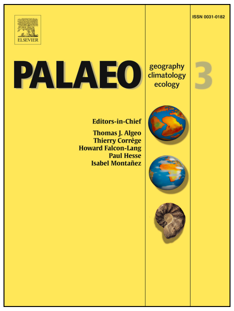

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Bivalve bioerosion in Cretaceous-Neogene amber around the globe, with implications for the ichnogenera *Teredolites* and *Apectoichnus*

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ABSTRACT

Amber samples with bivalve borings from six localities around the world, ranging in age from Hauterivian to Miocene, have been studied. The possible assignment to

Teredolites or *Gastrochaenolites* is discussed considering the type of substrate as an ichnotaxobase. It is proposed to regard amber or similar resins as a variant of xylic substrates and to maintain the separation between the two ichnogenera and their different paleoecological implications. The amber borings are assigned to *Teredolites clavatus* Leymerie, 1842 and *Apectoichnus longissimus* (Kelly and Bromley, 1984), respectively. The presence of bioglyphs in a few borings suggests a mechanical production process, with pholadid bivalves such as *Martesia* preserved inside many of the samples representing the producer. In general, the amber-producing trees mostly grew along a forested coastline, where they were occasionally flooded by seawater or even transported from rivers into the sea and later deposited.

Keywords: Borings, Bivalvia, ichnotaxonomy, Cretaceous, Neogene, fossil resin, substrate.

1. Introduction

Bivalves are the most common ichnotaxon trace makers in xylic substrates (Savrda and King, 1993) with multiple examples in the literature (e.g., Leymerie, 1842, Kelly and Bromley, 1984; Buatois and Mángano, 2011; Donovan, 2018, among others). *Teredolites* is described from woody substrates including – according to Kelly and Bromley (1984) – the following categories: driftwoods, mangrove roots, submerged forests, nutshells, pilings and ship hulls. For ichnofacies, Bromley et al. (1984) proposed the term woodground to distinguish wood from other i.e. softground, firmground and hardground. Later on, Savrda et al. (1993) discriminated two subtypes as xylic peatgrounds (“relatively laterally persistent composite wood substrates that correspond to the *Teredolites* ichnofacies”) and log-grounds (“relatively small, non-composite substrates represented by isolated logs”).

The material studied herein consists of *Teredolites* and *Apectoichnus* recorded in another, yet closely related type of substrate – amber. Up to now, there are very few works addressing this phenomenon: Woodward (1880, p. 394) mentioned that *Pholas* could bore in amber and referred to the “Highgate resin, in the cabinet of Mr Bowerbank”, which is a fossil resin from the London Clay (Ypresian, Eocene) in England, similar to copal. Villamil and Hasiotis (1993) reported minute *Teredolites* in late Turonian amber from transgressive deposits of Columbia. They reported the borings as if made in xylic substrate. Bandel et al. (1997), recognised club-shaped boreholes in mid-Cretaceous amber from Jordan quite like those excavated by modern Pholadidae, but they did not name them. Jahnke and Füldner (2004) described a series of borings in Baltic amber (Eocene in age), which they interpreted as being produced by insects. However, their morphology and size coincide with those presented in this work as *Teredolites clavatus* (especially the specimens from Mexico and Lebanon). Ross et al. (2010) and Smith and Ross (2017) described pholadid (Martesiinae) borings, assigned as *Teredolites* in earliest Cenomanian (Late Cretaceous) Burmese amber. Maksoud et al. (2017) displayed the existence of amber with shipworm borings, from Chambouk (North of Lebanon). Such borings occur as well indifferent fossiliferous amber from different outcrops of other Lebanese localities. Lately, Mao et al. (2018) in their study of Burmese amber, mentioned pholadids, but did not elaborate in their systematic details.

2. Materials and methods

Amber samples from five locations around the world from Hauterivian to Early Miocene in age are studied here, complemented by the records of Columbian Andes (Villamil and Hasiotis, 1993) (Table 1).

The available borings in amber were measured directly on the samples (Spanish and French amber) or images (Mexican, Mr John DeCosta private collection; Lebanon and Burmese amber) using the measurement tools in the ImageJ 1.46r software according to the diagram shown in Figure 1. The French amber (Albian of Archingeay, Charente-Maritime, SW France, Perrichot, 2004) is represented by two pieces (MNHN.F. A70078, MNHN.F. A70081) available in the palaeoentomological section of the Muséum National d'Histoire Naturelle in Paris. They contain 23 and 52 borings, respectively and were studied under the binocular microscope and in latex casts prepared in the museum and housed in the Nature Education Centre of the Jagiellonian University (CEP) – Museum of Geology in Kraków, Poland.

Micro-CT scans of bivalves included in Burmese amber slab Nr. F2854/BU/CJW housed in Jörg Wunderlich private collection (Hirschberg, Germany) were performed with a GE Phoenix nanotome X-ray|s tube at 90 kV and 150 µA, generating 2500 projections with 750 ms per scan and a useful voxel size of 4.6 µm. The cone beam reconstruction was performed using the GE datos|x 2 reconstruction software, and the data were visualised in Volume Graphics Studio Max 3.0. High-resolution and high-depth-of-field images of clay fill in some borings observed in Spanish amber were obtained using SEM EDX Hitachi S-3400 N with a variable pressure up to 270 Pa with EDX analyzer Röntec XFlash Si(Li).

3. Ichnotaxonomy

Ichnofamily: Gastrochaenolitidae Wisshak, Knaust and Bertling, 2019

Ichnogenus: *Teredolites* Leymerie, 1842

Type ichnospecies: *Teredolites clavatus* Leymerie, 1842

Revised diagnosis: Macroborings in xylic substrates and their derivate copal, amber or similar solid resins, clavate, straight or slightly curved, circular to oval in cross-section, narrowing from the base of the main chamber to the aperture, either abruptly and symmetrically, or gradually and less symmetrically (modified from Kelly and Bromley, 1984, Pickerill et al., 2003, and Kříž and Mikuláš, 2006).

Remarks: The diagnosis had to be revised, as amber or similar resins were not included in the original descriptions as a material derived from and related to a xylic substrate. This approach is considered more practical than to regard amber as a narrowly defined particular type of substrate on its own and thus avoids using (and adding) a new term such as amberground, as proposed and used by Smith and Ross (2017) and Mao et al. (2018). We argue that *Teredolites* is justified and essential to be conserved together with its analogue in lithic substrates, *Gastrochaenolites*, since we consider principal substrate types a valid ichnotaxobase at ichnogenus level.

Teredolites clavatus Leymerie, 1842

Figs. 2A–I, 3A–I, 4A–H, 5A–B, 6

Revised diagnosis: *Teredolites* predominantly perpendicular to the fibres in woody substrates or the resin surface, having a length/width ratio of less than 5.

Material: The Lebanon material (ALTC-01–02, Department of Palaeontology, The Natural History Museum, London) is a cuboid piece of amber (Fig. 2A) and an isolated mould of a boring (Fig. 2B) from Kfar Selouan (Central Lebanon), in “Grès de Liban” (Sandstone of Lebanon; Granier et al., 2015) that appear in primary deposits of the early Barremian (Maksoud et al., 2017). The piece is 17 x 13 x 9 mm in size, which contains one specimen.

The Spanish material is housed at the Palaeontological Museum, University of Zaragoza (MPZ), samples MPZ 2017/571 to MPZ 2017/726 and at Dinópolis Foundation, Aragonian Palaeontological Museum (MAP), Teruel, samples MAP-7594 to MAP-7596. All material is represented by three slabs and two small fragments from the San Just mountain pass, located to 2 km SW from Escucha (Teruel) and belonging to the Regachuelo Member, Escucha Formation, northern margin of the Aliaga Subbasin, (Peñalver et al., 2007) early-middle Albian in age. MPZ 2017/571 to MPZ 2017/726 contain 157 specimens distributed in three successive layers of amber that form a cluster 50 x 55 x 35 mm in size (Figs. 2C–F, 3A–D, 4G–H). The inner layer, whose thickness varies between 8 and 18 mm, holds 73 specimens. The middle layer, with a thickness between 2 and 9 mm, has 54 specimens, and the outer layer, with a thickness between 4 and 8 mm, contains 34 specimens. MAP-7594 is a piece of amber 80 x 45 x 35 mm in size that shows 48 borings distributed irregularly along surface (Figs. 2G, 3E–F). MAP-7595; MAP-7596 are two shards of the previous fragment (Fig. 2H–I) with 16 specimens with empty or partially filled borings.

The French amber is from the Albian of Archingeay (Charente-Maritime, SW France, Perrichot, 2004) and it comprises two pieces of amber containing at least 23 and 52 borings, respectively (Figs. 3G–I, 4D-F).

The main amber-producing area in Myanmar is the Hukawng valley (Hukawng Basin) in the Kachin region, northern Myanmar (Noetling, 1892; Chhibber, 1934; Cruickshank and Ko, 2003; Shi et al., 2012), whose most recent dating is from Albian to Cenomanian (Shi et al., 2012). The samples from this area are constituted by one rounded piece of amber from 15 x 30 x 26 mm in size, with 131 borings (In.20205. Department of Palaeontology, The Natural History Museum, London, Fig. 4A), as well as six pieces (BuB 1511–1549, from the Patrick Müller private collection, Käshofen, Germany), and sixteen pieces (F3091/BU/CJW- F3044/BU/CJW, from the Jörg Wunderlich private collection, Hirschberg, Germany. Table 1), respectively.

The Mexican amber is from the early Miocene Balumtun Sandstone and the late Oligocene La Quinta Formation coming from the Mr John DeCosta private collection, London. The exact origin of the sample is unknown, although it has been collected from the region of Chiapas. It is composed of one rounded piece of amber 21 x 120 x 70 mm size, which contains 18 specimens (Fig. 4B).

Description: Borings oriented more or less vertically to the surface, with the axis straight or slightly curved. In the longitudinal view, they have a typical bottle-bag-shape (Figs. 2B, G, 3E–F, H–I, 4E–F). Both aperture (proximal) and basal (distal) regions are circular to oval in cross-section (Figs. 1, 3B, G, 4A, C). The development of these regions can show irregularities due to the proximity and degree of occupation of each other, without exhibiting intersections. The diameter generally increases gradually to a maximum in the distal region. This maximum is located 0.25–0.33 mm from the base (Fig. 4D–F).

The length (L) of the Spanish specimens varies from 2.1 to 6.0 mm, with a mean of 3.6 mm on 221 measurements (Table 2). The width in the proximal region (Wp, Fig. 1) ranges from 0.4 to 1.9 mm, with a mean of 1.1 mm. The maximum diameter of the chambers or width distal (Wd) ranges from 0.3 to 2.6 mm, with a mean value of 0.5 mm. Mean L/Wd is 2.4. All borings are open or partially filled by loose, whitish clayey material. X-ray diffraction analyses indicate the presence of at least three types of phyllosilicates: pure kaolinite, illite (with very scarce Fe, and fillings that could derive from biotite. The detected sulfur is a stray signal from the ambient amber. This composition is different from that observed by Smith and Ross (2017) in the Burmese amber. These authors found that the filling of the clavate forms is formed by very fine to coarse sand, or by spare calcite cement.

Mexican amber has an L from 12.0 to 19.2 mm, with 17.4 mm on average. Wp between 3.0 and 4.2 mm, with 3.3 mm on average. Wd varies from 8.7 to 9.6 mm, with a mean value of 9.4 mm. Mean L/Wd is 1.9.

Burmese specimens have lengths that vary between 0.8 and 4.2 mm, with a mean of 2.7 mm, Wp is between 0.2 and 1.1 mm, at a mean of 0.6 mm: Wd varies from 0.5 to 2.6 mm, with 1.6 mm in average, the mean L/Wd is 2.7. The Lebanon amber piece has an L of 8.1 mm, a Wp of 2.5 mm, a Wd of 2.6 to 5.6 mm and a mean L/Wd of 1.9.

Finally, measurements of two latex casts of French amber show a Wd range from 0.9 to 3.5 mm, mean = 2.2. L ranges from 1.8 to 4.0 mm, at a mean of 2.9 mm. Wp could not be measured. Mean L/Wd is 1.3.

In general, the largest specimens are from Mexico and the Lebanon, the Spanish and Burmese amber being more similar. However, when the mean length/width distal ratio is analysed, the Spanish specimens present a higher degree of elongation proportionally.

The surfaces of the borings show striations in the form of a series of very thin ridges and grooves that are subparallel to each other and perpendicular to the axis of the chamber (Fig. 4G). Their spacing varies between 300–320 μm and their width varies between 70–80 μm. In the basal part of the chamber, several specimens show these striae more distinctly but with similar spacing (Fig. 5A). In the basal region, there often is an additional series of 15 to 20 ridges, which are oriented perpendicular to the previous ones, are less distinct and much finer (4–5 μm), and more densely aligned, with a spacing of only 20–25 μm (Fig. 4H).

