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ORIGINAL PAPER

A new turtle confirms the presence of Bothremydidae (Pleurodira) in the Cenozoic of Europe and expands the biostratigraphic range of Foxemydina

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Abstract Pleurodira is a clade of Gondwanan turtles that reached Europe at the beginning of the Late Cretaceous. It is recognized as the most abundant and diverse group of freshwater turtles in the uppermost Cretaceous record of this continent, being represented by several members of Bothremydidae. Two well-preserved and relatively complete skulls are studied in this paper. They come from lower Eocene levels of the French locality of Saint-Papoul (Aude). These specimens are recognized as attributable to a new taxon, *Tartaruscola teodorii* gen. et sp. nov., identified as a bothremydid. This new form constitutes the only known unambiguous and valid representative of Bothremydidae in the Cenozoic of Europe. The new taxon is diagnosed by several autapomorphies and also by an exclusive combination of characters. It is one of the few members of Bothremydini identified in the Cenozoic record and the only one described for the Eocene outside of the Ouled Abdoun Basin of Morocco. *Tartaruscola teodorii* is identified as a member of Foxemydina, a clade recognized here as exclusive of the European record, and whose presence in post-Mesozoic levels is demonstrated in this paper. The European Foxemydina *T. teodorii* and the African Bothremydina *Bothremys kellyi*, both from the Ypresian, are the youngest members of Bothremydini hitherto known.

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Keywords Pleurodira · Bothremydidae · *Tartaruscola teodorii* gen. et sp. nov · Europe · Cenozoic record · Early Eocene

Introduction

Pleurodira (the Crown group of Pan-Pleurodira) is a clade of turtles with a Gondwanan origin (Romano et al. 2014). It is represented by two main groups: Pelomedusoides and Chelidae. Pelomedusoides developed in the north of Gondwana. The record of this clade is relatively rich and diverse in both the Cretaceous and the Paleogene (Fuente 2003). Although the distribution of Pleurodira is limited to more restrictive climatic conditions than those of the representatives of Cryptodira (Broin 1988), this group significantly expanded its paleobiogeographic distribution in periods characterized by relatively high global temperatures (Broin 1988; Lapparent de Broin 2000; Pérez-García and Lapparent de Broin 2014). In this regard, representatives of Bothremydidae dispersed to Europe during the Late Cretaceous, Bothremydidae being the group of freshwater turtles most abundant during the Campanian and Maastrichtian of Europe (Gaffney et al. 2006; Pérez-García et al. 2012). Another lineage of Pelomedusoides reached Europe during the Cenozoic: Podocnemididae. The dispersal of this clade took place during the Paleocene-Eocene Thermal Maximum (Lapparent de Broin 2001; Pérez-García and Lapparent de Broin 2014). Thus, Podocnemididae was abundant and diverse in the Eocene of Europe (Pérez-García and Lapparent de Broin 2015).

Several taxa described in the Cenozoic record of Europe were preliminarily attributed to Bothremydidae. *Tahrosphys ambiguus* (Gaudry 1890) was described from a partial plastron from Mont-Aimé (Champagnes, France). It represents the only evidence of Taphrosphyini so far recognized in the European record. Although it was recognized as coming from Danian (early Paleocene) levels (Broin 1977), the vertebrate fossils from this locality are currently recognized as Maastrichtian forms (Martin and Delfino 2010). *Palaeaspis bowerbanki* Owen 1842 is a taxon from the Ypresian (early Eocene) of the London Clay (England). It was recognized as a representative of both Podocnemididae (Broin 1988) and Bothremydidae (Lapparent de Broin 2001). None of these attributions was justified. In fact, considering the scarcity of available information, this taxon was recently identified as Pelomedusoides incertae sedis (Gaffney et al. 2006). Gaffney et al. (2006) also identified "*Chrysemys*" *montolivensis* Roman 1897, a taxon from the Oligocene of France, as Pelomedusoides incertae sedis. This form had previously been referred as Bothremydidae (Lapparent de Broin 2001), this attribution not having been justified. "*Podocnemis lata*" Ristori 1895 is a form from the Miocene of Malta, attributed to Bothremydidae by Lapparent de Broin and Werner (1998) and Lapparent de Broin (2001), without justification. Gaffney et al. (2006) questioned this allocation, the taxon being considered as a nomen dubium. Therefore, none of the European Cenozoic taxa previously attributed to Bothremydidae is currently considered as representatives of this group. Similarly, the preliminary identification of specimens of the Cenozoic of Europe as Bothremydidae indet., such as those of the Lutetian of Avesa (Verona, Italy) (Lapparent de Broin and Werner 1998; Lapparent de Broin 2001), or of the Bartonian of Osona (Catalonia, Spain) (Lapparent de Broin et al. 2014), has not been justified.

A new taxon, from the early Eocene of Saint-Papoul (Aude, France; Fig. 1), is presented here. It is recognized as the only unambiguous member of Bothremydidae known in the European Cenozoic record. The new taxon represents the youngest members of Foxemydina so far described.

Institutional abbreviations MNHN.F., Paleontology Collection of the Muséum national d'Histoire naturelle, Paris, France.

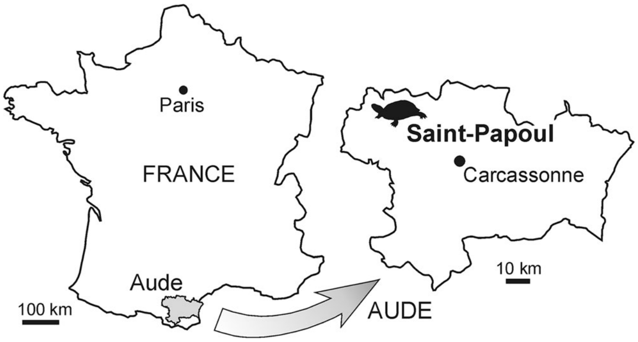

Fig. 1 Geographical position of the type locality of *T. teodorii* gen. et sp. nov. (Pleurodira, Bothremydidae), the early Ypresian (early Eocene) site of Saint-Papoul (Aude, France)

Materials and methods

Two skulls from early Ypresian levels of the French locality of Saint-Papoul (Aude, Languedoc-Roussillon-Midi-Pyrénées; Fig. 1) are presented and analyzed in detail here (Figs. 2 and 3). They are attributed to a single taxon, corresponding to a new member of Bothremydidae (see "Discussion"). These skulls are detailed compared with those of the other known members of Bothremydidae, considering the information available in the literature and, especially, by the first-hand study of the holotypes and other specimens attributed to many of these taxa. In addition, in order to confirm the phylogenetic position of the taxon from Saint-Papoul obtained by the comparative study, this new bothremydid is coded in the version of the data matrix of Gaffney et al. (2006) as revised by Pérez-García et al. (2012), which pursues the study of the phylogenetic relationships among the representatives of Bothremydidae (Appendix 1). Two recently described members of Bothremydini are included, *Puentemys mushaisaensis* and *Foxemys trabanti* Rabi, Tong and Botfalvai 2012, based on the coding given by Cadena et al. (2012) and Rabi et al. (2012), respectively. Characters 36 and 120 for *Foxemys mechinorum* are recoded as proposed by Rabi et al. (2012). Some character states are recoded for several taxa, based on the direct re-examination of the specimens. Thus, the character 95 of *F. mechinorum* (Prootic, quadrate-pterygoid-basisphenoid exposure), previously coded as 1 (exposure of prootic small, surrounded by pterygoid, basisphenoid, and quadrate, with foramen nervi facialis exposed), is recoded as 0 (complete exposure of prootic or no exposure of prootic) (see Fig. 3a and b in Rabi et al. 2012). For *Chedighaii barberi*, the character 147 (Carapace, length of contact between peripheral 1 and costal 1 in dorsal view), previously coded as 1 (wide contact so that anterior margin of peripheral 1 is less than twice the length of costal 1 contact), is recoded as 2 (narrow contact, so that anterior margin of peripheral 1 is twice or more the length of costal 1 contact) (see Fig. 2 in Schmidt 1940). For *Bothremys maghrebiana*, the character 74 (Pterygoid, position of the foramen posterius canalis carotici interni), previously coded as 1 (in pterygoid-quadrate suture), is also coded as 5 (in pterygoid-basisphenoid-quadrate suture) (see Fig. 143D in Gaffney et al. 2006). Following the methodology used in some analyses by Gaffney et al. (2006), Cadena et al. (2012), and Rabi et al. (2012), no taxon only known by the shell is considered here. Thus, the data matrix used here is composed by 180 characters and 29 taxa.

