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The first Early Jurassic (late Hettangian) theropod dinosaur remains from the Grand Duchy of Luxembourg

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ABSTRACT. Body fossils of earliest Jurassic (Hettangian) dinosaurs are scarce worldwide. Here we report two isolated dinosaur remains from the marine upper Hettangian (the *Schlotheimia angulata* ammonite Zone) Luxembourg Sandstone Formation, collected at Brouch, Grand Duchy of Luxembourg. The small to medium-sized pedal phalanx III-1 is referred to a neotheropod dinosaur based on the combination of the following features: proximal end with a lateral margin formed by two straight margins meeting at a wide angle, distal end with a well-defined semilunate extensor fossa and a proximodistally elongated shaft. The isolated tooth crown most likely belongs to an indeterminate theropod, because of its labiolingually compressed shape and the presence of sharp mesial and distal carinae and denticles along its distal edge. These remains represent the first Jurassic dinosaur specimens reported from the Grand Duchy of Luxembourg, enlarging the meagre record of the group immediately after the Triassic-Jurassic mass extinction event.

KEYWORDS: Dinosauria, Theropoda, Early Jurassic, Grand Duchy of Luxembourg, Europe.

1. Introduction

The Triassic-Jurassic mass extinction event seems to have prompted the success of dinosaurs during the Jurassic and Cretaceous (Benton, 1983; Brusatte et al., 2008; Langer et al., 2010). Nevertheless, earliest Jurassic (Hettangian) dinosaur bones are scarce worldwide (Table 1), being represented unambiguously by the holotype of *Sarcosaurus andrewsi* and by an indeterminate *Syntarsus* species from the Moenave Formation in Arizona, USA. The holotype of *Lophostropheus airelensis* (Carrano & Sampson, 2004; Ezcurra & Cuny, 2007) probably also belongs to this list, although a somewhat older age (latest Rhaetian) is not excluded. By contrast, the coetaneous theropod ichnofossil record is relatively rich and widely distributed on a global scale (e.g. Hitchcock, 1836, 1848, 1858; Ellenberger, 1965; Bassoullet, 1971; Gierlinski, 1991; Demathieu & Sciau, 1992, 1999; Avanzini & Leonardi, 1993; Gierlinski & Ahlberg, 1994; Dalla Vecchia, 1995; Olsen, 1995, 2005; Smith et al., 1996; Gierlinski & Sawicki, 1998; Pienkowski, 1998; Le Loeuff et al., 1999; Leonardi & Mietto, 2000; Gierlinski et al., 2001; Kirkland et al., 2002; Dalman & Getty, 2003; Niedzwiedzki & Pienkowski, 2004; Gierlinski & Niedzwiedzki, 2005; Avanzini & Petti, 2008). The reasons for this meagre earliest Jurassic dinosaur bony record is not well understood, but an improved fossil record from this time span is crucial to obtain a better knowledge of the recovery fauna in the aftermath of the Triassic-Jurassic mass extinction event and the macroevolutionary patterns and processes related with it.

In the present paper we describe theropod dinosaur remains from the marine beds of the lowermost Jurassic (upper Hettangian; *Angulata* Zone) Luxembourg Sandstone Formation, cropping out at Brouch, near Mersch, Grand Duchy of Luxembourg (Meier & Meiers, 1988; Faber & Weis, 2005) (Fig. 1A). Until now, the Mesozoic archosaur record from Luxembourg was restricted to specimens collected in Upper Triassic beds (Hahn et al., 1984; Godefroit et al., 1998). The non-ungual pedal phalanx (MHNL BR778) and the shed tooth (MHNL BR924) described here thus constitute the first post-Triassic dinosaur remains of the country. Both specimens, which appear to have belonged to small to medium-sized theropods, are housed in the collections of the Luxembourg Natural History Museum.

2. Institutional abbreviations

FMNH: Field Museum of Natural History, Chicago, USA; MB: Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; MCP: Museo de Ciencias e Tecnología, Porto Alegre, Brazil; MHNL BR: Luxembourg Natural History Museum, Luxembourg, Grand Duchy of Luxembourg; NHMUK: The Natural History Museum, London, UK; PVL: Paleontología de Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina; PVSJ: División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; UCMP: University of California Museum of Paleontology, Berkeley, USA.

