



Asthenopodichnium in fossil wood: Different trace makers as indicators of different terrestrial palaeoenvironments

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ABSTRACT

The ichnospecies *Asthenopodichnium xylobiontum* comprises U-shaped traces in wood, usually attributed to the activity of mayfly nymphs (Insecta, Ephemeroptera), which indicate the presence of freshwater palaeoenvironments. The record of a new ichnospecies in wood, *Asthenopodichnium lignorum*, in the Miocene of New Caledonia, strongly indicates that it may correspond to other trace makers because the potential producing Ephemeroptera are absent around these Miocene oceanic islands and in a wide area comprising New Zealand and Australia. We present herein the evidence for wood rotting fungi as potential trace maker of the new ichnospecies that has been previously recorded from Argentina, Egypt, Czech Republic, USA, and Lithuania. The new ichnospecies *A. lignorum*, in contrast with *A. xylobiontum*, is an indicator of terrestrial, humid to subhumid, palaeoenvironments.

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1. Introduction

Determining the organism(s) that could have produced trace fossils is frequently a difficult challenge (Buatois and Mángano, 2011) and in some cases trace makers of very different taxa or even realms are proposed for the same ichnotaxon. This is the case of some trace fossils included in *Asthenopodichnium xylobiontum* Thenius, 1979, a quite characteristic trace in wood the origin of which will be matter of discussion herein. This ichnotaxon, which comprises U-shaped structures and depressions with different shapes (Genise, 2004; Uchman et al., 2007), has been usually attributed to the activity of some wood boring Ephemeroptera (Moran, 2009; Moran et al., 2010; Thenius, 1979, 1988, 1989, 2011), which is potentially of great interest for palaeoecological reconstructions and the fossil record of Ephemeroptera. Wood boring mayflies belong to highly specialised families living in freshwater environments. Consequently

Moran et al. (2010) inferred the presence of “moving freshwater” after the discovery of fossil wood fragments with *Asthenopodichnium* in the palaeoenvironments of the Late Cretaceous Wahweap Formation, Utah, USA. In addition, Uchman (2011) mentioned gammarids as other producers of U-shaped traces in wood from Poland.

Two of us (PM and DC) recently discovered in the Miocene of New Caledonia some wood fragments with pouch-like *Asthenopodichnium*. If these trace fossils are attributed to mayflies, they could have a strong biogeographical significance, since the wood boring species of this group are presently absent from this old oceanic island and the region around (McCafferty and Edmunds, 1976; Hubbard, 1984; Grandcolas et al., 2008). Additionally, this material is comparable with other trace fossils in wood previously recorded from Argentina, Egypt and Czech Republic preliminary attributed to fungi (Genise, 2004; Mikuláš and Zasadil, 2008), and also material from Lithuania of unknown origin (Uchman et al., 2007), and USA attributed to mayflies (Moran et al., 2010). These records of *Asthenopodichnium* share with the New Caledonian material similar morphological characters that are not present in the holotype of *A. xylobiontum*.

The objective of this contribution is (1) to create a new ichnospecies of *Asthenopodichnium* from wood to include this material, (2) to present the evidence to attribute it to fungi as proposed preliminarily by Genise

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(2004), and (3) to point out the different palaeoenvironmental meaning for the different ichnospecies.

2. Geological setting

In New Caledonia the Miocene sediments crop out in the bay of Nepoui peninsulas and islets where they form gently southwest-dipping layers (<5°) (Coudray, 1976, in: Paris, 1981). The material comes from the northern part of small Didot Islet (GPS 161° 01' 16", 21° 22' 20") (Fig. 1). The Nepoui series is divided into two subunits. The lower subunit corresponds to c. 100 m thick reefal and lagoonal limestones that represent the earliest reefal settlement in New Caledonia when the island reached the intertropical region during the northward drift of the Australian Plate (Davies et al., 1987). The upper subunit, c. 100 m thick, has an erosive lower boundary and starts with 50 m thick, unconformable fluvialite to torrential cobble

conglomerate, overlain by bioclastic limestone. Silicified and ferruginous fossil woods fragments are common in the conglomerate, the deposition context of which being clearly continental. The age of both lower and upper limestones and thus of the conglomerate is Early Miocene.

3. Systematic ichnology

Ichnogenus *Asthenopodichnium* Thenius, 1979

3.1. Included species

Asthenopodichnium xylobiontum Thenius, 1979 (type ichnospecies), *Asthenopodichnium ossibiontum* Thenius, 1988, *Asthenopodichnium lithuanicum* Uchman et al., 2007, *Asthenopodichnium lignorum* isp. n.