The data matrix was analyzed using TNT 1.0 (Goloboff et al. 2008), in order to find the most parsimonious trees (MPTs). A heuristic tree search has been used, performing 1000

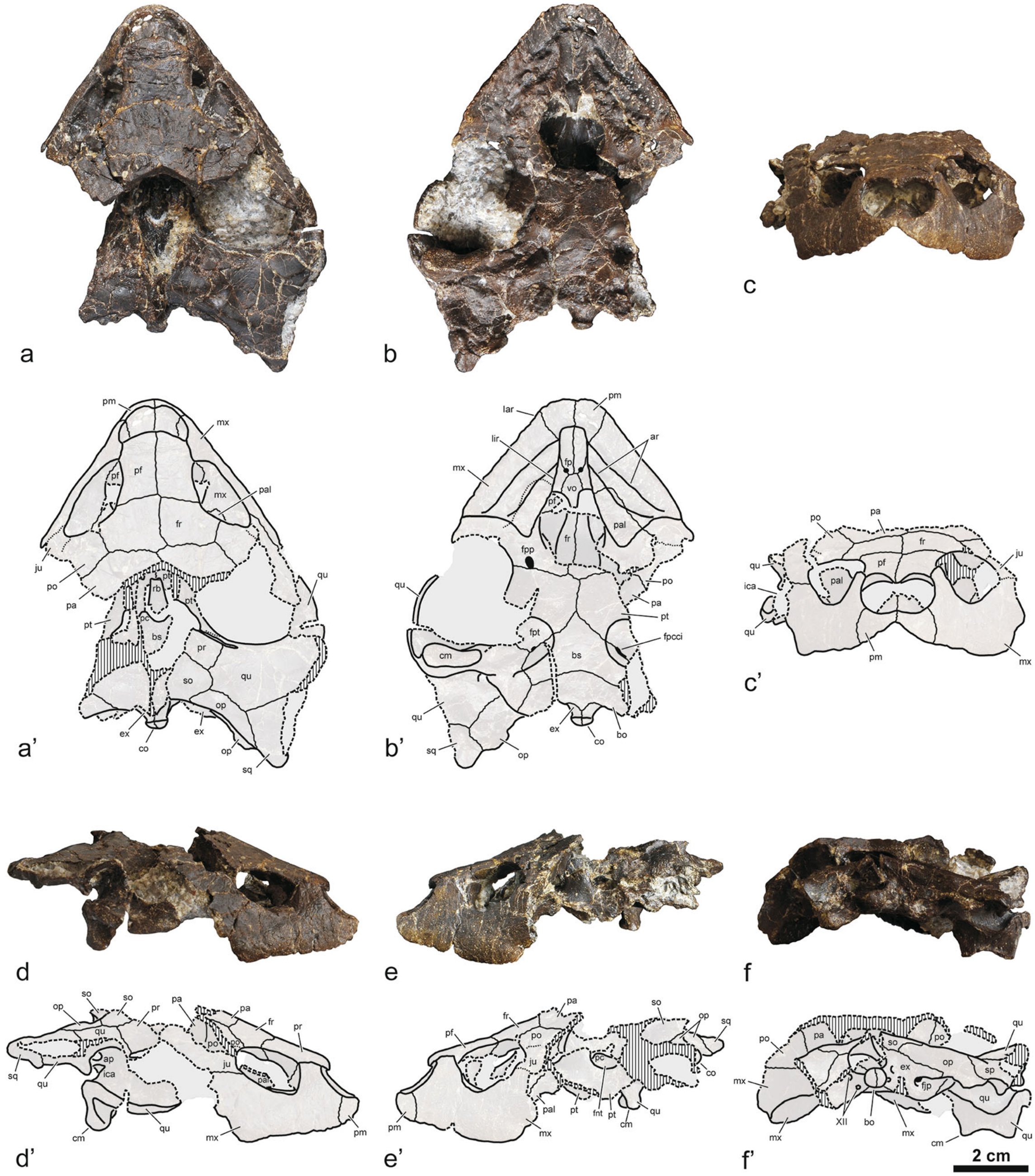

Fig. 2 Skull MNHN.F.SPP33, holotype of *T. teodorii* gen. et sp. nov. (Pleurodira, Bothremydidae), from the early Ypresian (early Eocene) of Saint-Papoul (Aude, France), in dorsal (**a**), ventral (**b**), anterior (**c**), right lateral (**d**), left lateral (**e**), and posterior (**f**) views

replications of Wagner trees (using random addition sequences) followed by Tree Bisection Reconnection (TBR) as swapping algorism, serving 100 trees per replication. To test the robustness of the phylogenetic hypotheses, Bremer support and bootstrap frequencies (absolute frequencies based on 1000 replications) values were also obtained using TNT.

Three nuchal plates also found in the early Ypresian levels of Saint-Papoul, identified as belonging to different ontogenetic stages of a single taxon, are also analyzed (Fig. 4a–f). The possible systematic allocation of this taxon is discussed.

Anatomical abbreviations ap, antrum postoticum; ar, accessory ridge; bo, basioccipital; bs, basisphenoid; cm, condylus mandibularis; co, condylus occipitalis; ex, exoccipital; fjp, foramen jugulare posterius; fnt, foramen nervi trigemini; fp, foramen praepalatinum; fpcci, foramen posterius canalis carotici interni; fpp, foramen palatinum posterius; fpt fossa pterygoidea; fr, frontal; ica, incisura columellae auris; IP, interparietal scute; ju, jugal; lar, labial ridge; lir, lingual ridge; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pc, processus clinoideus; pf, prefrontal; pm, premaxilla; po,

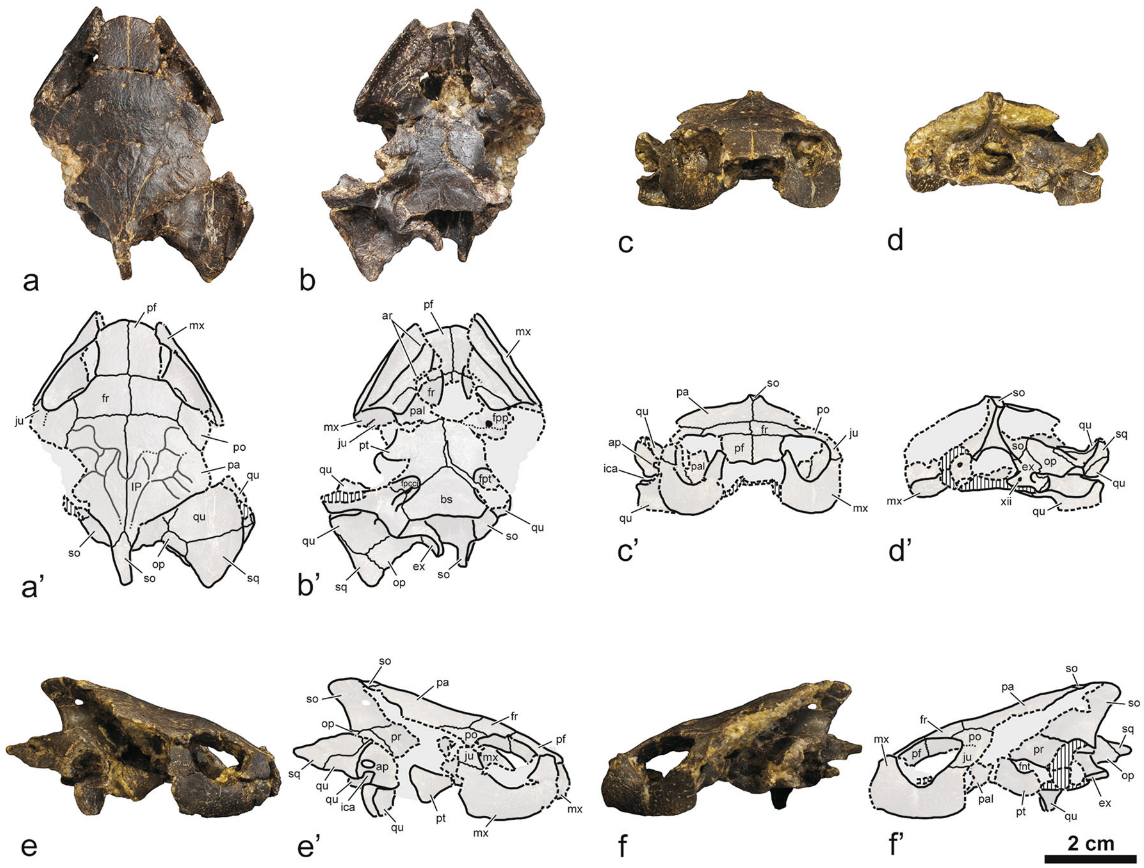

Fig. 3 Skull MNHN.F.SPP34, paratype of *T. teodorii* gen. et sp. nov. (Pleurodira, Bothremydidae), from the early Ypresian (early Eocene) of Saint-Papoul (Aude, France), in dorsal (**a**), ventral (**b**), anterior (**c**), posterior (**d**), right lateral (**e**), and left lateral (**f**) views

postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; rb, rostrum basisphenoidale; so, supraoccipital; sq, squamosal; vo, vomer; XII, foramen nervi hypoglossi.

