

**New insights on the only bothremydid turtle (Pleurodira)
identified in the British record:
Palemys bowerbankii new combination**

Adán Pérez-García

ABSTRACT

The British record of Pleurodira is very limited compared to that of Continental Europe. It is restricted to two lower Eocene coastal forms, corresponding to two lineages of Pelomedusoides: Podocnemididae and Bothremydidae. One of them is a recently recognized indeterminate species of the podocnemidid *Eocnochelus*, represented by a single individual from Bracklesham Bay (Sussex). *Eocnochelus* is a lineage of African origin that reached Europe during the Paleogene and is recognized in several European countries. The other British form is represented by several specimens from the London Clay of the Isle of Sheppey (Kent). Several shells were identified there, since the 19th century, allowing the description of four putative new species. The detailed study of the classic and subsequently found specimens, including unpublished individuals, confirms their attribution to a single species, for which the new combination *Palemys bowerbankii* is proposed. It is the only pleurodiran turtle recognized in the British record at a specific level. A neotype is designated, and a new diagnosis is provided. Photographs of most of the classic specimens of *Palemys bowerbankii* are included here for the first time. The detailed study of all these specimens improves the knowledge of this species. With this information, this exclusively British form is included for the first time in a cladistic analysis. It is not interpreted as the result of a Cenozoic dispersal event from Africa, as was the case with *Eocnochelus*, but as a member of a well-established lineage present in Europe during the Late Cretaceous, which lived in this continent at least until the early Eocene.

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INTRODUCTION

The British turtle record includes several Mesozoic members of the stem group of Testudines, as well as a great diversity of representatives of Cryptodira, both from Mesozoic and Cenozoic horizons (Lapparent de Broin, 2001; Joyce et al., 2011; Pérez-García, 2012; Bardet et al., 2014). However, the British record of Pleurodira is very limited, being restricted to only a few relatively poorly known and poorly represented forms from the lower Eocene (Gaffney et al., 2006; Pérez-García and Chapman, 2017). Several events of dispersion of this group of Gondwanan origin to continents that were part of Laurasia are known, and more specifically to Europe, both during the Mesozoic and the Cenozoic (Pérez-García, 2016a, 2017). Two successful lineages of Pleurodira are identified in the Eocene levels of Europe: Bothremydidae and Podocnemididae (Lapparent de Broin, 2001). The podocnemidids are the best represented, showing a relatively wide diversity. This group is represented in Continental Europe both by freshwater forms (i.e., several species of *Neochelys* Bergounioux, 1954) and by the recently described coastal genus *Eocnochelus* Pérez-García, Lapparent de Broin and Murelaga 2017 (Pérez-García et al., 2017). *Eocnochelus* is known in the Belgian, French, Spanish and Italian records, as well as a single specimen from the upper Ypresian (early Eocene) of Bracklesham Bay (Sussex, England) (Pérez-García et al., 2017; Pérez-García and Chapman, 2017; Pérez-García and Smith, 2017). This recently identified fossil, corresponding to an indeterminate species, represents the only podocnemidid specimen currently known in the British record (Pérez-García and Chapman, 2017).

Several shells and partial shells of coastal bothremydid turtles have been found in the lower Eocene British record, since the 19th century, from the London Clay of the Isle of Sheppey (see Owen, 1842, 1858; Owen and Bell, 1849). They were attributed to four different species, '*Platemys*' *bowerbankii* Owen, 1842, '*Emys laevis*' Bell in Owen and Bell, 1849, '*Emys delabechii*' Bell in Owen and Bell, 1849, and '*Emys conybearii*' Owen, 1858. Williams (1954) indicated that all of them could represent a single species. No detailed review of these specimens has been made after the study of Williams (1954). In fact, although drawings of some of the classic specimens were included in several works (presented by Owen and Bell, 1849, and reproduced in subsequent papers, see Owen, 1849; Williams, 1954), no photographs of any of

these classic specimens had been previously published. With the exception of its holotype, which is identified as lost since the 19th century (Lydekker and Boulenger, 1887), photographs of all the classic specimens are included here for the first time. In addition, shells subsequently found, including several previously unpublished specimens that add to the knowledge about both the shell anatomy and variability of this species, are also analyzed here. Photographs and schematic drawings of the more recently discovered specimens are also provided. The detailed study of all these specimens supports their interpretation as belonging to a single species, represented by both juvenile and adult individuals. A reconstruction of the complete shell of this taxon is done. The new combination *Palemys bowerbankii* (Owen, 1842) is proposed, and a neotype is designated. Additionally, this coastal bothremydid turtle is incorporated, for the first time, in a phylogenetic analysis.