In the Mexican amber, some specimens show a series of closely spaced (100 μm) short ridges (500 μm in average) in the basal part, forming a very characteristic chevron pattern (white arrows in Fig. 5B). On the contrary, towards the proximal part, the ridges of approximately same length show a direction perpendicular to the boring axis and are more widely spaced (280 μm), discontinuous, and with a broken trajectory (black arrows in Fig. 5B).

The French amber contains borings that are partly truncated at the present substrate surface. Their length (L) ranges from 1.0 to 5.8 mm, the minimum width (Wp) from 0.8 to 1.6 mm, and the maximum width (Wd) from 0.9 to 3.6 mm. The surface of the borings are partly or entirely covered with a thin, white lining, which is also present on the surface of some amber pieces. Occasionally, some borings contain a white mineralic substance, which fills most of the chamber. Most chamber surfaces devoid of bioglyphs. Only rarely, rings can be seen in the proximal and middle part of the chamber. The chamber tapers gradually from the perimeter, located in the distal region, to the entrance of the boring. Some chambers touch each other in their widest parts or even slightly overlap. The boring openings are circular to elliptical. Some of the openings can be partly fused.

As for the *Teredolites* of the Columbian amber (Villamil and Hasiotis, 1993), the characteristics are very similar, although the borings are smaller. The average of the WP is 0.4 mm, the Wd, is 0.6 mm and the mean L/Wd is: 3:1, but may be as small as 2:1. This latter ratio is closer to the Spanish specimens, where L mean / Wd is 2.4). The density of borings is similar in all cases except for the Mexican amber, where the large size of the borings reduces the density to only 1–2 specimens/cm^2. In the Spanish amber, densities range from 7 to 20 specimens/cm^2 (Figs. 2C-E, G, 3B), and the

Burmese amber (Fig. 4A) shows densities of 6 to 16 specimens/cm^2. Lebanese amber contains only one specimen/cm^2, and the French amber varies between 2 and 4 specimens/cm^2. For the Columbian case, no exact figures are given, although a piece of amber was reported to contain about 100 specimens closely packed and evenly spaced.

Remarks: In the Spanish amber, the striations transverse to the axis of the chamber can be interpreted as xenoglyphs (*sensu* Bromley et al., 1984). Although the microstructure of amber is unlike that of wood, i.e. amber is an amorphous substance, which has no grain or fibre orientation, it is usually arranged in successive layers. For this reason, the series of observed striae might be regarded as bioglyphs at superficial examination, but a detailed observation excludes this possibility.

True bioglyphs were observed by Villamil and Hasiotis (1993) in *Teredolites* from the Upper Cretaceous amber of the Magdalena Basin, Colombia, and attributed the grooved texture to the drilling mechanism. Bertling and Hermanns (1996) have reported similar structures from Rhenish lignites.

Also, Röder (1977), Bandel et al. (1997) and Savazzi (1999) have observed the mechanical abrasion of the substrates often resulting in visible tool marks on the surfaces of the boring. More recently, Smith and Ross (2017) mention that traces of the grinding process are visible on the surface of the borings containing pholadid bivalves inside the Burmese amber, although they did not consider details of this striation production process.

On the other hand, the little crests perpendicular to the previous ones in the Spanish amber (Fig. 4H) pose a greater uncertainty. Their disposition and orientation are not compatible with a xenomorphic structure. They could probably be related to some minor ornamental element of the producer's shell, although usually boring bivalves produce bioglyphs whose lines set some 2 mm apart.

The probable explanation could perhaps be related to the fact that most pholadid shells possess commarginal rows of sharp teeth that are arranged in radial series in rock or hard substrates. According to Savazzi (1999) revolving of the shell produces a set of ring-shaped furrows, which are gradually excavated by an individual tooth or by a series of homologous teeth during growth.

In the same way, similar bioglyphs in the uncompressed borings in the Mexican amber demonstrate scratches and grooves made by the rugose sculpture of the trace-makers' valves during boring (Fig. 5B).

The presence of bioglyphs preserved on the inner surface of some of the traces (Fig. 5B) indicates that the substrate must have been indurated by the moment of trace production.

Smith and Ross (2017) made a similar observation by a pair of articulated shells floating in the amber suggesting that the resin was not hard when the bivalves were boring into it. A possible alternative explanation could be that the resin was liquefied after the solid phase, e.g. due to a slight increase in temperature, pressure or natural chemical changes. These small transformations are possible because in some cases insect fossils inside amber are deformed by heat and because resin polymers can change by the destruction of the double carbon bind.

Jahnke and Füldner (2004) in the description of the borings in Baltic amber deduced that the wood resin was already hard at least at time of the decomposition of the tree. Mao et al. (2018) suggested that ambers may or may not be hardened entirely when borings were produced, although it is hard to conceive how a mechanical bioeroder should be able to rasp away 'liquid' or 'plastic' resin without totally clogging its ornament.

For this reason and because the model proposed in this paper offers an explanation for shells seemingly floating in the resin, we maintain that the amber was a hard substrate at the time of ichnogenesis.

Ichnofamily: Gastrochaenolitidae Wisshak, Knaust and Bertling, 2019

Ichnogenus: *Apectoichnus* Donovan, 2018

Type ichnospecies: *Apectoichnus longissimus* (Kelly and Bromley, 1984)

Revised diagnosis: Elongate borings in xylic substrates and its derivate amber, or other solid resins, commonly circular in cross-section, curved to contorted and intertwined, may have a calcareous lining, usually of more or less constant diameter.

Apectoichnus longissimus (Kelly and Bromley, 1984)

Figs 2I, 5C–E

Revised diagnosis: *Apectoichnus* predominantly parallel to the grain or fibres in a xylic substrate, length/width ratio greater than 5. Sinuous to contort.

Material: Only present in the Albian Spanish material. Five specimens, four of them located in the outer layer of the amber ball (MPZ-723–726) (Figs. 2D, 5C) and one in the middle layer (MPZ-722). One specimen is incomplete and appears in a fragment of amber (MPA-7596; Fig. 2I).

Description: The borings are arranged parallel to the substrate surface in their proximal part and inclined to more vertical course in the distal region (Figs. 2D, 5C–D, 6). Slightly contorted and straight in longitudinal section, similar to *Teredolites clavatus*. In cross-section, the aperture is almost circular, while the basal part is oval to elliptical. When the degree of occupation is high coexisting with *T. clavatus*, the two types of boring may come into contact with each other but never intersect (Figs. 2C, E–F, I, 5C). The length (L) (Table 1) varies from 2.4 to 9.5 mm, with a mean of 4.9 mm. The width in the proximal region (Wp) ranges from 0.4 to 0.7 mm, with a mean of 0.6 mm. This progressive increase in diameter from apertural to distal zones has already been observed by Savrda and King (1993). Width distal~~,~~ (Wd) varies from 0.7 to 1.6 mm, with a mean value of 1.2 mm. Mean L/Wd is 4.1. All of them are entirely or partially filled by clayey sediment material of kaolinite type (Fig. 5C–E). Interior of the borings shows (especially in the distal portion) similar series of ridges and grooves as observed in *T. clavatus*, with same size and spacing, giving the borings a slightly ringed appearance. Savrda and Smith~~,~~ (1996), noted similar vestiges of weak linings in woody substrates of Panama City Beach, Florida, and only two specimens show more pronounced linings, 20–40 μm in thickness, present in both the neck and main chamber (Fig. 5E).

Remarks: The relationship L/Wd is slightly higher than 5.2 on average, which, as established by Kelly and Bromley (1984), would include it within the ichnospecies *longissimus*. The apertural region of the borings is not perpendicular to the surface such as described by Savrda and King (1993) and Gingras et al. (2004), but has a more parallel course to it. This apparent path is most likely due to erosion, which has removed the first millimetres of the surface where the entrance probably was more vertically oriented.

4. *Teredolites* versus *Gastrochaenolites*

Substrate type is considered an essential ichnotaxobase for trace fossils in general, and bioerosion trace fossils in particular, where the principal substrate types lithic/skeletal (mostly biogenic and abiogenic carbonates), osteic (bone, teeth, scales), and xylic (wood, seeds) are a suitable ichnotaxobase particularly at ichnogenus level (e.g., Bertling et al., 2006; Höpner and Bertling, 2017; Wisshak, 2017). Most recently, Wisshak et al. (2019) subdivided the largest and somewhat incoherent group of ‘lithic/skeletal’ substrates into calcareous substrates (biogenic and abiogenic carbonates) and siliceous substrates (sensu lato; biogenic and abiogenic silica, silicate minerals and rocks, siliciclastic rocks). This argument is grounded on the fact that for the majority of bioerosion ichnospecies, the presence of calcium governs the mode of penetration (chemical and mechanical versus mechanical only) and thus, behaviour. Amber is a hard, fossil resin, soluble in acetone or toluene and essential oils. These properties are not shared by common xylic substrates, a term included in the current diagnosis of the ichnogenus *Teredolites* (Kelly and Bromley, 1984; Kříž and Mikuláš, 2006). The term “xylic”, refers to the classical Greek "xylos" (= wood) for this reason amber cannot be considered a xylic substrate, but a substance derived from it. Amber is an organic multi-compound product of the polymerisation of the resin of different higher plants. Its composition of carbon (78.8%), hydrogen (10.2 %) and oxygen (11%), is similar to wood (average composition of 50% carbon, 42% oxygen, 6% hydrogen and the remaining 2% nitrogen and other elements).

Furthermore, amber derives from wood, although differing from it in structure, lacking the fibrous architecture. Consequently, Wisshak et al. (2019) considered amber within the category of xylic substrates in the sense that it is a wood derivative, just like seeds. In support of this line of reasoning, we here argue that (1) amber is a product of a tree, (2) amber (former resin or its precursor, copal) may be found in and on wood, and (3) there are individuals of *Teredolites* that pass through wood and amber as it is the case of a slab of Burmese amber from the Patrick Müller collection. This piece was not available for study because it is on display at the amber exhibition at the Stuttgart Natural History Museum (P. Müller, pers. comm., Sept. 2018).

For this reason, we include amber as a substance derived from a xylic material (wood), similar in composition, but not in structure.

Bromley et al. (1984) and Bromley (2004) discussed the affinities and differences between *Gastrochaenolites* and *Teredolites*, justifying their taxonomic separation based on the different principal kind of substrate involved. The authors also established the ichnotaxobases to discriminate the two ichnogenera, proposing to keep the name *Teredolites* for xylic substrates and *Gastrochaenolites* for lithic ones. The majority of authors (e.g., Kelly and Bromley, 1984; Mikuláš, 1993, 2006; Mikuláš et al., 1995; Lavigne, 1999; Buatois et al., 2002; Gingras et al., 2004; Ferrer and Gibert, 2005; Bertling et al., 2006; Kříž and Mikuláš, 2006; Buatois and Mángano, 2011; Buatois et al., 2016; Minter et al., 2016) have accepted this proposal. As amber is genetically related to trees, traces made on it could be considered as belonging to the *Teredolites* ichnofacies. Nevertheless, Kelly and Bromley (1984) and Savrda et al. (1993), did not consider amber in woodgrounds. By assigning borings in amber to *Teredolites*, Villamil and Hasiotis (1993), implicitly accepted amber as a xylic-related substrate. In addition to this, the material presented here shows not only the typical morphology of *T. clavatus* but also the ichnofabrics developed (Figs. 2C–E, 3B, G, 4A–C).

In contrast to this traditional view, Donovan and Ewin (2018) considered all types of substrate a poor ichnotaxobase, and they exemplify this by the case of clavate borings commonly produced by bivalves across substrate types. They consider *Gastrochaenolites* morphologically indistinguishable from *Teredolites*, and thus synonymise the two ichnogenera, giving priority to *Gastrochaenolites*. There is little doubt that Donovan and Ewin (2018) were right concerning the given morphological similarity of *Teredolites* and *Gastrochaenolites*. By synonymising them, they employ the exception (i.e., a boring crossing different substrate types) to ground a rule upon (i.e., rejecting substrate as suitable ichnotaxobase), even though most of the bioerosion traces and the respective ichnotaxa are restricted to a specific type of substrate. On the other hand, Carmona et al. (2007) identified *Gastrochaenolites*-like traces in unconsolidated substrates and consequently advocated that the ichnogenus *Gastrochaenolites* should even be extended into the bioturbation realm.