Systematic paleontology.

Testudines Batsch 1788
  Pan-Pleurodira Joyce et al. 2004
  Pleurodira Cope 1864
  Pelomedusoides Cope 1868
  Podocnemidoidea Cope 1868
  Bothremydidae Baur 1891
  Bothremydodda Gaffney et al. 2006
  Bothremydini Gaffney et al. 2006
  Foxemydina Gaffney et al. 2006
  Tartaruscola teodorii gen. et sp. nov.
  (Figs. 2 and 3)

Holotype. MNHN.F.SPP33, a skull lacking the posterior half of the cranial roof and the left latero-posterior region (Fig. 2).

Paratype. MNHN.F.SPP34, a skull lacking the left latero-posterior region (Fig. 3).

Type locality and horizon. Saint-Papoul, Aude, Languedoc-Roussillon-Midi-Pyrénées, France (Fig. 1). Clays of Saint-Papoul. Upper part of the early Ypresian (MP 8–9), early Eocene (Pérez-García and Lapparent de Broin 2015).

Etymology. The generic name is composed of the Latin words Tartărus (the underworld, the Hell, a deep abyss representing a dungeon for the wicked and a prison for the Titans) and -cola (inhabitant of), in relation to one of the most consensual hypothesis about the origin of the words Turtle (English), Tortue (French), Tortuga (Spanish), Tartaruga (Portuguese), and other determinations for this reptile, having been identified as an infernal animal. According to this hypothesis, these words come from the Latin Tartarūcha or Tartarūchus, derived from the Greek Tartaroûkhos, meaning inhabitant of the Tartarus. The specific name is in honor of Dominique Teodori (Toulouse, France), who discovered and donated all the specimens studied here.

Diagnosis. Member of Bothremydini with the following autapomorphies: well-developed medial notch in the ventral margin of the premaxillae; high cheek emargination, reaching the level of the orbit; wide opening of the incisura columellae

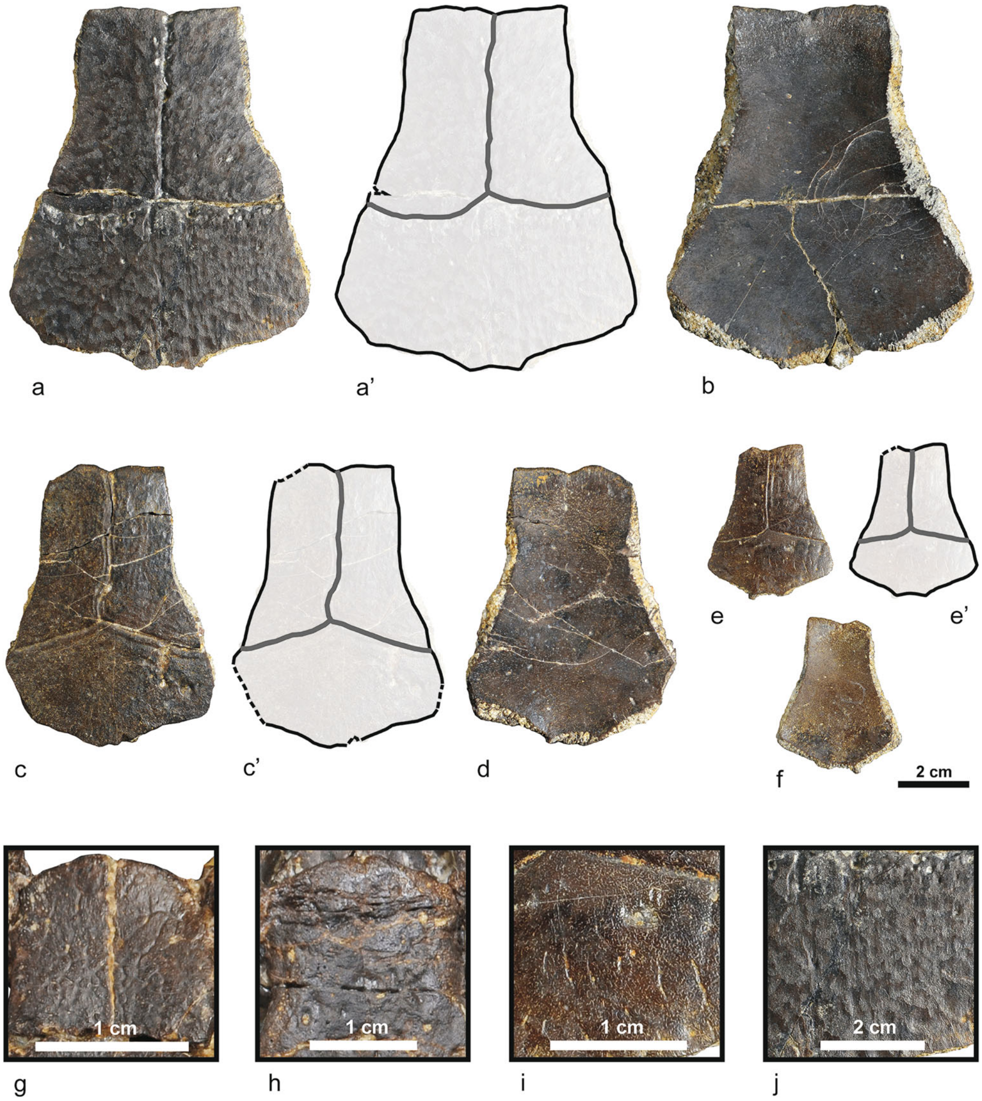

Fig. 4 Plates and details of the outer surface of skulls and plates from the early Ypresian (early Eocene) of Saint-Papoul (Aude, France). **a**–**f** Nuchal plates of cf. Foxemydina. **a**, **b** MNHN.F.SPP35, in dorsal (**a**) and ventral (**b**) views. **c**, **d** MNHN.F.SPP36, in dorsal (**c**) and ventral (**d**) views. **e**, **f** MNHN.F.SPP37, in dorsal (**e**) and ventral (**f**) views. **g**–**j**, details on the outer surface of the anterior region of the cranial roofs of the paratype, MNHN.F.SPP34 (**g**), and holotype, MNHN.F.SPP33 (**h**), of *T. teodorii* gen. et sp. nov., and of the posterior region of the nuchal plates MNHN.F.SPP37 (**i**) and MNHN.F.SPP35 (**j**) of cf. Foxemydina