Institutional abbreviations. GSM, British Geological Survey (BGS), Keyworth, Nottinghamshire, UK; NHMUK, Natural History Museum, London, UK.

MATERIALS AND METHODS

The detailed study of all the specimens of *Palemys bowerbankii* identified in this manuscript, including those previously published (except its holotype, now lost) and other unpublished specimens, is performed here. In this way, the shell of this generally considered problematic taxon can be characterized in detail.

In order to evaluate the systematic position of *Palemys bowerbankii*, it was coded in the data matrix proposed by Pérez-García (2016a), which pursues the study of the phylogenetic relationships among the representatives of Bothremydidae (Appendix 1. The recently described European Eocene bothremydid *Tartaruscola teodorii* Pérez-García (2016b) is also included, following the codification proposed by Pérez-García (2016b). Thus, the data matrix used here is composed of 180 characters and 31 taxa (Appendix 2).

This data matrix was analyzed using TNT 1.0 (Goloboff et al., 2008) in order to find the most parsimonious trees (MPTs). The outgroup of this analysis is *Proganochelys quenstedti* Baur, 1887. A heuristic tree search (Traditional search) was used, with 1000 replications of Wagner trees (using random addition sequences) followed by tree bisection recognition (TBR) as a swapping algorithm, saving 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. Equal weighting was used for the analysis.

SYSTEMATIC PALEONTOLOGY

Order TESTUDINES Batsch, 1788
 Suborder PLEURODIRA Cope, 1864
 Hyperfamily PELOMEDUSOIDES Cope, 1868
 Superfamily PODOCNEMIDOIDEA Cope, 1868
 Family BOTHREMYDIDAE Baur, 1891
 Infracfamily BOTHREMYDODDA Gaffney, Tong and Meylan, 2006
 Tribe BOTHREMYDINI Gaffney, Tong and Meylan, 2006
 Subtribe FOXEMYDINA Gaffney, Tong and Meylan, 2006
 Genus *PALEMYS* Gray, 1870
Palemys bowerbankii (Owen, 1842) new combination
 Figures 1-2

Holotype. A partial shell, now lost, first figured by Owen and Bell (1849, plate XXIII) (Figure 1.13-14).

Neotype. The almost complete shell NHMUK 39449, which is the holotype of '*Emys conybearii*' Owen, 1858 (Figure 1.1-8).

Other specimens attributed to this species. Five specimens, consisting of partial shells, including the holotypes of '*Emys delabechii*' and '*Emys laevis*' (Figure 1.9-12, 16-33). All of them from the type locality and horizon.

Type locality and horizon. Lower Eocene (Ypresian) London Clay of the Isle of Sheppey (Kent, England) (see Steurbaut and King, 2017; and references therein).

Main synonymies. *Platemys bowerbankii* Owen, 1842; *Emys laevis* Bell in Owen and Bell, 1849; *Emys delabechii* Bell in Owen and Bell, 1849; *Emys conybearii* Owen, 1858; *Podocnemis bowerbankii* (Owen, 1842) in Cope (1870); *Podocnemis laevis* (Bell in Owen and Bell, 1849) in Cope (1870); *Palemys laevis* (Bell in Owen and Bell, 1849) in Gray (1870); *Palaeaspis conybearii* (Owen, 1858) in Gray (1870); *Palaeochelys bowerbankii* (Owen, 1842) in Gray (1870); *Peltocephalus laevis* (Bell in Owen and Bell, 1849) in Rüttimeyer (1873); *Podocnemis bowerbanki* (Owen, 1842) in Lydekker and Boulenger (1887); *Podocnemis delabechi* (Bell in Owen and Bell, 1849) in Lydekker and Boulenger (1887); *Dacochelys delabechi* (Bell in Owen and Bell, 1849) in Lydekker (1889a); *Palaeaspis bowerbanki* (Owen, 1842) in Williams (1954); *Palaeaspis bowerbanki* (Owen, 1842)

(*Podocnemis bowerbanki* (Owen, 1842)) in Rayner et al. (2009).