3. Geological and palaeogeographical setting

The Grand Duchy of Luxembourg is divided into two main geological areas (see Duffin & Delsate, 1993; Monari et al., 2011): the peneplained Devonian cropping out in the north as part of the London-Brabant-Ardennes Massif (Fig. 1B), and the overlying marginal Triassic and Jurassic rocks in the centre and south of the country. The Jurassic sequence is dated as Hettangian to early Bajocian (Gründel, 2012) and overlies the Triassic deposits with an approximately NW-SE strike. The sedimentary units become progressively younger south-westwards and extend laterally into coeval units in the Belgian and French Lorraine, to

***Sarcosaurus andrewsi* Huene, 1932**: Wilmcote (*Angulata* Zone, late Hettangian), Warwickshire, England (Huene, 1932; Carrano & Sampson, 2004).

Coelophysis rhodesiensis (Raath, 1969): Kwengula River, Southcote farm, Forest Sandstone (Hettangian–Sinemurian), northeast to Bulawayo, Nyamandhlovu District, Rhodesia, Zimbabwe (Raath, 1969).

Lophostropheus airelensis (Cuny & Galton, 1993): Airel Quarry (Manche) (latest Rhaetian–early Hettangian), Moon-Airel Formation, Carentan Basin, southeast of the Cotentin Peninsula, Normandia, France (Cuny & Galton, 1993; Ezcurra & Cuny, 2007).

Cryolophosaurus ellioti Hammer & Hickerson, 1994: lower levels of the Hanson Formation (Hettangian–Toarcian), Beardmore Glaciar Region of the Central Transantarctic Mountains, Antarctica (Smith et al., 2007).

***Syntarsus* sp.**: Dinosaur Canyon Member (Hettangian), Moenave Formation, Arizona, United States of America (Lucas & Heckert, 2001).

Theropod remains described in the present paper: Feidt Quarry in Reckingerwald (*Angulata* Zone, late Hettangian), Luxembourg Sandstone Formation, Brouch, Luxembourg.

Table 1. Hettangian (earliest Jurassic) theropod records, arranged according chronology of discovery (unambiguous Hettangian records are in bold).

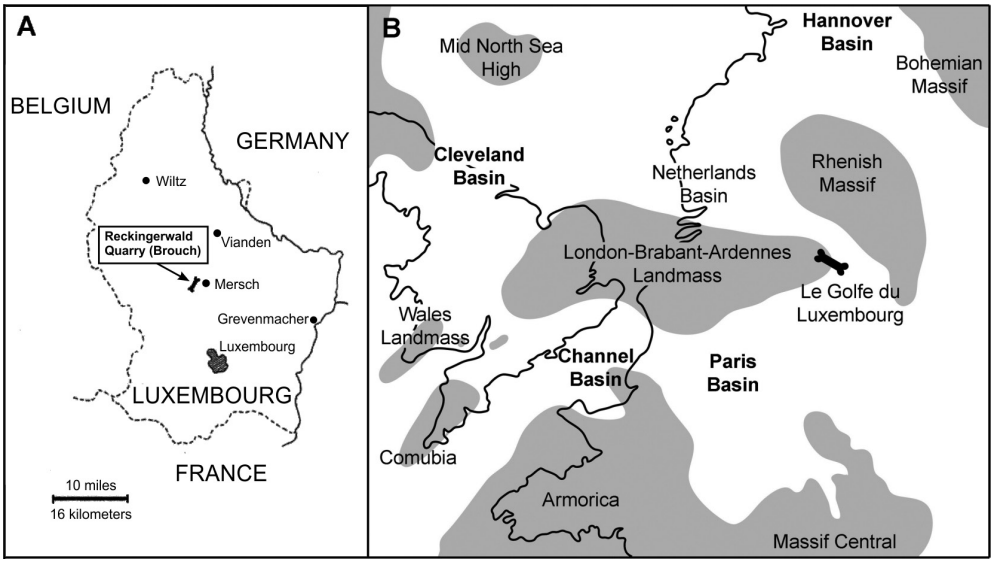


Figure 1. A: Map of Luxembourg showing the provenance (black bone) of the specimens described here. B: Palaeogeographical reconstruction of part of western Europe during earliest Jurassic times. Exposed landmasses during the earliest Jurassic are indicated in grey and the position of the Luxembourg area is indicated by a black bone in B. Maps redrawn and simplified from Bradshaw et al. (1992), De Graciansky et al. (1998), Dercourt et al. (2000), and Monari et al. (2011).

