



# Jurassic *Teredolites* from Cuba: New trace fossil evidence of early wood-boring behavior in bivalves

Jorge Villegas-Martín<sup>a</sup>, Jordi M. de Gibert<sup>b,\*</sup>, Reinaldo Rojas-Consuegra<sup>c</sup>, Zain Belaústegui<sup>b</sup>

<sup>a</sup> Instituto de Ecología y Sistemática, Carretera de Varona km. 31/2, Capdevila, Boyeros, A.P. 8029, C.P. 10800, Ciudad de La Habana, Cuba

<sup>b</sup> Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, Martí Franquès s/n, 08028 Barcelona, Spain

<sup>c</sup> Museo Nacional de Historia Natural, Obispo 61, Habana Vieja, Ciudad de la Habana, Cuba

## ARTICLE INFO

### Article history:

Received 17 April 2012

Accepted 5 June 2012

### Keywords:

*Teredolites*

Borings

Bioerosion

Bivalves

Wood

## ABSTRACT

*Teredolites clavatus* is described from log fragments preserved in carbonate concretions in the Oxfordian (Upper Jurassic) Jagua Formation in western Cuba. The trace fossils are interpreted as borings produced by marine bivalves inhabiting floating wood substrates, probably pholadids belonging to the subfamily Martesiinae. This report constitutes one of the few known occurrences of the ichnogenus in the Jurassic and contributes to a better knowledge of the early history and evolution of wood-boring behavior in bivalves.

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## 1. Introduction

Bivalves are a major bioerosive force in marine settings today. They are capable of boring in a variety of substrates including rock, invertebrate and vertebrate skeletons, firm sediments and wood (e.g., Fischer, 1990; Savazzi, 1999; Belaústegui et al., 2012). In particular, teredinids are specialized in boring on wood substrates for protection and nutrition, while several pholadids, mainly martesiinins and xylophagains, also inhabit this kind of substrates (Evans, 1999). The body fossil record of wood boring clams goes back to the Middle Jurassic (Haga and Kase, 2011, and references therein), while ichnological evidences predate these age with some *Teredolites* borings known from the Lower Jurassic (Vahldiek and Schweigert, 2007).

Here we report a new finding of *Teredolites* from the Upper Jurassic (Oxfordian) Jagua Formation in western Cuba, which previously had been only mentioned by Kulicki and Wierzbowski (1983) as pelecypod borings. A younger occurrence of this trace fossil was already known from the Upper Cretaceous of Cuba (Villegas-Martín and Rojas-Consuegra, 2011), but the new data are remarkable because of the limited knowledge of Jurassic *Teredolites*. Herein, this occurrence is described and discussed in the context of the early evolution of bivalve wood-borers.

## 2. Geological setting

The specimens come from the Jagua Vieja Member of the Jagua Formation in the vicinity of the city of Viñales in the Pinar del Río province, western Cuba (Fig. 1). The Jagua Formation crops out along la Sierra de los Órganos, and was first named and described by Palmer (1945). The Jagua Vieja Member was dated as middle Oxfordian by Wierzbowski (1976) based on ammonite faunas. Detailed description of the unit was provided by Pszczółkowski (1978) who characterized it as consisting of black shales and marly limestones with carbonate concretions. The member contains an abundant fossil fauna of ammonites, bivalves and fish, and it is well known for its exceptional record of marine reptiles (e.g. Kulicki and Wierzbowski, 1983; Iturralde-Vinent and Norell, 1996; Fuente and Iturralde-Vinent, 2001; Gasparini, 2009). Pszczółkowski (1978, 1999) interpreted deposition as produced in a low-energy offshore environment with deltaic influence as indicated by the abundance of wood fragments.

## 3. The borings

### 3.1. Description

The studied material is housed in the paleontological collection of the Museo Nacional de Historia Natural de Cuba (MNHN Cu). Examination of near 25 specimens of fossil wood from the Jagua Vieja Member revealed the presence of borings in four specimens.