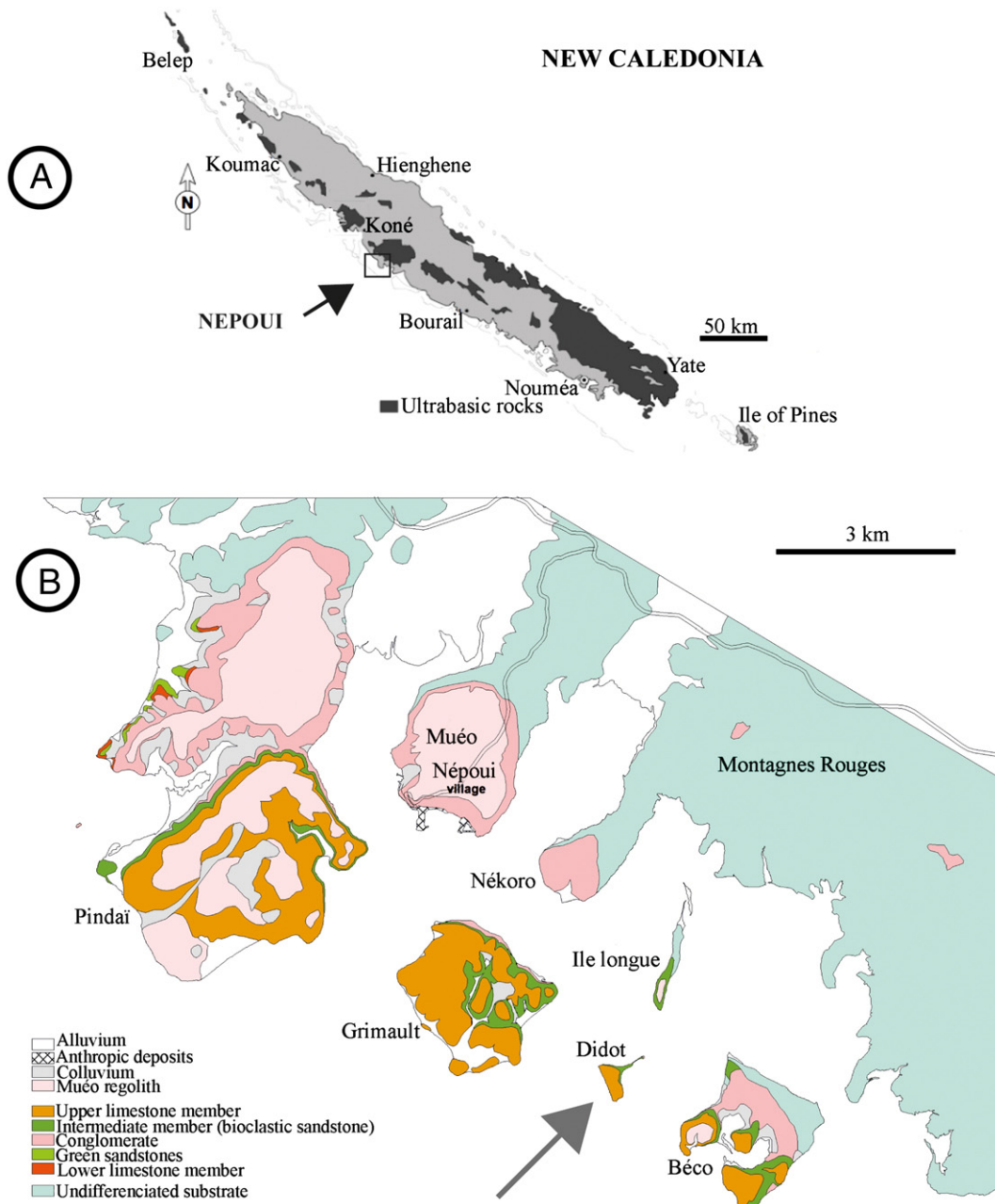


Fig 1. New Caledonia map and geological settings of Nepoui area. (A) New Caledonia map. (B) Geological map of Nepoui. Arrow shows Didot Islet, holotype locality.

3.2. Comments

The original ichnogenus diagnosis is as follows: “U-förmige Spreitenbauten in Holz, senkrecht zur Stammoberfläche angeordnet.” (U-shaped spreiten structures in wood, perpendicular to the trunk surface) (Thenius, 1979: 185). Later, Uchman et al. (2007: 331–332) emended this diagnosis to include “small, U-shaped spreiten” or “pouch-like structures in wooden, organic-rich or bone substrates” considering that “The spreiten, however, are not obvious because

even in the type material, the trace fossil appears as a tongue filled with other, non-xylic material”.

3.3. *Asthenopodichnium lignorum* isp. n

Figs. 2–4, Supplementary 1.