However, there is general agreement, as already expressed in the first workshop on ichnotaxonomy (WIT) held on Bornholm, Denmark, and in Kraków and Tymbark, Poland, that substrate is essential to distinguish burrows and borings of identical morphology. This view was published by Bertling et al. (2006) who recommended to keep trace fossils found in the principal types of lithic, woody and soft substrates separate regardless of morphologic similarity (not identity). Subsequently, Höpner and Bertling (2017) argued that osteic substrates should be regarded as another distinct type of substrate, and most recently, Wisshak et al. (2019), divided lithic substrates into the calcareous and siliceous substrate categories. We herein follow the perspective that substrate is an important and valid ichnotaxobase, particularly on the ichnogenus level, and in due course retain *Teredolites* and *Gastrochaenolites* as separate ichnogenera, despite them sharing a common morphology. Also, we here follow Donovan (2018) who established the ichnogenus *Apectoichnus* for the long, slender forms, usually parallel to fibres, now represented by the type ichnospecies *T. longissimus*.

Apart from this purely ichnotaxonomical reasoning, we see clear advantages of keeping *Teredolites* and *Gastrochaenolites* as separate ichnogenera, in that *Teredolites* lends its name also a distinct substrate-controlled type of ichnofacies, while *Gastrochaenolites* can appear in both the *Glossifungites* firmground ichnofacies, as well as of the *Trypanites* hardground ichnofacies, being most frequent in the latter. In addition, *Teredolites* as a woodground boring is primarily related to the herbivorous search for food (fodinichnion), while hardground borings are commonly produced for protection (domichnion), produced by organisms whose trophic type is suspension feeding (MacEachern et al., 2007; Buatois et al., 2016). These are not ichnotaxonomical arguments, but palaeoecological ones, but they do show that often more information is attached to an ichnogenus than just the pure shape – and we would lose this gain of information when restricting ourselves to alone.

5. Potential trace-makers of the amber borings

Fortunately, in the Mexican and Burmese amber, specimens of bivalves have been preserved to allow an adequate systematic approach. Thus, all of them exhibit the characteristics of the family Pholadidae (Kennedy, 1974), subfamily Martesiinae Grant and Gale, 1931, specifically with the genus *Martesia* Sowerby, 1824. Although its conservation is good, there is no record of the inside of the valves, which means a particular handicap when establishing systematic precisions at a specific level. *Martesia* is the oldest known genus of Pholadidae, occurring in the Carboniferous (questionably) and from Jurassic to Recent (Turner, 1969). Adult Mexican specimens (Late Oligocene–Early Miocene) show the mesoplax broadly oval (Fig. 7A), and flat, similar to a cushion with the metaplax and hypoplax pointed or truncated posteriorly (Fig. 8D, F, G). Palmer and Brann (1965) refer to several references from *Martesia* for the Paleocene (*Martesia* Gardner, 1935) and Eocene (*M. elongata* Aldrich, 1886), *M.*? *laredoensis* Gardner, 1923, *M. recurva* Aldrich, 1921, *M. texana* Harris, 1895) from eastern and southeastern of the United States. Kennedy (1974) also described in the West American Cenozoic deposits, the existence of two Eocene species of *Martesia*, *M. meganosensis* Clark and Woodford, 1927 and *M.* (*Particoma*) *tolkieni* Kennedy, 1974. The latter differs from

Martesia by the presence of a non-bifurcate metaplax and hypoplax, and by the shape of the mesoplax.

All these Paleocene-Eocene species display external morphological characteristics (for more details see Turner, 1969; Kennedy, 1974) that are different from those observed in their Oligocene–Miocene counterparts.

Other Pholadidae with this stratigraphic range may be according to Turner (1955), *Barnea* Leach in Risso, 1826, *Parapholas* Conrad, 1848, *Jouannetia* Des Moulins, 1828 and *Xylophaga* Turton, 1822. However, *Martesia* differs from these related genera by the presence of the mesoplax, metaplax, hypoplax, funnel-shaped pit below the umbonal reflection, and complete callum in adult specimens. The umbonal-ventral sulcus and its corresponding ridge is the only radial division of the shell (Fig. 7B).

In the case of the Cretaceous Burmese specimens, young individuals showing the typical large pedal gape (Figs. 7B, 8C, E) represent the most common. Adult individuals have a subtriangular mesoplax, pointed towards the anterior part and rounded towards the posterior one. Kennedy (1974) in his review on the Cretaceous Pholadidae of North America only identifies the genera *Opertochasma* Stephenson, 1952, and *Xylophagella* Meek, 1864 with a genus, *Turnus* Gabb, 1864 of uncertain systematic position. All of them are also of very different morphologies to *Martesia*.

The current species of *Martesia, M. (Martesia) striata* Linnaeus, 1758 and *M.* (*Martesia*) *fragilis* Verrill and Bush, 1898, show apparent differences in the mesoplax, which is nearly circular, and inflated in the adult specimens and semicircular in the young of the former, while it is concentrically sculptured in the latter.

For all these reasons, and taking into account the limitations for the observation of the internal structures of the valves, it is considered appropriate to classify the specimens of Cenozoic amber as *Martesia* sp. 1 (made up of adult specimens) and those of Mesozoic amber as *Martesia* sp.2 (includes young and adult specimens). In the latter case, according to Crampton (1990), an in-depth review is necessary for Mesozoic Pholadidae.

This implies that in this case, *Teredolites* can be associated with the work of martesiine bivalves (also see Smith and Ross, 2017). The striations and ring structures indicate that the producer owned a rugose sculpture similarly to *Martesia.* This is not characteristic of other bivalve borers such as *Gastrochaena*, which is a frequent producer of *Gastrochaenolites*.

Boring cycle of *Martesia* (Ansell and Nair, 1969) comprises first the retraction of the shell to the base of the boring, and second, the abrasion of the boring margin by movements of the shell caused by a single consecutive contraction of each of the adductor muscles. On the other hand, *Apectoichnus longissimus* (formerly *Teredolites longissimus*) has been classically associated with boring bivalves of the family Teredinidae (e.g., *Teredo*, *Nototeredo*, *Bankia*, see Savrda and King, 1993; Gingras et al., 2004; Kříž and Mikuláš, 2006) and xylophagaines (Evans, 1966). The coexistence of both ichnospecies in the same layers, with a clear dominance of *T. clavatus*, seems to indicate colonisation of the substrate with a standard behaviour (domichnion). Some of the factors that influence the form of the borings are the density of colonisation and the degree of substrate compaction (Evans, 1970; Lavigne, 1999). For this reason, morphological differences observed in the borings are due to the isotropic nature of amber (Mexican, Lebanese and Burmese amber) versus its concentric structure in layers (Spanish amber), rather than to the type of behaviour of the producers. It must be taken into account that in some cases, as in the Mexican amber, borings are compressed and thus appear very closely spaced. This indicates that the amber was plastically deformed or compressed after the traces had been produced, as also observed in the Burmese amber (Smith and Ross, 2017). A reason for the dense occupation of the amber is the gregarious larval behaviour of *Martesia* (and Martesiinae in general) when lighted, sciaphilous larvae prefer to settle on the underside of horizontal surfaces (Nagabhushanam, 1959). It should be noted that not only martesiine bivalves seem to be potential trace makers, but also amphipods and marine isopod crustaceans (Bromley, 1970). However, the borings of the isopods have a much larger diameter (2–3 mm), and their tunnels are much longer (up to 10 cm) and tend to be arranged en-echelon. Their course usually follows the direction of the wood fibres until they hit another boring or until they return to the wood-water or wood-air interface (Gingras et al., 2004). On the other hand, amphipods (represented by Cheluridae) are usually associated with isopods of the genus *Limnoria* (Coleman and Renz, 2009). This causes the chelurids to enlarge the burrows initiated by the limnoriids (Thomas, 1979).

Further comparisons can be made with some of the more or less elongated clavate borings produced by insects, since these arthropods have been found fossilized in the amber of the studied sites (Grimaldi et al., 2002; Perrichot, 2004; Peñalver and Delclòs, 2010; Azar et al., 2003, 2010). However, as described by Kříž and Mikuláš (2006), the ichnogenera *Anobichnium* Linck, 1949 (see also Rajchel and Uchman, 1998), *Carporichnus* Genise, 1995 and *Eocavum* Buchholz, 1986, differ significantly from *Teredolites,* since they are both more asymmetrical and cylindrical (*Anobichnium* case) or have radial tunnels (*Carporichnus*) or are much larger and show slightly different shape (*Eocavum*).

6. Taphonomic model

On the base of the rich available material of bored Burmese amber, we propose a general taphonomic model (Fig. 9), explaining the various observed and hypothetical modes of preservation of pholadids and their borings in amber. Our model predicts that the pholadids bored into a living, resin-secreting tree, which was at least periodically immersed in seawater. In the first phase, pholadid borings in wood with both valves preserved in situ were variably filled with sediment or remained unfilled (Fig. 9A) (it is noteworthy to mention that the disarticulated valves of the bivalves generally remain in place within the boring because their size (if intact) exceeds that of the boring aperture). In the next stage, fresh resin fills the empty space within the borings or seals the borings at the level of the wood surface (Fig. 9B). Subsequently, while the resin hardens, wood and other organic remains may gradually decay (Fig. 9C). In the final stages, wood is replaced by subsequent episodic flows of resin, which after hardening may repeatedly be bored by pholadids (Fig. 9D). The final result is an amber slab showing borings including preserved pholadid body fossils, preserved wood remains, borings completely or incompletely (geopetally) filled with sediment and borings neither filled with resin nor with sediment, encapsulated by a final flow of resin (Fig. 9E).

7. Palaeoenvironmental setting

Teredolites and *Apectoichnus* are considered indicators of marine to marginal marine environments (e.g., Breddin, 1935; Philipp and Wehrli, 1936; Bradshaw, 1980; Bromley et al., 1984; Urreta, 1987; Arua, 1991; Savrda, 1991; Mikuláš, 1993; Gingras et al., 2004; Kříž and Mikuláš, 2006; Savrda et al., 1993; Mikuláš et al., 1995; Lavigne et al., 1998; Pirrie et al., 1998; Obata, 2000). However, occurrences of *Teredolites* in deep-sea sediments are also noticed (e.g., Turner, 1973). Other authors linked the presence of these trace fossils to marine transgressions (Philipp and Wehrli, 1936; Panos and Skacel, 1966; Bromley et al., 1984; Savrda, 1991; Savrda et al., 1993). *Teredolites* in allochthonous logs, usually indicate a transitional environment between a truly terrestrial and a marine-influenced setting (e.g., Ferrer and Gibert, 2005). However, deep-sea occurrences are also present (e.g., Uchman, 1995).

In the Columbian amber, the specimens appear associated with driftwoods, which have been interpreted by Villamil and Hasiotis (1993) as indicators of transgressive pulses that would cause the flooding of a forested coastline, as well as the drift towards the basin of potential xylic substrates. Most probably, this is the most plausible explanation, since only a few representatives of Martesiinae are able to withstand brackish water, in such a way that after the advance of the sea into coastal forests the juveniles died when the salinity decreased again.

On the other hand, and according to the previous authors, small *Teredolites* could represent young populations that ceased by the sinking of the woods in oxygen-poor waters. Another alternative explanation for the dwarfing of the population would be their production in an environment whose oxygen content was quite low. It is also possible that both wood and amber can be transported from rivers into the sea, can float in saline water and later deposited.

The presence of *Apectoichnus* and *Teredolites* in the Spanish material indicates an episode of marine influence during the deposition of this member, initially consisting of freshwater swamp deposits (Querol et al., 1992). Such a transgressive pulse would entail the transition from terrestrial conditions to tide-influenced ones. In a first phase (Fig. 10A) boring bivalves colonised the external surface of the amber looking for dwelling (*T. clavatus*). Subsequently, a new layer of amber covered the previous one, repeating the colonization process. Finally, a third and last layer covered the previous ones, with the installation of *Apectoichnus longissimus* together with *T. clavatus* (Fig. 10B–E). A slight further transport eroded the amber ball prior to its final burial.

Nevertheless, the reworking of amber pieces and bioerosion under fully marine conditions and deposition elsewhere cannot be ruled out. In this case, amber-bearing beds would only indicate a marine source near in space and time. It is important to emphasise that the presence of these isolated pieces does not necessarily indicate a marine influence, especially if it is shown to have an allochthonous origin. Therefore, the appearance of *Teredolites* and *Apectoichnus* in amber does not prove a marine deposit, but a derivation from a marine source only, next to the area where they appear. A similar interpretation has been held by Jahnke and Füldner (2004) for the Baltic amber. According to these authors, this amber could be transported by streams and rivers from the resin-producing “amber forest” into the Oligocene river delta and the nearby shallow sea.

