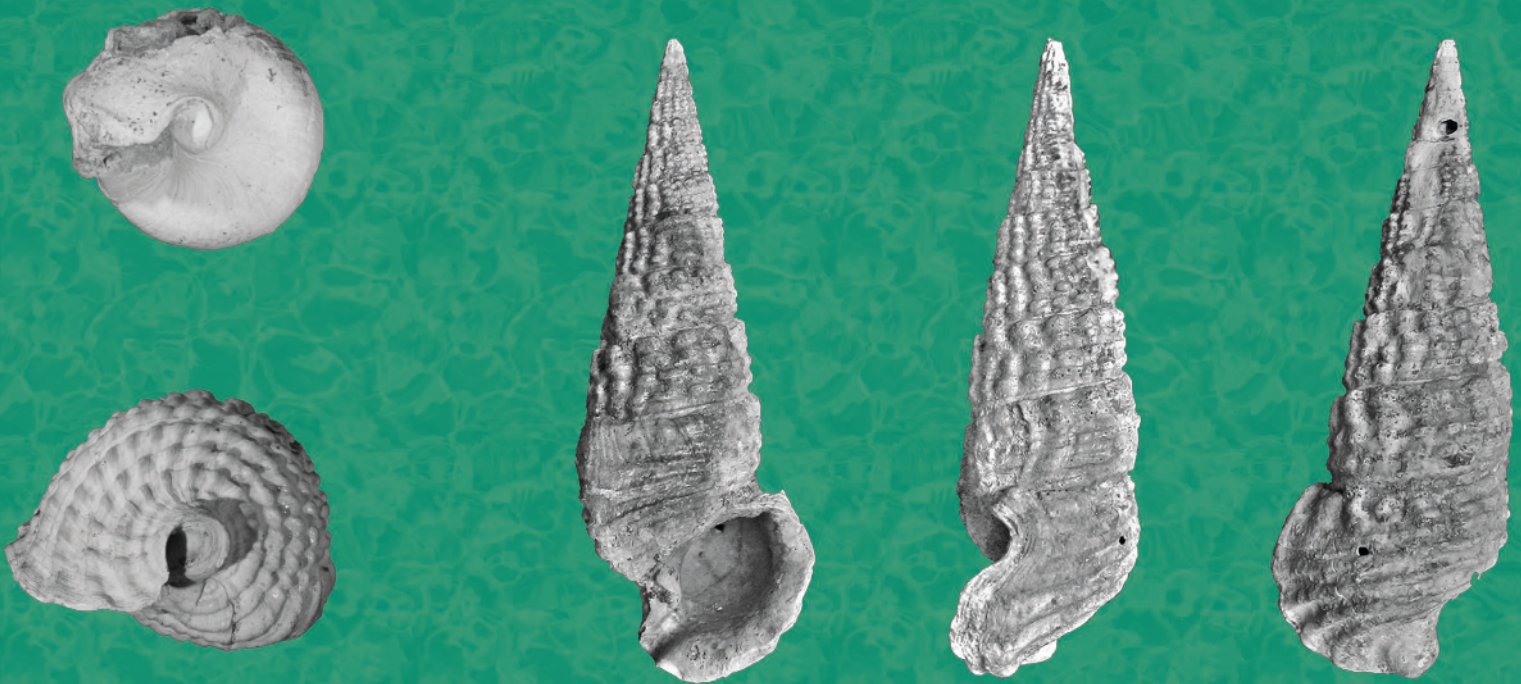


Cenozoic diversity and distribution
of the mangrove- and mudflat-associated
gastropod genus *Terebralia* Swainson, 1840
(Potamididae: Caenogastropoda) in Europe

Danae THIVAIYOU, Mathias HARZHAUSER & Efterpi KOSKERIDOU



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Terebralia paradoxa Kadolsky, 1995 (Credit: Dietrich Kadolsky); *Terebralia vielensis* Belliard & Gain, 2006 (MNHN); *Terebralia rahti* Kadolsky, 1995 (Credit: Dietrich Kadolsky).

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Cenozoic diversity and distribution of the mangrove- and mudflat-associated gastropod genus *Terebralia* Swainson, 1840 (Potamididae: Caenogastropoda) in Europe

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ABSTRACT

We analyse the distribution of the potamidid genus *Terebralia* Swainson, 1840 in the European fossil record (middle Eocene to Miocene). Extant *Terebralia* contains species restricted to mangroves and mudflats, rendering it a reliable element for detecting these coastal environments in the fossil record. Our contribution summarizes the European fossil record of this taxon and highlights the presence of this genus within coastal environments in the European realm. Distribution in the Cenozoic is interpreted based on ecological preferences, dispersal modes and climatic restrictions of recent species. Maximum geographical distribution is reached during the Early and Middle Miocene with two species being present from the southernmost parts of Europe and Anatolia to the North Sea Basin and the Paratethys. During the Late Miocene, the distribution of *Terebralia lignitarum* (Eichwald, 1830) is patchy and limited to the South of Europe. The Messinian Salinity Crisis coupled with a changing climate caused the disappearance of *Terebralia* in the Mediterranean first, and then marked the end of mangrove environments in this province.

KEY WORDS

Mollusca,
Tethys,
Indo-West Pacific,
systematics,
climate,
biogeography.

RÉSUMÉ

Diversité et distribution au Cénozoïque du genre Terebralia Swainson, 1840 (Potamididae: Caenogastropoda), gastéropode associé aux mangroves et aux vasières, en Europe.

Nous analysons les représentants européens de *Terebralia* Swainson, 1840 dans le registre fossile (Éocène moyen – Miocène). *Terebralia* comprend des espèces vivant dans des mangroves et des vasières, le rendant ainsi fiable pour détecter de tels environnements dans le registre fossile. Notre contribution résume les données fossiles des espèces européennes et souligne leur importance au sein des environnements côtiers du domaine européen. L'interprétation de la distribution des taxons est basée sur les préférences écologiques et climatiques, mode de dispersion des espèces actuelles. La répartition maximale est atteinte pendant la première moitié du Miocène, avec *Terebralia lignitarum* (Eichwald, 1830) et *Terebralia duboisi* (Hörnes, 1855) présentes depuis le sud de l'Europe jusqu'à la Mer du Nord et la Paratéthys. Pendant le Miocène Supérieur, on ne retrouve plus que *Terebralia lignitarum* dans le sud européen, avec une distribution éparse. La Crise de Salinité Messinienne et les changements climatiques ont précipité la disparition des mangroves de la côte méditerranéenne, ce qui a marqué la fin de la présence de *Terebralia* au sein de cette province.

MOTS CLÉS
Mollusques,
Téthys,
Océan Indo-Ouest
Pacifique,
systématique,
climat,
biogéographie.

INTRODUCTION

Mangrove ecosystems are important resilient coastal environments, considered as “hotspots” because of their contribution to organic carbon sequestration (Alongi 2012; Collins *et al.* 2017). Modern-type mangrove ecosystems were established during the early Eocene in the Tethyan realm from where they spread quickly to tropical and subtropical latitudes (Plaziat *et al.* 2001; Reid *et al.* 2008). These particular environments were colonized by a low number of molluscan species, possibly due to the demanding ecological conditions (Reid *et al.* 2008). The family Potamididae is considered the most ecologically specialised to live in these environments, found almost exclusively in mangrove forests and associated tidal habitats (Reid *et al.* 2008; Strong *et al.* 2011). It is composed of 19 recognized genera (MolluscaBase 2020), of which *Terebralia* Swainson, 1840 is one of the most commonly found in the European Cenozoic fossil record (Kadolsky 1995; Harzhauser & Kowalke 2001; Lozouet *et al.* 2001; Kowalke 2005; Dominici & Kowalke 2014).

The extant species of the genus *Terebralia* play an important ecological role in the mangrove and mangrove-associated environments of the Indo-West Pacific (including the Red Sea), consuming considerable amounts of leaves and litter, thus contributing to nutrient recycling within these ecosystems (Slim *et al.* 1997; Raw *et al.* 2017). Recent representatives of the genus have been extensively investigated from different aspects, including coastal environment management (Ratsimbazafy & Kochzius 2018), sea-level changes in relation to human settlements (Berger *et al.* 2013; Manne & Veth 2015) or ecological preferences (Houbrick 1991; Bandel & Kowalke 1999; Fratini *et al.* 2001; Wells 2003; Reid *et al.* 2008; Wilson 2013; Raw *et al.* 2017). In modern environments, *Terebralia* species live in proximity to or in mangroves (Houbrick 1991; Reid *et al.* 2008) and for this reason they have been used as indicators

of habitats favourable for the development of mangrove swamps, even when mangrove fossils are lacking (Ellison *et al.* 1999). *Terebralia* are typically found associated with specific species of the families Potamididae H.Adams & A.Adams, 1854, Batillariidae Thiele, 1929 and Ellobiidae L.Pfeiffer, 1854 (1822) in variable abundances (Kowalke 2005). Furthermore, this taxon is believed to have always lived in such restricted environments (Reid *et al.* 2008). Recent potamidids are of great ecological interest since they are among the most specialized molluscan inhabitants of mangrove ecosystems, mainly because of their contribution to litter removal from the substrate surface (Reid *et al.* 2008; Wilson 2013).

The first European representatives of *Terebralia* emerged shortly after mangroves appeared in the area, in the early Eocene (Plaziat *et al.* 2001; Reid *et al.* 2008). In Europe, *Terebralia* has a stratigraphic distribution limited between the middle Eocene and the Late Miocene (Glibert 1952; Dermitzakis 1972; Bałuk 1975; Le Renard & Pacaud 1995; Harzhauser 2002; Bandel 2006; Belliard *et al.* 2006; Esu & Girotti 2010; Moths *et al.* 2010; Landau *et al.* 2013). The family Potamididae has existed at least since the Late Cretaceous and includes genera that live in restricted environments such as mangroves, estuarine mudflats, and salt marshes of tropical and subtropical regions (Houbrick 1991; Healy & Wells 1998; Reid *et al.* 2008; Dominici & Kowalke 2014).

In the fossil record, it is difficult to attribute some specimens to a given genus because the morphological traits – including protoconch structure – are often poorly described or absent in the existing literature. In contrast to recent species, which are well defined and their morphology has been analysed in detail (Houbrick 1991), fossil representatives are not as well understood and some confusion persists concerning the diagnosis of the genus. The abundance of shells and the morphological variation of the members of the genus were noted by 19th-century authors, who erected

several subspecies and varieties (some of which were originally placed in *Cerithium*) (Deshayes 1833; Sacco 1888; Cossmann 1889).

This work pieces together the diversity and distribution of *Terebralia* in the European Cenozoic. The aims are to:

- describe the morphological features of the genus;
- assess the history of diversity of the genus through a taxonomic and systematic update;
- reconstruct its geographical distribution in the European realm;
- review the ecology and environmental restrictions of recent taxa to infer palaeoecology and palaeoclimate.