2004 *Asthenopodichnium xylobiontum*: Genise, p. 37.

2007 Form A Uchman et al., p. 332.

2008 Almond-shaped hollows Mikuláš and Zasadil, p. 124.

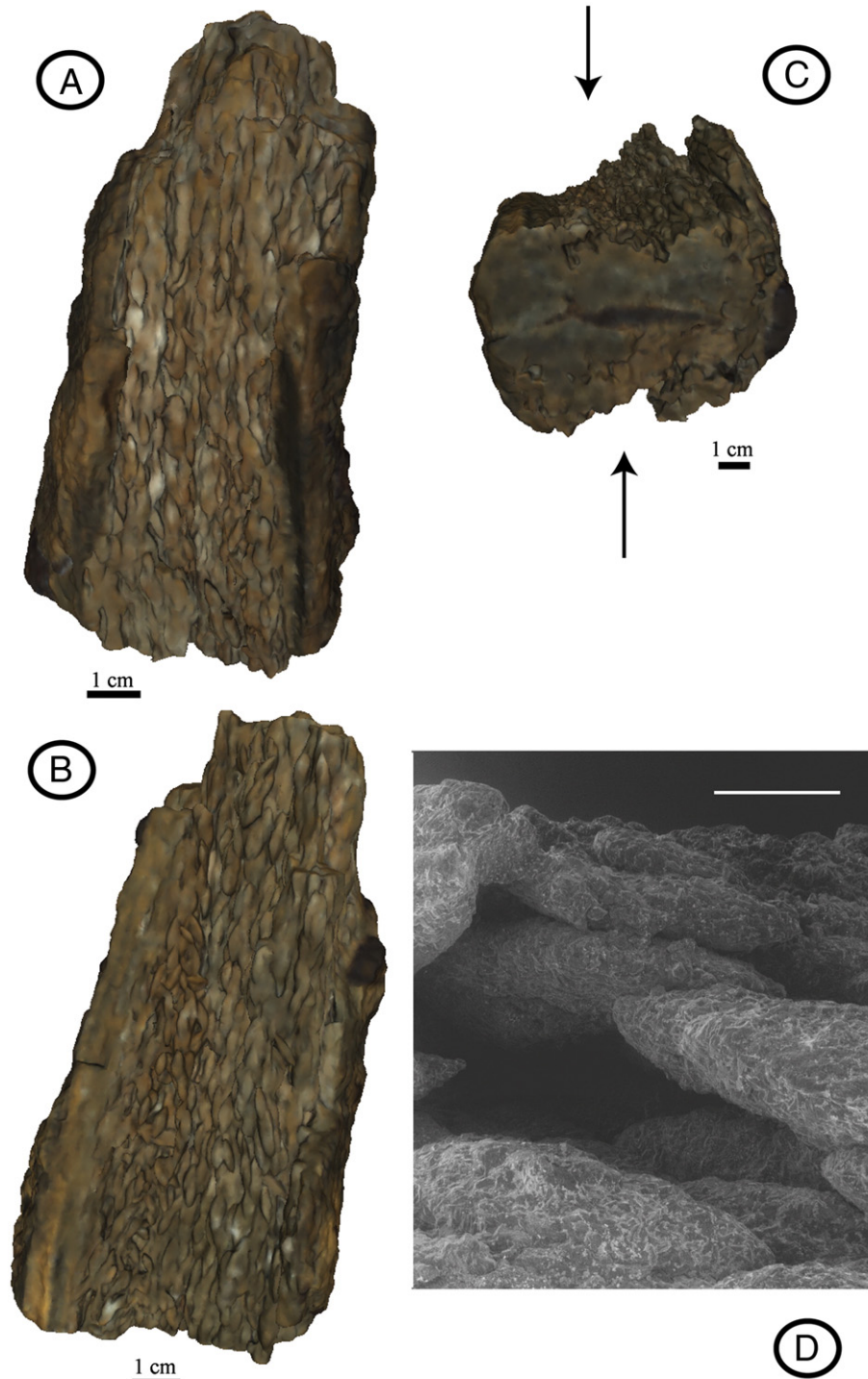


Fig. 2. *Asthenopodichnium lignorum* isp. n., holotype NC-NEP-01, 3D reconstruction by surface scanning. (A and B) Two sides with scoops. (C) Section view; arrows indicate the position of views A and B. (D) Details of scoops in SEM (VEGA/TESCAN LSU, Low vac, LVSTD detector, 20 kV). 3D PDF file available in supplementary material.

