western lineage to *Dortoka* (*Dortoka vasconica* Lapparent de Broin & Murelaga, 1996) and those of the eastern lineage to *Ronella* (*Ronella botanica* Lapparent de Broin, 1999 and *Ronella vremiri* (Augustin et al. 2021)).

CONCLUSIONS

The costal 1 from the Massecaps locality, Cruzy is assigned to *Dortoka vasconica*. The comparisons with other dortokids from Europe support the hypothesis that two lineages were present in that family during the Late Cretaceous – Paleocene interval: a western lineage represented by *Dortoka vasconica* and *Dortoka* sp. from the Late Cretaceous of Spain and France, and an eastern lineage consisting of *Ronella botanica*, *Ronella vremiri*, and dortokid remains from Iharkut, Hungary, Muthmannsdorf, Austria and the Transylvanian and Haţeg basins, Romania. The split between these two lineages occurred prior to the Santonian.

ACKNOWLEDGMENTS

We thank the members of ACAP (the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois (Cruzy)) for their help in the excavation at the Massecaps locality in Cruzy. Financial support was provided by CNRS (UMR 8538) and ACAP.

BIBLIOGRAPHY

Augustin, F.J., Csiki-Sava, Z., Matzke, A.T., Botfalvai, G., Rabi, M., 2021. A new latest Cretaceous pleurodiran turtle (Testudinata: Dortokidae) from the Haţeg Basin (Romania) documents end-Cretaceous faunal provinciality and selective survival during the K-Pg extinction. Journal of Systematic Palaeontology 19, 1059-1081. https://doi.org/10.1080/14772019.2021.2009583

Buffetaut, E., 1998. First evidence of enantiornithine birds from the Upper Cretaceous of Europe: postcranial bones from Cruzy (Hérault, southern France). Oryctos 1, 131-136.

Buffetaut, E., 2008. Late Cretaceous pterosaurs from France: a review. Zitteliana 249-255.

Buffetaut, E., Le Loeuff, J., Tong, H., Duffaud, S., Cavin, L., Garcia, G., Ward, D., 1999. Un nouveau gisement de vertébrés du Crétacé supérieur à Cruzy (Hérault, Sud de la France). Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science 328, 203-208. https://doi.org/10.1016/S1251-8050(99)80097-4

Cadena, E., Joyce, W.G., 2015. A review of the fossil record of turtles of the clades Platychelyidae and Dortokidae. Bulletin of the Peabody Museum of Natural History 56, 3-20. https://doi.org/10.3374/014.056.0101

Cavin, L., Buffetaut, E., Dutour, Y., Garcia, G., Le Loeuff, J., Méchin, A., Méchin, P., Tong, H., Tortosa, T., Turini, E., 2020. The last known freshwater coelacanths: New Late Cretaceous mawsoniid remains (Osteichthyes: Actinistia) from southern France. Plos one 15, e0234183. https://doi.org/10.1371/journal.pone.0234183

Cavin, L., Forey, P.L., Buffetaut, E., Tong, H., 2005. Latest European coelacanth shows Gondwanan affinities. Biology Letters 1, 176-177. https://doi.org/10.1098/rsbl.2004.0287

Csiki-Sava, Z., Buffetaut, E., Ösi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous-faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. ZooKeys 1-161. https://doi.org/10.3897/zookeys.469.8439

Díez Díaz, V., Tortosa, T., Le Loeuff, J., 2013. Sauropod diversity in the Late Cretaceous of southwestern Europe: The lessons of odontology. Annales de Paléontologie 99, 119-129. https://doi.org/10.1016/j.annpal.2012.12.002

Gaffney, E.S., Tong, H., Meylan, P.A., 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae; Bulletin of the American Museum of Natural History, no. 300. https://doi.org/10.1206/0003-0090(2006)300[1:EOTSTT]2.0.CO;2

Gheerbrant, E., Astibia, H., 2012. Addition to the Late Cretaceous Laño mammal faunule (Spain) and to the knowledge of European "Zhelestidae"(Lainodontinae nov.). Bulletin de la Société géologique de France 183, 537-546. https://doi.org/10.2113/gssgfbull.183.6.537

Gheerbrant, E., Codrea, V., Hosu, A., Sen, S., Guernet, C., Lapparent de Broin, F., Riveline, J., 1999. Découverte de vertébrés dans les Calcaires de Rona (Thanétien ou Sparnacien), Transylvanie, Roumanie: les plus anciens mammifères cénozoïques d'Europe Orientale. Eclogae geol. Helv 92, 517-535.