Emended diagnosis. Member of Bothremydini characterized by the following combination of characters: relatively large shell, exceeding 45 cm; elongated and elliptical carapace, its length being almost 1.4 times that of its width; slightly wider than long nuchal plate; seven neurals, the first five being notably longer than wide, especially the first, which is more than twice as long as wide; antero-lateral margins of the first vertebral scute reaching the second pair of peripherals; first vertebral as wide as the second; first to third vertebrae wider than long; overlap of the first pair of marginals on more than half of the nuchal anterolateral margins; outer surface of the carapace and plastral plates lacking a well-developed ornamental pattern; long plastral bridge, longer than the plastral lobes; broad plastral lobes (the anterior being more than twice as wide as it is long), with sub-straight lateral margins; trapezoidal anterior lobe; short and wide anal notch; posterior end of the entoplastron anterior to the plastral bridge level; longer than wide mesoplastra; medial contact of the humeral scutes; overlap of the anterior region of the pectorals on the epiplastra; long overlap of the pectorals on the entoplastron; pectorals not reaching the anterior margins of the mesoplastra.

DISCUSSION

Attribution of the Pleurodiran Turtles from the lower Eocene London Clay to a Single Species

The detailed study of all the pleurodiran shells from the lower Eocene London Clay of the Isle of Sheppey (England) analyzed here, including the previously published specimens and other unpublished individuals (Figure 1), support their attribution to a single taxon. Adult specimens (e.g., Figure 1.1-6), but also juveniles (e.g., Figure 1.21-33), are identified. These juveniles show a lower degree of ossification between the plates, with disarticulations between some of the neurals, costals and peripherals, as well as between the peripherals and the plastral plates. As generally occurs during the ontogenetic development of extinct and extant taxa, the vertebral scutes of the juveniles are generally wider than those of the adults (pers. observ.). In addition, the presence of discontinuous, sinuous and anastomosed furrows is also generally better developed in the juveniles (Figure 1.27) than in the adults (Figure 1.7-8). The characters preserved in both juveniles and adults, recognized as being part of the exclusive diagnosis of this species, are com-



FIGURE 1. All currently known specimens of the coastal bothremydid turtle *Palemys bowerbankii*, from the lower Eocene London Clay of the Isle of Sheppey (Kent, England). 1-8, NHMUK 39449, neotype of *Palemys bowerbankii* and holotype of *'Emys conybearii'*, in dorsal (1-2), ventral (3-4), right lateral (5) and posterior (6) views. 7-8, details of the outer surface, near the second (7) and the fifth neurals (8). 9-10, dorsal view of the holotype of *'Emys delabechii'*, GSM 6634. 11-12, dorsal view of the previously unpublished specimen NHMUK 39451. 13-14, drawings corresponding to the currently lost holotype of *'Platemys bowerbankii'*, in dorsal (13) and ventral (14) views. Taken from the plate XXIII of Owen and Bell, 1849. 15-20, the previously unpublished specimen NHMUK 39452, in dorsal (15-16) ventral (17-18), right lateral (19), and anterior (20) views. 21-26, holotype of *'Emys laevis'*, NHMUK 37209, in dorsal (21-22), ventral (23-24), anterior (25), and right lateral (26) views. 27, details of the outer surface, near the left mesoplastron. 28-33, shell without collection number, previously published by Clouter et al. (2000, page 73) and by Rayner et al. (2009, pag. 167), in dorsal (28-29) ventral (30-31), anterior (32), and left lateral (33) views. The scale for 1-26 and 28-33 is the same.