The European fossils being the most thoroughly studied to this day, combining the available data will provide a unified record, thus facilitating further research on the genus and its environments.

MATERIAL AND METHODS

The study is largely based on bibliographical references to cover occurrences from the European fossil record, as well as extra-European occurrences. These include the large monographs of the 19th and early 20th centuries (i.e., Sacco [1888, 1895] for Italy, Deshayes [1833], Cossmann [1889], Cossmann & Pissaro [1913], Cossmann & Peyrot [1922] for France). Additionally, some unpublished material is included, collected in the Mesohellenic Basin, NW Greece, hosted at the National and Kapodistrian University of Athens.

The ecology and distribution data of modern species are mainly based on the large monograph of Houbriek (1991), with additional information on the ecology and distribution of species in Australia by Wells (2003).

Illustrations of French specimens were obtained from the stratigraphic and historical collections of the Muséum national d'Histoire naturelle, Paris, France. Illustrations of Italian specimens were obtained from the historical Bellardi-Sacco collections housed at the Regional Museum of Natural Sciences, Torino, Italy. Photographs of *Terebralia duboisi* (Hörnes, 1855) and *T. lignitarum* (Eichwald, 1830) from the Paratethys were obtained from the Natural History Museum of Vienna, Vienna, Austria.

ABBREVIATIONS

IWP	Indo-West Pacific;
MCT	Miocene Climatic Transition;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMV	National History Museum of Vienna;
NKUoA	National and Kapodistrian University of Athens;
MRNS	Regional Museum of Natural Sciences, Torino.

SYSTEMATIC PALAEOLOGY

We provide taxonomic remarks on species of *Terebralia* based on recent taxonomic revisions, and discuss potential synonymies as well as taxa that likely do not belong in the genus.

Class GASTROPODA Cuvier, 1795
Subclass CAENOGASTROPODA Cox, 1960
Superfamily CERITHIOIDEA Fleming, 1822

POTAMIDIDAE H.Adams & A.Adams, 1854

Potamididae H.Adams & A.Adams, 1854: 286.

REMARKS

Monophyly of recent Potamididae is commonly accepted and supported by molecular data (Reid *et al.* 2008; Ozawa *et al.* 2009; Strong *et al.* 2011). Potamidid species usually display a very high morphological variability (Sälgeback & Savazzi 2006). There is poor basal resolution, and sister groups to the Potamididae are not resolved (Reid *et al.* 2008). Nevertheless, *Terebralia* seems to be a basal group within the family (Reid *et al.* 2008; Ozawa *et al.* 2009).

Genus *Terebralia* Swainson, 1840

Terebralia Swainson, 1840: 315.

REMARKS

Species of the genus present shells of medium size, ranging from *c.* 20 to *c.* 100 mm, with high-spined turreted or bulky shapes with flat to moderately convex teleoconch whorls. The protoconch is rarely preserved even for recent species (Houbriek 1991), although a direct development is described for the veligers of the type species, *T. palustris* (Linnaeus, 1767), and for *T. sulcata* (Born, 1778) (Houbriek 1991). Harzhauser & Kowalke (2001) noted that *T. palustris* has a very bulbous embryonic shell of 0.75 whorls, measuring 170–180 µm in diameter. This suggests a very short planktotrophic stage, which appears to have remained undetected by Houbriek (1991). The protoconch of *T. lignitarum* shows a clear demarcation between the embryonic and larval shell and a sinusigera notch, which suggests a planktonic veliger stage (Harzhauser & Kowalke 2001). Furthermore, the larval shell bears two strong spiral keels on the lower part of the whorls (Harzhauser & Kowalke 2001). Teleoconch sculpture comprises several broad spiral cords separated by narrow interspaces and densely spaced axial ribs; prominent beads typically form at the intersections of spiral cords and axial ribs; in a few species beads may grade into short spines in the adapical half of whorls. The last whorl is often somewhat inflated with a convex base. The aperture is ovate, the outer lip expanding, moderately to strongly thickened, forming a continuous peristome in some species, or in others it can be interrupted by a moderately deep anterior canal. The inner lip is thin to moderately thickened, rarely expanding on the base. Columella morphology is straight to slightly concave, with a columellar fold. Distinct varices on which axial sculpture is usually weak, coincide with axial rows of internal denticles, which are not developed on the internal surface of the outer lip (for descriptions see Houbriek 1991; Healy & Wells 1998;

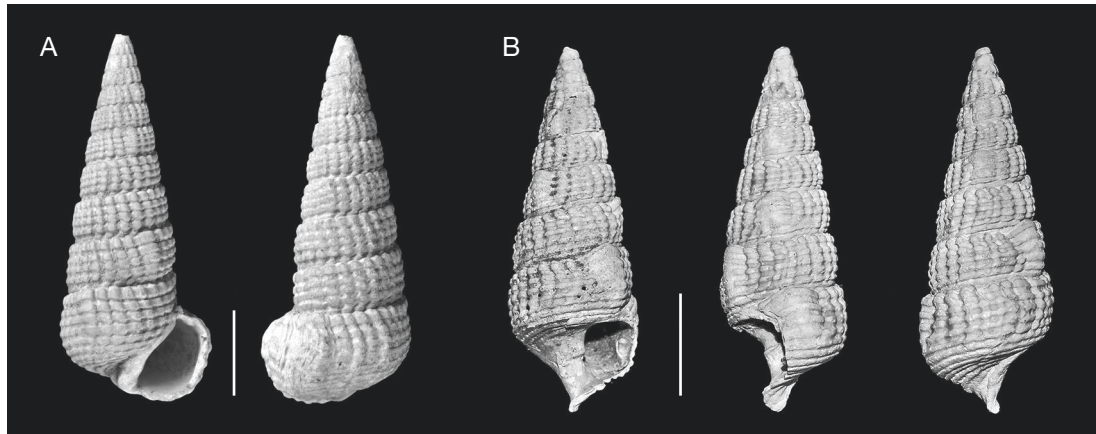


FIG. 1. — **A**, *Terebralia duboisi* (Hörnes, 1855), Paratethys of Austria (NHMV); **B**, *Terebralia gibberosa* (Gratoloup, 1832), Paris Basin, France (MNHN). Scale bars: 1 cm.

Vermeij 2007, 2014; Reid *et al.* 2008; for anatomical data see Houbrick 1991). According to Vermeij (2007) the siphonal canal is tubular and closed for *Terebralia sulcata*. This feature – associated with olfactory organs that detect chemical signals from a distance in recent species – appeared during the Early Miocene and has been lost for the recent *Terebralia palustris* (Vermeij 2007).

The genus is not speciose (Houbrick 1991; Reid *et al.* 2008). MolluscaBase (2020) lists only three extant species, all of which are restricted to the IWP. Similarly, the fossil record of the genus suggests that *Terebralia* has never been rich in species. However, the morphological variability of fossil *Terebralia* species (Sälgeback & Savazzi 2006) has led to the description of numerous subspecies and varieties (e.g. Sacco 1888), which have hampered biogeographical and stratigraphic analyses. The same problem arose for recent species, especially during the 19th century, but was overcome during the last decades by revisions and improved knowledge (Houbrick 1991; Bandel 2006; Reid *et al.* 2008).

SYNOPSIS OF EUROPEAN *Terebralia* SPECIES

This list gives an overview of species-level taxa in alphabetical order.

Terebralia bonelli (Deshayes, 1833)

Cerithium bonelli Deshayes, 1833: 319, pl. 50, figs 21-23.

Terebralia bonelli – Cossmann & Pissarro 1913: pl. 29, fig. 151-1.

Terebralia (*s. str.*) *bonelli* – Le Renard & Pacaud 1995: 111.

DISTRIBUTION. — North-eastern Atlantic: Lutetian to Bartonian of France (Deshayes 1833; Cossmann & Pissarro 1913; Le Renard & Pacaud 1995).

REMARKS

This species was placed in *Terebralia* by Cossmann & Pissarro (1913) and Le Renard & Pacaud (1995), which is followed herein. The illustrations in Deshayes (1833) show a typical *Terebralia* with prominent varices and flaring aperture with a distinct siphonal canal.

Terebralia duboisi (Hörnes, 1855) (Fig. 1A)

Cerithium duboisi Hörnes, 1855: 399, pl. 42, figs 4, 5.

Terebralia duboisi – Landau *et al.* 2013: 53, pl. 4, fig. 12 (cum syn.).

POTENTIAL SUBJECTIVE JUNIOR SYNONYMS. — (according to Švagrovský 1971; Landau *et al.* 2013; and present work) *Cerithium pauli* Hoernes, 1875; *Potamides monregalensis* Sacco, 1888; *Potamides Melii* Sacco, 1888; *Terebralia monregalensis* Sacco, 1895; *Clava dollfusi* Hoernes, 1901; *Clava holleri* Hoernes, 1901; *Terebralia andrzejowskii* Friedberg, 1914; *Terebralia praebidentata* Seneš in Steininger *et al.* 1971, non *Cerithium* (*Clava*) *bidentatum* var. *abbreviata* Schaffer, 1912 [likely a synonym of *Granulolabium plicatum* (Bruguière, 1792) according to D. Kadolsky, pers. comm. 2018].

PALAEOENVIRONMENT. — *Terebralia duboisi* is believed to have inhabited mudflats and brackish palaeoenvironments (Landau *et al.* 2013; Harzhauser *et al.* 2014).

DISTRIBUTION. — North-eastern Atlantic. Early Miocene and Middle Miocene of France (Cossmann & Peyrot 1922; Glibert 1949). Proto-Mediterranean Sea: Burdigalian of Italy (Sacco 1895) and Turkey (İslamoğlu & Taner 2003); Middle Miocene (Serravallian) of Turkey (Landau *et al.* 2013); Tortonian of southern Italy (D’Amico *et al.* 2012). — Paratethys Sea. Early Burdigalian (Eggenburgian) of Gauderndorf (Austria) and Vélka Čausa (Slovak Republic) (Steininger *et al.* 1971). An Ottnangian (mid-Burdigalian) record was reported by Rupp *et al.* (2008). Late Burdigalian (Karpatian) of Austria co-occurring with *Terebralia lignitarum* (Harzhauser 2002). Middle Miocene (Badenian) of the Central Paratethys (Harzhauser & Piller 2007). Middle Miocene (lower Sarmatian – 12.5 Ma) of Austria (Papp 1974); virtually absent from the Sarmatian sea thereafter, it reappears during the Bessarabian (late Middle Miocene – middle Sarmatian) roughly around 11 Ma in Ukraine, Romania, Moldova (Kolesnikov 1935; Simionescu & Barbu 1940). — Early Indian Ocean. Early Miocene of Iran (Landau *et al.* 2013).