\* Corresponding author. Tel.: +34 934035870; fax: +34 934021340.

E-mail address: [jmdegibert@ub.edu](mailto:jmdegibert@ub.edu) (J.M. de Gibert).



Fig. 1. Map of western Cuba showing the location of the area from where the studied material comes from in the surroundings of the city of Viñales.

The wood corresponds to carbonized and partly silicified logs preserved as the nuclei of carbonate concretions (Fig. 2).

The best preserved and most abundant borings were found in a wood fossil specimen (cataloged as MNHNCu-96.000803, Fig. 3) collected by Manuel Iturralde-Vinent from the locality of El Hoyo de San Antonio (see Iturralde-Vinent and Norell, 1996, for situation of the locality). The fossil occurs in a dark, carbonate concretion, which also contains fossils of ammonites and bivalves. The wood fragment is elongated and approximately 4 cm wide and 15 cm long. The longitudinal fibers of the wood can be seen, while in thin section the cellular structure of the tissue is also identifiable. Such original anatomic attributes are partly degraded by an incomplete process of silicification resulting in features somewhat similar to those figured and described by Sweeney et al. (2009). The wood displays several cracks and veins filled by crystalline calcite. The borings are seen as cross sections with morphologies either circular-to-ovate or teardrop-shaped (Fig. 3C), what allows interpreting their morphology as conical to short, clavate, and with a maximum diameter of 2–6 mm and a length of 6–7 mm. They cut the wood fibers perpendicularly and are concentrated in one of the margins of the fragment. Some of the borings exhibit a thin mineral lining about 50  $\mu$ m thick (Fig. 3E). The cavities are infilled by crystalline calcite arranged radially from the walls of the boreholes, similar to that seen in some ammonites in the same sample (Fig. 3C). In some cases, the calcite does not completely fill the void and a dark, shiny, metallic mineral occurs in the center (Fig. 3D). In one of the borings, the section of what seems to be a bivalve can be recognized (Fig. 3C).

Additional material exhibits similar morphological features, dimensions and preservational characteristics. Specimen MNHNCu-96.000842 (Fig. 4A, B) presents at least 9 circular-to-oval cross-sections of borings clustered in the margin of the log with calcitic infill and preservation in some of them of a thin carbonate lining. Meanwhile, the wood fragment in MNHNCu-96.001829 bears numerous but dispersed, circular cross-sections of boreholes with

calcitic infill. Another specimen (MNHNCu-96.003889) displays a single boring.

### 3.2. Ichnotaxonomy

The morphology interpreted for the borings as a short club with a narrow aperture, widening distally and with a rounded termination allows for the determination of the borings as *Teredolites* cf. *clavatus* Leymerie, 1842 (see Kelly and Bromley, 1984 for diagnosis). The short profile allows ruling out *Teredolites longissimus* Kelly and Bromley, 1984, the other valid ichnospecies of *Teredolites*, which typically bears long, contorted morphologies parallel to the wood grain. On the other hand, the quasi-triangular shape of some cross-sections is not the most typical in *Teredolites clavatus*, although more material would be needed to evaluate if that may be a feature significant enough to erect a new ichnospecies.