auris; presence of a well-developed accessory ridge on each triturating surface; presence of a second pair of poorly developed accessory ridges on the triturating surfaces. It differs from the other members of Bothremydini by the following character combination: straight lateral edge of the maxilla, generating a relatively narrow preorbital area (shared with *Araiochelys hirayamai*); ventral edge of the apertura narium externa located significantly ahead the dorsal edge (shared with *Zolhafah bella*, *Chedighaii* spp., and *A. hirayamai*); absence of midline dorsal process of the premaxillae (shared with *Foxemys* spp., *Polysternon provinciale*, *Z. bella*, and *Rosasia soutoi*); midline process in the dorsal margin of the apertura narium externa (shared with *A. hirayamai*, *Bothremys* spp., and *Chedighaii* spp.); laterally oriented orbits (shared with *Foxemys* spp., *Po. provinciale*, *R. soutoi*, *Z. bella*, and *A. hirayamai*); absence of a prefrontal-palatine contact or of proximity between both bones (shared with *Foxemys* spp., *R. soutoi*, and *Z. bella*); supraoccipital-quadrate suture (shared with all Bothremydini except *Z. bella*); distinct posterior process of the squamosal (shared with all Bothremydini except *Pu. mushaisaensis*); high sulcus palatinopterygoideus (shared with *Foxemys* spp. and *R. soutoi*); ossified processus clinoideus (shared with *R. soutoi* and *Z. bella*); distinct margin in the ventral rim of the orbit (shared with *Po. provinciale* and *Bothremys arabicus*); low maxilla below the orbit, lower than the orbit diameter (shared with *Foxemys* spp., *Po. provinciale*, *R. soutoi*, *Z. bella*, *A. hirayamai*, and some *B. maghrebiana*); relatively large antrum postoticum (shared with *Foxemys* spp., *Po. provinciale*, and *Z. bella*); very low verticalized surface of the quadrate below the cavum tympani (shared with *A. hirayamai*); high processus articularis (shared with *A. hirayamai*, *Bothremys* spp., and *Chedighaii* spp.); stapes not completely enclosed (shared with *Foxemys* spp. and *Po. provinciale*); laterally open foramen jugulare posterius (shared with *Foxemys* spp. and *Po. provinciale*); lingual ridges of the triturating surfaces defining a narrow midline depression (shared with *Bothremys cooki*, *B. maghrebiana*, *R. soutoi* and *A. hirayamai*); triturating surfaces no more than two times wider posteriorly than anteriorly (shared with *Po. provinciale*, *C. barberi*, some *B. maghrebiana* and *A. hirayamai*); absence of pits on the triturating surface (shared with *Foxemys* spp., *Po. provinciale*, and *Chedighaii* spp.); absence of exposure of the jugal on the triturating surface (shared with *Foxemys* spp., *Po. provinciale*, and *Chedighaii* spp.); vomer-maxilla contact (shared with all Bothremydini except *Chedighaii hutchisoni*); foramen praepalatinum located in the premaxilla-maxilla suture (shared with *R. soutoi*); relatively long medial contact of the pterygoids (shared with *Foxemys* spp., *Po. provinciale*, *B. cooki*, *Bothremys kellyi*, *Chedighaii* spp., *R. soutoi*, and *Z. bella*); deep and narrow fossa pterygoidea (shared with *Foxemys* spp. and *Po. provinciale*); foramen posterius canalis carotici interni in the pterygoid-basisphenoid suture (shared with *Foxemys* spp., *Po. provinciale*, *R. soutoi*, and some *B. maghrebiana*); condylus mandibularis well anterior to the basioccipital-basisphenoid suture (shared with *Po. provinciale*); pentagonal basisphenoid (shared with *Foxemys* spp. and *Po. provinciale*); relatively long basisphenoid-quadrate suture (shared with *Foxemys* spp., *Po. provinciale*, *Pu. mushaisaensis*, *R. soutoi*, and *Z. bella*).

Description. The length of the skull MNHN.F.SPP33, from the anterior margin of the premaxillae to the posterior edge of the squamosals, is about 95 mm (Fig. 2). That of the preserved region of MNHN.F.SPP34 is about 60 mm (Fig. 3). The outer surface of the cranial roof of MNHN.F.SPP33 is roughened (Fig. 4h). Millimetric grooves, discontinuous and anastomosed, are preserved in the outer surface of the cranial roof of MNHN.F.SPP34 (Fig. 4g). The larger specimen is interpreted as an adult, not only considering its size but also the described outer surface and the presence of strongly sutured skull bones. The development of the sutures between these bones is weaker in the smaller specimen, being recognized as a probably subadult (which is supported by the described ornamentation of its outer surface). The skull of *T. teodorii*, from its anterior end to the rear edge of the cavum tympani, has a triangular morphology in dorsal and ventral views (Figs 2a, b and 3a, b). Thus, the lateral edge of the maxilla is straight, and the preorbital part of the skull is relatively narrow. A medial high and narrow notch is present in the ventral margin of the premaxillae (Fig. 2c). The ventral margin of the apertura narium externa is positioned clearly more anteriorly than the dorsal margin (Fig. 2a). In dorsal view, the snout is very broad (Figs. 2a and 3a). A midline dorsal process of the premaxillae is absent (Fig. 2c). *T. teodorii* has a medial protrusion in the anterior margin of the prefrontals (Figs. 2c and 3c). The orbits open laterally, in a vertically oriented face (Figs. 2 and 3). This taxon lacks nasal and lacrimal bones. In the skull roof, the prefrontals, frontals, and parietals have a midline contact (Figs. 2a and 3a). The descending process of the prefrontal is small, not being in contact with the vomer or palatine. The parietal is not in contact with the orbital margin. The temporal emargination is relatively slight (Fig. 3a). The crista supraoccipitalis is well-developed (Fig. 3). The supraoccipital contacts the quadrate in the dorsal surface of the otic chamber (Figs. 2a and 3a). A distinct canal for the foramen stapedio-temporale is present (Fig. 2a). This foramen lies on the anterior surface of the otic chamber. The foramen stapedio-temporale is separated of the foramen nervi trigemini by a narrow bar of the prootic. The squamosal of *T. teodorii* forms a posterior process that extends well posterior to the short processus paroccipitalis of the opisthotic (Figs. 2a, b and 3a, b).

The maxilla of *T. teodorii* is broadly exposed in the fossa orbitalis, forming most of the orbital floor (Figs. 2a and 3a). The foramen interorbitale is low, being reduced in height by a relatively high palate and a low sulcus olfactorius (Figs. 2d, e and 3e, f). The septum orbitotemporale is distinctly posterior to the orbital rim, due to the posterior enlargement of the fossa orbitalis (Figs. 2c and 3c). This septum is completely closed. A high sulcus palatinopterygoideus is present (Fig. 2a). *Tartaruscola teodorii* has a well-defined and relatively deep sella turcica concavity, with a distinct dorsum sellae at its posterior margin. A processus clinoideus is present.

The anterior wall of the premaxilla, between the labial ridge and the apertura narium externa, is subvertical (Figs. 2d, e and 3e, f). A well-developed ridge is present in the edge corresponding to the contact between the nearly horizontal floor of the fossa orbitalis and the lateral surface of the maxilla (Figs. 2a, d, e and 3a, e, f). The height of the maxilla below the orbit is lower than that of this structure (Figs. 2d, e and 3e, f). *Tartaruscola teodorii* has a high cheek emargination, reaching at least the level of the orbit. It lacks a fossa precolumellaris. The quadrate does not completely surrounds the stapes (Figs. 2d and 3e). The incisura columellae auris shows a wide opening. The antrum postoticum is relatively large. The verticalized surface of the quadrate located below the cavum tympani is very low. The processus articularis is high, the height of its anterolateral margin being twice as large as the maximum length of the condylus mandibularis.

The foramen jugulare posterius is surrounded by the exoccipital, being open laterally, so it is continuous with the fenestra postotica (Figs. 2f and 3d). The fenestra postotica is medially closed by the opisthotic-quadrate contact. A relatively long suture between the exoccipital and the quadrate is present. The condylus occipitalis is exclusively constituted by the exoccipitals (Fig. 2a, b, f).

Tartaruscola teodorii has well-defined lingual ridges of the triturating surfaces, extending onto the premaxillae, and constituting a long and narrow midline depression, with parallel lateral sides along the anterior half (Fig. 2b). The triturating surfaces are triangular, about twice as wide posteriorly than anteriorly (Figs. 2b and 3b). This taxon has a well-developed accessory ridge on each triturating surface, and also a poorly developed second accessory ridge. It lacks pits on the triturating surface. The palatine forms a significant part of the triturating surface, constituting its posteromedial region. The jugal is not exposed on the triturating surface. *Tartaruscola teodorii* has a vomer. This bone contacts the maxillae. The foramen praepalatinum is located in the premaxilla-maxilla suture. The foramen palatinum posterius is located in the floor of the sulcus palatinopterygoideus. This taxon has a well-developed processus trochlearis pterygoidei. The midline contact of the pterygoids is relatively long. A cavum pterygoidei is absent. The prootic is not exposed in the ventral surface of the skull. The fossa pterygoidea is well-developed. It is relatively deep and narrow. The foramen posterius canalis carotici interni is located in the suture between the pterygoid and the basisphenoid. The condylus mandibularis is placed well anterior to the basioccipital-basisphenoid suture. The basisphenoid is pentagonal in ventral view, and lacks ventral tubercles. Relatively long basisphenoid-quadrate and basioccipital-quadrate sutures are present. The basioccipital is short, being three times wider than long.

A complex pattern of scutes is partially recognized in the cranial roof of the paratype (Fig. 3a). Thus, numerous scutes are located on the parietals. The interparietal scute is longer than wide. A relatively large distance separates it from the frontals. A deep notch is developed in its anterior margin.

cf. Foxemydina

(Fig. 4a–f)

Material. MNHN.F.SPP35, MNHN.F.SPP36 and MNHN.F.SPP37, three nuchal plates (Fig. 4a–f).