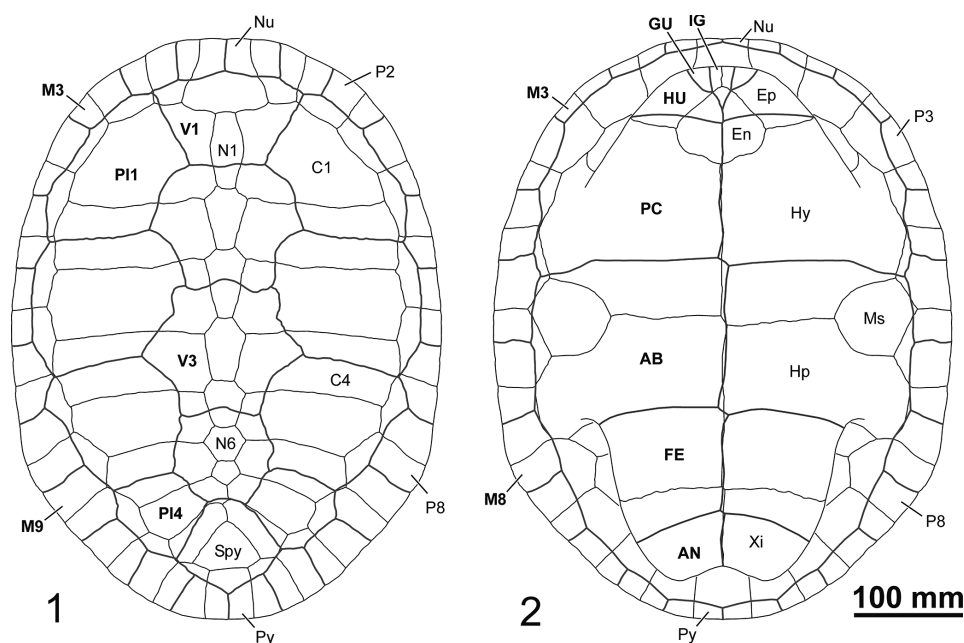


FIGURE 2. Reconstruction of the complete dorsal (1) and ventral (2) shell of an adult specimen of *Palaemys bowerbankii*, from the lower Eocene London Clay of the Isle of Sheppey (Kent, England). Abbreviations for the plates: C, costal; En, entoplastron; Ep, epiplastron; Hp, hypoplastron; Hy, hyoplastron; N, neural; Nu, nuchal; Ms, mesoplastron; P, peripheral; Py, pygal; Spy, suprapygal; Xi, xiphoplastron. Abbreviations for the scutes (in bold and capital letters): AB, abdominal; AN, anal; FE, femoral; GU, gular; HU, humeral; IG, intergular; M, marginal; PC, pectoral; PL, pleural; V, vertebral.

patible with its attribution to a single taxon. Thus, all of the specimens show the presence of seven neurals, the first five being noticeably longer than wide, especially the first one, which is more than twice as long as wide; the first to third vertebral scutes are wider than long; and the mesoplastra are longer than wide.

The presence of a supernumerary vertebral scute in the specimen NHMUK 39449 (Figure 1.1-2), located between the first and second vertebrals, is here considered as an anomaly. In addition to the variability in the width/length ratio of the vertebral scutes exhibited by the adult individuals (being especially wide in the lost holotype of *Platemys bowerbankii* based on the plate XXIII of Owen and Bell, 1849; Figure 1.13-14), variability in the morphology and disposition of these scutes is identified. Thus, the contact between the third and fourth vertebrals is located on the posterior area of the fifth neural in the specimen NHMUK 39452 (Figure 1.15-16), but in a more anterior position in other specimens (e.g., Figure 1.1-2, 11-12, 21-22, 28-29).

One of the specimens analyzed for the first time in this manuscript is NHMUK 39452 (Figure 1.15-20), which documents the subrhombic morphology of the entoplastron of this taxon, being

wider than long. In addition, the arrangement of the humeral-pectoral sulcus on this plate can be recognized, the most probable locations of the intergular and gular scutes being interpreted (Figure 1.17-18).

Generic and Specific Attribution of the Pleurodiran Turtle from the lower Eocene London Clay

In 1842, Owen defined *Platemys bowerbankii* Owen (1842) by a single shell from the lower Eocene London Clay of the Isle of Sheppey, currently lost. A drawing of the specimen that had been attributed to *Platemys bowerbankii* was subsequently published by Owen and Bell (1849, plate XXIII). The species *Emys laevis* Bell in Owen and Bell (1849) and *Emys delabechii* Bell in Owen and Bell (1849) were defined in 1849, by two shells from the same fossiliferous area. A drawing of the only specimen attributed to *Emys laevis* (now NHMUK 37209) was presented in the plate XXII of Owen and Bell (1849). The plate XXVIII of Owen and Bell (1849) is the drawing of *Emys delabechii* (now specimen GSM 6634). The paper of Owen and Bell (1849) was published in July 1849. Another work of Owen was also published that month (i.e., Owen, 1849), in which the same draw-