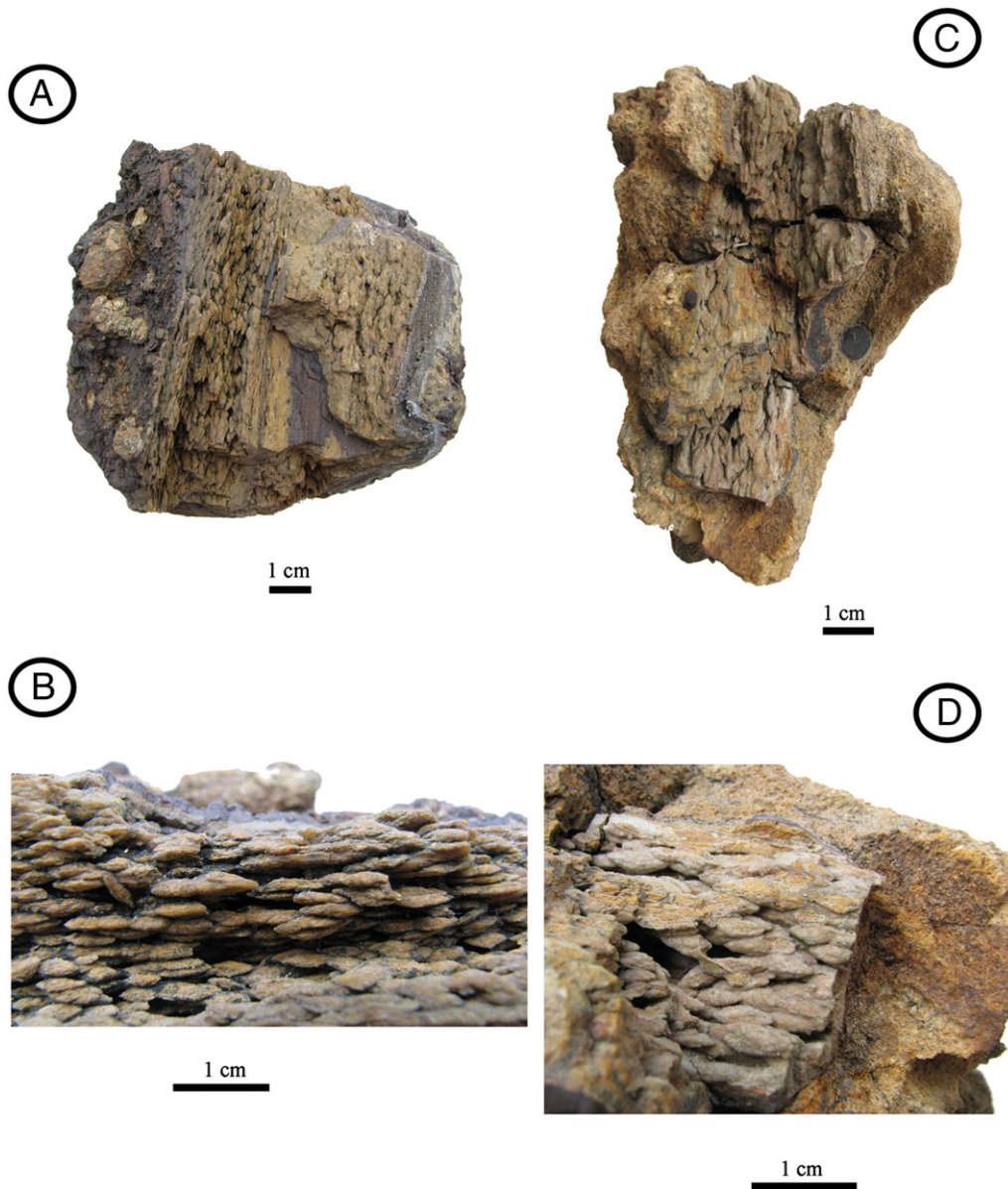


Fig. 3. *Asthenopodichnium lignorum* isp. n., NC-NEP-02 and NC-NEP-03. (A and B) Specimen NC-NEP-02 (B détails of the scoops). (C and D) Specimen NC-NEP-03 (D détails of the scoops).

2009 *Asthenopodichnium xylobiontum*: Moran, p. 262.

2010 *Asthenopodichnium*: Moran et al., p. 663.

3.4. Material

Holotype specimen NC. NEP 01 (Fig. 2, Supplementary 1), other specimens NC. NEP 02 and NC. NEP 03, SGNC (New Caledonia Geological Survey) (Fig. 3), Nouméa.

3.5. Examined material

Several trunks and branches with *A. lignorum* observed in the field from the Upper Cretaceous Allen Formation of Argentina (Fig. 4C). The casts shown in Fig. 4D and E examined in outcrops of the Eocene-Oligocene Jebel Qatrani Formation (El Fayum) and from the Miocene Moghra Formation (Qattara) in Egypt. A trunk with *A. lignorum* from the Miocene Most Formation of Czech Republic examined in the Museum of the Petrified Forest at Louny.