form the north eastern tip of the Paris Basin (Fig. 1B). During the early Mesozoic, marine deposition took place in a rather narrow stretch of water between two land masses, respectively known as the London-Brabant-Ardennes Landmass and the Rhenish Massif (Fig. 1B). The southern part of the Grand Duchy of Luxembourg was covered by this water mass (often termed "Le Golfe du Luxembourg" or Luxembourg seaway) during the Early Jurassic, connecting the Paris Basin with the epicontinental seas of the Netherlands and northern Germany (De Graciansky et al., 1998; Van den Bril & Swennen, 2009). The predominant Lower Jurassic sedimentary facies consists of strongly diachronous (cf. Berners, 1985), cross-stratified calcarenites, representing the Luxembourg Sandstone Formation or "Grès de Luxembourg". The deposition of this unit occurred mostly during Hettangian time (in the quadrilateral area defined by Mondorf-Oberpallen-Bigelbach-Echternach), although, in the extreme west of its depositional area, the uppermost levels have been dated as early Sinemurian (Guérin-Franiatte & Muller, 1986, 2005; Guérin-Franiatte et al., 1991). The Luxembourg Sandstone Formation is composed of yellowish poorly cemented sandstone and grey to whitish, well cemented sandy limestone (Colbach, 2005), reaching a thickness of 110 metres in the centre of Luxembourg (Faber & Weis, 2005). The unit is a complex of sand waves and bars, deposited diachronically, east to west, on a shallow marine shelf under tidal deltaic environmental conditions (Colbach, 2005; Van den Bril et al., 2007; Van den Bril & Swennen, 2009). The top of the Luxembourg Sandstone Formation is marked by a bioturbated level (Bintz & Muller, 1970), belonging to the *Schlotheimia angulata* ammonite Zone (upper Hettangian) in the south-east (near Welfrange), but located near the Hettangian-Sinemurian boundary in the north-west (around Luxembourg and Strassen).

The vertebrate remains described in this paper were found in beds of the Luxembourg Sandstone Formation, cropping out in the Feidt Quarry at Reckingerwald, near Brouch (Mersch), 20 kilometres north of Luxembourg city (49°44'38.97"N, 6° 2'59.36"E) (Fig. 1A, Fig. 2). During the 1980s, more than 40 metres of the Luxembourg Sandstone Formation were exposed in this quarry (Meier & Meiers, 1988, p. 11), consisting of sands and calcarenites with intercalated clays, overlain by conglomeratic lumachelle horizons (i.e. coarse-grained coquina layers yielding concentrations of fossils) and cross-bedded sands and marls. A 20-cm-thick lumachelle horizon of late Hettangian age (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone)



Figure 2. View of the Reckingerwald Quarry near Brouch. The white lower levels are the sands and calcarenites of the Luxembourg Sandstone Formation (Hettangian) and the blue-grey upper levels are the Strassen Marl and Limestone Formation (Sinemurian).

(Guérin-Franiatte & Weis, 2010) has yielded a rich invertebrate fauna (sponges, corals, bryozoans, bivalves, gastropods, cephalopods, echinoderms) and rare vertebrate fossils, including the dinosaur remains described here. This lumachelle horizon is situated 38.7 metres above the base of the section and around 10 metres below the transition to the Sinemurian Strassen Marl and Limestone Formation or "Marnes et Calcaires de Strassen".

Vertebrate remains previously described from the Brouch beds consist of plesiosaur bones, more precisely a dorsal vertebra (MNHL BR795) (Delsate, 2000) and a proximal end of humerus (MNHL BR777), two hybodontiform fin spines (MNHL BR738, 749) (Delsate, 1992), an ichthyosaur tooth assigned to *Temnodontosaurus* (MNHL BR 794), and a myriacanthid tooth plate referred to *Halonodon luxembourgensis* (MNHL BR739) (Duffin & Delsate, 1993). We enlarge here the taxonomic diversity of vertebrate remains from the Brouch vertebrate assemblage with the description of a neotheropod dinosaur pedal phalanx (BR778), and a shed tooth, most likely belonging to a theropod (BR924).