The French amber deposits are interpreted as a deltaic sandy environment (Perrichot, 2004), probably in arid conditions within a predominantly warm and humid climate (Frakes, 1979; Jenkyns et al., 1994; Fenner, 2001). In addition, Girard et al. (2008) found various marine microfossils that were probably introduced by wind, spray, or high tide from the beach or the sea onto the resin flows of the coastal mixed forests dominated by conifers. Truncated borings on the surfaces of amber pieces suggest abrasion during transport, and deposition.

In this way, French and Spanish amber borings seem to have been produced in forests growing very close to the sea beach in a similar analogy to what happens today in araucaria forest in New Caledonia (Nel pers. comm.) or in SE Asia (Schmidt et al., 2018).

The Cenomanian amber of Salignac (Alpes-de-Haute-Provence) is found in deep marine palaeoenvironment, with ammonites and marine reptiles (Nel pers. obs.). It was produced some kilometres away, thus amber can go far from its production area into sea. A similar fact is reported by Yu et al., (2019) in the Burmese amber, where they found the presence of an ammonite together with marine gastropods, intertidal isopods, and diverse terrestrial arthropods.

Martesia striata can tolerate low salinities in mangrove forests (e.g., Singh and Sasekumar 1994; Sivakumar and Kathiresan 1996; Ḉevik et al., 2015). Smith and Ross (2017) concluded that resin-producing trees grew very close to an environment in which the pholadid bivalves lived, possibly a brackish water bay or inlet. In a similar context, *Martesia* is known to bore into living mangrove roots in India and Australia, (Dharmaraj and Balakrishnan, 1981; Santhakumaran, 1983; Brearley et al., 2003). However, keeping in mind that mangroves did not yet exist in the mid-Cretaceous, the increasing record of marine biota preserved in Burmese (e.g., Xing et al., 2018) and Mexican amber (Huys et al., 2016), suggests coastal swamp habitats which were regularly flooded by sea water. In this line, Mao et al. (2018) mentioned that the shape of the Burmese amber suggests that it has not been transported over long distances, and the amber-producing plants grew not far from the beach or just by the sea. Amber would be deposited with debris from marine organisms, and some pholadid bivalves could bore into its surface during the relatively short exposure time. On the other hand, shallow water environments with plants, resin, and roots decomposing in the sea or on the beach near a forest could also be adequate.

The Mexican amber is associated with a sequence of marine calcareous sandstones and silt with beds of lignite (Poinar, 1992). According to Langenheim (1995) and Solórzano Kraemer (2010), it represents a coastal setting with resin-producing trees similar to the Burmese amber.

7. Conclusions

The studied amber samples ranging in age from Early Cretaceous to Miocene show bivalve borings. As amber and similar solid resins have to be considered as a derivative of xylic substrates. The borings are included in *Teredolites clavatus* Leymerie, 1842 and *Apectoichnus longissimus* (Kelly and Bromley, 1984). To this end, the diagnosis of both ichnotaxa was reviewed and updated. It is proposed to maintain the type of substrate as a valid ichnotaxobase and to exclude *Gastrochaenolites* from borings in xylic substrates. The palaeoenvironmental significance (trophism, ichnofacies) of these ichnotaxa is thus maintained. A mechanical production process is deduced from the presence of bioglyphs in most samples, and its production is related to pholadid bivalves, specifically *Martesia* sp. 1 for Cenozoic amber and *Martesia* sp. 2 for Mesozoic, respectively, which are found in situ inside borings in the Mexican and Burmese amber. The palaeoenvironmental conditions, except for small differences, can be summarised in a context of a forested or marshy coast, where the amber-producing plants grew close to the sea, with occasional marine ingressions or at least seaward riverine transport.

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References

Aldrich, T.H., 1886. Notes on the distribution of Tertiary fossils in Alabama and Mississippi. Cincinnati. Soc. Nat. Hist., Jour. 8 (4), pp. 256–257.

Aldrich, T.H., 1921. New Eocene species from Alabama. Bull. Amer. Paleont. 9 (37), 32 pp.

Ansell, A.D., Nair, N.B., 1966. The mechanisms of boring in *Martesia striata* Linne (Bivalvia: Pholadidae) and *Xylophaga dorsalis* Turton (Bivalvia: Xylophaginidae). Proc. R. Soc. Lond. B 174, 123–133.

Arua, I., 1991. The trace fossil *Teredolites longissimus* in calcareous concretions from the Eocene Ameki Formation, southeastern Nigeria. J. Afr. Earth Sci. 12, 605–608.

Azar, D., Nel, A., Gèze, R., 2003. Use of Lebanese amber inclusions in paleoenvironmental reconstruction, dating and paleobiogeography. Acta Zool. Cracov. 46, 393–398.

Azar, D., Geze, R., Acra, F., 2010. Lebanese amber. In: Penney, D. (Ed), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 271–298.

Bandel, K., Shinaq, R., Wetschat, W., 1997. First insect inclusions from the amber of Jordan (Mid Cretaceous). Mitt. Geol. Paläont. Inst. Uni. Hamburg 80, 213–23.

Bertling, M., Hermanns, K., 1996. Autochthonous bivalve borings in the Rhenish Lignite District and their sedimentological implications. Zbl. Geol. Paläont. Teil I 1995 (1/2), 33–44.

Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G.R., Genise, J., Mikuláš, R., Nielsen, J.K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M., Uchman, A., 2006. Names for trace fossils: a uniform approach. Lethaia 39, 265–286.

Bradshaw, M.A., 1980. Boring bivalves in the New Zealand Cenozoic with a redefinition of *Teredolites*. Rec. Canterbury Mus. 9, 289–294.

Brearley, A., Chalermwat, K., Kakhai, N., 2003. Pholadidae and Teredinidae (Mollusca: Bivalvia) collected from mangrove habitats on the Burrup Peninsula, Western Australia. In Proceedings of the eleventh International Marine Biological workshop: The marine flora and fauna of Dampier, Western Australia 345, p. 361.

Breddin, H., 1935. Die paralische Entwicklung der Niederrhenischen Braunkohle. Braunkohle 34, 851–862.

Bromley, R.G., 1970. Borings as trace fossils and *Entobia cretacea* Portlock, as an example. In: Crimes, T.P., Harper, J.C. (Eds.), Trace fossils. Geological Journal Special Issue 3, 49–90.

Bromley, R.G., 2004. A stratigraphy of marine bioerosion. In: McIlroy, D. (Ed.), The application of ichnology to palaeoenvironmental and stratigraphic analysis. The Geological Society, London, Special Publications 228, 455–479.

Bromley, R.G., Pemberton, S.G., Rahmani, R.A., 1984. A Cretaceous woodground: The *Teredolites* ichnofacies. J. Paleontol. 58, 488–498.

Buatois, L., Mángano, M.G., 2011. Ichnology: Organism-Substrate Interactions in Space and Time. Cambridge University Press, Cambridge (358 pp).

Buatois, L., Mángano, G., Aceñolaza, F.G., 2002. Trazas Fósiles. Señales de comportamiento en el registro estratigráfico. Edición especial Museo Paleontológico Egidio Feruglio 2, pp. 382.

Buatois, L., Carmona, N., Curran, A., Netto, R., Mángano, G., Wetzel, A., 2016. The Mesozoic marine revolution. In: Buatois, L., Mángano, G. (Eds.), Trace-Fossil record of major evolutionary events. Volume 2: Mesozoic and Cenozoic. Topics in Geobiology 40, 19–134.

Buchholz, H., 1986. Die Höhle eines Spechtvogels aus dem Eozäm von Arizona, USA (Aves, Piciformes). Verh. Naturwiss. Vereins Hamburg N. S. 28, 5–25.

Carmona, N.B., Mángano, M.G., Buatois, L.A., Ponce, J.J., 2007. Bivalve trace fossils in an early Miocene discontinuity surface in Patagonia, Argentina: Burrowing behaviour and implications for ichnotaxonomy at the firmground-hardground divide. Palaeogeogr. Palaeoclim. Palaeoecol. 255, 329–341.

Ḉevik, C., Ozcan, T., Gündoğdu, S., 2015. First record of the striate piddock *Martesia striata* (Linnaeus, 1758) (Mollusca: Bivalvia: Pholadidae) in the Mediterranean Sea. Bioinvasions Records 4, 277–80.

Chhibert, H.L., 1934. The mineral resources of Burma. London: Macmillan & Co., pp. 320.

Clark, B.L., Woodford, A.O., 1927. The geology and paleontology of the type section of the Meganos Formation (lower Middle Eocene) of California. University of California Publications in Geological Sciences 17(2), 63–142.

Coleman, C.O., Renz, A., 2009. Cheluridae. Zootaxa 2260, 339–343.

Conrad, T.A., 1848. Descriptions of two new genera and new species of Recent shells. Proc. Acad. Nat. Sci. Philadelphia 4(6): 121.

Crampton, J.S., 1990. A new species of Late cretaceous wood-boring bivalve from New Zealand. Palaeontology 33, 981–992.

Cruickshank, R.D., Ko Ko, 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. J. Asi. Earth Sci. 21, 441–455.

Des Moulins, C., 1828. Description de trois genres nouveaux de coquilles fossils du terrain tertiaire de Bordeaux. Soc. Linnéenne Bordeaux, Bull. Hist. Nat. 2, 226–255.

Dharmaraj, K., Balakrishnan, N., 1981. Timber boring animals of Talapady mangroves and adjoining areas with a record of *Martesia* sp. (Bivalvia: Pholadidae) boring into living trees. Mahasagar 14.2, 159–162.

Donovan, S.K., 2018. A new ichnogenus for *Teredolites longissimus* Kelly and Bromley. Swiss J. Paleont. 137, 95–98.

Donovan, S.K., Ewin, T.A.M., 2018. Substrate is a poor ichnotaxobase: a new demonstration. Swiss J. Paleont. 137, 103–107.

Evans, J.W., 1966. The ecology of the rock-boring clam *Penitella penita* (Conrad 1837). Thesis, University of Oregon, 111 pp.

Evans, J.W., 1970. Palaeontological implications of a biological study of rock-boring clams (Family Pholadidae). In: Crimes, T.P., Harper, J.C. (Eds.), Trace fossils. Geological Journal Special Issue 3, 127–140.

Fenner, J., 2001. Middle and Late Albian geography, oceanography, and climate and the setting of the Kirchrode I and II borehole sites. Palaeogeogr. Palaeoclim. Palaeoecol. 174, 5–32.

Ferrer, O., Gibert, J.M. de, 2005. Presencia de *Teredolites* en la Formación Arcillas de Morella (Cretácico inferior, Castellón). Rev. Esp. Paleont. Nº especial X, 39–47.

Frakes, L.A., 1979. The Cretaceous period. In: Frakes, L.A. (Ed.), Climates Throughout Geological Time. Amsterdam, Elsevier, pp. 168–178.

Gabb, W.M., 1864. Description of the Cretaceous fossils. Paleontology of California 1, section 4, pp. 57–243.

Gardner, J.A., 1923. New species of Mollusca from the Eocene deposits of southwestern Texas. U.S. Geol. Sun, Prof. Paper 131-D, pp. 109–115.

Gardner, J.A., 1935. The Midway group of Texas, including a chapter on the coral fauna by Thomas Wayland Vaughan and Willis Parkinson Popenoe. Univ. Texas Bull. 3301, 403 pp.

Genise, J.F., 1995. Upper Cretaceous trace fossils in permineralized plant remains. Ichnos 3, 287–299.

Gingras, M.K., MacEachern, J.A., Pickerill, R.K., 2004. Modern perspectives on the *Teredolites* ichnofacies: Observations from Willapa Bay, Washington. Palaios 19, 79–88.

Girard, V., Schmidt, A.R., Saint Martin, S., Struwe, S., Perrichot, V., Saint Martin, J.P, Grosheny, P., Bréton, G., Neraudeau, D., 2008. Evidence for marine microfossils from amber. Proc. Natl. Acad. Sci. 105, 17426–17429.

Granier, B., Azar, D., Maksoud, S., Gèze, R., Habchi, R., 2015. New fossiliferous sites with Barremian Charophyta in the “Grès du Liban” (Lebanon), with a critical perspective regarding the nature of *Munieria* Hantken ex Deecke, 1883. Carnets de Géologie 15, 199–229.

Grant, U.S., IV, Gale, H.R., 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Mem. San Diego Soc. Nat. Hist. 1, 1–1036.

Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. Am. Mus. Novit. 3361, 1–71.

Harris, G.D., 1895. New and otherwise interesting Tertiary Mollusca from Texas. Acad. Nat. Sci. Philadelphia, Proc. 47, 45–88.