## 4. Discussion

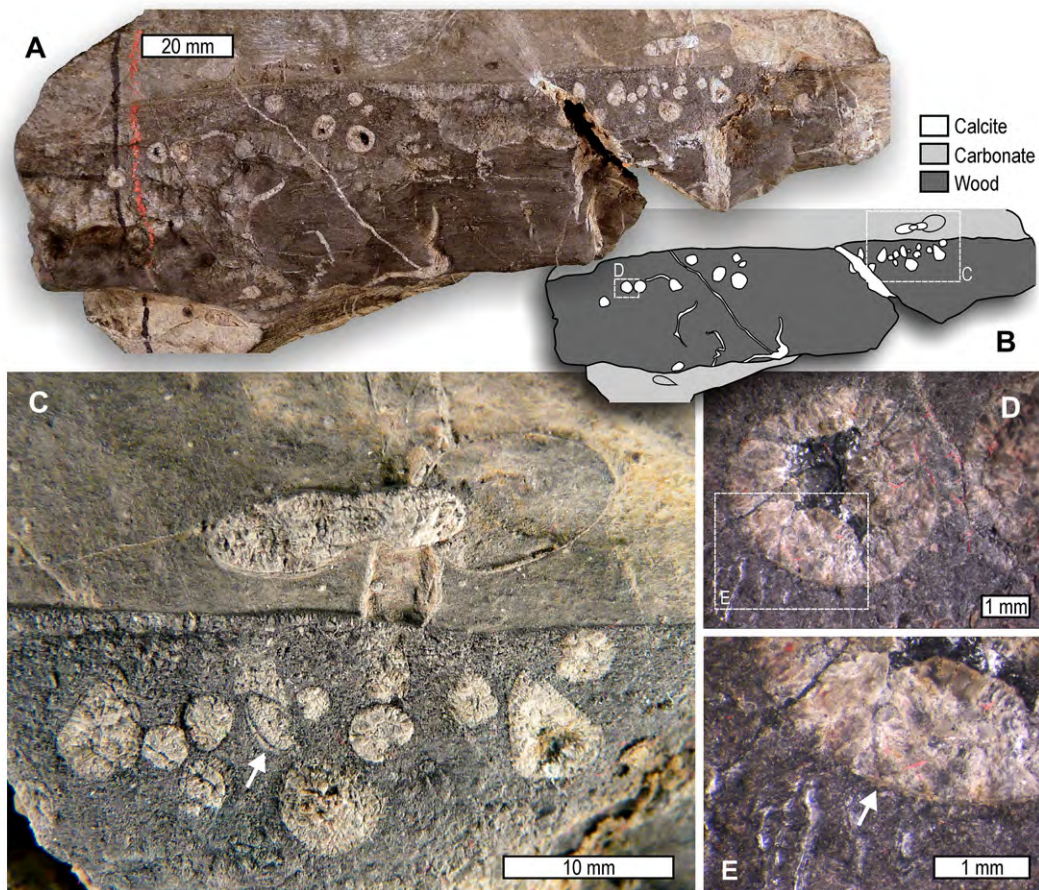
### 4.1. Tracemaker

The ichnogenus *Teredolites* is known to be produced by bivalves (e.g., Kelly and Bromley, 1984). In the material studied from the Jagua Formation, the general club-shaped morphology and the presence of a bivalve inside one of the boreholes support this interpretation. Also, the existence of a thin calcareous lining, which is a common feature in bivalve borers, provides additional evidence. The wood-boring habit occurs in two families of pholadacean bivalves, namely the teredinids and the pholadids (Evans, 1999). Teredinidae (shipworms) are obligate wood borers capable of digesting cellulose (Waterbury et al., 1983). They typically produce long, sinuous-to-meandering borings with morphologies more similar to *T. longissimus* (Kelly and Bromley, 1984; Savazzi, 1999) and, thus are not likely tracemakers for the boreholes described herein. Pholadidae (piddocks) are able to bore in a variety of substrates by mechanical means (e.g., Fischer, 1990) and are thus, facultative wood borers. Nevertheless, the wood-boring habit occurs in subfamilies Xylophaginae and Martesiinae. Xylophaginae are specialized deep-sea wood-borers probably capable of cellulose digestion (Turner, 1977), while Martesiinae produce short dwelling traces preferentially in wood, which are more similar to the morphology of *T. clavatus* (Kelly and Bromley, 1984). The bivalve shells preserved in one of the boreholes from Cuba (Fig. 3C) do not allow for a taxonomic determination of the potential tracemaker, assuming that the bivalve is the actual tracemaker and not a nestler. Interestingly, the subtriangular morphology of some sections of the specimens studied herein compare well to that of the borings of the Kimmeridgian martesiinid *Opertochasma somaensis* as described



Fig. 2. Log fragment preserved within a carbonate concretion, Oxfordian, Jagua Fm. Both figures correspond to the same specimen (MNHNCu-96.000831).