4. Systematic Palaeontology

Archosauria Cope, 1869
Dinosauria Owen, 1842
Theropoda Marsh, 1881
Neotheropoda Bakker, 1986

Neotheropoda indet.
(Figs 3A, C, E)

Material: MHNL BR778, isolated left pedal phalanx III-1 from the late Hettangian Luxembourg Sandstone Formation at Brouch, Grand Duchy of Luxembourg.

Description: MNHL BR778 corresponds to an isolated phalanx lacking its medial surface and most of its distal portion (Fig. 3A, C, E). It was originally identified as a left manual phalanx IV-3 by Delsate (2000, fig. 1a). However, this bone is more similar to a dinosaur pedal phalanx rather than the proportionally transversely narrower bipedal dinosaur manual phalanges. As a result, BR778 is re-identified as a pedal phalanx. The presence of a shallowly concave, undivided proximal articular facet indicates that the phalanx is a proximal element. It is not a phalanx I-1 or IV-1 because the bone is too proximodistally-elongated and neither a phalanx II-1 because it is not medially curved, as observed in the feet of *Liliensternus liliensterni* (MB R 2175) and *Dilophosaurus wetherilli* (UCMP 37302). MHNML BR778 is reinterpreted as a pedal phalanx III-1 on the basis of the following characters: presence of a slightly concave proximal articular surface in combination with the lateral margin of its proximal end, showing two conspicuous straight margins, meeting at a wide angle. It belongs to the left foot because the lateral edge of its proximal facet possesses a wide angle formed by two straight margins, which is also found on the lateral edge of the left pedal phalanges III-1 in other theropods (e.g. *Liliensternus liliensterni*: MB R 2175 7.17.7, 7.18.7; *Dilophosaurus wetherilli*: UCMP 37302; *Allosaurus fragilis*: Madsen, 1976, plate 54).

At preserved, the phalanx has a total length of 61 mm. The proximal end has a dorsoventral height of 23.9 mm and its surface is ornamented by shallow longitudinal wrinkles of about 0.25 mm in width. The preserved portion of the proximal articular facet is smooth and slightly concave (Fig. 3, paf). The dorsal margin of the proximal facet is strongly transversely convex and the ventral one incipiently transversely concave. The lateral margin is formed by the two straight borders described above. The proximal end of MHNL BR778 possesses a well developed lateroventral flange that confers a sigmoid ventral profile to the phalanx in lateral view (Fig. 3, lvf). This flange is also present in *Dilophosaurus wetherilli* (UCMP 37302). The dorsal margin of MHNL BR778 is straight in lateral view, resembling the condition in *Liliensternus liliensterni* (MB R 2175 7.17.7, 7.18.7), but contrasting with the concave margin of *Dilophosaurus wetherilli* (UCMP 37302) (Fig. 3B). The dorsal surface of the distal end possesses a well-developed, semilunate extensor fossa (Fig. 3, ef). This fossa is situated immediately proximal to the distal articular surface, as it is usually found in basal saurischian dinosaurs (e.g. *Herrerasaurus ischigualastensis*: PVSJ 373). The distal end of the bone has a square section as preserved (14 x 14 mm), but it should have been transversely broader than tall because the medial portion is missing. The lateral surface of the distal end has a deep and well defined, teardrop-shaped collateral pit (Fig. 3, cp), closely resembling the condition observed in *Dilophosaurus wetherilli* (UCMP 37302) and *Allosaurus fragilis* (Madsen, 1976, plate 54). The preserved portion of the distal trochlea has smooth dorsal and ventral surfaces for articulation with the phalanx III-2 (Fig. 3, dat).

Taxonomic affinities: MHNL BR778 is referred to a neotheropod dinosaur because of the combination of several features, including the configuration of the lateral margin of the proximal end of the phalanx, which consists of two straight margins, meeting at a wide angle, a semilunate extensor fossa at its distal end, and a proximodistally elongated shaft. In sauropodomorph dinosaurs, pedal phalanges have also a semilunate extensor fossa, but the phalanges are proportionally shorter proximodistally (e.g. *Saturnalia tupiniquim*: MCP 3845-PV; *Adeopaposaurus mognai*: PVSJ 569; *Pantydraco caducus*: Yates, 2003, fig. 20) and, in at least some basal forms, the lateral margin of phalanx III-1 has a continuously straight border (e.g. *Saturnalia tupiniquim*:

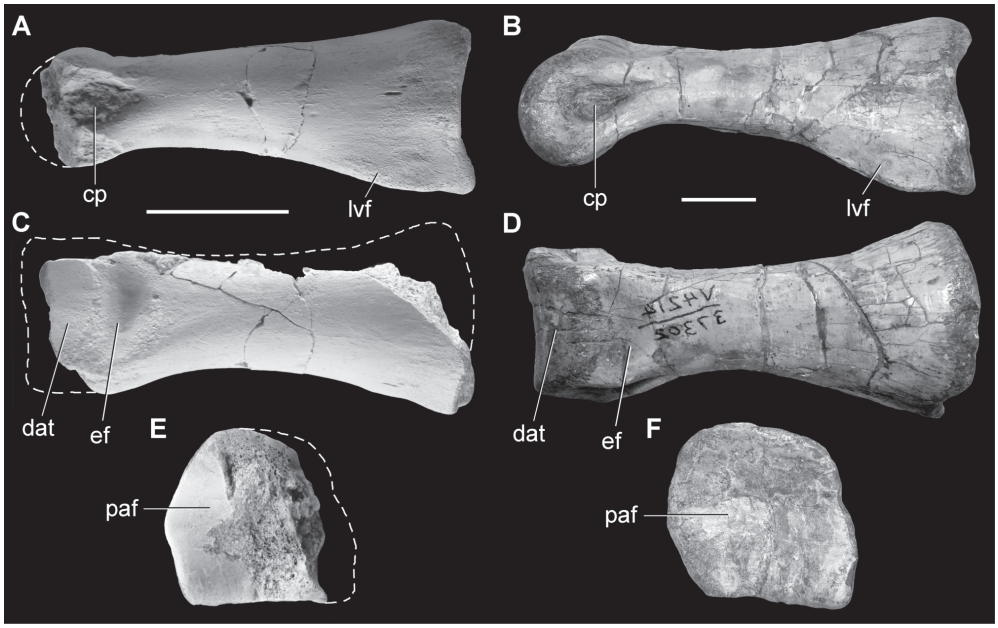


Figure 3. Pedal phalanges of Neotheropoda indet. BR778 (A,C,E) and *Dilophosaurus wetherilli* UCMP 37302 (B, D, F). A-B: lateral; C-D: dorsal and E-F: proximal views. Abbreviations: cp = collateral pit, dat = distal articular trochlea, ef = extensor fossa, lvf = lateroventral flange, paf = proximal articular facet. Scale bars equal 2 cm.

MCP 3845-PV). In basal ornitischian dinosaurs (e.g. *Eocursor parvus*: Butler, 2010, fig. 17; *Heterodontosaurus tucki*: Santa Luca, 1980, fig. 20) and basal crocodylomorph pseudosuchians (*Terrestrisuchus gracilis*: NHMUK R10002; *Hesperosuchus gracilis*: Colbert, 1952) the distal end of the pedal phalanges have a circular and not distally defined extensor fossa.

***cf.* Theropoda indet.**
(Figs 4A, C, E)

Material: BR924, maxillary or dentary shed tooth from the late Hettangian Luxembourg Sandstone Formation at Brouch, Grand Duchy of Luxembourg.