Höpner, S., Bertling, M., 2017. Holes in bones: ichnotaxonomy of bone borings. Ichnos 24, 259–282.

Huys, R., Suárez-Morales, E., Serrano-Sánchez, M. de L., Centeno-García, E., Vega, F.J., 2016. Early Miocene amber inclusions from Mexico reveal antiquity of mangrove-associated copepods. Sci. Rep. 6, 34872.

Jahnke, H., Füldner, K., 2004. Trace fossils of insects in Baltic amber? In: Mikuláš, R. (Ed.), 4th International Bioerosion Workshop, Prague, August 30 – September 3, 2004, Abstract Book. Institute of Geology, Academy of Sciences of the Czech Republic, Prague, pp. 20–23.

Jenkyns, H.C., Gale, A.S., Corfield, R.M., 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. Geol. Mag. 131, 1–34.

Kelly, S.R.A., Bromley, R.G., 1984. Ichnological nomenclature of clavate borings. Palaeontology 27, 793–807.

Kennedy, G.L., 1974. West American Cenozoic Pholadidae (Mollusca: Bivalvia). San Diego Society of Natural History, Memoir 8, 1–128.

Kříž, J., Mikuláš, R., 2006. Bivalve wood borings of the ichnogenus *Teredolites* Leymerie from the Bohemian Cretaceous Basin (Upper Cretaceous, Czech Republic). Ichnos 13, 159–174.

Langenheim, J.H., 1995. Biology of amber-producing trees: focus on case studies of *Hymenaea* and *Agathis*. In: Anderson, K.B., Crelling, J.C. (Eds.), Amber, Resinite and Fossil Resins. ACS Symposium Series 617, American Chemical Society, Washington, D.C., pp. 1–31.

Lavigne, J.M., 1999. Aspects of marginal marine sedimentology, stratigraphy and ichnology of the Upper Cretaceous Horseshoe Canyon Formation, Drumheller, Alberta. Ph. Doctoral Thesis, Department of Earth and Atmospheric Sciences, Edmonton, Canada, 146 p.

Lavigne, J.M., Gingras, M.K., Pemberton, S.G., Eberth, D.A., 1998. Woodgrounds, log grounds and the *Teredolites* ichnofacies. Bull. Am. Assoc. Petrol. Geol. 82, 691.

Leymerie, M.A., 1842. Suite de mémoire sur le terrain Crétacé du département de l'Aube. Mém. Soc. Géol. France 5, 1–34.

Linck, O., 1949. Fossile Bohrgänge (*Anobichnium simile* n. g. n. sp.) an einem Keuperholz. Neues Jahrb. Min. Geol. Pal. 90B, 180–185.

Linnaeus, C., 1758. Systema naturae per regna tria naturae. Editio decima, reformata: Stockholm, Tomus I, Regnum animale, 824 pp. [Facsimile reprinted by the British Museum (Natural History), London, 1956].

MacEachern, J.A., Pemberton, S.G., Gingras, M.K., Bann, K.L., 2007. The ichnofacies paradigm: a fifty-year retrospective. In: Miller, W., III (Ed.), Trace Fossils. Concepts, Problems, Prospects. Elsevier, Amsterdam, pp. 52–77.

Maksoud, S., Azar, D., Granier, B., Gèze, R., 2017. New data on the age of the Lower Cretaceous amber outcrops of Lebanon. Palaeoworld 26, 331–338.

Mao, Y., Liang, K., Su, Y., Li, J., Rao, X., Zhang, H., Xia, F., Fu, Y., Cai1, C., Huang, D., 2018. Various amberground marine animals on Burmese amber with discussions on its age. Palaeoentomology 1, 091–103.

Meek, F.B., 1864. Check list of the invertebrate fossils of North America, Cretaceous and Jurassic. Smithsonian Misc. Coll. 177, 40 pp.

Mikuláš, R., 1993. *Teredolites* from the Upper Cretaceous near Prague (Bohemian Cretaceous Basin, Czechoslovakia). Vestn. Česk. Geol.Úst. 68, 7–10.

Mikuláš, R., 2006. Bivalve wood borings of the ichnogenus *Teredolites* Leymerie from the Bohemian Cretaceous Basin (Upper Cretaceous, Czech Republic). Ichnos 13, 159–174.

Mikuláš, R., Pek, I., Zimák, J., 1995. *Teredolites clavatus* from the Cenomanian near Maletín (Bohemian Cretaceous Basin), Moravia, Czech Republic. Vestn. Česk. Geol. Úst. 70, 51–57.

Minter, N.J., Buatois, L.A., Mángano, M.G., 2016. The conceptual and methodological tools of ichnology. In: Mángano, M.G., Buatois, L.A. (Eds.), The Trace-Fossil Record of Major Evolutionary Events, Volume 1: Precambrian and Paleozoic, Topics in Geobiology 39, 1–26.

Nagabhushanam, R., 1959. Settlement of marine borers (Mollusca) in the Visakhapatnam Harbour in relation to light and gravity. Zool. Soc. India, 30–31.

Noetling, F., 1892. Preliminary report on the economic resources of the amber and jade mines area in Upper Burma. Rec. Geol. Surv. India 25, 130–135.

Obata, K., 2000. The Miocene trace fossils from the area of the River Yokoze-gawa in Chichibu Basin, Saitama Pref., Central Japan. Saitama Kenritsu Shizenshi Habubutsukan Kenkyu Hokoku 18, 31–39.

Palmer, K. v. W., Brann, D.G., 1965. Catalogue of the Paleogene and Eocene Mollusca of the Southern and Eastern United States. Part I. Pelecypoda, Amphineura, Pteropoda, Scaphopoda, and Cephalopoda. Bulletins of American Paleontology 48, 466 pp.

Panos, V., Skacel, J., 1966. Zur Frage der Entstehung der Steinsäulen “Pobiti Kameni” und anderer eigenartiger Formem zwischen Varna und Beloslav in Nordost-Bulgarien. Z. Geomorph. 10, 105–118.

Peñalver, E., Delclòs, X., 2010. Spanish amber. In: Penney, D. (Ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 236–270.

Peñalver, E., Delclòs, X., Soriano, C., 2007. A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. Cretaceous Res. 28, 791–802.

Perrichot, V., 2004. Early Cretaceous amber from southwestern France: insight into the Mesozoic litter fauna. Geol. Acta 2, 9–22.

Pickerill, R.K., Donovan, S.K., Portell, R.W., 2003. *Teredolites longissimus* Kelly & Bromley from the Miocene Grand Bay Formation of Carriacou, the Grenadines, Lesser Antilles. Scripta Geologica 125, 1–9.

Pirrie, D., Marshall, J.D., Crame, J.A., 1998. Marine high Mg calcite cements in *Teredolites*-bored fossil wood: evidence for cool paleoclimates in the Eocene La Meseta Formation, Seymour Island, Antarctica. Palaios 13, 276–286.

Philipp, H., Wehrli, H., 1936. Bohrlöher von Pholadiden in Ligniten aus dem Dach und dem Hangenden der Grube Fischbach (Ville). Zbl. Miner. 1936 (1), 15–20.

Poinar, G.O. Jr., 1992. Life in Amber. Stanford University Press, Stanford, California, pp. 350.

Querol, X., Salas, R., Pardo, G., Ardevol, L., 1992. Albian coal-bearing deposits of the Iberian Range in northeastern Spain. In: McCabe, P.J., Parrish, J.T. (Eds.), Controls on the distribution and quality of Cretaceous coals. Geological Society of America, Special Paper 267, pp 193–208.

Rajchel, J., Uchman, A., 1998. Insect borings in Oligocene wood, Kliva Sandstones, Outer Carpathians, Poland. Ann. Soc. Geol. Pol. 68, 219–224.

Risso, A., 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, Vol. 4. Aperçu sur l'histoire naturelle des mollusques qui vivent sur les bords de la méditerranée boréale et des coquilles terrestres, fluviatiles et marines, subfossiles, fossiles et pétrifiées, qui gisent dans les diverses formations des Alpes Maritimes. F.-G. Levrault, Paris et Strasbourg. 4: vii +1–439.

Röder, H., 1977. Zur Beziehung zwischen Konstruktion und Substrat bei mechanisch bohrenden Bohrmuscheln (Pholadidae, Teredinidae). Senckenbergiana Maritima 9: 105–213

Ross, A., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (Ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 208–235.

Santhakumaran, L.N., 1983. Incidence of marine wood-borers in mangroves in the vicinity of Panaji Coast, Goa. Mahasagar 16, 299–307.

Savazzi, E., 1999. Boring, nestling and tube-dwelling bivalves. In: Savazzi, E. (Ed.), Functional Morphology of the Invertebrate Skeleton. Wiley & Sons, Chichester, 205–237.

Savrda, C.E., 1991. *Teredolites*, wood substrates, and sea-level dynamics. Geology 19, 905–908.

Savrda, C.E., King, D.T.Jr., 1993. Log-ground and *Teredolites* lagerstätte in a transgressive sequence, Upper Cretaceous (Lower Campanian) Mooreville Chalk, central Alabama. Ichnos 3, 69–77.

Savrda, C.E., Ozalas, K., Demko, T.H., Huchison, R.A., Scheiwe, T.D., 1993. Loggrounds and the ichnofossil *Teredolites* in transgressive deposits of the Clayton Formation (Lower Paleocene), western Alabama. Palaios 8, 311–324.

Savrda, C.E., Smith, M.W., 1996. Behavioral implications of branching and tube lining in *Teredolites*. Ichnos 4, 191–198.

Schmidt, A., Grabow, D., Beimforde, C., Perrichot, V., Rikkinen, J., Saint Martin, Thiel, V. Seyfullah, L. J., 2018. Marine microorganisms as amber inclusions. Fossil Record 21, 213-221.

Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang Jing, Wang Jun, Yang, M.C., Lei, W.Y., Li, Q.L., Li, X.H., 2012. Age constraints on Burmese amber based on U-Pb dating zircons. Cretaceous Res. 37, 155–163.

Singh, H.R., Sasekumar, A., 1994. Distribution and abundance of marine wood borers on the west coast of peninsular Malaysia. Hydrobiologia 285, 111–121.

Sivakumar, A., Kathiresan, K., 1996. Mangrove wood bored by molluscs, southeastern coast of India. Phuket Marine Biological Centre Special Publication 16, 211–214.

Smith, R.D.A., Ross, A.J., 2017. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin producing forests to brackish waters, and the age of the amber. Earth Environ. Sci. Trans. Royal Soc. Edinburgh, 1–9.

Solórzano Kraemer, M.M., 2010. Mexican amber. In: Penney, D. (Ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, pp. 42–56.

Sowerby, G.B., 1821–1834. The genera of Recent and fossil shells. G.B. Sowerby [I], London, v. 1, unpaginated text, pls. 1–126 (1821–1825); v. 2, unpaginated text, pls. 127–262 (1825–1834).

Stephenson, L.W., 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. U.S. Geol. Surv., Prof. Paper 242, pp. 226.

Thomas, J.D., 1979. A redescription of the wood-rasping amphipod *Tropichelura gomezi* Ortiz, 1976 (Cheluridae) from the Florida Keys, with notes on its distribution and ecology. Proceedings of the Biological Society of Washington 92, 863–872.

Turner, R.D., 1955. The Family Pholadidae in the Western Atlantic and the Eastern Pacific. Part Ii — Martesiinae. Jouannetiinae and Xylophaginae. Johnsonia 3, 65–160.

Turner, R.D., 1969. Superfamily Pholadacea Lamarck, 1809. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Mollusca 6, Part N, Bivalvia, Volume 2. Geological Society of America and University of Kansas Press, Lawrence, pp. 702–741

Turner, R.D., 1973. Wood-boring bivalves, opportunistic species in the deep sea. Science 180, 1377–1379.

Turton, W., 1822. Conchylia insularum Britannicarum. The shells of the British Islands, systematically arranged. Combe and Son, Leicester, and M.A. Nattali, London, pp. 279.

Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: The Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). Beringeria 15, 3–115.

Urreta, M.B.A., 1987. La icnofacies *Teredolites* en el Cretácico de la Cuenca Austral, Argentina. Actas del Congreso Geológico Argentino 10. Asoc. Geol. Argentina. Buenos Aires 3, 143–147.

Verrill, A.E., Bush, K.J., 1898. Revision of the deep-water Mollusca of the Atlantic coast of North America, with descriptions of new genera and species. Part I.—Bivalvia. Proc. U.S. Natl. Mus. 20 (1139), 775–901.

Villamil, T., Hasiotis, S., 1993. Miniature *Teredolites* in amber and associated microborings, Late Turonian, Colombia. Geol. Soc. Am., Abstracts with Programs 25, pp. 30257.