Locality and horizon. Saint-Papoul, Aude, Languedoc-Roussillon-Midi-Pyrénées, France (Fig. 1). Clays of Saint-Papoul. Upper part of the early Ypresian (MP 8–9), early Eocene (Pérez-García and Lapparent de Broin 2015).

Description. The three nuchal plates have a similar morphology (Fig. 4a–f). They are subhexagonal and demonstrate a very shallow to absent medial anterior notch. The latero-anterior margin of each nuchal is the longest, being more than twice longer than the latero-posterior. The shortest edge is the posterior, being three times shorter than the anterior. These plates are longer than wide, the length being about 20 % higher than the maximum width. The length of the anterior margin is similar to half of the maximum width of these plates. The lateral margins of the anterior third of these plates are subparallel to each other. All these proportions are shared by the three specimens presented herein, as well as by other unpublished nuchals from the same locality. Since the nuchal plates presented here have different sizes (the maximum length of MNHN.F.SPP35 is 100 mm, Fig. 4a, b; that of MNHN.F.SPP36 is 80 mm, Fig. 4c, d; and that of MNHN.F.SPP37 is 41 mm, Fig. 4e, f), corresponding to individuals of different ontogenetic stages, the described characters are recognized as not subject to ontogenetic variability. As in the outer surface of the cranial roofs of the specimens studied here, millimetric grooves, discontinuous and anastomosing, are preserved in the outer surfaces of the small specimens (Fig. 4i), but those of the plates interpreted as belonging to adult individuals are roughened (Fig. 4j). This taxon lacks cervical scute. The first pair of marginal scutes is very long, overlapping more than the 65 % of the latero-anterior margin of the nuchal plate. Thus, these scutes overlap over half of the length of this plate. The first pair of pleural scutes does not overlap the nuchals.

Discussion

Identification of *Tartaruscola teodorii* as a member of Foxemydina

The new taxon studied here can be attributed to Pleurodira due to several exclusive character of this group, such as the presence of sulcus palatinopterygoideus and associated septum orbitotemporale, absence of epipterygoid, foramen palatinum posterius located posterior to the fossa orbitalis, and development of a processus trochlearis pterygoideus (Figs. 2 and 3). The absence of nasals, the presence of prefrontals meeting on the midline, and the absence of contact between the parietal and the squamosal allow its identification as a member of Pelomedusoides. It corresponds to a Podocnemidoidea by characters such as the absence or poorly develop exposure of the prootic in the ventral surface of the skull, and the presence of contact between the quadrate and the basioccipital. The presence of a member of Podocnemidoidea in Saint-Papoul was previously notified (see Tong 1998; Pérez-García and Lapparent de Broin 2015), a representative of Podocnemididae having been defined there, *Neochelys laurenti* (Tong 1998). *Tartaruscola teodorii* gen. et sp. nov. differs from the members of Podocnemididae by the presence of open incisura columellae auris, the absence of basioccipital-opisthotic contact, and the absence of cavum pterygoidei. However, these and other characters allow its attribution to Bothremydidae. Thus, *T. teodorii* shares with the members of Bothremydidae exclusive characters for this clade of Pelomedusoides (e.g,. wide exoccipital-quadrate contact, processus paroccipitalis not projected posterior to the squamosal), and also a unique combination of characters, including the following: supraoccipital-quadrate contact, relative wide triturating surfaces, moderate to large palatine contribution to the triturating surface, prootic partially or completely covered in ventral view, foramen posterius canalis carotici interni not located in the prootic, and basisphenoid-quadrate suture present (Gaffney et al. 2006).

Four clades of Bothremydidae are currently recognized: Kurmademydini, Cearachelyini, Taphrosphyini, and Bothremydini, the last two constituting Bothremydodda. Gaffney et al. (2006) recently proposed new diagnoses for all these clades. Thus, *T. teodorii* differs from the members of

Kurmademydini due to the absence of exclusive characters for this clade such as extreme temporal emargination, presence of fossa precolumellaris, and prootic partially exposed on the ventral surface. In addition, the representatives of Kurmademydini differ from the taxon analyzed here, and from the other representatives of Bothremydodda, due to absence of proximity between the foramen stapedio-temporale and the foramen nervi trigemini. They also differ from *T. teodorii* and from the other members of Bothremydini due to the presence of narrower triturating surfaces. *Tartaruscola teodorii* differs from the members of Cearachelyini due to the absence of some exclusive characters of that clade: jugal not contacting the orbital margin, and fenestra postotica open but formed as a short slit. In addition, the representatives of Kurmademydini differ from the taxon analyzed here, and from the other representatives of Bothremydodda, due to the presence of a longer temporal emargination (but shorter than in Kurmademydini), exoccipitals not completely forming the neck of the condyle occipitalis, and absence of proximity between the foramen stapedio-temporale and the foramen nervi trigemini. Thus, all the states on the aforementioned characters allow the attribution of *Tartaruscola teodorii* to Bothremydodda. *T. teodorii* differs from the members of Taphrosphyini, a clade lacking supraoccipital-quadrate contact, but with relatively high fenestra interorbitale, relatively narrow triturating surfaces, and a small palatine contribution to triturating surfaces. However, the states of these characters for *T. teodorii* are compatible with those of the members of Bothremydini. Thus, its attribution to this clade is performed.

Characters such as the absence of cervical scute allow excluding the attribution of the nuchal plates analyzed here to Cryptodira, this character being shared with most clades of Pleurodira (Fig. 4a–f). They cannot be attributed to the representative of Pleurodira previously recognized in Saint-Papoul, *N. laurenti*. Thus, the latero-anterior margin of the nuchal plate of *N. laurenti* is less than twice the length of the latero-posterior margin; the anterior marginal is less than two times wider than the posterior; the nuchal plates are as wide as long or wider than long; the length of the anterior margin is approximately one third of the maximum width of these plates; the lateral margins of the anterior third of these plates are not subparallel to each other, but anteriorly convergent; the maximum length of the nuchal plate of the adult specimens of *N. laurenti* is slightly greater than half of the maximum length of the nuchals of the adult specimens of the taxon presented here; the first pair of marginal scutes is noticeably shorter, overlapping a length considerably lower than half of the latero-anterior margin of the nuchal plate, usually close to a third or a quarter of that length. The characters observed in the nuchal plates presented here are consistent with those of some representatives of Foxemydina, as, for example, *F. mechinorum* Tong, Gaffney and Buffetaut 1998 or *Iberoccitanemys convenarum* (Laurent et al. 2002) (see Pérez-García et al. 2012). The presence of discontinuous millimetric grooves in the outer surface of the younger individuals, but of a roughened pattern in the adults, is compatible with the condition observed for the skulls of *T. teodorii* (see Fig. 4g–j). However, considering the limited information provided by these plates, they are recognized as cf. Foxemydina.

Comparison of *T. teodorii* with the other members of Bothremydini

The development of a straight lateral margin of the maxilla of *T. teodorii*, generating a relatively narrow preorbital part of the skull, is shared with *A. hirayamai* Gaffney, Tong and Meylan 2006, but not with the other representatives of Bothremydini. A well-developed, high relative to its width, medial notch in the labial margin of the premaxillae is not shared with any other member of Bothremydini. The presence of the ventral edge of the apertura narium externa not located approximately at the same level as the dorsal margin, or slightly ahead, but significantly ahead, is shared with *Z. bella* Lapparent de Broin and Werner 1998, *Chedighaii* spp., and *A. hirayamai*, but not with *Foxemys* spp. and *R. soutoi* Carrington da Costa 1940. The absence of a midline dorsal process of the premaxillae is shared with *Foxemys* spp., *Po. provinciale* (Matheron 1869), *Z. bella*, and *R. soutoi*, but not with *Bothremys* spp. and *A. hirayamai*, in which a well-developed process is developed, partially (in *B. cooki* Leidy 1865 and *B. maghrebiana* Gaffney, Tong and Meylan 2006) or totally (in *B. kellyi* Gaffney, Tong and Meylan 2006 and *A. hirayamai*) separating the nares. The development of a midline process in the dorsal margin of the apertura narium externa is shared with *A. hirayamai* and the representatives of *Chedighaii* Gaffney, Tong and Meylan 2006 and *Bothremys* Leidy 1865 in which this region is known (i.e., *C. hutchisoni* Gaffney, Tong and Meylan 2006, *B. cooki*, *B. maghrebiana*, and *B. kellyi*), but not with *Po. provinciale*, *Foxemys* spp., and *R. soutoi*, in which this margin is straight or convex. The orbits of *Foxemys* spp., *Po. provinciale*, *R. soutoi*, *Z. bella*, and *A. hirayamai* are also clearly laterally oriented. This condition is not shared with *Bothremys* spp. and *Chedighaii* spp., in which the orbits face dorsally and only slightly laterally. The absence of a prefrontal-palatine contact, or of a very close position between both bones, is shared with *Foxemys* spp., *R. soutoi*, and *Z. bella*; but not with *A. hirayamai* and the representatives of *Bothremys* and *Chedighaii* in which this region is known (i.e., *B. cooki*, *B. maghrebiana*, *B. kellyi*, and *C. hutchisoni*). The presence of contact between the supraoccipital and the quadrate is shared with all Bothremydini except *Z. bella*. The development of a distinct posterior process of the squamosal is present in all Bothremydini except *Pu. mushaisaensis*. A high sulcus palatinopterygoideus is also present in *Foxemys* spp. and *R. soutoi*, but not in the representatives of *Bothremys* and *Chedighaii*. The presence of an ossified processus clinoideus is shared with *R. soutoi* and *Z. bella*, but not with *C. barberi* (Schmidt 1940), *B. cooki*, and *B. maghrebiana*.