Description: MHNL BR924 is a shed tooth (i.e. the root is missing) with an apicobasally tall and blade-like crown (Figs. 4A, C, E), resembling the condition in most theropod dinosaurs, but also in some basal crocodylomorphs. The tip of the crown is blunt and the edges of the mesial and distal borders are eroded probably during transportation before burial. The crown has a maximum preserved height of 46 mm, a basal mesiodistal length of 15.5 mm, and a labiolingual width of 7 mm. The height of the mesial carina is 45 mm and that of the distal carina is 43 mm. The crown is distally curved, with a concave distal margin and a convex mesial margin. The enamel is smooth and does not possess wrinkles, ridges or other kind of ornamentation, as also observed in most basal theropods (e.g. *Dilophosaurus wetherilli*: UCMP 37302) (Figs. 4A, B). The preserved portion of the base of the crown indicates that the tooth apparently lacked a constriction between the crown and the root, resembling the condition of non-coelurosaurian theropods (Holtz, 1994) (Fig. 4, cr). Both edges possess distinct carinae. Although the distal margin of the crown is strongly weathered (Fig. 4C, wd) the bases of denticles can be faintly discerned, being regularly disposed along the margin, indicating that it is not a taphonomic artefact. The average density of the denticles is 2.6 per mm close to the base of the crown and 2.0 per mm at the apical portion of the tooth, resembling the condition in several theropod dinosaurs, in which a lower density of denticles is observed towards the apex of the crown (e.g. *Dilophosaurus weterilli*: UCMP 37302; *Piatnitzkysaurus floresi*: MACN-Pv-CH 895). The mesial margin is better preserved and seems to lack denticles. The absence of mesial denticles is observed among averostran theropods, such as the megalosauroid *Sciurumimus albersdoerferi*, the megaraptoran *Orkoraptor burkei*, compsognathids and dromaeosaurids (Novas et al., 2008; Rauhut et al., 2012). However, this condition should be considered with caution in MHNL BR924 because their absence may be an artefact of preservation. Both carinae are aligned to each other, indicating that BR924 does not belong to a premaxillary or an anterior dentary tooth. The crown is well labiolingually compressed, acquiring an oval cross-section (Fig. 4E), as usually occurs in archosauriforms (Dilkes, 1998). In mesial or distal view, the crown possesses a gentle lingual bowing.

Taxonomic affinities: MHNL BR924 closely resembles the tooth morphology usually found among basal archosauriforms, contrasting with plesiosaurs and ichthyosaurs, in which tooth crowns are conical, strongly longitudinally striated and lack or have poorly developed cutting edges or serrated margins (e.g. McGowan & Montani, 2003; *Rhomaleosaurus megacephalus*: Cruickshank, 1994; *Thalassiodracon hawkinsi*: Storrs & Taylor, 1996; *Guizhouichthyosaurus tangae*: Maisch et al., 2006; *Meyerasaurus victor*: Smith & Vincent, 2010). However, the identification of blade-like teeth is problematic because this morphology is widespread among basal archosauromorphs and rather homoplastic. MHNL BR924 has a strongly labiolingually compressed crown and denticles at its distal margin, which are considered archosauriform synapomorphies (Gauthier et al., 1988; Dilkes, 1998). However, the presence of both traits can also be extended to, at least, some non-archosauriform archosauromorphs with leaf-shaped crowns (e.g. *Azhendosaurus madagaskarensis*: FMNH PR 2751). Within Archosauriformes, phytosaur teeth are usually distally curved but differ from BR924 in being circular in cross-section to gently labiolingually compressed (Hungerbühler, 2000). Crocodylomorph tooth crowns are generally straight, but some basal forms (e.g. *Pseudhesperosuchus jachaleri*: PVL 3830; *Dibothrosuchus elaphros*: Wu & Chaterjee, 1993; *Dromicosuchus grallator*: Sues et al., 2003) have labiolingually compressed and distally curved crowns, resembling the condition of MHNL BR924. Thalattosuchian crocodylomorph tooth crowns differ from BR924 in the usual presence of enamel bands, facets, strongly sharp and tapering carina and the absence or poor degree of distal curvature (e.g. Andrade et al., 2010). Pterosaur tooth crowns are generally more conical, less tapering apically and