ings of the specimens of '*Emys laevis*' (plate 3), '*Emys delabechii*' (plate 37) and '*Platemys bowerbankii*' (plate 39) were included. In addition, Owen (1849) recognized a partial skull as possibly attributable to '*Platemys bowerbankii*' (plate 40, 1-2 in Owen, 1849; subsequently reproduced as figures 1 and 2 of the plate XXIX of Owen, 1850). This skull is currently recognized not as attributable to Pleurodira, but to Cryptodira (Gaffney et al., 2006). A new taxon from the lower Eocene London Clay, '*Emys conybearii*' Owen, 1858, also from the Isle of Sheppey, was defined in 1858. Drawings of this shell, currently identified as NHMUK 39449, were represented on the plate XXVIII A-B of Owen (1858).

Cope (1870) proposed the new combinations '*Podocnemis bowerbankii*' and '*Podocnemis laevis*' for '*Platemys bowerbankii*' and '*Emys laevis*', respectively. Gray (1870) defined two new genera, *Palemys* and '*Palaeaspis*', proposing the new combinations '*Palemys laevis*' (represented by the holotype of '*Emys laevis*', NHMUK 37209) and '*Palaeaspis conybearii*' to which he attributed the holotype of '*Emys conybearii*', NHMUK 39449. In addition, he correctly indicated that the genus *Platemys* Wagler, 1830, should not be employed for the species '*Platemys bowerbankii*' (*Platemys* is currently recognized as a monospecific genus, represented by the extant chelid *Platemys platycephala* (Schneider, 1792)]. Therefore, he proposed a putative new genus for this species, *Palaeochelys*, generating the new combination '*Palaeochelys bowerbankii*'. However, this generic name was previously employed by von Meyer (1847) for a well-represented member of Geoemydidae in the European Miocene record (Hervet, 2004). Rüttimeyer (1873) recognized '*Emys laevis*' as belonging to the extant South American genus *Peltocephalus* Duméril and Bibron (1835) proposing the new combination '*Peltocephalus laevis*'. He considered that it probably corresponded to the same form as '*Platemys bowerbankii*'. This synonymy was supported by Lydekker and Boulenger (1887). However, these authors reassigned this taxon to the genus *Podocnemis* Wagler (1830) as was previously proposed by Cope (1870). So, they supported the combination '*Podocnemis bowerbankii*'. In addition, they indicated that '*Emys conybearii*' appears specifically identical to '*Emys delabechii*', proposing the new combination '*Podocnemis delabechii*'. In 1889, Lydekker attributed a partial and isolated lower jaw to the new genus *Dacochelys*, indicating that it could correspond to the same taxon as '*Emys delabechii*'.

Thus, he indicated that, if this could be confirmed, the combination '*Dacochelys delabechii*' would be established (Lydekker, 1889b). In the Catalogue of the Fossil Reptilia and Amphibia in the British Museum, Lydekker (1889a) supported his previous identification of two possible forms, *Podocnemis bowerbankii* and '*Dacochelys delabechii*'. Although the lower jaw of *Dacochelys* is lost, the information provided by Lydekker (1889a, b) refutes its attribution to Pleurodira (de Broin, 1977).

Williams (1954) reproduced the previously published drawings of '*Emys conybearii*' (figure 1), '*Emys laevis*' (figure 2), '*Emys delabechii*' (figure 3) and '*Platemys bowerbankii*' (figure 4). The comparison between all previously published specimens led him to the belief that all the pleurodires of the London Clay were synonymous. Taking into account the absence of a detailed study of these forms, and the lack of new specimens, subsequent authors indicated that more than one species could be represented (de Broin, 1977; Gaffney et al., 2006). The attribution of all these specimens to a single species is supported here (see above). Assuming this, and considering the proposal of the two new generic names *Palemys* and '*Palaeaspis*' in a single publication (see Gray, 1870), Williams (1954) chose '*Palaeaspis*' as the valid generic name, because it included the most complete specimen. Therefore, he proposed the new combination '*Palaeaspis bowerbankii*'. The name *Palemys* was proposed by Gray (1870) in pages 49-51, but *Palaeaspis* was proposed in pages 71 and 73. Therefore, the priority should be that of *Palemys*, the identification of one specimen as more complete than the other not being relevant. Considering Article 23.9.1.2. of the International Code of Zoological Nomenclature, the proposal of Williams (1954) could only be correct if the putative junior synonym (i.e., '*Palaeaspis*') was used for the taxon, as the presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years of that publication, and encompassing a span of not less than 10 years. Because this condition was not met, the first proposed generic name, *Palemys*, is considered here as the valid. Thus, the new combination *Palemys bowerbankii* is proposed.