3.6. Type locality and strata

Northern part of small Island Didot, Early Miocene, New Caledonia.

3.7. Derivation of name

After the Latin *lignum* for wood.

3.8. Diagnosis

Shallow elongate ellipsoidal or almond-shaped scoops corresponding to the filling of pouches or depressions in the surface and inside wood substrates, usually oriented parallel to the wood fibers along the branch or trunk longitudinal axis. In many cases densely grouped, less commonly up to forming an alveolar structure. Always devoid of associated galleries.

3.9. Comments

The original diagnosis of *A. xylobiontum* is as follows (Thenius, 1979: 185): “U-förmige Spreitenbauten mit einem Röhrendurchmesser von 1,5–3 mm. Höhe (Tiefe) der U-Bauten bis zu 20 mm”. (U-shaped structures with a tube diameter of 1.5–3 mm. Height (depth) of the excavations up to 20 mm). Two different structures have been included until now in *A. xylobiontum*: U-shaped and pouch-like (tongue-shaped) borings in wood. In fact, Thenius (1979) was speaking about notches for the specimen that he figured in his text-Fig. 1 (see also Schenk, 1937: text-Fig. 6), while he indicated the presence of U-shaped tubes for the holotype that he figured in his text-Fig. 2. In this last figure, some U-shaped tubes remain clearly visible, while in others on the same piece of wood the part between the two branches of the tube are filled with sediments so that it looks like a pouch-like structure and thus it better looks like a counterprint of a notch. The new ichnospecies, *A. lignorum*, is represented by shallower ellipsoid depressions in contrast to the deeper tongue notches and U-tubes of *A. xylobiontum*.

3.10. Description

The New Caledonian material consists of several pieces of wood preserved as iron hydroxide, silica rind casts with scoop-shaped counter-imprints of pouch-like traces (Figs. 2 and 3). The piece of wood corresponding to the holotype (NC. NEP 01) is 12.5 cm long, with a broadly elliptical section 6 cm × 4.5 cm. The structures are elongate ellipsoidal scoops, with long axes typically aligned parallel or sub-parallel to the long axis of the preserved wood. These scoops occupy nearly all the volume of the wood. The length of the structures is 4.0–6.0 mm, and the depth/width is 1.5–2.0 mm. The surface of NC EP 01 is covered by a thin layer of calcium carbonate, indicating a secondary concretion. The specimen NC. NEP 02 is 10 cm long, with structures of the same shape but smaller than in the holotype, 1.0–3.0 mm long, 1.0 mm wide, and 0.5 mm high (Fig. 3A and B); the specimen NC. NEP 03 is 15 cm long, with structures identical to those of NC. NEP 02 (Fig. 3C and D).

The material from Argentina (Fig. 4C) is composed mostly of elongated, ellipsoid and relatively shallow depressions, 15–18 mm long, 5–6 mm wide and 2–5 mm deep, in the surface of trunks and branches. The depressions are in many cases densely grouped and aligned longitudinally, covering the entire surface of trunks. In some cases the coalescence of depressions may compose short channels. The El Fayum material was preserved as sandstone casts. In one sample, casts of individual traces were 25–30 mm long and 11–14 mm wide, whereas in the other sample showing only two traces they were 17 mm long and 3 mm wide (Fig. 4D). The Moghra material was preserved as a sandstone cast with counter-imprints of small depressions (Fig. 4E). Individual casts ranged from 4 mm to 10 mm in length and 2.5 mm to 4 mm width. The Czech material was a single piece of trunk showing aligned, ellipsoid shallow depressions in most of its surface, 15–17 mm long and 5–6 mm wide.

4. Discussion

Until now, the ichnogenus *Asthenopodichnium* Thenius, 1979 comprised three ichnospecies. The type species *Asthenopodichnium xylobiontum* Thenius, 1979 was described for traces in Miocene fossil