REMARKS

Terebralia menestrieri d’Orbigny, 1844 described from the Bessarabian (Sarmatian) of Letytschiw, Oblast Chmelnyzkyj (Ukraine) differs from *T. duboisi* in its smaller size and delicate sculpture. Although we regard it as a possible synonym of *T. duboisi*, a re-examination of the Ukrainian material would be useful for assessing the possibility that it might represent a distinct offshoot of *T. duboisi*.

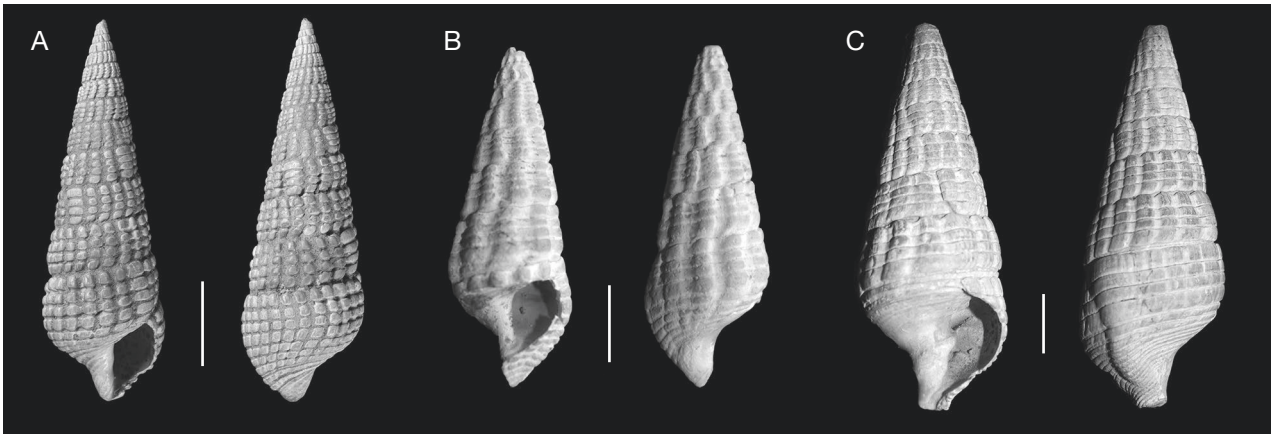


FIG. 2. — *Terebralia lignitarum* (Eichwald, 1830) and morphotypes: **A**, *Terebralia lignitarum* Paratethys of Austria (NHMV); **B**, *Terebralia* 'dertonensis', Proto-Mediterranean, Italy (MRNS); **C**, *Terebralia* 'palustris lineata', Proto-Mediterranean, Italy (MRNS). Scale bars: 1 cm.

Terebralia duboisi is among the few taxa that survive the Badenian-Sarmatian Extinction Event (Harzhauser & Piller 2007).

Terebralia gibberosa (Grateloup, 1832)
(Fig. 1B)

Cerithium gibberosum Grateloup, 1832: 272, no. 278.

Terebralia gibberosa – Lozouet & Maestrati 2012: 278, fig. 179, 16, 17.

DISTRIBUTION. — North-eastern Atlantic. Early Oligocene (Rupelian) of France (Grateloup 1832; Lozouet & Maestrati 2012).

REMARKS

The description given by Grateloup (1832) is very brief; two forms are presented, corresponding to a wide morphotype (variety A) and a narrow morphotype (variety B). Morphologically, the species differs from *T. lignitarum* by its finer, more prominent sculpture and slightly thinner shell.

Terebralia lignitarum (Eichwald, 1830)
(Fig. 2)

Cerithium lignitarum Eichwald, 1830: 224.

Terebralia lignitarum – Landau *et al.* 2013: 51, pl. 4, fig. 11 (cum syn.).

POTENTIAL SUBJECTIVE JUNIOR SYNONYMS. — (according to Landau *et al.* 2013) *Cerithium bidentatum* DeFrance in Grateloup, 1832; *Potamides lignitarum* var. *sulfurea* Sacco, 1888; *Potamides lignitarum* var. *cingulati* Sacco, 1888; *Potamides lignitarum* var. *planulata* Sacco, 1888; *Potamides colligens* Sacco, 1888; *Potamides colligens* var. *fasciculata* Sacco, 1888; *Terebralia bidentata* var. *cingulati* Sacco, 1895; *Terebralia bidentata* var. *margaritifera* Sacco, 1895; *Terebralia vighali* Cossmann, 1906; *Cerithium* (*Clava*) *bidentatum* var. *fusiformis* Schaffer, 1912. *Terebralia dertonensis* (Sacco, 1888) and its variations is most probably just a morphotype of *T. lignitarum* with predominant axial sculpture. *Terebralia palustris lineata* Borson, 1821 seems to be another morphotype of *T. lignitarum* with predominant axial sculpture and marked spiral grooves (Landau *et al.* 2013).

PALAEOENVIRONMENT. — Plaziat *et al.* (2001) mention that it is possible that this species had not yet developed an exclusive association with mangrove environments, as its distribution largely exceeded that of *Avicennia*. Stable isotope data from estuary environments of the Korneuburg Basin (Austria) in Latal *et al.* (2006) indicate a preference for brackish-water environments. *Terebralia lignitarum* coexisted from the late Oligocene (Chattian) to the earliest Miocene (Aquitainian) with *T. subcorrugata* in the Aquitaine Basin (SW France) and in the Mesohellenic Basin (NW Greece). From the Burdigalian on, it is frequently found associated with *T. duboisi* (Landau *et al.* 2013).

DISTRIBUTION. — North-eastern Atlantic. Early Miocene of France (Cossmann & Peyrot 1922; Lozouet *et al.* 2001); Middle Miocene (Langhian and Serravallian) of France (Cossmann & Peyrot 1922; Glibert 1949). Tortonian of Portugal (Pereira da Costa 1866). — North Sea. Late Early Miocene (early Hemmoorian) (Moths *et al.* 2010). — Proto-Mediterranean Sea. Oligocene (late Rupelian to early Chattian) and early to Middle Miocene of Turkey (Mandic *et al.* 2004; İslamoğlu 2008; Landau *et al.* 2013). Late Oligocene (Chattian) and Early Miocene (Aquitainian) of Greece (Harzhauser & Kowalke 2001; Harzhauser 2004; Thivaoui *et al.* 2019) and Italy (Sacco 1895). Late Miocene (Tortonian – early Messinian) of Italy (Sacco 1895; D'Amico *et al.* 2012) and Greece (Dermitzakis 1972; E. K. pers. obs.). — Paratethys Sea. Egerian (Chattian-Aquitainian) of Máriahalom in Hungary (Báldi & Steininger 1975; Janssen 1984). Early Burdigalian (Eggenburgian) and late Burdigalian (Karpatian) of Austria (Steininger *et al.* 1971; Harzhauser 2002). — Early Indian Ocean. Occurrences described by Vredenburg (1928) from the Burdigalian of Pakistan might rather represent another species (Harzhauser *et al.* 2017).

REMARKS

This species was intensively discussed by Landau *et al.* (2013). The list of subjective synonyms (as presented above) is a result of the morphological variability and wide geographical distribution of the species.

Terebralia paradoxa Kadolsky, 1995
(Fig. 3B, E)

Terebralia paradoxa Kadolsky, 1995: 18, figs 26, 30, 31 (cum syn.).

PALAEOENVIRONMENT. — Euryhaline, lagoonal with subtropical semi-arid climate (Kadolsky 1989).

DISTRIBUTION. — An endemic species of the Chattian of the Mainz Basin (Oppenheim-Nierstein, Hochheim; Germany), it co-occurs with *T. rabti* according to Kadolsky (1995).

Terebralia prolignitarum (Sacco, 1888)
(Fig. 3C)

Potamides prolignitarum Sacco, 1888: 3, pl. 4, figs 1-3.

Terebralia bidentata var. *prolignitarum* Sacco, 1895: 54, pl. 3, fig. 33.

POTENTIAL SUBJECTIVE JUNIOR SYNONYMS. — *Potamides prolignitarum* var. *reticulata* Sacco, 1888; *P. p.* var. *perrandi* Sacco, 1888; *P. p.* var. *turrita* Sacco, 1888; *P. p.* var. *cingulosa* Sacco, 1888; *Potamides clerichi* Sacco, 1888.

PALAEOENVIRONMENT. — Specimens from Greece are found co-occurring with *Terebralia lignitarum* in brackish assemblages, dominated by taxa such as *Mesohalina margaritacea*, *Granulolabium plicatum* and *Potamides papaveraceum*, accompanied by *Nerita plutonis* (D. T. pers. obs.). A brackish environment is inferred possibly in a mudflat setting because of the co-occurrence of the species (Esu & Girotti 2010).

DISTRIBUTION. — Rupelian of Liguria (northern Italy) (Sacco 1888, 1895); Rupelian/Chattian of the Mesohellenic Basin (north-western Greece, southern Albania) (D. T. pers. obs.).

REMARKS

This species is poorly known due to its rare occurrence and incomplete preservation. The rather small and slender morphology is characterized by weakly convex teleoconch whorls and subquadrate interspaces between comparatively small nodes. A space between the first and second abapical cords is noticeable in larger specimens, sometimes bearing a fine, smooth spiral thread. Specimens from the Mesohellenic Basin (NW Greece) show a regular spacing of the varices of about 2/3 of a whorl, resulting in a triangular aspect of the shell in apical view. Part of the colour of the shell is preserved in some specimens, which seems to be uniformly brown and darker on the inner surface of the shell. Morphologically it is closer to the Miocene *T. duboisi* than to *T. lignitarum*.

Terebralia rabti (Braun *in* Walchner, 1851)
(Fig. 3A, G)

Cerithium rabti A. Braun, 1851 – Walchner 1851: 1128.

Terebralia rabti – Kadolsky 1995: 16, pl. 2, fig. 19-23; pl. 3, figs. 24, 25, 28, 29 (cum. syn.).

SYNONYMS. — (according to Kadolsky 1995) *Cerithium rabti calvum* Braun *in* Walchner, 1851; *Cerithium rabti eminens* Braun *in* Walchner, 1851; *Cerithium curvicostatum* Sandberger, 1858; *Cerithium arcuatum* Sandberger, 1859.

PALAEOENVIRONMENT. — Euryhaline, lagoonal environment with subtropical semi-arid climate (Kadolsky 1989).

DISTRIBUTION. — An endemic species from the Chattian of the Mainz Basin (Oppenheim-Nierstein, Hochheim; Germany) (Kadolsky 1995). The occurrence from the Early Miocene of the

Aquitaine Basin (SW France) listed by Reid *et al.* (2008) needs confirmation.

Terebralia subcorrugata (d'Orbigny, 1852)
(Fig. 3D)

Cerithium subcorrugatum d'Orbigny, 1852: 80.

Terebralia subcorrugata – Esu & Girotti 2010: 158, pl. 6, figs 4-7 (cum. syn.).