Gheerbrant, E., Teodori, D., 2021. An enigmatic specialized new eutherian mammal from the Late Cretaceous of Western Europe (Northern Pyrenees). Comptes Rendus Palevol 20, 207-223. https://doi.org/10.5852/cr-palevol2021v20a13

Joyce, W.G., 2017. A review of the fossil record of basal Mesozoic turtles. Bulletin of the Peabody Museum of Natural History 58, 65-113. https://doi.org/10.3374/014.058.0105

Lapparent de Broin, F. de, Codrea, V.A., Murelaga, X., 2004. Presence of Dortokidae (Chelonii, Pleurodira) in the earliest Tertiary of the Jibou Formation, Romania: paleobiogeographical implications. Acta Palaeontologica Romaniae 4, 203-215.

Lapparent de Broin, F. de, Murelaga, X., 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. Comptes rendus de l'Académie des sciences. Série 2. Sciences de la terre et des planètes 323, 729-735.

Lapparent de Broin, F. de, Murelaga, X., 1999. Turtles from the upper cretaceous of Laño (Iberian peninsula). Estudios del Museo de Ciencias Naturales de Alava 14, 135-211.

Martin, J.E., 2007. New material of the Late Cretaceous globidontan *Acynodon iberoccitanus* (Crocodylia) from southern France. Journal of Vertebrate Paleontology 27, 362-372. https://doi.org/10.1671/0272-4634(2007)27[362:NMOTLC]2.0.CO;2

Martin, J.E., Buffetaut, E., 2005. An overview of the Late Cretaceous crocodilian assemblage from Cruzy, southern France. Kaupia 14, 33-40.

Martin, T., Buffetaut, E., Tong, H., 2015. A Late Cretaceous eutherian mammal from southwestern France. Paläontologische Zeitschrift 89, 535-544. https://doi.org/10.1007/s12542-014-0231-7

Ösi, A., Prondvai, E., Butler, R., Weishampel, D.B., 2012. Phylogeny, histology and inferred body size evolution in a new rhabdodontid dinosaur from the Late Cretaceous of Hungary. PLoS One. https://doi.org/10.1371/journal.pone.0044318

Pérez-García, A., Cobos, A., Royo-Torres, R., 2017. The oldest evidence of a dortokid turtle (stem Pleurodira) from the uppermost Hauterivian-basal Barremian El Castellar Formation (Teruel, Spain). Journal of Iberian Geology 43, 139-146. https://doi.org/10.1007/s41513-017-0013-7

Pérez-García, A., Gasulla, J.M., Ortega, F., 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. https://doi.org/10.1016/j.cretres.2013.12.004

Pérez-García, A., Scheyer, T.M., Murelaga, X., 2012. New interpretations of *Dortoka vasconica* Lapparent de Broin and Murelaga, a freshwater turtle with an unusual carapace. Cretaceous Research 36, 151-161. https://doi.org/10.1016/j.cretres.2012.03.006

Pincemaille-Quillevéré, M., Buffetaut, E., Quillevere, F., 2006. Description ostéologique de l'arrière-crane de *Rhabdodon* (Dinosauria, Euornithopoda) et implications phylogénétiques.

Bulletin de la Société géologique de France 177, 97-104. https://doi.org/10.2113/gssgfbull.177.2.97

Rabi, M., Vremir, M., Tong, H., 2013. Preliminary overview of Late Cretaceous turtle diversity in eastern central Europe (Austria, Hungary, and Romania). In: Morphology and Evolution of Turtles. Springer, pp. 307-336. https://doi.org/10.1007/978-94-007-4309-0_19

Smektala, F., Buffetaut, E., Deconinck, J.-F., 2014. Rivers as repositories for fossil vertebrates: a case study from the Upper Cretaceous of southern France. Proceedings of the Geologists' Association 125, 567-577. https://doi.org/10.1016/j.pgeola.2014.10.004

Vremir, M., 2010. New faunal elements from the late Cretaceous (Maastrichtian) continental deposits of Sebes area (Transylvania). Acta Musei Sabesiensis 2, 635-684.

Vremir, M., 2013. An Early Eocene freshwater turtle assemblage from the Şimleu Basin (NW Romania): paleobiogeographic significance. Acta Musei Sabesiensis 5, 597-625.

Vremir, M., Codrea, V., 2009. Late Cretaceous turtle diversity in Transylvanian and Haţeg basins (Romania). Presented at the 7th International Symposium of Paleontology, Abstract Volume, Cluj-Napoca, Romania, pp. 122-124.

Walker, C.A., Buffetaut, E., Dyke, G.J., 2007. Large euenantiornithine birds from the Cretaceous of southern France, North America and Argentina. Geological Magazine 144, 977-986. https://doi.org/10.1017/S0016756807003871