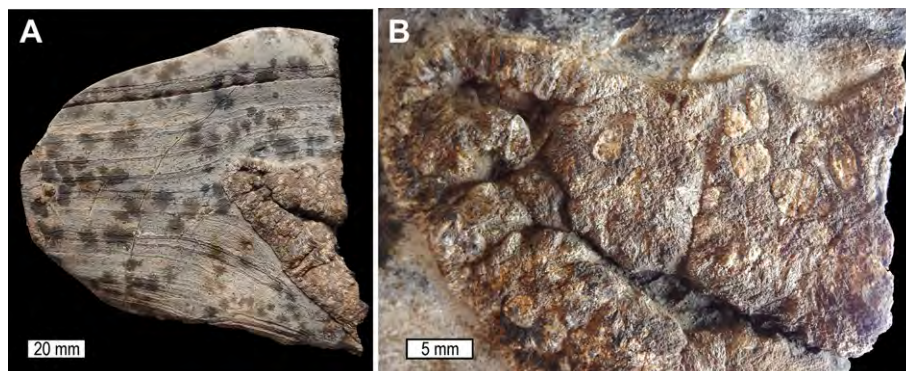
**Fig. 3.** Wood fragment with *Teredolites clavatus* (MNHNCu-96.000803). (A) Complete specimen showing numerous borings. (B) Schematic drawing of the specimen. (C) Detail of some of the borings. White arrow indicates the presence of a bivalve fossil preserved within one of them. A cross-section of an ammonite is seen above the fossil log. (D) Detail of one of the borings showing the calcitic infill. (E) Detail of boring in D. White arrow indicates the presence of a thin calcitic lining. Dashed boxes indicate positions of close-ups.

and figured by Haga and Kase (2011). Thus, it is concluded that the most probable tracemaker for the Cuban *Teredolites* is a martessinid bivalve.

#### 4.2. Paleoecological and taphonomic interpretation

The fossils found in the Jagua Formation are commonly preserved in carbonate concretions and include primarily ammonites as well as other cephalopods (nautiloids and sepioids), small-size gastropods, bivalves (mainly *Liostrea*), fishes and reptiles

(Wierzbowski, 1976; Kulicki and Wierzbowski, 1983; Iturralde-Vinent and Norell, 1996). Kulicki and Wierzbowski (1983), who also referred the presence of planktic foraminifera in thin sections, pointed out the remarkable dominance of nekctic and planktic forms, and interpreted the common *Liostrea* as a pseudoplanktic bivalve when found attached to ammonite shells. The same authors remarked that these features, together with the good preservation of original lamination indicating the absence of burrowers, the articulated or partly articulated vertebrate fossils, and the presence of disperse pyrite, were evidence of an oxygen-depleted seafloor.



**Fig. 4.** Wood fragment with *Teredolites clavatus* (MNHNCu-96.000842). (A) Concretion preserving the log fragment inside. Primary lamination is preserved and deformed by the presence of the wood. (B) Detail showing the abundant borings.

Wierzbowski (1976) estimated a water depth of less than 100 m. In this context, the borings described herein are interpreted as produced by bivalves that colonized floating logs. This pseudo-planktic mode of life is common in modern wood borers, which has been historically a common threat for wooden boats (e.g., Cobb, 2002), although they may also inhabit living marine plants or in situ dead stumps and roots in coastal environments (e.g., Gingras et al., 2004). The logs of the Jagua Formation were drifted from an emerged land area in the vicinity and would have sunk down onto the seafloor taking down with them their boring guests. Carbonate concretions formed early after burial, preventing compression of the logs and allowing them to be preserved as tridimensional entities.