POTENTIAL SUBJECTIVE JUNIOR SYNONYMS. — *Terebralia subcorrugata* var. *tuberculosa* Grateloup, 1846 (*sensu* Cossmann & Peyrot, 1922); *Terebralia subcorrugata* var. *subinterruptum* d'Orbigny, 1852 (*sensu* Cossmann & Peyrot, 1922).

PALAEOENVIRONMENT. — Oligo- to mesohaline, very shallow tropical environments subjected to tide fluctuations, rich in organic matter and vegetation such as mangroves (Esu & Girotti 2010).

DISTRIBUTION. — North-eastern Atlantic: Cossmann & Peyrot (1922) listed numerous localities in France (Aquitaine Basin). — Proto-Mediterranean Sea. Chattian of southern Italy (Esu & Girotti 2010). Late Oligocene (Chattian) and Early Miocene (Aquitainian) of Greece (Thivaïou *et al.* 2019; D. T. unpublished data).

REMARKS

Some specimens from the Mesohellenic Basin (Greece) and the Esfahan-Sirjan Basin (Iran) illustrated in Harzhauser (2004) although incomplete are most likely conspecific. A Burdigalian record from the western Taurids (Turkey) mentioned by İslamoğlu & Taner (2003) needs verification. A specimen from the Early Miocene of Anatolia attributed to *T. subcorrugata* by Gürsoy (2017) is too poorly preserved to be placed with certainty in the species. A record from the Middle Miocene Badenian of Hungary, reported by Kecskeméti-Körmendy (1962), is almost certainly a misidentification, based on an aberrant morphotype of *Terebralia duboisi* or *T. lignitarum* as presented in the mentioned work.

Specimens of *Cerithium corrugatum* Brongniart, 1823 have been placed in this species after re-examinations (e.g. Esu & Girotti 2010). Indeed, *C. corrugatum* Brongniart, 1823 from northern Italy has a similar morphology to that of *T. subcorrugata* but lacks a columellar fold and basal sculpture.

Terebralia vielensis Belliard & Gain
in Belliard, Dugué & Gain, 2006
(Fig. 3F)

Terebralia vielensis – Belliard *et al.* 2006: 47, 48, pl. 18, figs 1, 2.

DISTRIBUTION. — North-eastern Atlantic: Lutetian of the English Channel, Northern France (Belliard *et al.* 2006).

REMARK

This is the oldest known species that bears the distinctive characters of *Terebralia*, i.e., the presence of varices, the distinct siphonal canal and the wide aperture.

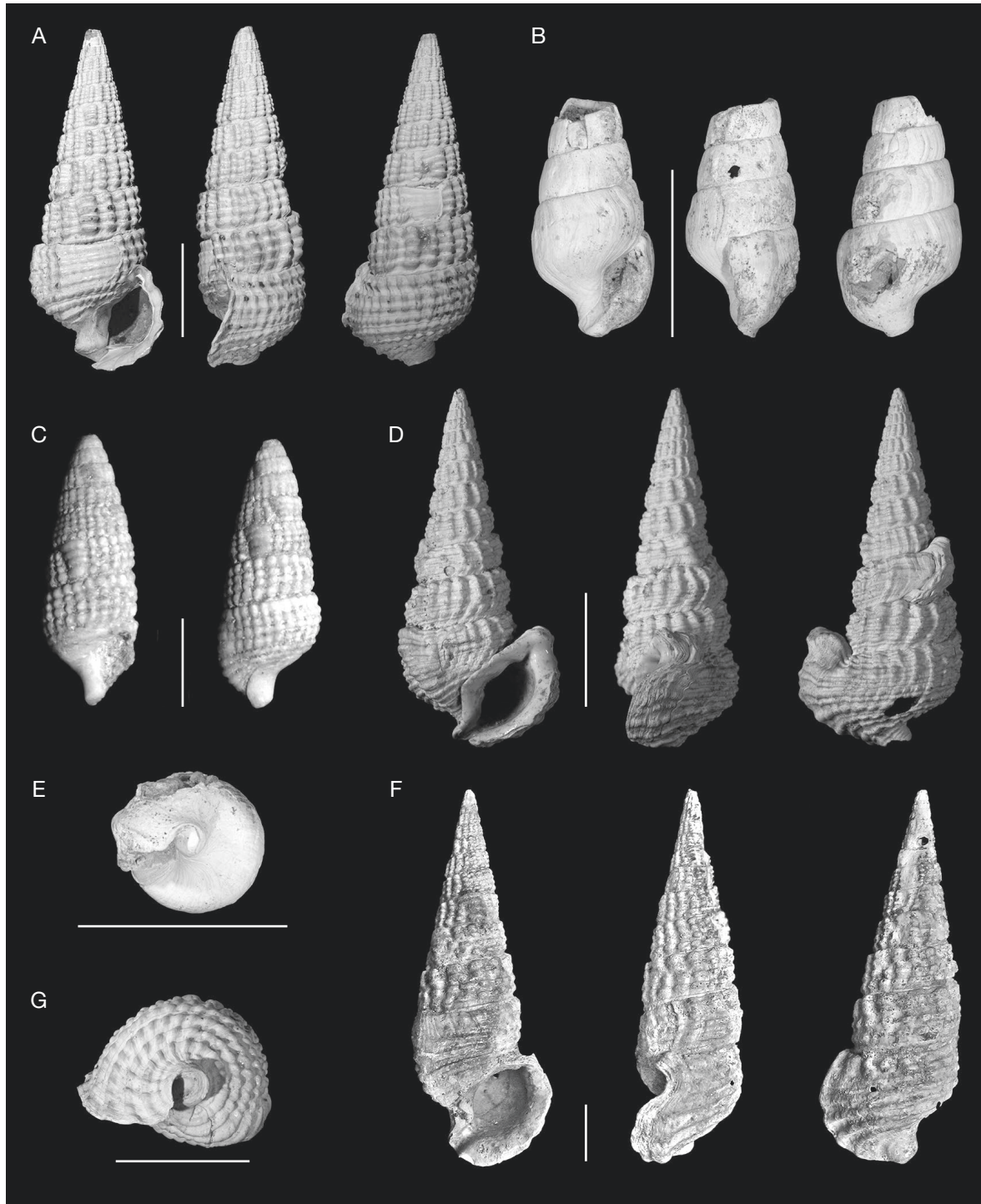


FIG. 3. — **A**, *Terebralia rahti* Kadolsky, 1995, Mainz Basin, Germany; **B**, *Terebralia paradoxa* Kadolsky, 1995, Mainz Basin, Germany; **C**, *Terebralia prolignitarum* (Sacco, 1888), Proto-Mediterranean, Italy (MRNS); **D**, *Terebralia subcorrugata* (d'Orbigny, 1852); **E**, *Terebralia paradoxa*, bottom view; **F**, *Terebralia vielensis* Belliard & Gain, 2006 (Belliard et al. 2006), NW France (MNHN); **G**, *Terebralia rahti*, bottom view. Scale bars: 1 cm.

SPECIES ERRONEOUSLY OR DOUBTFULLY PLACED IN *TEREBRALIA*

Species previously considered as *Terebralia s.s.* are included in this section; members of the fossil subgenus *Terebralia* (*Gravesicerithium*) Charpiat, 1923 are not treated as their systematic position merits a separate specific analysis. Their

teleoconch morphology includes elements such as crenulated spiral threads, one row of prominent, large adapical beads and a lack of a columellar tooth; these are not found in *Terebralia s.s.* Additionally, the morphological characteristics of the adult shells placed in this subgenus do not match those of *Terebralia* as described herein.

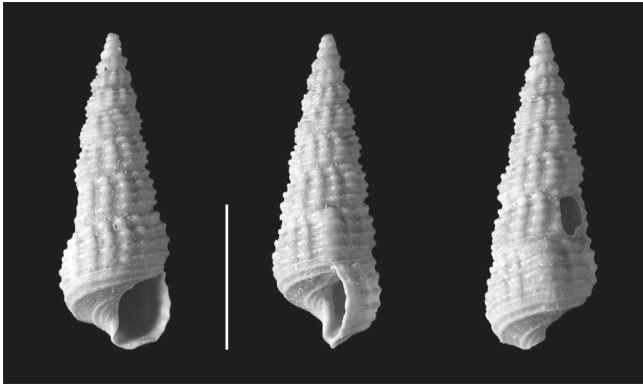


FIG. 4. — ‘*Terebralia*’ *bouryi* (Cossmann, 1889), Paris Basin, France (MNHN). Scale bar: 2 mm.

‘*Terebralia*’ *bourdettensis* Doncieux, 1908

Terebralia Bourdettensis Doncieux, 1908: 149, 150, pl. 8, fig. 9a-c.

DISTRIBUTION. — North-eastern Atlantic. Ypresian of SW France (Doncieux 1908).

REMARKS

The incomplete specimens illustrated by Doncieux (1908) and the description provided does not allow for an accurate generic attribution. The author is noting similarities with ‘*Terebralia*’ *tritaenia* which is also doubtfully placed in *Terebralia*.

‘*Terebralia*’ *bouryi* (Cossmann, 1889)
(Fig. 4)

Potamides Bouryi Cossmann, 1889: 73, pl. 2, fig. 5.

Terebralia bouryi Cossmann & Pissarro, 1913: pl. 29, fig. 151 bis 3.

Terebralia (*s. str.*) *bouryi* – Le Renard & Picaud 1995: 111.

DISTRIBUTION. — North-eastern Atlantic. Lutetian of the Paris Basin (Cossmann 1889; Le Renard & Picaud 1995).

REMARKS

The syntypes of *Potamides bouryi*, figured in the online database of the Muséum national d’Histoire naturelle (MNHN.FA29179), do not fall into *Terebralia*. They rather seem to have more affinities with the subfamily Bittiinae, such as the wide apertural canal, a finer spiral sculpture – including fine lines between spiral chords, and spiral cords at the base of the shell, closely resembling those of *Bittium*.

‘*Terebralia*’ *curvicostata* (Deshayes, 1833)

Cerithium curvicostatum Deshayes, 1833: 311, 312, pl. 50, figs 4, 5.

Terebralia (*s. str.*) *curvicostata* – Le Renard & Picaud 1995: 111.

DISTRIBUTION. — North-eastern Atlantic: Bartonian of the Paris Basin (departments Île-de-France and Oise) (Cossmann & Pissarro 1913; Le Renard & Picaud 1995).

REMARK

The taxonomic position of this species cannot be verified with certainty but the original illustration and description suggest a placement in another genus.

‘*Terebralia*’ *morleti* (Cossmann, 1889)
(Fig. 5)

Potamides morleti Cossmann, 1889: 73, pl. 2, fig. 8.

Terebralia Morleti Cossmann & Pissarro, 1913: pl. 29, fig. 151 quat. 4.

Terebralia (*s. str.*) *morleti* – Le Renard & Picaud 1995: 111.