Phylogenetic Position of *Palemys bowerbankii* and Comparison with Other European Paleogene Forms

Owen (1842) indicated that '*Platemys bowerbankii*' probably belonged to the 'Platemydian' division of the family 'Chelonia'. A few years later,

Owen (1849) included this species, and the others here recognized as synonymous, as belonging to the order 'Chelonia' and the family 'Paludinosa'. Gray (1870) attributed '*Palemys laevis*' to the family 'Dermatemydidae', '*Palaeochelys bowerbankii*' to 'Chelydrade' and '*Palaeaspis conybearii*' to 'Hydraspididae'. The same year, Cope (1870) recognized '*Podocnemis bowerbankii*' and '*Podocnemis laevis*' as members of Pleurodira, including them in the Podocnemididae. Rüttimeyer (1873) supported the attribution of both species to Podocnemididae. However, he indicated that it was difficult to say whether '*Emys conybearii*' and '*Emys delabechii*' belonged to the Emydidae or the 'Chelydidae'. Lydekker and Boulenger (1887), which recognized the presence of two species ('*Podocnemis bowerbankii*' and '*Podocnemis delabechii*'), supported the interpretation that they were members of Podocnemididae. Williams (1954) considered the only form recognized by him, '*Palaeaspis bowerbankii*', as a member of Pelomedusidae, an attribution supported by de Broin (1977). However, de Broin (1988) indicated its possible attribution to Podocnemididae, subsequently reattributing it to Bothremydidae (Lapparent de Broin and Werner 1998; Lapparent de Broin, 2001). Gaffney et al. (2006) recognized these shells as belonging to Pelomedusoides incertae sedis because these attributions were not justified, due to the lack of information about the pleurodires from the lower Eocene London Clay, and taking into account the doubt whether they could correspond to single or more than one forms. Several characters recognized by Lapparent de Broin et al. (under preparation), including those relative to the morphology of both the carapace and the plastron, and the length of the plates of the anterior region of the carapace, confirms the attribution of this taxon to Bothremydidae. However, it was never included in a cladistic analysis, so its phylogenetic position within this clade is not known.

The phylogenetic analysis performed as part of this study resulted in 16 most parsimonious trees, with a length of 306 steps (CI=0.696; RI=0.771; RC=0.537) (Figure 3). *Palemys bowerbankii* is obtained as a member of Bothremydini Foxemydina, a clade composed of several Santonian to lower Eocene European forms. The Colombian Paleocene *Puentemys mushaisaensis* Cadena et al., 2012 is also obtained as a member of this clade (as in some previous phylogenetic hypotheses, such as those of Cadena et al., 2012, and Pérez-García, 2016a; but not in Pérez-García, 2016b). In addition to several cranial characters,

Foxemydina is defined here by the overlap of the anterior region of the pectoral scutes on the epiplastra (character 166, state 1; not shared with some specimens of *Puentemys mushaisaensis*), and by the presence of the first vertebral scute wider than the second (character 178, state 2; not shared with some specimens of *Foxemys mechinorum* Tong et al., 1998 and with *Palemys bowerbankii*). *Palemys bowerbankii* is obtained as part of a polytomy, composed of three branches: this species, the node composed by the French Campanian *Polysternon provinciale* (Matheron, 1869) and the French Ypresian *Tartaruscola teodorii*, and that composed by the Hungarian Santonian *Foxemys trabanti* Rabi et al., 2012, the French Campano-Maastrichtian *Foxemys mechinorum*, and *Puentemys mushaisaensis*. Both nodes are defined, in this analysis, by cranial characters. *Palemys bowerbankii* is characterized by the presence of the first vertebral scute as wide as the second (character 178, state 1). This state of character is also shared with some specimens of *Foxemys mechinorum*.