#### 4.3. Jurassic *Teredolites* and the origin of the wood-boring behavior in bivalves

Haga and Kase (2011) recently reviewed the body fossil record of pholadacean bivalves in the Jurassic, which includes the Bajocian '*Teredo*' *australis* Moore, 1870, two Kimmeridgian species of *Operotochasma* – *O. somaensis* Haga and Kase, 2011, and *O. mallonianum* (Cragin, 1905) –, two Tithonian species of the teredinid *Turnus* – *T. davidsoni* (Loriol and Pellat, 1875), and *T. waldheimii* (D'Orbigny, 1845) –, and a possible Tithonian xylophagainid. In contrast, the oldest trace fossil that may be attributed to a bivalve wood borer corresponds to *T. longissimus* from the Lower Jurassic (Upper Pliensbachian) of Germany (Vahldiek and Schweigert, 2007), thus predating the oldest known body fossil from the Bajocian. Kelly (1988a) also referred to the presence of *T. longissimus* borings in wood from the Lias (probably Upper Pliensbachian as well) of Portugal. Additional occurrences of *Teredolites* in the Jurassic are few, including only two Middle Jurassic occurrences from the Bajocian of Australia (Moore, 1870; Kelly, 1988a), and the Bajocian-Bathonian of Argentina (*T. isp.*; McIlroy et al., 2005), and two Upper Jurassic records from the Tithonian of France (*T. clavatus*; Schlirf, 2003) and the Volgian (Tithonian) of England (Kelly, 1988b). Hence, the new material presented herein from the Oxfordian (Upper Jurassic) of western Cuba provides additional data about the early fossil record of the ichnogenus. Both the body and trace fossil record coincide in providing evidence of the presence of several groups of wood-boring pholadaceans in the Jurassic. Haga and Kase (2011) hypothesized that wood-boring pholadaceans evolved directly from sand-dwelling ancestors.

An analysis of the occurrences of *Teredolites* recorded in the literature (see Appendix for complete list; Fig. 5) may provide a rough estimation of the relative abundance of wood-boring bivalves through time. To construct the graph of Fig. 5 the total number of occurrences per Epoch has been normalized taken into account its temporal extent. The resulting diagram was compared with a pholadid and teredinid diversity curve (Fig. 5). The latter was constructed with the aid of the software Fossil Plot 2.0 developed by Leif Tapanila at Idaho State University ([www.fossilplot.org](http://www.fossilplot.org)), which uses Sepkoski's compendium of marine animal genera (Sepkoski, 2002) as the underlying database. All pholadids and teredinids were selected from the database to construct the generic diversity curve.

The diagram of recorded occurrences of *Teredolites* reveals that the trace fossil became more common after the Jurassic and shows a noteworthy abundance increase in the Late Cretaceous. This distinct Late Cretaceous rise parallels a distinct increment in the diversity of pholadid and teredinid genera (Fig. 5). Despite the graphics being qualitatively different (abundance of trace fossils vs. diversity of biotaxa), the shared trend supports the well established relation between these bivalve groups and the ichnogenus *Teredolites*, and shows the validity of the use of ichnological data in the