DISTRIBUTION. — North-eastern Atlantic. Lutetian of the Paris Basin (Cossmann 1889; Cossmann & Pissarro 1913; Le Renard & Picaud 1995).

REMARKS

This species has been described and illustrated by Cossmann (1889) and Cossmann & Pissarro (1913), who placed it in *Terebralia*. This was followed by Le Renard & Picaud (1995). The syntype figured in the online database of the Muséum national d’Histoire naturelle (MNHN.FA29167) is a *Potamides*-like species with weak sculpture, a thinner shell than most representatives of *Terebralia*, rare varices and is most probably not a *Terebralia*.

‘*Terebralia*’ *praxensis* Doncieux, 1908

Terebralia Praxensis Doncieux, 1908: 149, pl. 8, fig. 8.

DISTRIBUTION. — North-eastern Atlantic. Lutetian? of SW France (Doncieux 1908).

REMARKS

Although the general aspect of the shell is *Terebralia*-like, the specimen illustrated by Doncieux (1908) is incomplete, presenting only a slightly developed inner lip. None of the information on shell structure provided is sufficient for a certain generic attribution.

‘*Terebralia*’ *robusta* Dainelli, 1901

Terebralia robusta Dainelli, 1901: 274, pl. 33, figs 10, 11.

Cerithium robustum – Kühn 1946: 77.

DISTRIBUTION. — Oligocene (Rupelian), Promina Mountain (Šibenik-Knin), Croatia.

REMARKS

The species is based on two poorly preserved specimens, internal moulds with few parts of the shell present, mainly on the basal part of the shell. The illustrated specimens are reminiscent of

Campanile species, which are common in the Oligocene of the Western Tethys. Kühn (1946) placed this species in *Cerithium* Bruguière, 1789 but without mentioning characters proper to *Terebralia*. Moreover, this combination would be a junior secondary homonym of *Cerithium robustum* (Sowerby, 1865).

'*Terebralia*' *subcorvina* (Oppenheim, 1894)

Cerithium subcorvinum Oppenheim, 1894: 395 (*nov. nom pro Cerithium corvinum* Zittel, 1863, *non* Brongniart, 1823).

Terebralia subcorvina – Bandel 2006: 84, pl. 6, fig. 10. — Reid *et al.* 2008: 691, table 4.

DISTRIBUTION. — Western Tethys: Lutetian (middle Eocene) of Hungary (Kowalke 2001).

REMARKS

This is one of the rare species for which the protoconch is preserved and described by Bandel (2006). This author placed it in *Terebralia* based on similarities of the protoconch with that of the type species *Terebralia palustris*, but he also mentioned similarities with the protoconch of *Pyrazus* Montfort, 1810. This Eocene species was described by Zittel (1863) from the middle Eocene of Hungary as *Cerithium corvinum* (Brongniart, 1823). Although the early spire whorls bear a *Terebralia*-like sculpture, most of the teleoconch of this large and slender species is smooth and the whorls are flat-sided (Szöts 1953). Moreover, the characters of the aperture are missing, therefore the structure of the canals remains unknown (Vermeij 2007).

'*Terebralia*' *tritaenia* (Cossmann, 1889)

Potamides tritaenia Cossmann, 1889: 74, 75, pl. 2, fig. 14.

Terebralia tritaenia – Cossmann & Pissarro 1913: pl. 29, fig. 29 quat. 6.

Terebralia (*s. str.*) *tritaenia* – Le Renard & Pacaud 1995: 111.

DISTRIBUTION. — North-eastern Atlantic: Lutetian of the Paris Basin (Cossmann 1889; Le Renard & Pacaud 1995).

REMARKS

Cossmann (1889) described the protoconch of the species as a flat button, which suggests a short larval stage and possibly a direct development. The attribution of the species to *Terebralia* was suggested by Cossmann & Pissarro (1913) and followed by Le Renard & Pacaud (1995) in their revision of the Paleogene taxa of the Paris Basin. The tetragonal aperture, comparatively thin outer lip and the absence of an inner lip are features that exclude placement in the genus.

DISCUSSION

The genus *Terebralia* has been extensively studied in Europe, leaving many synonyms for each species but also the highest diversity in the fossil record.

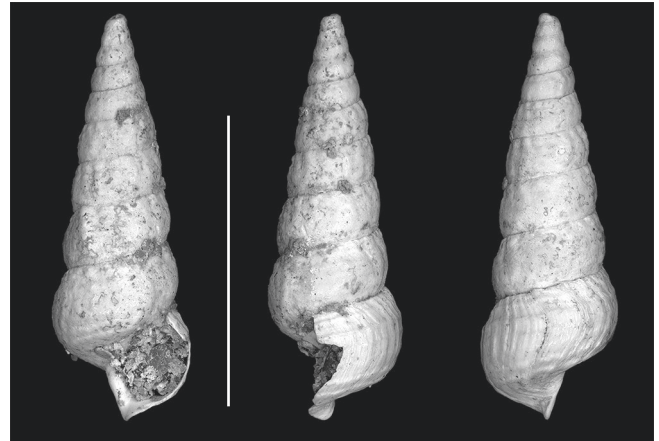


FIG. 5. — '*Terebralia*' *morleti* (Cossmann, 1889), Paris Basin, France (MNHN). Scale bar: 1 cm.

The first appearance of a well-preserved representative of the genus in Europe is dated back to the middle Eocene with *Terebralia vielensis* Belliard & Gain, 2006 from the Lutetian (47.8–41.2 Ma) of Normandy (France). The genus is likely to be represented by two species in the early Eocene Kırkkavak Formation in the Ankara region of Turkey (İslamoğlu *et al.* 2011). However, the fragmentary preservation of the specimens cannot confirm with certainty their systematic position, while the teleoconch structure falls in the range of *Terebralia*.

Representatives of the genus (fossil and extant) often display morphological similarities with other cerithiform cerithioid-eans, something that is reflected by the erroneous attribution of several potamidid-like species to *Terebralia*.

Specimens are usually found in clayey marls, marly sands to conglomerating sands of coastal environments (D'Amico *et al.* 2012; Landau *et al.* 2013; Thivaïou *et al.* 2019). Well preserved and diverse mudflat- or mangrove-related cerithioid-ean assemblages of early Eocene age lack *Terebralia* (e.g. Dominici & Kowalke 2014). *Terebralia* can also be a rare element of subtidal associations apparently unrelated to mangrove environments, as was the case for *Terebralia* sp. in the Early Miocene Korneuburg Basin in Austria (Zuschin *et al.* 2014). In general, the most widespread species (*Terebralia lignitarum*, *T. duboisi*) seem to be more independent of mangrove environments than those with more restricted distributions.

Herein, we give an overview of geographical and stratigraphic occurrences of *Terebralia* in Europe, Western Asia, Anatolia and Arabia to summarize the existing circum-European fossil record of this environmentally restricted genus. In addition, non-European occurrences are briefly presented so as to provide an overview of its global distribution in the geological past.

GEOGRAPHICAL DISTRIBUTION OF RECENT SPECIES

The distribution of extant *Terebralia* is limited to the tropics, in tropical and subtropical latitudes (Fig. 6) (Houbrick 1991). The mean winter sea surface temperatures range between 20°C (south-eastern South Africa and north-eastern, eastern and western Australia) and 28°C (central Indian Ocean, Philippines) in the southern hemisphere and lies around 20° in the

Persian Gulf, the Red Sea and the south of Japan (Okinawa islands) (Fig. 6). In the Indian Ocean Warm Pool in Indonesia and Borneo, temperatures are as high as 28°C all year long (Roxy *et al.* 2014; De Dekker 2016; Li *et al.* 2018).

The global pattern of species distribution largely overlaps with that of mangroves, in longitudes between 30° and 180° (Ellison *et al.* 1999) and ranging through the whole of the Indo-West Pacific from the eastern coast of South Africa to Vanuatu (Houbrick 1991). Their latitudinal spread ranges from the Okinawa islands (Japan) in the North (28°) to eastern South Africa in the South (27°). The distribution observed today is a consequence of a good dispersal potential inherited by the larval development of the Potamididae, which allows for the planktotrophic marine larvae to be transported over long distances (Houbrick 1991). Berger *et al.* (2013) hypothesised that the limited distribution of *T. semistriata* could be a consequence of direct larval development that only allows short-distance dispersal.

Few potamidids are present in New Zealand (Morrisey *et al.* 2007) – possibly because of the climatic restrictions of the family; however, there are some occurrences from the warmer Early Miocene of New Zealand (Powell & Bartrum 1929).

ECOLOGY OF RECENT SPECIES

Three species of *Terebralia* inhabit the IWP today, i.e., *Terebralia palustris*, *Terebralia sulcata*, and *Terebralia semistriata* (Mörch, 1852). Feeding habits and ecology of these species have been studied in detail by Houbrick (1991), while recent studies have focused on more specialized aspects of their ecology such as population structure, feeding, or olfaction (Fratini *et al.* 2001, 2004; Penha-Lopes *et al.* 2009; Raw *et al.* 2017).

Ecologically, the three species are restricted to mangrove swamps, mangroves, mudflats in front of mangrove tree lines, warm-temperate saltmarshes and adjacent tidal flats (Houbrick 1991; Reid *et al.* 2008; Wilson 2013). *Terebralia palustris* and *T. semistriata* are occasionally sympatric, occurring together on the mangrove floor (Healy & Wells 1998; Wells 2003). *Terebralia sulcata* and *T. semistriata* are parapatric in that they occupy different microhabitats within an individual mangrove forest as it has been observed in Northern Australia (Wells 2003). More precisely, *T. sulcata* lives in the seaward margin of mangroves, whereas *T. semistriata* occupies shoreward parts of mangroves and co-occurs with *T. palustris* and other potamidids (Wells 2003).

The substrate around these areas has a high organic content, micro-algae and microbial activity, serving as food sources for these detritus feeders (Wilson 2013).

Terebralia palustris is the largest and most widespread of all living Potamididae (Houbrick 1991; Raw *et al.* 2017). It is the only species that consumes mangrove leaves in addition to mangrove litter, detritus, diatoms and bacteria; its juveniles are detritus-feeders of mangrove-derived detritus on mudflats adjacent to mangrove vegetation (Houbrick 1991; Fratini *et al.* 2004; Penha-Lopes *et al.* 2009; Raw *et al.* 2017). *Terebralia palustris* is considered to be an ecosystem engineer because of its capability of decomposing mangrove leaves and

interfering with other, infaunal animals of the meiofauna by moving on the sediment surface (Carlén & Olafsson 2002); this contributes to nutrient dynamics and the recycling of carbon (Penha-Lopes *et al.* 2009; Raw *et al.* 2017). Population structure studies have shown that with increasing age *T. palustris* individuals occupy microhabitats closer to the mangrove treeline (Penha-Lopes *et al.* 2009).