Tartaruscola teodorii shares with *Po. provinciale* and *B. arabicus* (Zalmout et al. 2005) the present of a distinct margin in the ventral rim of the orbit. A continuous slope between the floor of the fossa orbitalis and the lateral surface of the maxilla is present in *Foxemys* spp., *B. cooki*, and some *B. maghrebiana*. A relatively low maxilla below the orbit, roughly equal to or less than the orbital diameter, is shared with *Foxemys* spp., *Po. provinciale*, *R. soutoi*, *Z. bella*, *A. hirayamai*, and some specimens of *B. maghrebiana*. A high maxilla is present in *B. cooki*, *B. kellyi*, *C. hutchisoni*, and some specimens of *B. maghrebiana*. The presence of a high cheek emargination, reaching at least the level of the orbit, is not shared with any other member of Bothremydini. Thus, this structure is poorly developed or relatively low in comparison with the orbit level in *F. mechinorum*, *Po. provinciale*, and *C. hutchisoni*, but absent in *B. maghrebiana*, *B. kellyi*, and *R. soutoi*. The absence of stapes completely enclosed by the bony incisura columellae auris is shared with *Foxemys* spp. and *Po. provinciale*, but not with *Bothremys* spp., *Chedighaii* spp., *R. soutoi*, *Z. bella*, and *A. hirayamai.* The development of a wide opening of the incisura columellae auris is not shared with the other members of Bothremydini in which this structure is not completely enclosed (i.e., *Foxemys* spp. and *Po. provinciale*), due to the presence of a narrow fissure. The presence of a relatively large antrum postoticum is shared with *Foxemys* spp., *Po. provinciale*, and *Z. bella*, but not with *A. hirayamai* and the representatives of *Bothremys* and *Chedighaii* in which this character is known (i.e., *B. maghrebiana*, *B. kellyi*, and *C. barberi*). *Tartaruscola teodorii* shares with *A. hirayamai*, but not with *F. mechinorum*, *B. maghrebiana*, and *R. soutoi*, the presence of a very low verticalized surface of the quadrate located below the cavum tympani. The presence of a relatively high processus articularis, the height of its anterolateral margin being about twice the maximum length of condylus mandibularis, is shared with *A. hirayamai*, *Bothremys* spp., and *Chedighaii* spp. The processus articularis is low in *F. mechinorum*, *Po. provinciale*, and *R. soutoi*, the height of the anterolateral margin and the maximum length of the condylus mandibularis being subequal.

A thin horizontal flange is present on the posterior edge of the opisthotic of *Chedighaii* spp., *B. kellyi*, and some *B. maghrebiana*, this structure being absent in the new taxon studied here, *T. teodorii*, and in *Foxemys* spp., *A. hirayamai* and some *B. maghrebiana*. The presence of a laterally open foramen jugulare posterius is shared with *Foxemys* spp. and *Po. provinciale*, but not with *Bothremys* spp., *Chedighaii* spp., *Z. bella*, and *A. hirayamai*.

In ventral view, the premaxilla of *A. hirayamai* and *Bothremys* spp. projects anteriorly beyond the labial ridge. This condition is not shared with *T. teodorii*, *Foxemys* spp., *Po. provinciale*, *R. soutoi*, and *Z. bella*. A distinct and narrow midline depression, defined by the lingual ridges of the triturating surfaces, is also present in *B. cooki*, *B. maghrebiana*, *R. soutoi*, and *A. hirayamai*, but not in *F. mechinorum*, *Po. provinciale*, *B. arabicus*, *B. kellyi*, *C. hutchisoni*, and *Z. bella*, in which this depression is wider, lacking subparallel lateral margins. The presence of triangular triturating surfaces, about twice wider posteriorly than anteriorly, is shared with *Po. provinciale*, *C. barberi*, some *B. maghrebiana*, and *A. hirayamai*, but not with *Foxemys* spp., *R. soutoi*, *Z. bella*, *C. hutchisoni*, *B. arabicus*, *B. cooki*, *B. kellyi*, and some *B. maghrebiana*, in which these surfaces are wider. The only known Bothremydini with an accessory ridge on each triturating surface is *F. mechinorum*, the other representatives lacking this structure. However, the accessory ridges of *F. mechinorum* are poorly developed. Thus, the presence of both two pairs of accessory ridges, and also of a well-developed pair, is exclusive of *T. teodorii*. The absence of pits on the triturating surface is shared with *Foxemys* spp., *Po. provinciale*, and *Chedighaii* spp., but not with *Bothremys* spp., *R. soutoi*, *Z. bella*, and *A. hirayamai*. The absence of exposure of the jugal on the triturating surface is shared with *Foxemys* spp., *Po. provinciale*, and *Chedighaii* spp., but not with *Bothremys* spp., *R. soutoi*, *Z. bella*, and *A. hirayamai*. The presence of contact between the vomer and the maxillae is shared with all members of Bothremydini except *C. hutchisoni*. A foramen praepalatinum in the premaxilla-maxilla suture is also identified in *R. soutoi*, this condition not being shared with the other Bothremydini in which this foramen is known. Thus, this foramen is located on the premaxilla in *F. mechinorum*, *Po. provinciale*, *B. arabicus*, *B. maghrebiana*, and *A. hirayamai*. A relatively long medial contact between the pterygoids is shared with *Foxemys* spp., *Po. provinciale*, *B. cooki*, *B. kellyi*, *Chedighaii* spp., *R. soutoi*, and *Z. bella*, but not with *B. maghrebiana* and *A. hirayamai*.

The presence of a relatively deep and narrow fossa pterygoidea is shared with *Foxemys* spp. and *Po. provinciale*. It is moderate in *R. soutoi*, but very small or almost absent in *Bothremys* spp., *Chedighaii* spp., *Z. bella*, and *A. hirayamai*. The position of the foramen posterius canalis carotici interni in the pterygoid-basisphenoid suture is shared with *Foxemys* spp., *Po. provinciale*, *R. soutoi*, and some *B. maghrebiana*. This foramen is located in the pterygoid-quadrate suture in *A. hirayamai*, *Chedighaii* spp., *B. arabicus*, and some *B. maghrebiana*, but is in contact with the pterygoid, basisphenoid, and quadrate in *Z. bella*, *B. kellyi*, and some *B. maghrebiana*. The variability observed in *B. maghrebiana* is very large, and this foramen can also be located on the basisphenoid and on the prootic. The presence of the condylus mandibularis distinctly anterior to the plane of the suture between the basioccipital and the basisphenoid is shared with *Po. provinciale*, but not with the other members of Bothremydini, in which it is located near or in line with the basioccipital-basisphenoid suture. A pentagonal basisphenoid, in ventral view, is also present in *Foxemys* spp. and *Po. provinciale*, but not in *Bothremys* spp., *Chedighaii* spp., *R. soutoi*, *Z. bella*, and *A. hirayamai*, in which this bone has a triangular ventral outline. The presence of a relatively long basisphenoid-quadrate contact is shared with *Foxemys* spp., *Po. provinciale*, *Pu. mushaisaensis*, *R. soutoi*, and *Z. bella*, but not with *Bothremys* spp. and *Chedighaii* spp., in which this suture is narrow.

Results

Results of the phylogenetic analysis

The performed phylogenetic analysis resulted in two most parsimonious trees, with a length of 291 steps (CI = 0.698; RI = 0.773; RC = 0.539) (Fig. 5). The new taxon proposed here, *T. teodorii*, is obtained as a member of Foxemydina, being recognized as the sister taxon of *Po. provinciale*.