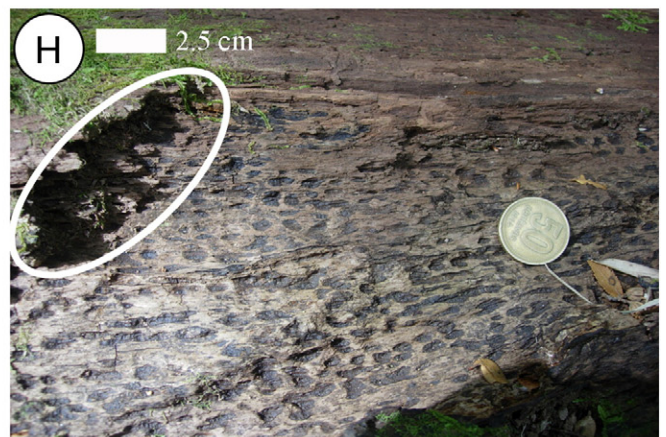
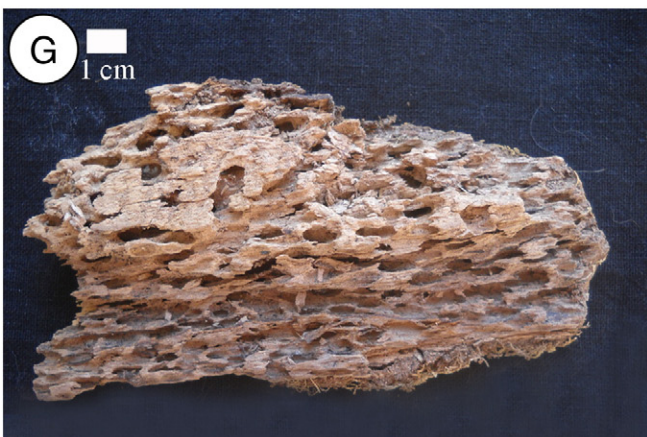
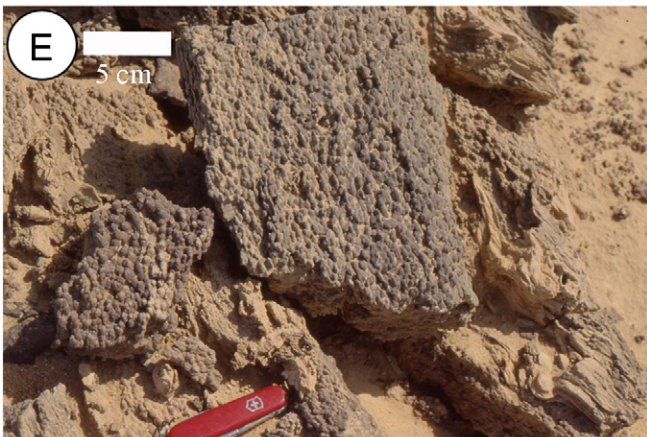
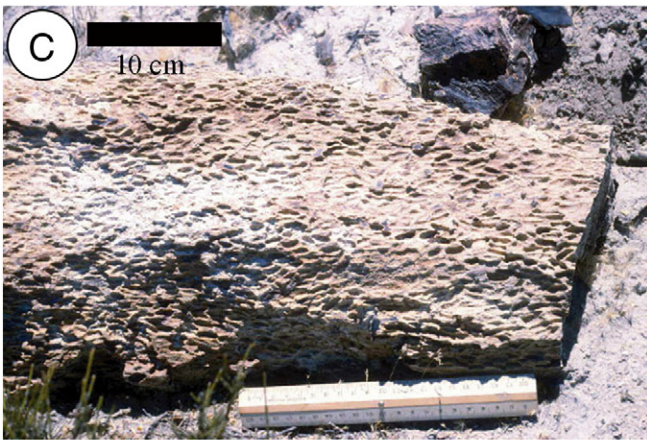
wood, but *Asthenopodichnium ossibiontum* Thenius, 1988 corresponds to traces in Miocene bones. Uchman et al. (2007) described a third ichnospecies, *Asthenopodichnium lithuanicum*, from Late Neogene organic-rich sediments of freshwater origin from Lithuania. Lastly Moran (2009) and Moran et al. (2010) attributed several Late Cretaceous traces of activities in woods to *Asthenopodichnium*.

Thenius (1979, 1988, 1989, 2011) and Moran et al. (2010) attributed *A. xylobiontum* and *A. ossibiontum* to the activity of ephemeropteran nymphs of the polymitarcid lineage. In contradiction, Bae and McCafferty (1995: 390) considered that *Asthenopodichnium* is “not even clearly insect burrows”, Zherikhin (2001: 310) indicated that the *Asthenopodichnium* described by Thenius (1979, 1988, 1989, 2011) and Nesson (1988), are “believed to be mayfly nymph domiciles”, but with some doubt, and Kluge (2004) considered *Asthenopodichnium* as an “Animalia incertae sedis”. Genise (2004) included with doubts the traces described herein in *A. xylobiontum* and proposed that they were produced by fungi, a hypothesis followed by Mikuláš and Zasadil (2008). Uchman et al. (2007: 334) indicated that the “interpretations of pouch-like trace fossils and lebensspuren exclusively as traces of mayfly larvae can be challenged” and later, Uchman (2011) attributed U-tubes of different sizes to mayflies and gammarids (crustaceans), respectively.