Terebralia sulcata is considered to be a generalist that can tolerate variations in salinity, desiccation and can feed on various food sources including algae, vascular plants, detritus (leaf litter) and sand (Houbrick 1991). It prefers coarser and firmer substrates than *T. palustris*, in mangrove environments or salt marshes, but can also live on similar substrates without mangrove vegetation (Houbrick 1991; Healy & Wells 1998; Wells 2003). It is the only one of the three species that climbs on mangrove trees and pneumatophores, up to 60 cm, with both adults and juveniles able to attach themselves to the plants (Wells 2003).

Terebralia semistriata lives on open mudflats and on mudflats in front of the mangrove tree line (Houbrick 1991; Wilson 2013). Less data on feeding habits are available for this species compared to its congeners (Houbrick 1991). It lives on muds of the shoreward upper parts (in terms of shore height) of the mangroves (Wells 2003).

THE STORY OF *Terebralia* AND MANGROVES

Mangroves and potamidid gastropods have had a largely concomitant distributions, and are believed to have originated in the Tethys at the Paleogene-Eocene transition (Ellison *et al.* 1999; Plaziat *et al.* 2001). However, we have to keep in mind that analyses on *Terebralia* are limited by the gaps of the fossil record that result in unequal representation of facies and the fact that the first occurrence and origination of the genus do not coincide.

Mangrove vegetation has been well established in Europe since the early Eocene (Plaziat *et al.* 2001), before the first occurrence of *Terebralia s.s.* In the middle and late Eocene, the European species of *Terebralia* occurred in areas with well documented and diverse mangrove vegetation (*Avicennia*, *Pelliciera*, *Aegiceras* and *Nypa*) (Plaziat *et al.* 2001). The European coasts witnessed a gradual impoverishment of mangroves from the Early to the Middle Miocene (Plaziat *et al.* 2001; Suc *et al.* 2018). This impoverishment can be paralleled with the presence of *Terebralia* in the European realm, yet not with the taxonomic diversity of vegetation in these mangrove environments (Plaziat *et al.* 2001). The close ecological association of mangroves and Potamididae in general is supported by recent observations and palaeontological phylogenetic reconstructions (Reid *et al.* 2008). That said, Potamididae members can be abundant and widespread also in the absence of mangroves, as the extant *Terebralia palustris* (Houbrick 1991).

North-eastern Atlantic

Mangroves were present in the north-eastern Atlantic as far north as the London clays, England (Ellison *et al.* 1999). They persisted along the western coast of Europe until the

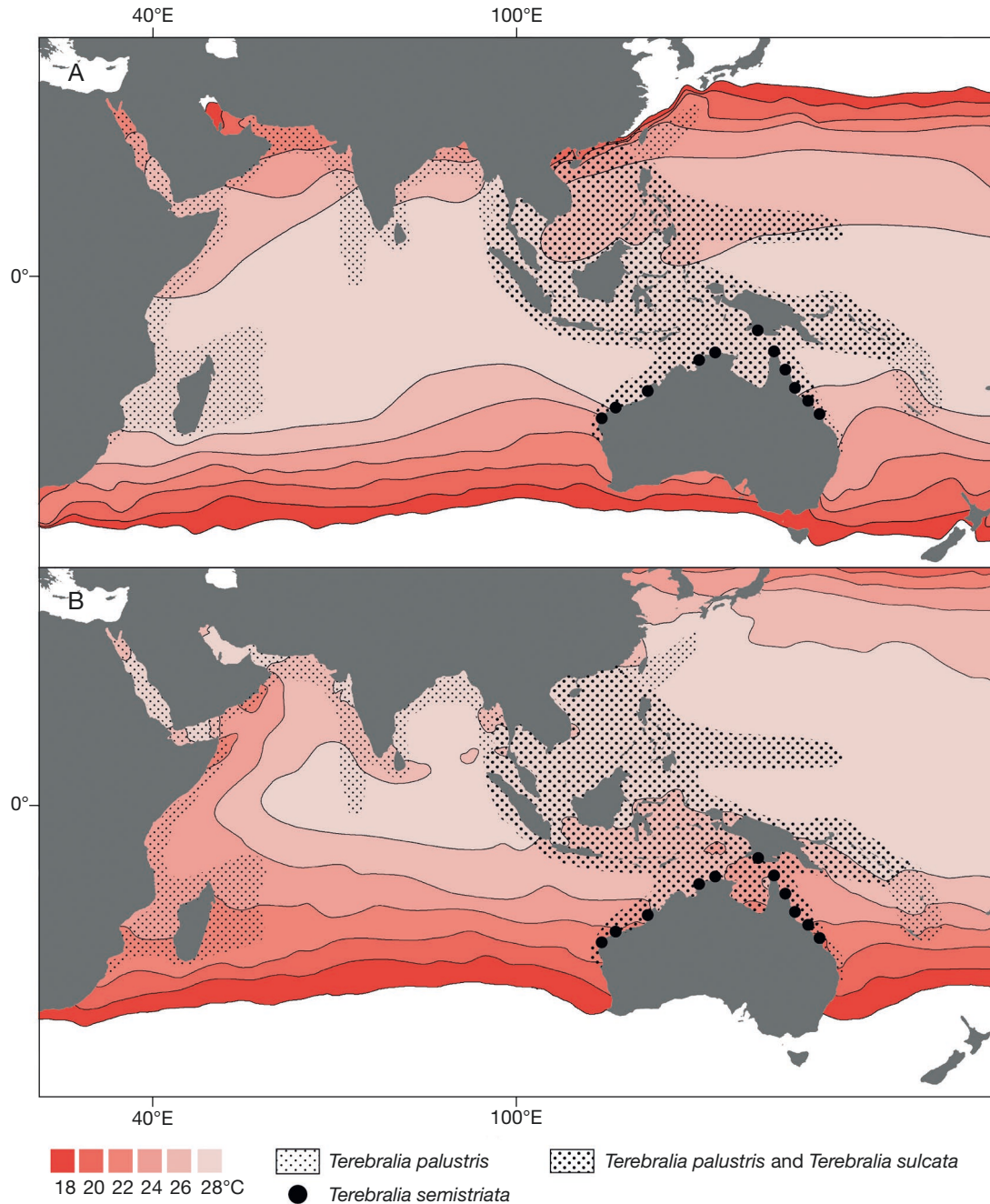


FIG. 6. — Geographical distribution of recent species of *Terebralia* and mean sea surface temperatures of the Indo-West Pacific. **A**, February corresponds to winter in the Northern Hemisphere; **B**, August corresponds to winter in the Southern Hemisphere. Occurrences after Houbrick (1991) and Wells (2003). Credits: maps modified after www.ospo.noaa.gov/Products/ocean/sst/contour/index.html, last consultation on 14 March 2023.

early Middle Miocene with mentions of their existence in France (Plaziat *et al.* 2001). This is consistent with the first appearance of *Terebralia* in Normandy, France, within such an ecosystem (Belliard *et al.* 2006). The retreat of this vegetation from the Atlantic coast occurred after the late Oligocene warming and during the cooler interval of the late Early Miocene; it is thus related to a decrease in temperature (Plaziat *et al.* 2001).

Two species of *Terebralia* remain in the Loire and Aquitaine basins in France until the Middle Miocene and in Portugal until the Tortonian (Fig. 7).

Mediterranean Sea

The disappearance of *Avicennia* mangroves from the southern coasts of France was dated to the beginning of the Serravallian around 13.6 Ma, while in the Central Mediterranean they persisted until the Messinian at 5.6 Ma (Suc *et al.* 2018). The impoverishment and retreat of the mangrove forest from the South of Europe seems to be correlated with temperature. The cooling that started with the MCT (Fig. 8) pushed the impoverished mangrove vegetation gradually southwards, to be found only in lower latitudes in the Late Miocene (Fig. 7) (Plaziat *et al.* 2001). The disappearance of mangroves and that

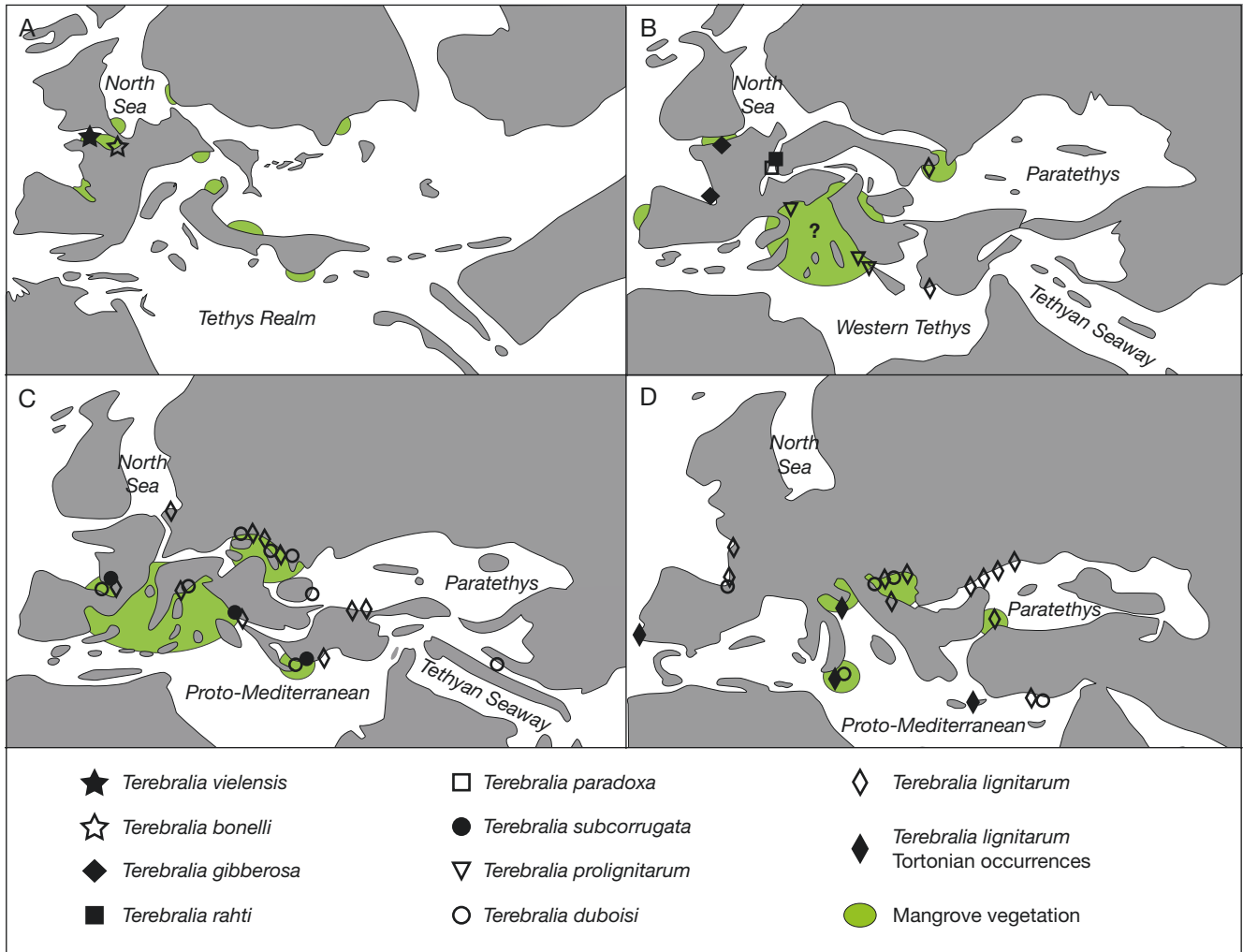


FIG. 7. — Palaeogeographical distribution of various species of *Terebralia* Swainson, 1840 in the fossil record of Europe: **A**, Middle Eocene; **B**, Oligocene; **C**, Early Miocene; **D**, Middle Miocene. Occurrences of *Terebralia lignitarum* (Eichwald, 1830) in the Late Miocene (Tortonian) are presented separately to emphasize their presence in the south of Europe. Credits: palaeogeographical maps modified after Meulenkamp *et al.* (2000) (Middle Eocene) and Popov *et al.* (2004).

of *Terebralia* in the Mediterranean Basin coincided with the onset of the Messinian Salinity Crisis (Fig. 7). Modern *Avicennia* trees can withstand a range of salinities but have a limit for hypersaline environments (Dos Santos Garcia *et al.* 2017).