Wisshak, M., 2017. Taming an ichnotaxonomical Pandora's Box: Revision of dendritic and rosetted microborings (ichnofamily: Dendrinidae). Eur J Taxonomy 390, 1–99.

Wisshak, M., Knaust, D., Bertling, M., 2019. Bioerosion ichnotaxa – review and annotated list. Facies 65, 2.

Woodward, S.P., 1880. A Manual of the Mollusca Being a Treatise of Recent and Fossil Shells, Fourth Edition with an Appendix of Recent and Fossil Conchological Discoveries. Crosby Lockwood and Co., London, 542 p. + 86 p.

Xing, L.D., Sames, B., McKellar, R.C., Xi, D., Bai, M., Wan, X., 2018. A gigantic marine ostracod (Crustacea: Myodocopa) trapped in mid-Cretaceous Burmese amber. Sci. Rep. 8, 1365.

Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F., Zhang, H., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. PNAS 116 23, 11345–11350.

Table Captions

Table 1. Localities, age and repository numbers of the amber samples studied.

Table 2. Measurements of proximal and distal width, length and mean length/ width ratio for *Teredolites clavatus* Leymerie, 1842 and *Apectoichnus longissimus* (Kelly and Bromley, 1984).

Figure Captions

Fig. 1. Schematic drawing of *Teredolites* boring with the parameters used in its description. L: length (L); Wp: width in the proximal region; Wd: width distal or maximum diameter of the chamber.

Fig. 2. General view of amber specimens. A) On the right side, basal view of the internal mould of *T. clavatus*. (ALTC-01. Lebanese amber. Early Barremian). Scale bar: 5 mm. B) An isolated specimen of *T. clavatus.* (ALTC-02from Lebanese amber).. Scale bar: 5 mm. . C-E) side views showing a complete image where the three amber layers containing *T. clavatus* and *Apectoichnus longissimus* can be appreciated. (MPZ 2017/571 to MPZ 2017/726. Spanish Amber. Early-middle Albian). Scale bar: 10 mm. (.). F) Schematic drawing indicating the position of *Teredolites* and *Apectoichnus.* Scale bar: 10 mm. G-I) One piece and two shards of Spanish amber with borings. G-H) *T. clavatus*. G) (MAP-7594. Early-middle Albian). Scale bar: 10 mm. ~~.~~ H)(MAP-7595). White arrow shows an incomplete section of *A. longissimus*. I) (MAP-7596). Scale bar for H-I: 2 mm.

Fig. 3. Longitudinal and cross-sections of *Teredolites clavatus*. A-F. (MPZ 2017/573 to MPZ 2017/575. Spanish Amber. Early-middle Albian). A) In the external layer, filled by clayey sediments. Scale bar: 2 mm. B) Borings closely packed in the intermediate layer. (MPZ 2017/576 to MPZ 2017/626). Scale bar: 5 mm. C) The internal layer is showing a longitudinal section. (MPZ 2017/627). Scale bar: 5 mm. D) Detail of the white box of figure 3. Scale bar: 5 mm. E-F. Longitudinal sections. E) (MPZ 2017/571-572). Scale bar: 2 mm. F) (MAP-7594). Scale bar: 2 mm. G) General view of *T. clavatus* (MNHN.F. A70081. French amber. Albian). Scale bar: 5 mm. H) Detail with three borings showing the margins entirely covered with a thin, white lining. (MNHN.F.

A70078). Scale bar: 5 mm. I) Another detail with *T. clavatus* slightly overlapping. (MNHN.F. A70078). Scale bar: 5 mm.

Fig. 4. A) General view of Burmese amber (In.20205. Albian-Cenomanian). Scale bar: 10 mm. B) General view of Mexican amber. The borings are located on the periphery of the sample (white arrows). (Not signed. Mr John DeCosta private Collection, London. Late Oligocene-early Miocene). Scale bar: 10 mm. C) Evenly spaced *T. clavatus* in Burmese amber. (In.20205). Scale bar: 2 mm. D-F. Latex replica of French amber. Albian. D) General view. (MNHN.F. A70078). Scale bar: 10 mm. E-F) View of the lateral and rounded basal moulds. (MNHN.F. A70081). Scale bar: 5 mm. G) SEM view of the transverse ridges (black arrows) inside *T. clavatus* from Spanish amber and interpreted as xenomorphic structures. MPZ 2017/580. Scale bar: 100 µm. H) SEM view of fine longitudinal grooves (white arrows) inside the boring from the previous specimen and that could be interpreted as micro-bioglyphs. Scale bar: 100 µm.

Fig. 5. A) Xenomorphic ridges and grooves (white arrows) in the distal region (basal part) of *T. clavatus*. (MPZ 2017/575. Spanish amber. Early-middle Albian). Scale bar: 1 mm. B) *T. clavatus* with chevron-like pattern of striae in the basal region (white arrows) and transverse, uneven striae (black arrows). Mexican amber. (Not signed. Mr John DeCosta private Collection, London. Late Oligocene-early Miocene). Scale bar: 1 mm. C) Close-up of a set of *Apectoichnus longissimus.* (MPZ 2017/716-719. Spanish amber. Early-middle Albian). Scale bar: 1 mm. D) Schematic diagram of the previous picture. - E.L: External layer, IL: Intermediate layer. Gray color: filling. E) Close-up view of the linings (white arrows) around the wall and the neck in *A. longissimus*. MPZ 2017/719. Scale bar: 500 µm.

Fig. 6. Schematic diagram illustrating the characteristics of *Teredolites clavatus* and *Apectoichnus longissimus* in the Spanish amber (MPZ 2017/571 to MPZ 2017/726).

Fig. 7. A) *Martesia* sp. 1 inside its boring. mt: metaplax, ms: mesoplax, hp: hypoplax; ur: umbonal reflection, pr: prora, d: disc, s: sulcus, pg: pedal gape. (Mexican amber, not signed. Mr John DeCosta private Collection, London. Late Oligocene-early Miocene). Scale bar: 2.5 mm. B) *Martesia* sp. 2 inside its boring. (Burmese amber, In 20205. Albian-Cenomanian). Scale bar: 2.5 mm.

Fig. 8. CT scan of bored Burmese amber slab (F2854/BU/CJW. Jörg Wunderlich private collection, Hirschberg, Germany. Cenomanian) with bivalves preserved in situ. A) side view. B) view from above. C) View from below with a larger magnification. D) Typical cluster or "bundle "of *Martesia* sp. 2. E) Three articulated young specimens seen from below. Fm: flat mesoplax; pg: pedal gape. F-J) Lateral, dorsal, ventral and anterior view of a *Martesia* sp. 2 specimen. K-L) Lateral views of young *Martesia* sp. 2 specimens. All Scale bars: 5 mm.

Fig. 9. Taphonomic model, explaining various modes of preservation of pholadids and their borings observed in Burmese amber. Further explanations see text.

Fig. 10. An idealised sequence of the bioerosion process in the Spanish amber ball. (MPZ 2017/571 to MPZ 2017/726. A) Initial state and production of *Teredolites clavatus*. B) Occurrence of later amber coating the initial borings and installation of a second generation of *Teredolites*. C-D) Complete development of the previous phase and coverage by a third layer of amber with the appearance of *Apectopichnus longissimus* together with *T. clavatus*. E). Final state after erosion.

Locality	Age	References	Repository
Chiapas, Mexico	Late Oligocene- Early Miocene	De Poinar, 1992	Not signed. Mr. John DeCosta private Collection, London
Magdalena Basin, Colombian Andes	Late Turonian	Villamil and Hasiotis 1993	Unknown
Kachin region, Myanmar	Cenomanian	Noetling, 1892; Chhibber, 1934; Cruickshank and Ko, 2003; Shi et al., 2012	In.20205. Department of Palaeontology, The Natural History Museum, London BuB 1511 BuB 1512 BuB 1133 BUB 1551 BuB 1550 BuB 1549 Patrick Müller private collection (Käshofen, Germany) F3091/BU/CJW F2854/BU/CJW F3050/BU/CJW F 3049/BU/CJW F2855/BU/CJW F2858/BU/CJW F2856/BU/CJW F2857/BU/CJW F3052/BU/CJW F3051/BU/CJW F3043/BU/CJW F3048/BU/CJW F3045/BU/CJW F3047/BU/CJW F3046/BU/CJW F3044/BU/CJW Jörg Wunderlich private collection (Hirschberg, Germany)

Archingeay, Charente-Maritime, (SW France)	Albian	Perrichot, 2004	MNHN.F. A70078, MNHN.F. A70081 National Museum of Natural History of Paris
Sant Just, Teruel, Spain	Early-Middle Albian	Peñalver et al., 2007	MPZ 2017/571 to MPZ 2017/726 Paleontological Museum, University of Zaragoza MAP-7594 to MAP-7596, Dinópolis Foundation, Teruel
Kfar Selouan, Central Lebanon	Early Barremian	Maksoud et al., 2017	ALTC-01-02 Department of Palaeontology, The Natural History Museum, London

Teredolites clavatus	Value	Wp (Width proximal)	Wd (Width distal)	L (Length)	MeanL/Wd
Mexico (n: 18)	minimum	3.0	8.7	12.0	
	maximun	4.2	9.6	19.2	
	mean	3.3	9.4	17.4	1.9
Columbian Andes (n: 98)	mean	0.4	0.6	---	3.0 to 2.0
Myanmar (n: 131)	minimum	0.2	0.5	0.8	
	maximun	1.1	2.6	4.2	
	mean	0.6	1.6	2.7	1.6
France (n: 51)	minimum	---	0.9	1.8	---
	maximun	---	3.5	4.0	---
	mean	---	2.2	2.9	1.3
Spain (n: 221)	minimum	0.4	0.3	2.1	
	maximun	1.9	2.6	6.0	
	mean	1.1	1.5	3.6	2.4
Lebanon (n:2)	minimum	---	2.6	---	
	maximun	2.5	5.6	8.1	
		2.5	4.1	8.1	1.9
Apectoichnus longissimus					
Spain (n: 5)	minimum	0.4	0.7	2.4	
	maximun	0.7	1.6	9.5	
	mean	0.6	1.1	5.8	5.27

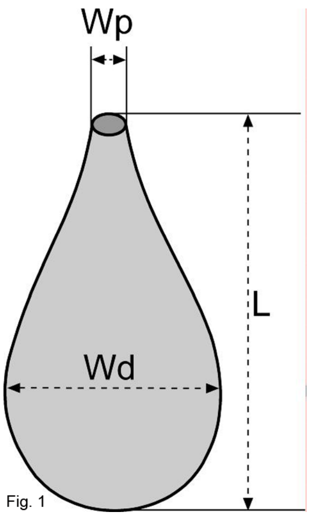
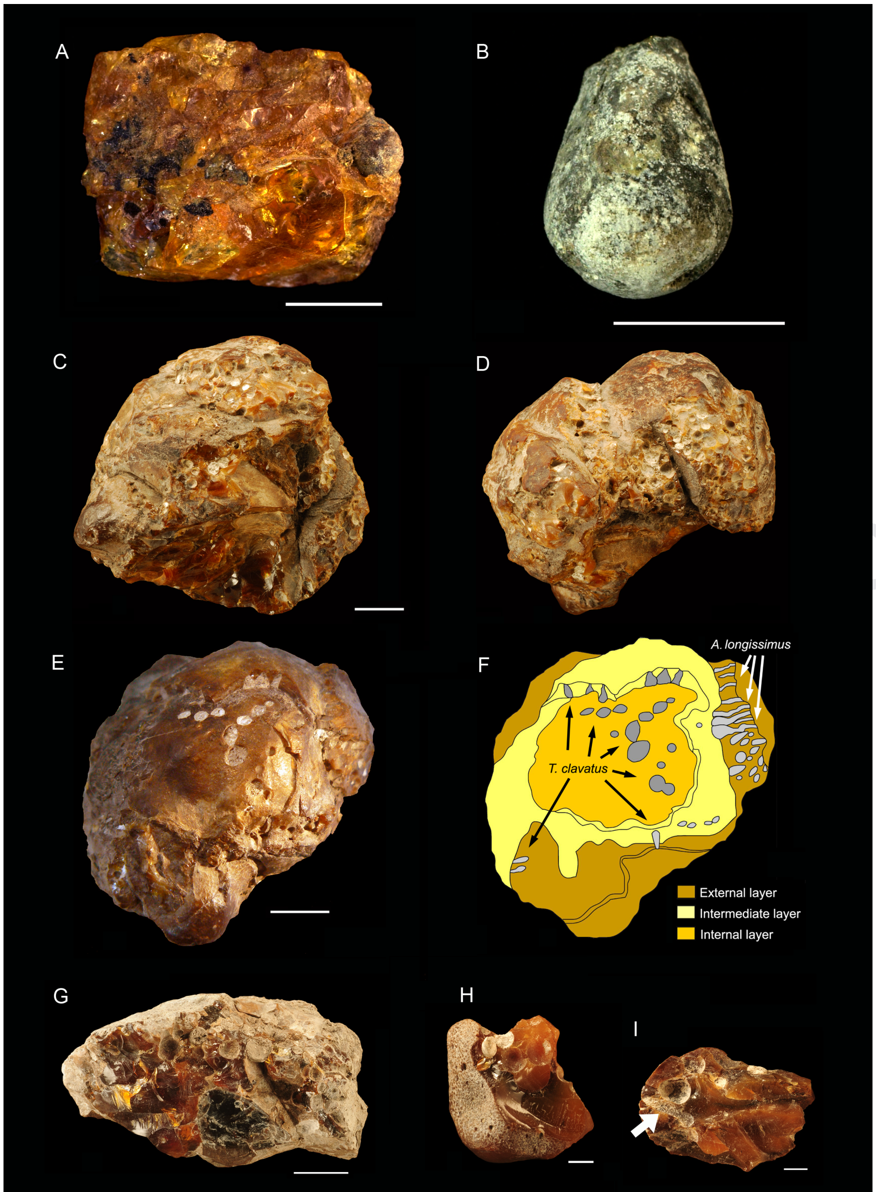