The burrowing mayflies belong to a very particular group of families (e.g. Polymitarcyidae, Ephemeridae, Palingeniidae and Euthyplociidae, in the clade Scaphphodonta sensu McCafferty (2004), or the clade Fossoriae sensu Ogden et al., 2009), characterized by having larval tusks (McCafferty, 2004). The taxa that are able to burrow into wood belong to the Polymitarcyidae, with also a record in the Palingeniidae (Edmunds and McCafferty, 1996), while some Ephemeridae have also very strong tusks (Bae and McCafferty, 1995). The presence of *Asthenopodichnium* in fossil New Caledonian woods would be challenging because the insular and disharmonious New Caledonian fauna comprises only mayfly representatives of the other families Leptophlebiidae and Baetidae (Peters, 2001). If some New Caledonian Leptophlebiidae are known to live in the benthic layer, none of the described species have larvae boring in wood. Only the larvae of the Australian leptophlebiid genus *Jappa* are known to “burrow along mud rock interfaces, and in gravel and sand” (Edmunds and McCafferty, 1996: 70). Thus the attribution of these New Caledonian Neogene structures to the activity of burrowing mayfly larvae of the families Polymitarcyidae or Palingeniidae is very unlikely because these two families are unknown in the large Australian and Pacific regions. New Guinea is the closest area with recent Palingeniidae, and the Andaman Islands for the Polymitarcyidae (Demoulin, 1965; McCafferty and Edmunds, 1976; Hubbard, 1984). These two families are probably groups of Asiatic origins that never reached the Oceania islands. Furthermore, New Caledonia is a relatively young Oligocene island, the “Grand Terre” emerging after 34 Ma and before 25 Ma (Cluzel et al., 1998; Grandcolas et al., 2008; Nattier et al., 2011; Sevin et al., 2011), which makes the past presence of mayflies more unlikely yet, since their Miocene record would mean that they have colonized the area from far away and became extinct in a quite short geological time.

The larvae of the recent Polymitarcyidae and Palingeniidae make U-shaped tunnels in the sediment (*Tortopus incertus*) (Scott et al., 1959; Russev, 1987; Bae and McCafferty, 1995; De, 2002) or in wood (*Asthenopodinae* of the genera *Asthenopus* and *Povilla*) (Hartland-Rowe, 1958; Sattler, 1967: Fig. 2). These U-shaped tunnels

Fig. 4. (A) Recent stem from Argentina, attacked by *Asthenops* larvae (Ephemeroptera, Polymitarcyidae) (white arrow) showing longitudinal tunnels instead of the discrete pouches of *A. xylobiontum* (photograph by C. Molina Arzabé). (B) Galleries and pupation chambers of *Pissodes castaneus* (Coleoptera, Curculionidae) in pine. Note the four pupation chambers with frass at the lower part of the picture (photograph by J. Farina). (C) *A. lignorum* isp. n. preserved as almond-shaped pits covering a piece of trunk from the Upper Cretaceous Allen Formation of Argentina (photograph by J.F. Genise). (D) *A. lignorum* isp. n. preserved as sandstone casts (center and right) from the Oligocene-Miocene Jebel Qatrani Formation of Egypt (photograph by J.F. Genise). (E) *A. lignorum* isp. n. preserved as a sandstone cast of an alveolar matrix from the Miocene Moghra Formation of Egypt (photograph by J.F. Genise). (F) Trunk of *Eucalyptus* sp. from Otamendi (Argentina) showing canker produced by *Coniothyrium* sp. Note at the left, where the bark is removed, the almond-shaped kino pockets (photograph by J.F. Genise). (G) Alveolar layer of wood from Puerto Blest (Argentina) attacked by white wood-rotting fungi. This external layer was removed from the trunk illustrated in (H). The surface shown was in contact with the trunk (photograph by J.F. Genise). (H) The healthy part of the trunk in (G) showing elliptical and aligned pockets that were in contact with the removed alveolar layer. The white ellipse shows the alveolar layer from which the piece was removed (photograph by J.F. Genise).



can be relatively regular or obliquely directed (Sattler, 1967: Fig. 7), resulting when filled (and replaced) by sediment into a regular U-shaped cast or a structure more looking like a tongue. In the Southern Hemisphere mayflies that attack wood or stems make straight tunnels (Fig. 4A) rather than U-tubes, which is a behavior recorded for mayflies of the Northern Hemisphere (E. Dominguez, pers. comm. 2011).