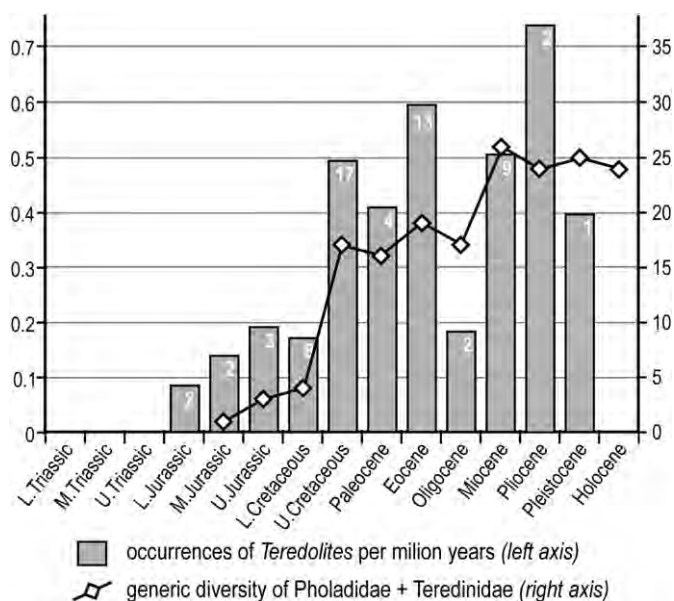


Fig. 5. Bar diagram showing the stratigraphic distribution of *Teredolites* occurrences per million years as recorded in the literature (see list of records in Appendix 1). Absolute number of occurrences is indicated within the bars. The line joining the grey rhombs shows the variation through time in generic diversity of teredinid and pholadid bivalves. This graph was constructed using FossilPlot 2.0 (developed by Leif Tapanila at Idaho State University) based in the database provided by Sepkoski (2002).

analysis of the evolutionary history of this group. Trace fossils provide additional evidence, which may be important taking into account that the taphonomic pathways followed by boreholes and shells are significantly different, and often trace fossils are preserved in absence of the skeletal parts of the borers.

#### Acknowledgments

The authors express their gratitude to Rosa Domènech and Jordi Martinell from the University of Barcelona for fruitful discussion about, and Stephen Donovan and Luis Buatois for helpful reviews. This research was partly funded by a research grant of the Geology School of the University of Barcelona and it is part of the research carried out by members of the project CGL 2010-15047 of the Spanish Ministry of Science and Innovation.

#### Appendix. Recorded occurrences of the ichnogenus *Teredolites*

The database used to construct the *Teredolites* abundance diagram of Fig. 5 consists of the following occurrences:

**Lower Jurassic:** Pliensbachian, Germany (Vahldiek and Schweigert, 2007); Pliensbachian?, Portugal (Kelly, 1988a).

**Middle Jurassic:** Bajocian, Australia (Moore, 1870; Kelly, 1988a); Bajocian-Bathonian, Lajas Fm, Argentina (McIlroy et al., 2005).

**Upper Jurassic:** Oxfordian, Jagua Fm, Cuba (this paper); Volgian (Tithonian), Shotover Grit Sands, England (Kelly, 1988b); Tithonian, Grès de la Crèche, France (Schlirf, 2003).

**Lower Cretaceous:** Hauterivian, Calcaire à Spatangues, France (Kelly and Bromley, 1984); Barremian, Kuhnpasset beds, Greenland (Kelly et al., 2000); Aptian, Wallumbilla Fm, Australia (Campbell and Haig, 1999); Aptian, Arcillas de Morella, Spain (Ferrer and Gibert, 2005; Poza et al., 2010); Aptian, Kentish Rag, England (Kelly and Bromley, 1984); Aptian, Hatira Fm, Israel (Lewy, 2003); Albion, Bluesky Fm, Canada (Hubbard et al., 2004); Albion, Kotick Point Fm, Antarctica (Kelly, 1988a; Buatois and Mángano, 1992).