The massive increase of salinity of the Late Messinian seems to have been the main factor for the disappearance of *Terebralia* rather than the decrease in temperature. Mean annual temperatures dropped in the Late Miocene, reaching about 23.5°C for the pre-evaporitic Messinian (Vasiliev *et al.* 2019), which are well within the tolerance range of modern *Terebralia* (Fig. 6). What could have affected the populations of *T. lignitarum* is a stronger seasonality during glacial periods of the Messinian (Roveri *et al.* 2014).

Paratethys

In the Paratethys, mangrove vegetation was well established during the late Oligocene and Early Miocene with a maximum spread during the late Burdigalian (Karpatian, 16.5 Ma), which coincided with the onset of the Miocene Climate Optimum (Fig. 8) (Kern *et al.* 2011; Suc *et al.* 2018). *Terebralia* was

present in the Central Paratethys during the late Oligocene (Egerian) and the Early Miocene (Eggenburgian) but was seemingly absent during the mid-Burdigalian/Ottungian. It reappeared in large populations during the late Burdigalian/Karpatian (Harzhauser 2002).

Although mangrove records became rare during the Middle Miocene in the Paratethys (Suc *et al.* 2018), *Terebralia* (mainly *T. lignitarum*) remained extraordinarily common during the early Langhian (early Badenian) and declined during the late Langhian (middle Badenian) (M. H. unpublished data), coinciding with the presence of an impoverished *Avicennia* mangrove vegetation (Jiménez-Moreno *et al.* 2008). Following the Badenian Salinity Crisis at about 13.8 Ma (De Leeuw *et al.* 2010), during the Miocene Climate Transition (Shevenell *et al.* 2004; Lear *et al.* 2010), *Terebralia* was rare in the Central Paratethys Sea. It became more widespread during the Sarmatian (late Serravallian) – which is otherwise characterized by high endemism (Harzhauser & Piller 2007) – as a rare element in mudflat environments, represented by small specimens and without forming large

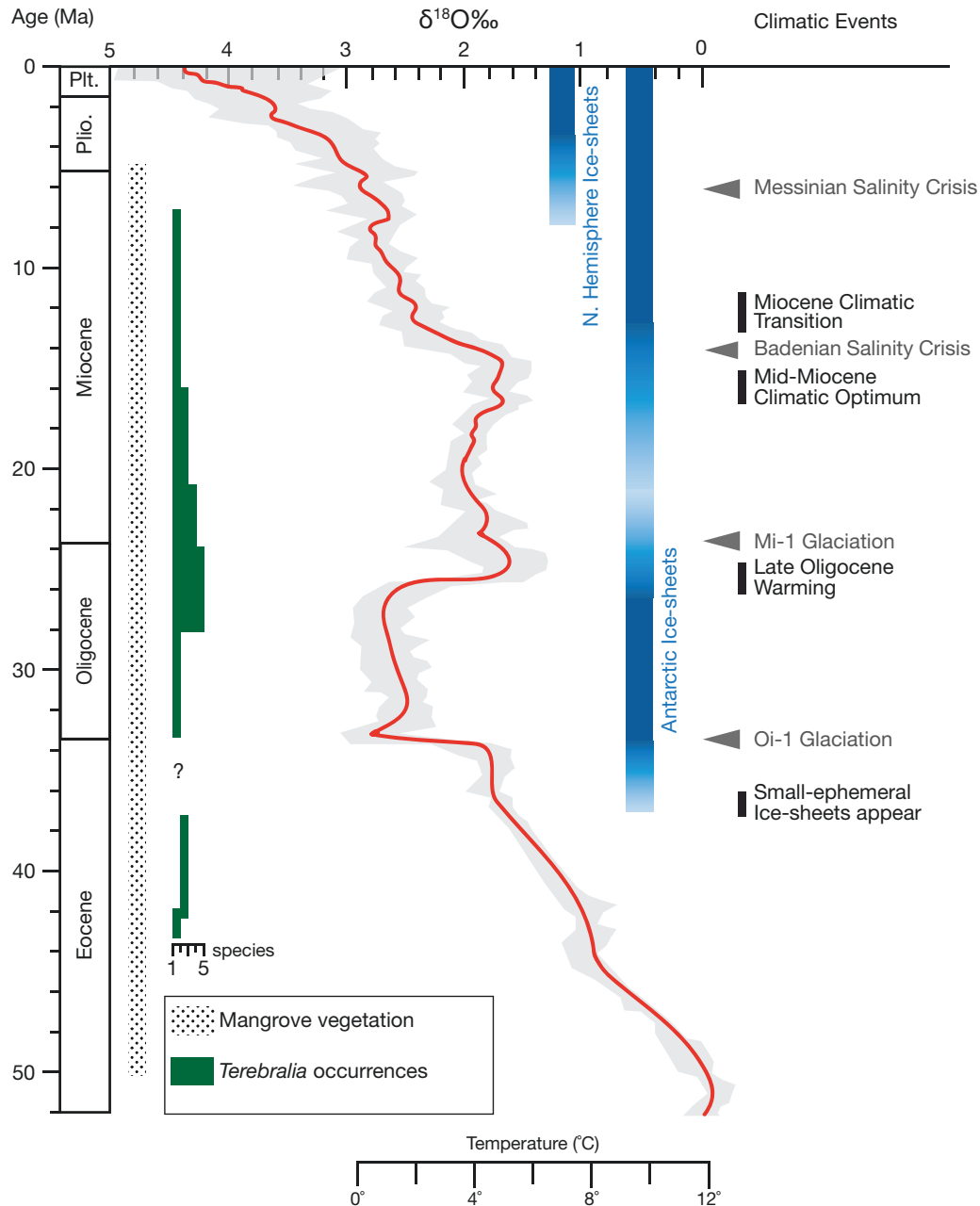


FIG. 8. — Climate curve showing the major climatic events with occurrences of *Terebralia* Swainson, 1840 and mangrove vegetation in Europe. Abbreviations: **Plio.**, Pliocene; **Plt.**, Pleistocene. Credits: modified after Zachos *et al.* (2001).

populations (Harzhauser 2002). The colonization may have been facilitated by a short warming period during the Sarmatian (Piller & Harzhauser 2005) and the availability of vast tidal flat environments. It finally became extinct in the Paratethys at the Sarmatian/Pannonian boundary around 11.6 Ma.

The presence of well-established communities of *Terebralia* in the Eastern Paratethys remains uncertain; a possible slenderer morphotype of *T. duboisi* is mentioned in the Sarmatian of south-western Ukraine by Kolesnikov (1935). This Sarmatian relic occurrence might represent an adaptation to habitats untypical for *Terebralia*.

Black Sea

Mangrove vegetation persisted in the Black Sea throughout the Miocene and until the earliest Pliocene at 4.8 Ma (Suc *et al.* 2018). North Anatolia is believed to have been a refuge for *Avicennia* mangroves in Europe, with impoverished mangroves crossing the Messinian-Pliocene boundary (Biltekin *et al.* 2015; Suc *et al.* 2018). The last representative of *Terebralia* in the Black Sea lived, however, during the Sarmatian and thus over one million years before the disappearance of mangroves there (Fig. 7). *Terebralia* persisted in the area until about 5.8 Ma when temperatures became too low for survival.

CLIMATE, DISTRIBUTION AND DIVERSITY

The minimum temperature that limits the distribution of recent species is 20°C (Fig. 6). This is best illustrated in the area between China and south Japan where the distribution of *T. palustris* and *T. sulcata* closely follows the 20°C-isotherm (Fig. 6A).

In the European fossil record, *Terebralia* species can indicate warm climatic conditions, having lived next to megathermic vegetation, which persisted in Europe up to the late Middle Miocene (Biltekin *et al.* 2015). The warm conditions that prevailed during the Early Miocene and up to the Middle Miocene Climate Optimum correlate with the northernmost distribution of the genus ever recorded (Fig. 7). The subsequent cooling of the Miocene Climate Transition around the Langhian/Serravallian boundary forced the retreat of the genus from northern latitudes as well as its decline in the Paratethys Sea. In the Mediterranean, *Terebralia* survived until the Tortonian (e.g. Crete, Calabria), often in large numbers (Dermitzakis 1972; D'Amico *et al.* 2012) (Fig. 7). In terms of species richness, the maximum diversity of five synchronous species was reached during the warmest period of the Oligocene (Fig. 8); the relatively high diversity also correlates with the wider geographical spread (Fig. 7).

THE NON-EUROPEAN FOSSIL RECORD

Fossil mentions of *Terebralia* outside of the European realm are briefly presented here so as to bring forward the diversity of the genus in the fossil record.

Twenty-two species are found in the fossil record outside of Europe (Table 1). The earliest mention is that of *Terebralia? juliana* Dailey & Popenoe, 1966 in the Late Cretaceous of the NE Pacific (California), and the next species mentioned in the same area is *Terebralia? susana* Squires & Kennedy, 1998. Both species are based on incomplete specimens, which bear general features of Cerithioidea (elongated turreted and relatively thick shells, axial and spiral sculptures) but lack diagnostic characters that would ascertain their placement in the genus. Another two species from the eastern Pacific (Peru) have been attributed to *Terebralia* by DeVries (2019); the few, incomplete specimens presented by the author lack protoconch and apertural characters, a columellar fold and varices, making the affiliation to the genus doubtful as well. The two species of the early Eocene of Anatolia (Turkey) presented by İslamoğlu *et al.* (2011), although incomplete, present a general morphology that does not exclude them from being true members of the genus. However, the lack of protoconch structure and aperture in *Terebralia* sp. 1 and absence of protoconch structure and sculpture of *Terebralia* sp. 2 cast doubt on their affiliation to the genus. Their affiliation with the genus would confirm accepted origination hypothesis (Ellison *et al.* 1999; Plaziat *et al.* 2001; Reid *et al.* 2008).