A second bothremydid had been described in the European lower Eocene record: the French Ypresian *Tartaruscola teodorii*. Although the type material corresponded to two skulls, several nuchal plates from the type locality, belonging to both juvenile and adult individuals, had been referred to this taxon (Pérez-García, 2016b). These nuchals are noticeably longer than wide, the length being about 20% higher than the maximum width. The lateroanterior margin of each nuchal is more than twice as long as the lateroposterior. The length of the anterior nuchal margin is similar to half of the maximum width of these plates. The outer surface of the plates belonging to adult individuals is markedly rough. Therefore, remarkable differences are recognized between *Palemys bowerbankii* and this synchronous taxon.

Another member of Bothremydidae has been recognized in the European Paleogene record: the French Oligocene '*Chrysemys*' *montolivensis* Roman (1897). This form is represented by a partial carapace, which lacks both the nuchal plate and a large part of the anterior plastral lobe. Its first neural is interpreted as noticeably shorter than that of *Palemys bowerbankii*, and the vertebral scutes are narrower, the second to fourth being as long as wide. In addition, their pectoral scutes overlap the anterior area of the mesoplastra. Therefore, *Palemys bowerbankii* differs from the other members of Bothremydidae so far defined in the European Paleogene record.

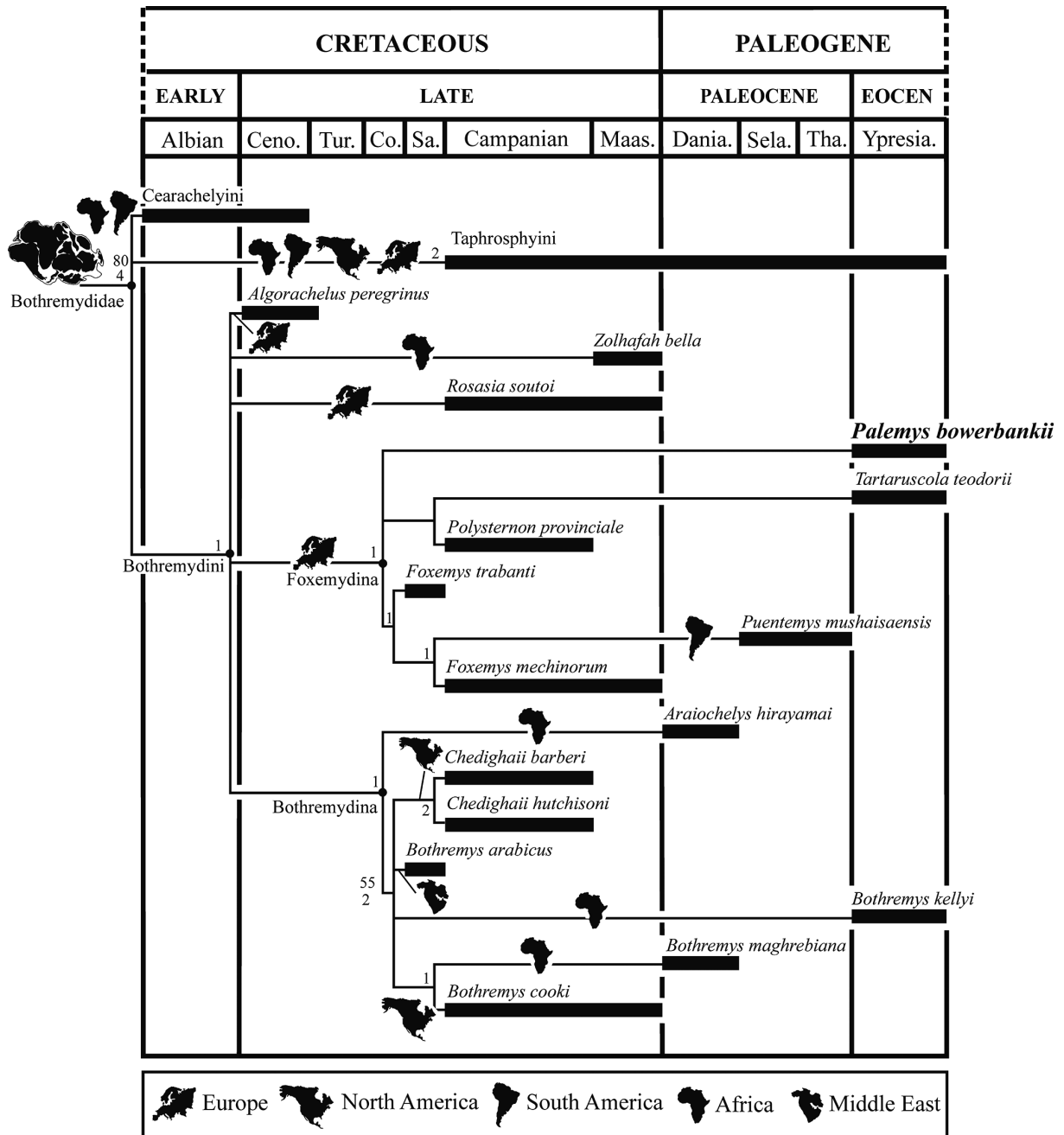


FIGURE 3. Phylogenetic position of *Palemys bowerbankii* (Pleurodira, Bothremydidae), from the lower Eocene London Clay of the Isle of Sheppey (Kent, England), in the strict consensus tree obtained by the cladistic analysis performed here. Bootstrap frequencies (top; only values equal to or greater than 50% shown) and Bremer support values (bottom) are indicated. The continents where each of these taxa were found are indicated.

Several dispersal events of Pelomedusoides from Africa to Europe are recognized in the Cenozoic record (see Pérez-García, 2017, and references therein). The identification of *Palemys bowerbankii* as a member of Foxemydina (i.e., a well-represented lineage in the European upper-

most Cretaceous record), suggests that this British coastal bothremydid probably does not represent the result of a Cenozoic dispersal event from Africa but that it could be the descendant of European Cretaceous forms.

CONCLUSIONS