In accordance with the unlikely mayfly hypothesis for the *Asthenopodichnium* from New Caledonia, its morphology is different from the holotype of *A. xylobiontum* described by Thenius (1979) and is actually resembling closely the Egyptian and Argentinean materials described and interpreted as fungus traces by Genise (2004) and the Czech material described by Mikuláš and Zasadil (2008). It is also similar to the USA material described by Moran et al. (2010), interpreted as mayfly traces, and the Form A traces described by Uchman et al. (2007). Clear differences in morphology, namely shallow, ellipsoidal depressions, longitudinally arranged in this material instead of the U-tubes, J-tubes, or tongue-shaped pouches in the holotype of *A. xylobiontum* and *A. lithuanicum* supported the creation of the new ichnospecies *A. lignorum*, which also would have another origin.

Genise (2004) already described material from the new ichnospecies, but attributing it to *A. xylobiontum*, although pointing out some differences. He discarded the mayfly hypothesis and also mentioned that those traces were also similar to coleopteran pupation chambers in wood (Fig. 4B). However pupation chambers are usually associated to galleries, which are lacking in *A. lignorum*, and the density of the depressions in some specimens of this ichnospecies is unlikely for pupation chambers.

Genise (2004) already described a specimen of *A. lignorum* from the surface of permineralized branches and trunks from the Upper Cretaceous Allen Formation (Río Negro) of Argentina (Fig. 4C), and as sandstone casts from the Eocene-Oligocene Jebel Qatrani Formation (Fayum) (Fig. 4D) and from the Miocene Moghra Formation (Qattara) (Fig. 4E) of Egypt. In the Allen Formation, the occurrence of *A. lignorum* is widespread in some of the petrified forests. Such attribution was based on similar traces produced by different types of fungal attacks in living trees on river banks (Otamendi, Buenos Aires) or near lakes (Puerto Blest, Río Negro) in humid environments of Argentina. The example of Otamendi (Argentina) (Fig. 4F) corresponds to a living *Eucalyptus* tree attacked probably by the stem canker *Conyothirium* (Deuteromycetes) (Marraro Acuña and Garran, 2004; Marraro, pers. comm., 2011), which produces lenticular kino pockets particularly observable at the left of the trunk.

Puerto Blest example (Fig. 4G and H), a white pocket rot produced by Polyporaceae (Basidiomycetes) (Rajchenberg, 2006; Rajchenberg, pers. comm. 2011), occurring in *Nothofagus* dead trunks is probably the most complete case to explain the different preservations of *A. lignorum*, either as pits in the surface of trunks or as casts similar to those of the New Caledonia material. The most attacked part of the wood is transformed into an alveolar structure composed of elongated alveoli aligned along the trunk longitudinal axis (Fig. 4G). Sediments filling this alveolar structure would result in specimens of *A. lignorum* preserved as internal casts from New Caledonia (Figs. 2 and 3). We show the surface of the healthy part of the trunk in contact with the attacked, alveolar, adjacent layer preserves pits that represent the cut ends of alveoli of the attacked part (Fig. 4F–H). Such traces are indistinguishable from specimens of *A. lignorum* of the Moghra Formation (Fig. 4E).

The fungi hypothesis was supported later by Mikuláš and Zasadil (2008), who showed a trunk from the Miocene Most Formation of Louny (Czech Republic) with the characteristic pits of *A. lignorum*. Later, Pujana et al. (2009) showed similar traces in a piece of Eocene wood from Argentina effectively associated to cellular decay produced by fungi. Previously, Creber and Ash (1990) have shown similar fungal attacks on Upper Triassic trees from the Chinle Formation (USA), but represented by elongated rods instead of pits.

Depressions are not made by physical erosion since they are formed between the most rotten external layer of the wood and the inner healthy part, a surface which is not exposed to weathering (physical factors) (Fig. 4H). Accordingly, the depression are produced by the primary activity of the fungi themselves and then *A. lignorum* can be qualified as trace fossils.

According to its present record involving different continents and ages since the Cretaceous, *A. lignorum* will probably result in a more widespread trace fossil in wood. It may be an indicator of humid or subhumid terrestrial palaeoenvironments according to its fungal origin. Particularly when the fungal attack is widespread in entire forests as those of the Chinle Formation (Creber and Ash, 1990) or the Allen Formation presented herein. *A. lignorum*, being fungus traces produced in continental settings, has a very different paleoenvironmental meaning than *A. xylobiontum*. Accordingly, paleoenvironmental interpretations of freshwater subaquatic settings inferred by Moran et al. (2010) based on *A. lignorum* should be reviewed.

In conclusion, the different ichnospecies of the ichnogenus *Asthenopodichnium* correspond to traces of activities of very different origins, caused by animals or fungi, even if the resulting traces look superficially very similar.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.09.025>.

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