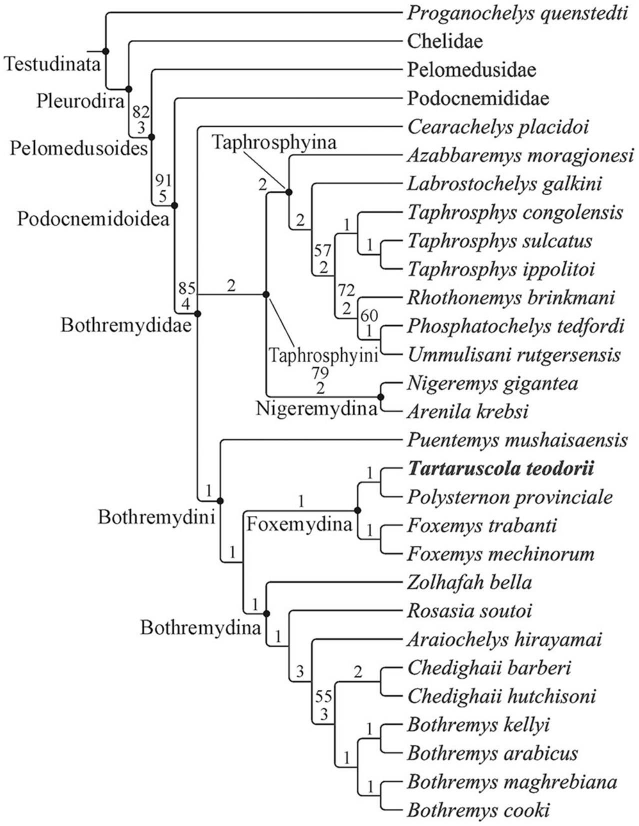

Fig. 5 Phylogenetic position of *T. teodorii* gen. et sp. nov. (Pleurodira, Bothremydidae), from the early Ypresian (early Eocene) of Saint-Papoul (Aude, France), in the strict consensus tree obtained by the cladistic analysis performed here. Bootstrap frequencies (*top*; only values equal to or greater than 50 % shown) and Bremer support values (*bottom*) are indicated

A polytomy at the base of Bothremydidae is obtained, composed by Cearachelyini, Taphrosphyini, and Bothremydini. The clade Bothremydini is defined here by the presence of anterior margin of plastron well posterior to the anterior margin of the carapace (character 173, state 1; not known in *T. teodorii*). Two branches compose Bothremydini. One of them corresponds to the South American taxon *Pu. mushaisaensis*. The second branch groups all the other representatives of this clade, corresponding to forms from Europe, Africa, Middle East, and North America. This branch is diagnosed by the presence of extension of the posterior projection of the squamosal well posterior to the opisthotic (character 24, state 1) and the absence of nuchal notch (character 154, state 1; not coded for *T. teodorii*). Two lineages are also recognized in this branch, Bothremydina and the exclusively European clade Foxemydina. In this analysis, Foxemydina is characterized by the presence of a deep and narrow fossa pterygoidea (character 68, state 2); foramen jugulare posterius formed by bone and open or partially closed (character 82, state 1); subpentagonal morphology of the basisphenoid (character 106, state 2); and pectoral scutes located on the epiplastra or on the epiplastra-hyoplastra sutures (character 166, state 1; not known in *T. teodorii*). *Tartaruscola teodorii* and *Po. provinciale* are grouped by the presence of triangular triturating surfaces, wider posteriorly than anteriorly (character 34, state 1; shared with the Bothremydina *A. hirayamai*, *C. barberi*, and some *B. maghrebiana*), and condylus mandibularis distinctly anterior to the plane of the basioccipital-basisphenoid suture (character 60, state 1; not shared with any other representative of Bothremydini). *Tartaruscola teodorii* is characterized by the presence of an anterior midline process of the prefrontals (character 6, state 1; shared with the Bothremydina *B. cooki*, *B. maghrebiana*, *B. kellyi*, *C. hutchisoni*, and *A. hirayamai*); distinct and narrow midline depression of the premaxillae (character 31, state 2, shared with the Bothremydina *B. cooki*, *B. maghrebiana*, *C. barberi*, *R. soutoi*, and *A. hirayamai*); presence of accessory ridges on each triturating surface (character 36, state 1; shared with the Foxemydina *F. mechinorum*); and well-developed opening of the incisura columellae auris (character 52, state 0; exclusive for this member of Bothremydodda).

Systematic, biostratigraphic, and paleobiogeographic implications

Foxemydina is recognized here as an exclusively European clade, the South American *Pu. mushaisaensis* not being identified as a representative of this lineage, but as the sister taxon of the clade consisting of Foxemydina + Bothremydina (Fig. 6). The specimens studied here represent the only unambiguous material of Bothremydidae in the European Cenozoic record. The new taxon, *T. teodorii*, corresponds to the only Cenozoic representative of Foxemydina so far identified, an abundant group of turtles in the European uppermost Cretaceous sites and, especially, in those of southern France and northeastern Spain (Gaffney et al. 2006; Pérez-García et al. 2012).

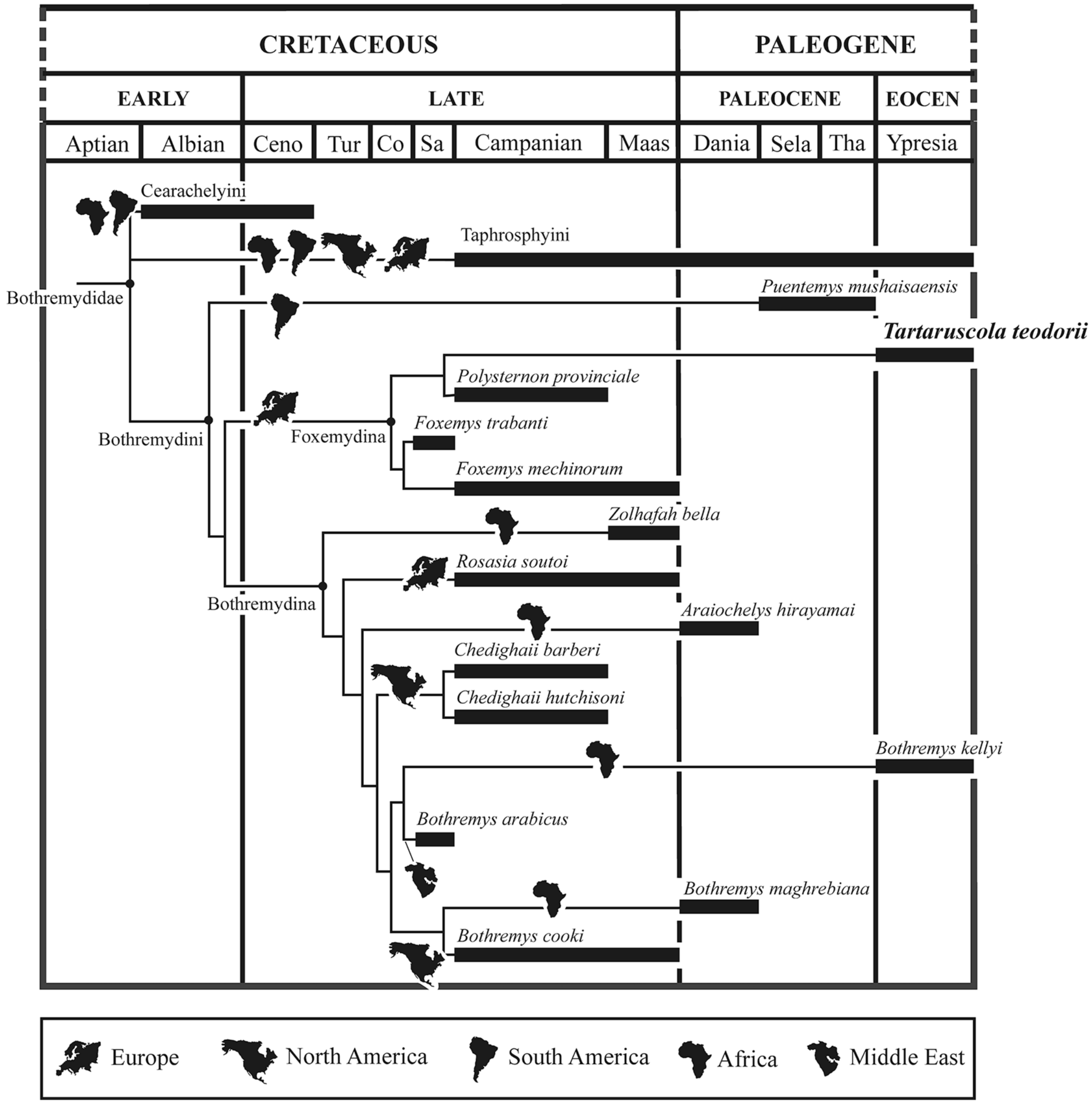

Fig. 6 Temporally calibrated cladogram, corresponding to the strict consensus tree of the analysis performed here, showing the position of *T. teodorii* gen. et sp. nov. (Pleurodira, Bothremydidae), from the early Ypresian (early Eocene) of Saint-Papoul (Aude, France). The continents where each of these taxa were found are indicated