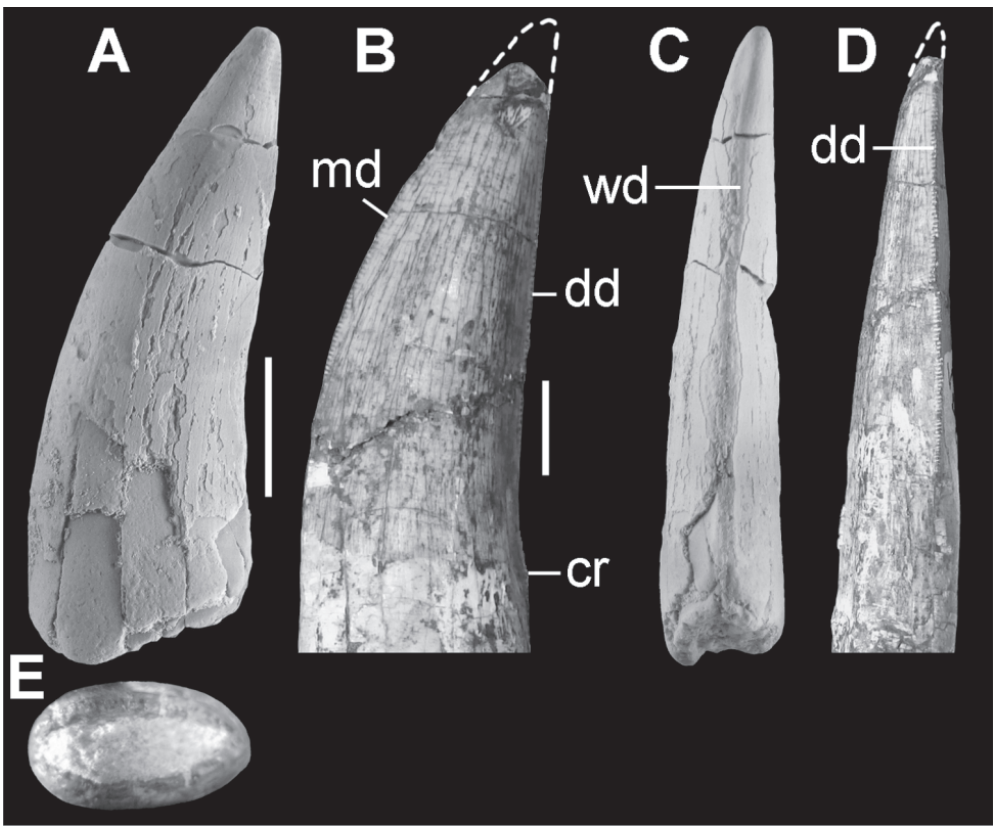


Figure 4. Tooth crown of *cf.* Theropoda indet. BR924 (A,C,E) and *Dilophosaurus wetherilli* UCMP 37302 (B, D). A-B: labial; C-D: distal and E: basal views. Abbreviations: cr = crown-root boundary, dd = distal denticles, md = mesial denticles, wd = weathered distal carena. Scale bars equal 1 cm.

lack denticles (e.g. Averianov et al., 2005) and those that possess denticles usually have lanceolate crowns in lingual or labial view (e.g. *Austriadactylus cristatus*: Dalla Vecchia et al., 2002; Dalla Vecchia, 2009).

The Brouch tooth crown closely resembles the morphology exhibited by basal theropods, with a labiolingually compressed crown, mesial and distal carena, denticles, distally curved and gradually apically tapering crown (e.g. *Liliensternus liliensterni*, *Lophostropheus airelensis*: MB R2175; Cuny & Galton, 1993). In particular, BR924 is very similar to the distinctly apicobasally tall crown of *Dilophosaurus wetherilli* (UCMP 37302) (Fig. 4). In addition, the size of the Brouch tooth matches those recorded among basal theropods and exceeds the sizes described for Early Jurassic "sphenosuchian" and protosuchian crocodylomorphs. Accordingly, MHNL BR924 very likely belongs to a theropod dinosaur, but a "sphenosuchian" and protosuchian crocodylomorph affinity cannot be completely ruled out.

5. Discussion

The presence of terrestrial animals in marine depositional settings suggests transportation of allochthonous elements. This might be due to transgressive pulses flooding inland areas and sweeping away carcasses of terrestrial life forms, or through floating carcasses introduced in coastal areas via river systems. The sedimentological data from the Feidt Quarry near Brouch bear evidence for such a coastal configuration, as the coarse-grained sediments that yielded the currently described fossil material were deposited under high energy conditions in a shallow marine environment (Van den Bril & Swennen, 2009). The recovery of terrestrial animal remains is not uncommon in the marine Jurassic beds of Europe, a situation that was probably favoured by its palaeogeography (Fig. 1B), as already discussed by Martill (1988), Buffetaut (1994) and Benton et al. (1995).

The here described phalanx, and most likely also the shed tooth, constitute the first theropod remains reported from Luxembourg. Together with *Sarcosaurus adrewsi*, *Syntarsus* sp. and probably *Lophostropheus airelensis* they constitute one of the few theropod records from unambiguously dated Hettangian beds around the world (Carrano & Sampson, 2004; Ezcurra & Cuny, 2007). The meagre dinosaur body fossil record immediately after the Triassic-Jurassic mass extinction event seems to be a non-biological signal because of the abundant and globally distributed coeval ichnofossil record of the group.

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