Pleurodiran turtles are relatively abundant in both the Upper Cretaceous and the Paleogene records of Continental Europe, being represented by continental and coastal members of two lineages of Pelomedusoides: Podocnemididae and Bothremydidae. However, the British record of Pleurodira is much more limited, being restricted to two lower Eocene coastal forms. One of them is an indeterminate species of the podocnemidid *Eocnochelus*, represented by a recently described single specimen from the Ypresian (early Eocene) of Bracklesham Bay (Sussex, England). *Eocnochelus* is a member of a lineage of African origin, which reached Europe during the Paleogene, and is present in several European countries: Great Britain, Belgium, France, Spain and Italy.

A second member of Pelomedusoides is recognized in the British Ypresian record. It is represented by several specimens from the London Clay of the Isle of Sheppey (Kent, England). Several shells were identified there, since the 19th century. Some of these classic specimens were the basis for the description of four putative new species. The detailed study of the classic specimens, as well as that of others found subsequently (including several unpublished ones), confirms that they can be attributed to a single species, for which the new combination *Palemys bowerbankii* (Owen, 1842) is proposed. Therefore, *Palemys bowerbankii*, is the only pleurodiran turtle currently recognized in the British record at specific level. A neotype is designated here, and a new diagnosis is

provided. Photographs of most of the classic specimens of *Palemys bowerbankii* are included here for the first time. In this way, knowledge about this form is improved and a reconstruction of its complete shell is performed. Characters and elements hitherto unknown for this species are described, and intraspecific variability, affecting several characters, is recognized. The comparison of this British form with the other Paleogene European bothremydids allows *Palemys* to be recognized as an exclusive form of the British record. Its inclusion in a cladistic analysis shows it belongs to a lineage well-represented in the European Upper Cretaceous record, Foxemydina, in contrast to the other member of Pelomedusoides present in the British record, *Eocnochelus*, which represented the result of a Cenozoic dispersal event from Africa to Europe.

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APPENDIX 1.

Coding of *Plemys bowerbanki* in the data matrix proposed by Pérez-García (2016a).
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2?1022?121 210????211 ?111111?10 10111?[01]10?

APPENDIX 2.

Nexus file corresponding to the data matrix used in this paper available in a zipped file at <https://palaeo-electronica.org/content/2018/2268-british-bothremydid-turtle>.