Fig. 1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T. clavatus
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Intermediate layer
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Fig. 2

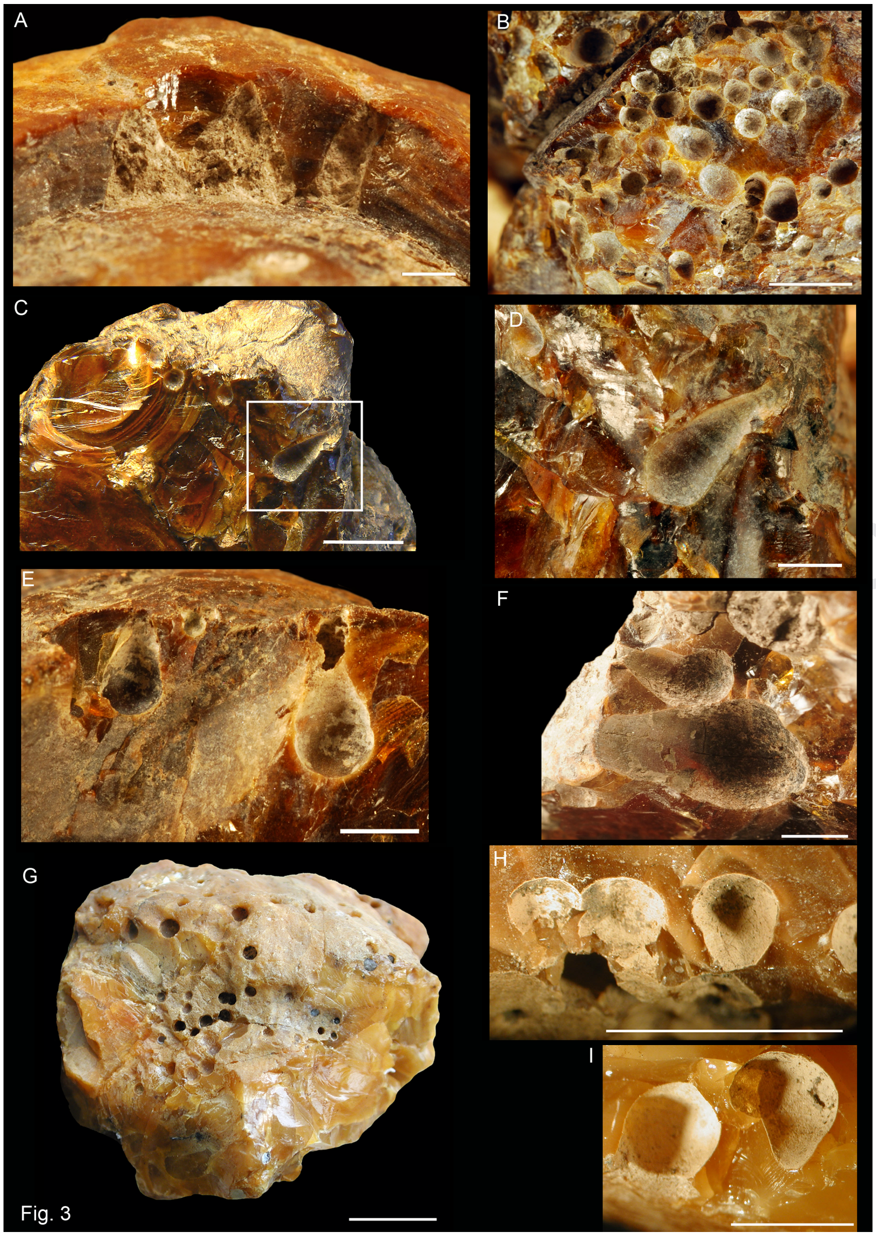
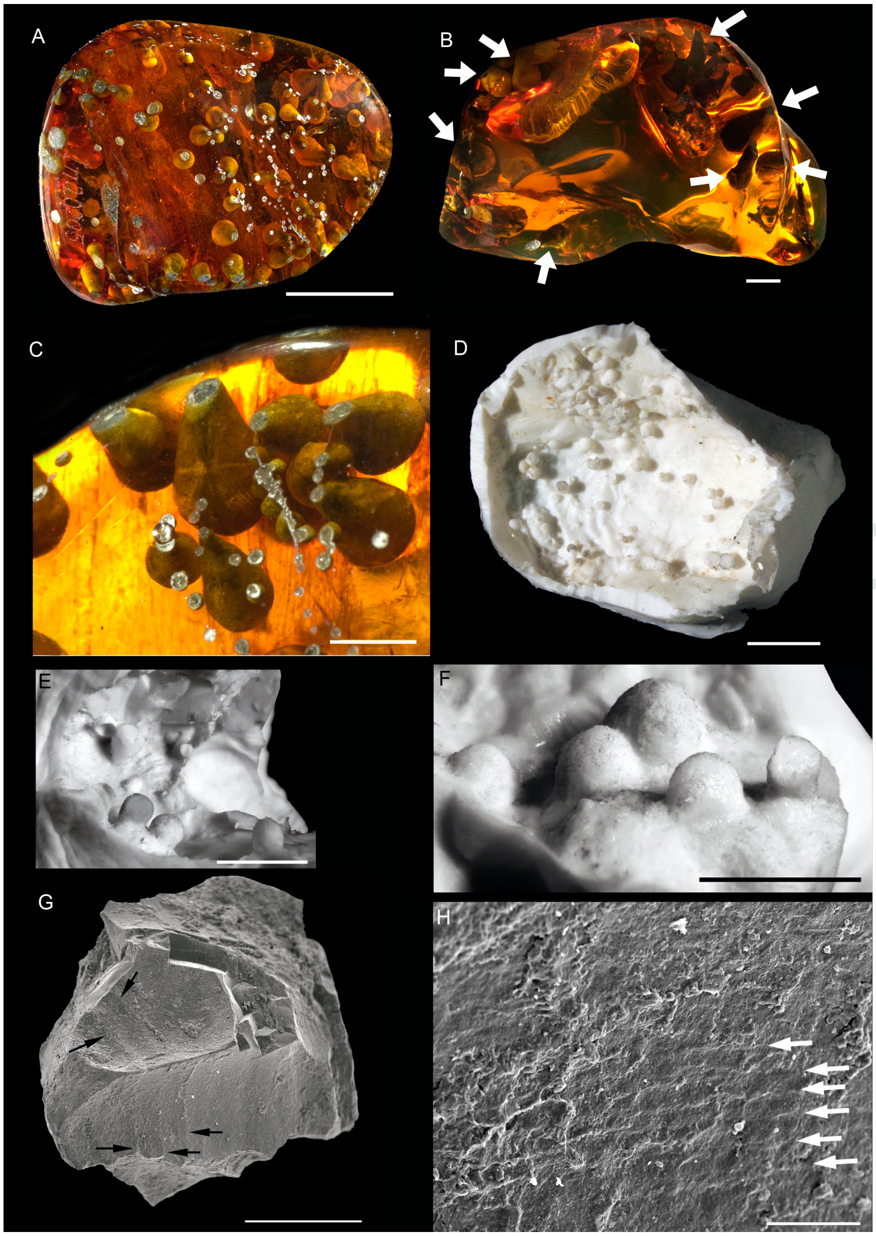


Fig. 3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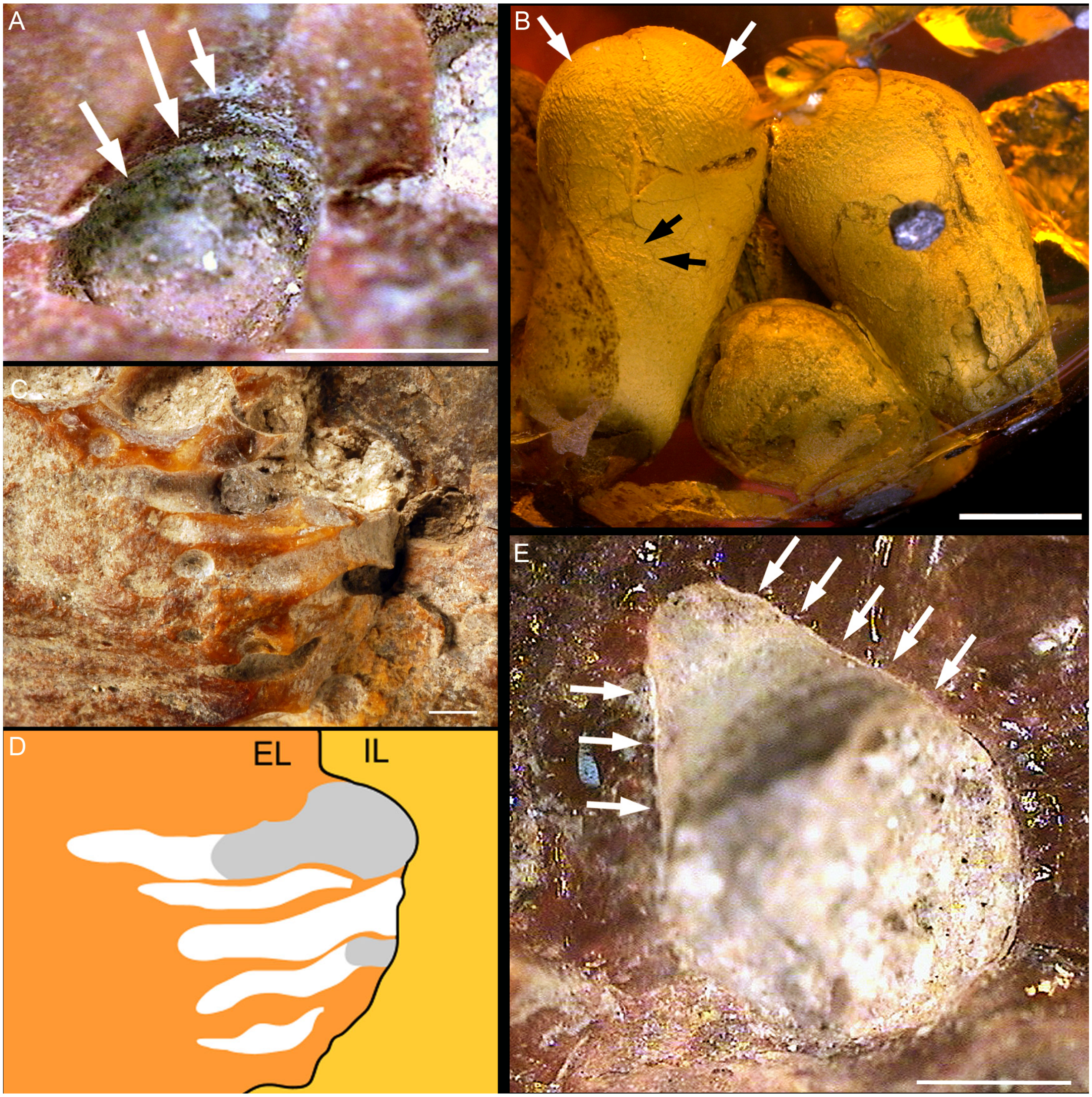
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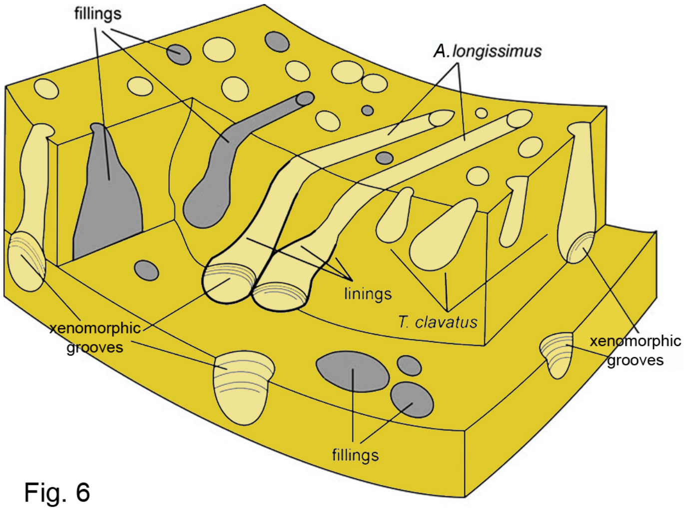
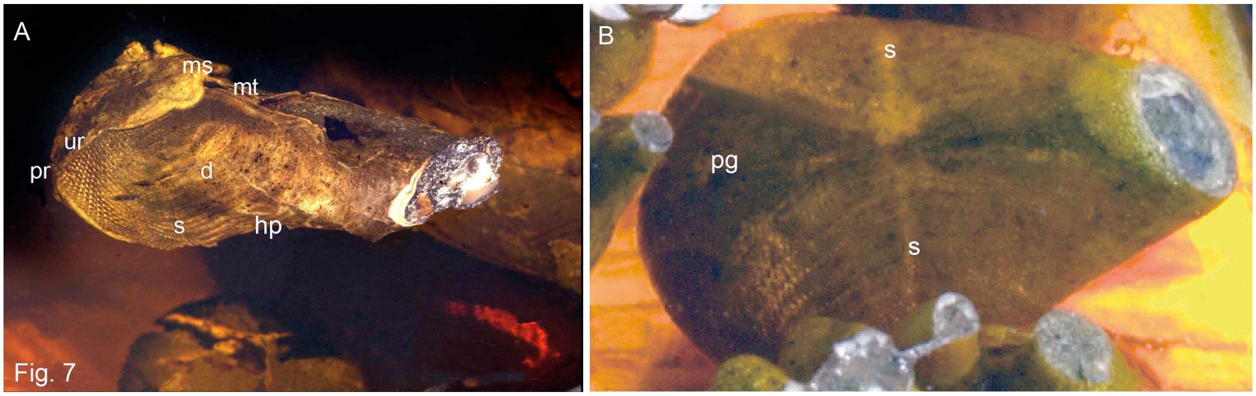