Two species are known from the Pliocene of the Caribbean and the Gulf of Mexico (Hoerle 1972; Landau & Marques Da Silva 2010).

Most fossil species occur in the IWP (Table 1), including Pakistan, India (Early Indian Ocean), Japan (Indo-NW Pacific), Australia and New Zealand (SE Pacific) (Harzhauser

et al. 2017). The earliest representative of the genus outside of Europe is *Terebralia sutherlandi* (Marwick, 1929), late Oligocene, New Zealand (Beu 2004).

BIOGEOGRAPHICAL REMARKS

The first appearance of *Terebralia* *s.s.* in Europe is marked by *Terebralia vielensis* from the middle Eocene of France. In this context, species would then have migrated southwards into the Tethys and the Paratethys, passing through the Tethyan seaway to the Indian Ocean some time during the Early Miocene. During the Early Miocene *Terebralia* colonized the Caribbean and Central America (Table 1). An alternative scenario would involve a first occurrence of the genus in the early Eocene of Anatolia (İslamoğlu *et al.* 2011), implying migration westwards to the Atlantic and eastwards to the IWP. The true origination story and early dispersal pathways need to be clarified by the analysis of better preserved material of the species presented by İslamoğlu *et al.* (2011). This would coincide with the first appearance and dispersion of mangrove ecosystems from the Tethyan realm to the IWP and the Caribbean (Ellison *et al.* 1999; Plaziat *et al.* 2001).

Lastly, a gap in time and geography is noted between the early Eocene (early Ypresian) occurrences of the Anatolian specimens (İslamoğlu *et al.* 2011) and the middle Eocene (Lutetian) occurrence of *Terebralia vielensis* in France (Belliard *et al.* 2006).

Pre-Oligocene occurrences of *Terebralia* in the Pacific coast of the Americas (Table 1) remain doubtful, and a point of origin in the Pacific coast is unlikely.

CONCLUSION

Terebralia has a long history in the European fossil record that traces back at least to the middle Eocene and ended in the Tortonian – early Messinian. The tight relationship with the mangrove ecosystem and the good preservation potential of the rather robust shells make the genus a useful proxy to infer the presence of mangrove vegetation in the absence of direct floral evidence. We hypothesise that this assumption holds true for most of the European Cenozoic especially if large populations are preserved. A rare exception could be that of a relic occurrence in the Sarmatian Sea, where it seems to have managed to survive in conditions of high salinity associated with a highly endemic mollusc fauna in this isolated area. *Terebralia* *s.s.* could have originated earlier than shown by the fossil record, and later became adapted to life in mangrove environments.

The genus' total diversity amounts to nine fossil European species; eight other taxa previously placed in *Terebralia* in the literature are excluded from the genus herein. The fact that the majority of systematic works has been carried out on European material, makes the study of this material a starting point for the revision of the genus. The diversity and palaeogeographical distribution of the genus and that of mangroves correlate with climatic conditions, low diversi-

TABLE 1. — Palaeogeographical and geochronological distributions of *Terebralia* species. Abbreviations: **E**, Early; **L**, Late; **M**, Middle; **Plei.**, Pleistocene; **Plio.**, Pliocene.

Species	Palaeogeographical distribution	Geochronological distribution												References		
		Cretaceous	Paleocene				Eocene		Oligocene		Miocene		Plio.		Plei.	
			E	M	L	E	L	E	L	E	M	L				
<i>Terebralia?</i> sp. 1	Anatolia	–	–	–	–	X	–	–	–	–	–	–	–	–	İslamoğlu <i>et al.</i> 2011	
<i>Terebralia?</i> sp. 2	Anatolia	–	–	–	–	X	–	–	–	–	–	–	–	–	İslamoğlu <i>et al.</i> 2011	
<i>Terebralia consorbina</i> (Powell & Bartrum, 1929)	South-West Pacific	–	–	–	–	–	–	–	–	–	X	–	–	–	Beu 2004	
<i>Terebralia dentilabris</i> Gabb, 1873	Caribbean, Gulf of Mexico	–	–	–	–	–	–	–	–	–	X	X	–	X	–	Hoerle 1972; Landau & Marques da Silva 2010; Hendy <i>et al.</i> 2015
– <i>Terebralia?</i> <i>dimorpha</i> Vredenburg, 1928	Early Indian Ocean	–	–	–	–	–	–	–	–	–	–	X	–	–	–	Vredenburg 1928
<i>Terebralia gajensis</i> Vredenburg, 1928	Early Indian Ocean	–	–	–	–	–	–	–	–	–	X	–	–	–	–	Harzhauser <i>et al.</i> 2017
<i>Terebralia harrisi</i> Maury, 1920	Caribbean	–	–	–	–	–	–	–	–	–	–	–	–	X	–	Landau & Marques da Silva 2010
<i>Terebralia itiogawai</i> (Taguchi, Osafune & Obayashi, 1981)	Indo-North-West Pacific	–	–	–	–	–	–	–	–	–	X	X	–	–	–	Taguchi 2002
<i>Terebralia?</i> <i>juliana</i> Dailey & Popenoe, 1966	North-East Pacific	X	–	–	–	–	–	–	–	–	–	–	–	–	–	Squires & Kennedy 1998
<i>Terebralia kakiensis</i> (Taguchi, Osafune & Obayashi, 1981)	Indo-North-West Pacific	–	–	–	–	–	–	–	–	–	X	X	–	–	–	Taguchi 2002
<i>Terebralia?</i> <i>kannoi</i> Nakagawa, 2009	Indo-North-West Pacific	–	–	–	–	–	–	–	–	–	X	X	–	–	–	Nakagawa 2009
<i>Terebralia marki</i> Devries, 2018	East Pacific (Peru)	–	X	–	–	–	–	–	–	–	–	–	–	–	–	DeVries 2019
<i>Terebralia?</i> <i>mekranica</i> Vredenburg, 1928	Early Indian Ocean	–	–	–	–	–	–	–	–	–	–	X	–	–	–	Vredenburg 1928
<i>Terebralia miosulcata</i> Vredenburg, 1928	Early Indian Ocean	–	–	–	–	–	–	–	–	–	X	X	X	–	–	Harzhauser <i>et al.</i> 2017
<i>Terebralia palustris</i> Linnaeus, 1767	Indo-West Pacific, South-West Pacific	–	–	–	–	–	–	–	–	–	X	X	X	X	X	Houbrick 1991; Reid <i>et al.</i> 2008
<i>Terebralia?</i> <i>pathani</i> Iqbal, 1969	Early Indian Ocean	–	–	–	–	X	–	–	–	–	–	–	–	–	–	Reid <i>et al.</i> 2008
<i>Terebralia pauli</i> Devries, 2018	East Pacific (Peru)	–	X	–	–	–	–	–	–	–	–	–	–	–	–	DeVries 2019
<i>Terebralia shibatai</i> Taguchi, 1992	Indo-North-West Pacific	–	–	–	–	–	–	–	–	–	X	X	–	–	–	Taguchi 1992, 2002
<i>Terebralia sulcata</i> Born, 1778	Indo-Pacific	–	–	–	–	–	–	–	–	–	–	–	X	X	X	Ladd 1972; Houbrick 1991
<i>Terebralia?</i> <i>susana</i> Squires & Kennedy, 1998	North-East Pacific	–	–	–	X	–	–	–	–	–	–	–	–	–	–	Squires & Kennedy 1998
<i>Terebralia sutherlandi</i> (Marwick, 1929)	South-West Pacific	–	–	–	–	–	–	–	–	X	–	–	–	–	–	Marwick 1929; Beu 2004
<i>Terebralia waitemataensis</i> (Powell & Bartrum, 1929)	South-West Pacific	–	–	–	–	–	–	–	–	–	X	–	–	–	–	Beu 2004; Ozawa <i>et al.</i> 2009

ties marking cooler intervals (late Eocene-early Oligocene). The maximum diversity of five species is observed during the warmest periods of the late Oligocene (Chatthian) and Early Miocene. No occurrences have been recorded from the terminal Eocene (Priabonian), possibly because of a lack of outcrops with mudflat deposits of that age. During the early Oligocene, the genus spread into a relatively wide geographic area, reaching the Western Tethys with at least one species (*T. prolignitarum*). During the late Oligocene, it maintained a wide geographical distribution and also spread into the Paratethys Sea. The largest geographical distribu-

tion of the genus in Europe occurred during the Early to Middle Miocene ranging from the north-eastern Atlantic to the Proto-Mediterranean, the Paratethys and further east into Anatolia. The last representatives are found in the Late Miocene of the south Atlantic coast and the Mediterranean, only to disappear before the major environmental perturbations of the Messinian Salinity Crisis. The extirpation of *Terebralia* in Europe predated the final disappearance of the mangrove environments.

No more than three species co-occur in the fossil record, which is also observed for extant representatives.

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APPENDIX

APPENDIX 1. —Supplementary occurrence data for species of *Terebralia* Swainson, 1840 with a larger geographic distribution.

Species	Occurrence		
	Country	Province	Formation/Localities
<i>Terebralia bonelli</i> (Deshayes, 1833)	France	Paris Basin	–
<i>Terebralia duboisi</i> (Hörnes, 1855)	France	Aquitaine Basin, Loire Basin	–
	Italy	Piedmont Basin, Calabria province	–
	Turkey	Antalya Basin	Altınkaya formation
		Karaman Basin	Tırtar Formation
	Austria	Korneuburg Basin, Styrian Basin, Vienna Basin	–
	Romania	Dacian Basin	–
	Moldova	Dacian Basin	–
	Ukraine	Dacian Basin	–
	Iran	Qom Basin	–
<i>Terebralia gibberosa</i> Grateloup, 1832	France	Paris Basin, Aquitaine Basin	–
<i>Terebralia lignitarum</i> (Harzhauser, 2002)	France	Aquitaine Basin	–
	Portugal	–	Cacella locality
	Germany	North Sea Basin	Krinke gravel-pit
	Turkey	Denizli Basin, Mut Basin, Erzincan Basin, Sivas Basin	–
	Greece	Mesohellenic Basin, Crete	Pentalofo Formation
	Italy	Po Basin, Calabria province	–
	Hungary	Máriahalom	–
	Austria	Eggenburg (various localities), Korneuburg Basin	–
<i>Terebralia subcorrugata</i> d'Orbigny, 1852	France	Aquitaine Basin	Saucats-Larrey, La Brède, Saucats-Peloua, Léognan
	Italy	Lecce province	Otranto
	Greece	Mesohellenic Basin	Pentalofo Formation