**Upper Cretaceous:** Cenomanian, Dunvegan Fm, British Columbia, Canada (Plint, 1996); Cenomanian to Coniacian, several Fms, Czech Republic (Kříž and Mikuláš, 2006; Mikuláš, 1993); Turonian-Coniacian, Garudamangalam Fm, India (Tewari et al., 1998); Coniacian-Santonian?, Czerna Fm, Poland (Leszczyński, 2010); Santonian, Eutaw Fm, Georgia, USA (Savrdá and Nanson, 2003); Santonian-Campanian, Mooreville Chalk Fm, Alabama, USA (Savrdá and King, 1993); Campanian, Kanguk Fm, Arctic Canada (Chin et al., 2008); Campanian, several Fms, (Howard and Frey, 1984; Anderson and Droser, 1998; Anderson et al., 1999; Roberts, 2007); Campanian, Ericson Fm, Wyoming, USA (Martinsen et al., 1999); Campanian-Maastrichtian, Horseshoe Canyon Fm, Alberta, Canada (Bromley et al., 1984); Campanian-Maastrichtian, Quiriquina Fm, Chile (Buatois and Encinas, 2011); Campanian-Maastrichtian, Marambio Group, Antarctica (Kelly, 1988b); Campanian-Maastrichtian, Aguja and Javelina Fms, Texas, USA (Wheeler and Lehman, 2005); Maastrichtian, Mamu Fm, Nigeria (Arua, 1989); Maastrichtian, Mali (Tapanila et al., 2008); Maastrichtian, Peñalver Fm, Cuba (Villegas-Martín and Rojas-Consuegra, 2011); Maastrichtian, Qahlah Fm, Arabia (Wilson and Taylor, 2001).

**Paleocene:** Danian, Kangilia Fm, Greenland (Donovan et al., 2009); Danian, Clayton Fm, Alabama, USA (Savrdá, 1991a,b; Savrdá et al., 1993); Danian, Moreno Fm, California, USA (Schwartz et al., 2003); Thanetian, Williamsburg Fm, South Carolina, USA (Erickson and Melchior, 1998).

**Eocene:** Paleocene to Middle Eocene, Turcau Fm, Romania (Buatois et al., 2001); Lower Eocene, Cambay Shale Fm, India (Kumar et al., 2011); Lower Eocene, Crescent Fm, Washington, USA (Kiel, 2008); Ypresian, Ameki Fm, Nigeria (Arua, 1991); Ilerdian (Ypresian), Serraduy Fm, Spain (Carrasco, 2004); Ypresian, London Clay Fm, England (Huggett and Gale, 1995); Middle? Eocene, Ceru di Cueba Fm, Curaçao (Donovan, in press); Middle Eocene, Hump-tulips Fm, Washington, USA (Kiel, 2008); Middle Eocene, Brackleshams, England (Plint and Pickerill, 1985); Lutetian, Tallahatta Fm, Alabama, USA (Savrdá et al., 2005); Lutetian, Croatia (Tarlao et al., 2005); Upper Eocene, La Meseta Fm, Antarctica (Pirrie et al., 1998; Uchman and Gaździcki, 2006); Eocene, Richmond Fm, Jamaica (Pickerill et al., 1992).

**Oligocene:** Rupelian, Poland (Radwański, 2009); Late Oligocene–Lower Miocene, Pysht Fm, Washington, USA (Kiel, 2008).

**Miocene:** Ottnangian (Lower Miocene), Hungary (Gecse and Bozsik, 2007); Burdigalian, Upper Marine Molasse, Switzerland (Pfister and Keller, 2010); Lower-Middle Miocene, Bhuvan Fm, India (Mehrotra et al., 2001); Middle Miocene, Punta Judas, Costa Rica (Krawinkel and Seyfried, 1996); Middle Miocene, Grand Bay Fm, Grenadines (Pickerill et al., 2003); Badenian (Middle Miocene), Skole Fm, Poland (Rajchel and Uchman, 1998); Tortonian, Ambelousos Fm, Greece (Reuter and Brachert, 2007); Tortonian, Navidad Fm, Chile (Encinas et al., 2008); Miocene, Chichibu Bonchi Group, Japan (Obata, 1999, 2000).

**Pliocene:** Zanclean, France (Gibert, 1995); Pliocene, Bowden Fm, Jamaica (Pickerill et al., 1996).

**Pleistocene:** Lower Pleistocene, “Chiani-Tevere” depositional cycle, Italy (Monaco et al., 2011).

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