The Cenozoic record of Bothremydidae is composed of a relatively small number of representatives, compared to the Cretaceous record. All of them are Paleogene forms. Both Taphrosphyini as Bothremydini are present (Fig. 7). A single valid form is known in the North American record. It is a representative of Taphrosphyini, *Taphrosphys sulcatus* (Leidy 1856), from the lower Paleocene record (probably Danian) of New Jersey. Taphrosphyini is also known in the Paleogene record of South America and Africa. In South America, it is represented by "*Taphrosphys*" *olssoni* (Schmidt 1931), from the Eocene of Mogollon (Peru). Several representatives of Taphrosphyini have been defined in the Paleogene record of Africa. Thus, this clade is represented by five taxa from the Ouled Abdoun Basin of Morocco: the Danian *Taphrosphys ippolitoi* Gaffney, Tong and Meylan 2006, the probably Paleocene *Labrostochelys galkini* Gaffney, Tong and Meylan 2006, the Ypresian *Phosphatochelys tedfordi* Gaffney and Tong 2003 and *Ummulisani rutgersensis* Gaffney, Tong and Meylan 2006, and *Rhothonemys brinkmani* Gaffney, Tong and Meylan 2006, from indeterminate levels of the Danian-Ypresian phosphate sequence. Two members of Taphrosphyini have been defined in the Paleocene of eastern Mali, *Azabbaremys moragjonesi* Gaffney, Moody and Walker 2001 and *Acleistochelys maliensis* Gaffney, Roberts, Sissoko, Bouaré, Tapanila and O'Leary 2007. In addition, Taphrosphyini is represented in Cabinda (Angola) by the Paleocene form *Taphrosphys congolensis* (Dollo 1913). The Cenozoic record of

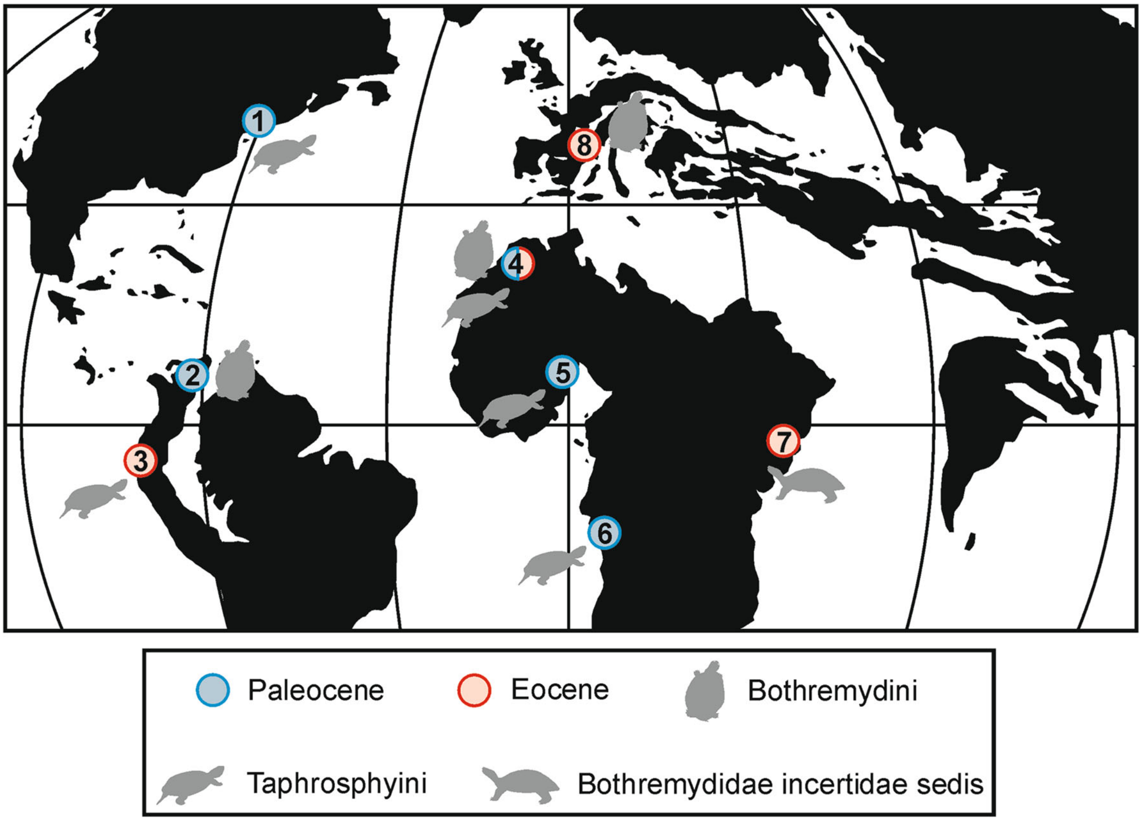

Fig. 7 Geographical position of the type localities of all Cenozoic Bothremydidae taxa currently recognized as valid. *1*, New Jersey (USA), probably Danian, type locality of *Taphrosphys sulcatus. 2*, La Guajira (Colombia), middle-late Paleocene, type locality of *Pu. mushaisaensis. 3*, Mogollon (Peru), Eocene, type locality of "*Taphrosphys*" *olssoni. 4*, Ouled Abdoun phosphate basin (Morocco), Danian to Ypresian, type locality of *B. maghrebiana*, *B. kellyi*, *A. hirayamai*, *Taphrosphys ippolitoi*, *Labrostochelys galkini*, *Phosphatochelys tedfordi*, *Ummulisani rutgersensis*, and *Rhothonemys brinkmani. 5*, Eastern Mali, Paleocene, type locality of *Azabbaremys moragjonesi* and *Acleistochelys maliensis. 6*, Cabinda (Angola), presumably Danian, type locality of *Taphrosphys congolensis. 7*, northern Somalia, middle Eocene, type locality of "*Podocnemis*" *somaliensis. 8*, Saint-Papoul (France), Ypresian, type locality of *T. teodorii* gen. et sp. nov

Bothremydini is much more limited than that of Taphrosphyini. Thus, the only unambiguous members of this clade so far defined came from the Ouled Abdoun Basin (Morocco) and La Guajira (Colombia). Several taxa have been described in the Ouled Abdoun Basin: *A. hirayamai* and *B. maghrebiana*, from the Danian, and *Bothremys kellyi*, from the Ypresian. As indicated, the South American taxon *Pu. mushaisaensis*, from the middle-late Paleocene of La Guajira (Colombia), is recognized here as the sister taxon of the clade consisting of Foxemydina + Bothremydina. The African form "*Podocnemis*" *somaliensis* Walker 1966, from the middle Eocene of Somalia, has recently been recognized as Bothremydidae incertae sedis. Thus, the Foxemydina *T. teodorii* and the Bothremydina *B. kellyi*, both from the Ypresian, are the youngest members of Bothremydini hitherto known.

Dispersal events of pleurodires from Africa to Europe are recognized for the Paleocene-Eocene Thermal Maximum, as is the case of several forms of Podocnemididae: the lineage of *Neochelys* Bergounioux 1954 and that of "aff. *Erymnochelys*" *eremberti* (Broin 1977) sensu Lapparent de Broin in Merle (2008), and Pérez-García and Lapparent de Broin (2015). The results of the cladistic analysis performed allow me to recognize the new taxon from Saint-Papoul as a member of a European linage originated from the migration of Gondwanan turtles at the beginning of the Late Cretaceous instead of as a Paleocene-Eocene immigrant (see Fig. 6). Thus, Foxemydina is identified as a lineage of Bothremydidae exclusive of Europe. This clade, abundant and relatively diverse in the uppermost Cretaceous of this continent, survived the Cretaceous-Paleocene extinction event. The information on the European Paleocene record of freshwater turtles is very limited (Pérez-García 2012). Therefore, the available evidences allow me to propose that the absence of record of Bothremydidae in the Paleocene of Europe does not indicate that this group was not present, but is the result of the limited information provided by the scarce record.

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