fillings
A. longissimus
linings
T. clavatus
xenomorphic grooves
xenomorphic grooves
fillings

Fig. 6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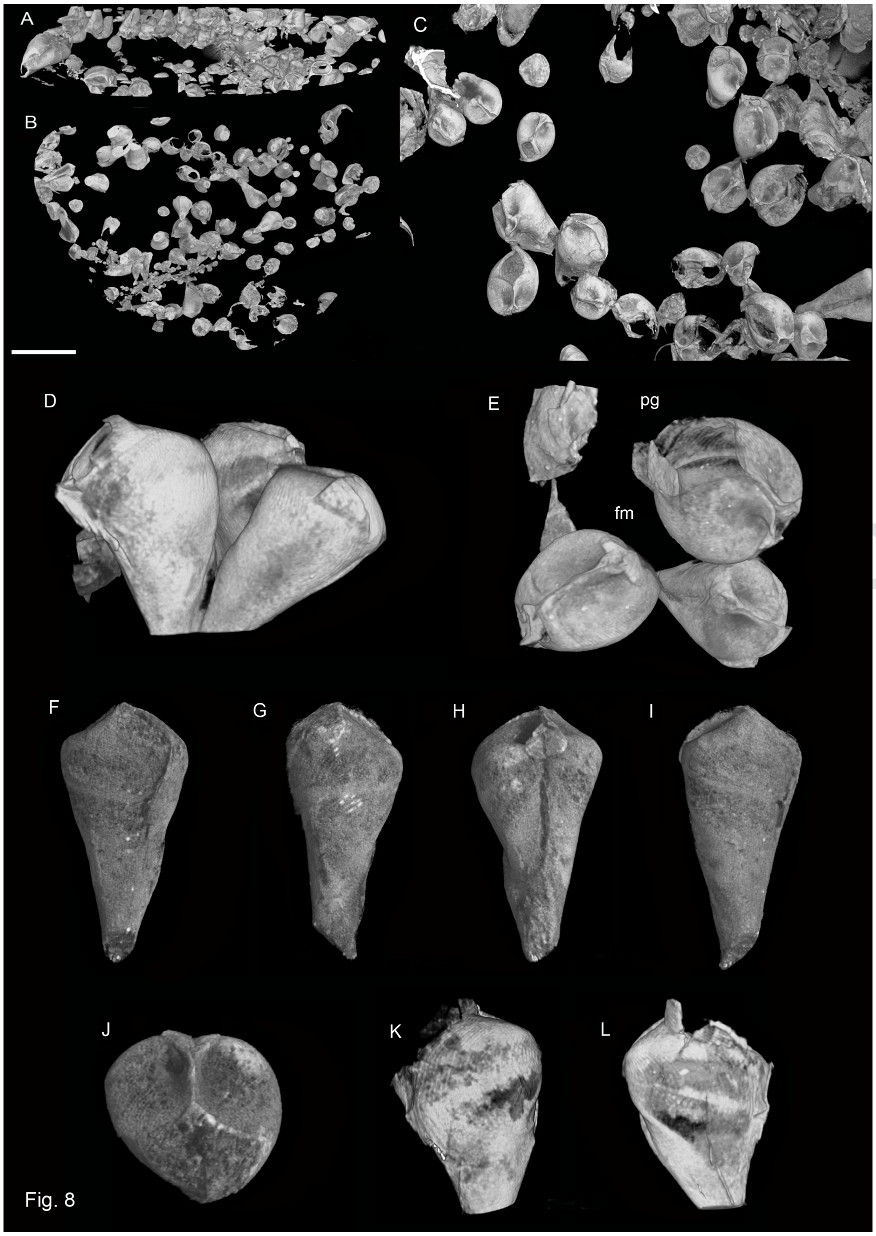
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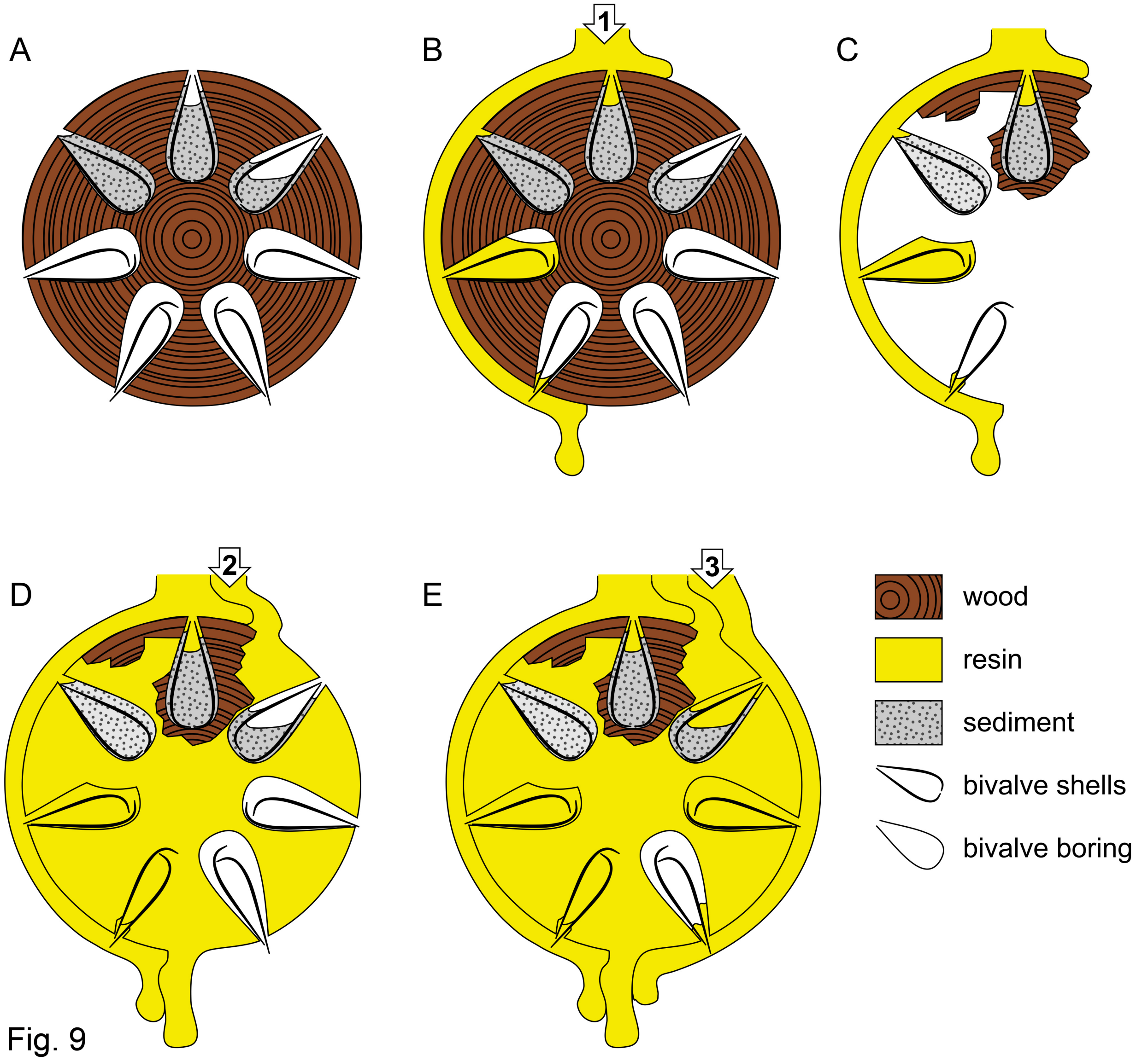
Fig. 8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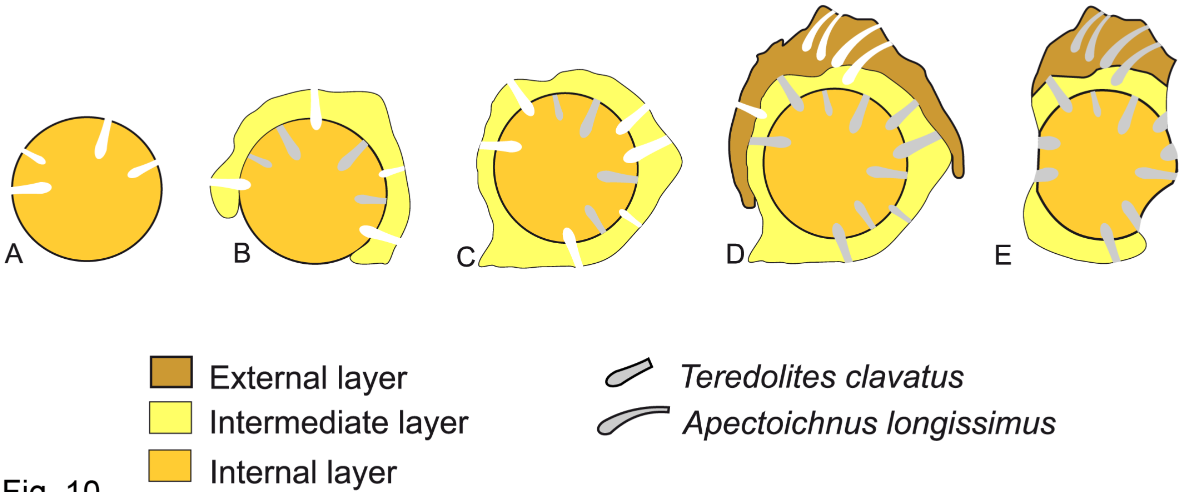
bivalve boring

Fig. 9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External layer
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Internal layer
Teredolites clavatus
Apectoichnus longissimus

Fig. 10

Highlights

* The existence of borings in amber from Early Cretaceous to Miocene is verified.

* Arguments are given in favour of separating *Teredolites* from *Gastrochaenolites*.

* Amber, copal or similar solid resins are considered a derivative of xylic substrates.

* Clavate borings in this type of substrates should be included in *Teredolites*.

* The separation between *Teredolites* and *Apectoichnus* is confirmed.

Conflict of Interest and Authorship Conformation Form

Please check the following as appropriate:

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