

EURAMERICAN LATE PENNSYLVANIAN / EARLY PERMIAN ARTHROPLEURID/TETRAPOD ASSOCIATIONS – IMPLICATIONS FOR THE HABITAT AND PALEOBIOLOGY OF THE LARGEST TERRESTRIAL ARTHROPOD

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Abstract—The giant arthropod *Arthropleura* was a common member of the late Paleozoic continental biota of paleo-equatorial biomes for more than 35 million years, from the Early Carboniferous late Viséan (FOD; Middle Mississippian, Asbian/Brigantian) up to the Early Permian lower Rotliegend (LOD = ?LAD; Asselian). In Upper Pennsylvanian red beds in Cañon del Cobre of northern New Mexico, trackways of *Arthropleura* are present in strata that also yield body fossils of the amphibian *Eryops*. We review the *Arthropleura* tracksite from Cañon del Cobre, New Mexico, as well as other tracksites of this animal and arthropleurid/eryopid associations in order to better interpret the paleoenvironmental preference and the paleobiology of *Arthropleura*. This review supports the conclusion that *Arthropleura* was well adapted to alluvial environments of ever wet humid to seasonally dry and semihumid climates. Preferred habitats of semi-adult and adult *Arthropleura* were open, vegetated, river landscapes. They co-occurred in these habitats with semi-aquatic eryopid amphibians and terrestrial pelycosaurs.

INTRODUCTION

Since the first description of *Arthropleura* (von Meyer, 1853; Jordan and v. Meyer, 1854; cf. Kraus and Brauckmann, 2003), most remains of this enigmatic giant arthropod were sampled by plant collectors and palaeobotanists in plant-rich roof shales of coal seams from mine dumps. This led to the assumption that this animal preferably lived in the tight hygrophilous to hydrophilous vegetation of Carboniferous coal-forming tropical forests (e.g., Rolfe and Ingham, 1967; Rolfe, 1969, 1980). However, an interesting observation, which would have modified this picture very early, has been overlooked: Guthörl (1940) reported from his detailed paleontological core investigation of the deep drilling Hangard No. 38 the discovery of *Arthropleura* remains at six levels in the depth interval between 50 to 350 m in the Westphalian D Saarbrücken Group of the Saar-Nahe basin. Remarkably, those finds do not come from roof shales of coal seams but from a 235-m-thick sequence of alluvial plain deposits without any indication of coal-forming forests and mires. Obviously, *Arthropleura* body remains are as common in alluvial plain deposits as they are in deposits of peat environments.

In contrast to body remains, which could be transported over large distances, tracks of animals are absolutely autochthonous. Since the first discovery of *Arthropleura* tracks in the Westphalian B (Bashkirian/Moscovian) of Nova Scotia, Canada (Ferguson, 1966), at least 11 more tracksites became known in North America and Europe, ranging from the Viséan of Scotland (Pearson, 1992) up to the Stephanian/Lower Rotliegend transition of Germany (Early Permian, Asselian: Walter and Gaitzsch, 1988) as well as the assumed Early Permian of Nova Scotia (Ryan, 1986). These track records considerably widen our knowledge of the locomotion and paleoenvironments of *Arthropleura* (Briggs et al., 1979, 1984; Wilson, 2003). The most recent description of an *Arthropleura* tracksite reports the co-occurrence with the eryopid amphibian track *Limnopus* in the Upper Pennsylvanian of Kentucky (Martino and Greb, 2009). It provides additional strong evidence of the co-existence of arthropleurids and eryopid amphibians in alluvial environments outside of coal-forming forests and swamps, which was discussed earlier by Schneider and Barthel (1997), and by Schneider and Werneburg (1998). Here, the *Arthropleura* tracksite from Cañon del Cobre, New Mexico (Lucas et al., 2005c) (Fig. 1) will be discussed in comparison with other tracksites of this animal as well as further arthropleurid/eryopid environ-

ments in order to better interpret the paleoenvironmental preference and the paleobiology of *Arthropleura*.

Institutional abbreviations: FG – Technische Universität Bergakademie Freiberg, Paleontological Collection, Germany; MfNC – Museum für Naturkunde, Chemnitz, Germany; MHNA – Musée d'Histoire naturelle, Autun, France; MTB - private collection M. Thiele-Bourcier, Kirel-Neuhäusel, Germany; NHMS - Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen, Germany; NMMNH – New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; SSB – Sammlungen Schloß Burgk, Feital, Germany.

LITHO- AND BIOFACIES OF THE *DIPLICHNITES* *CUITHENSIS* OCCURRENCE IN THE EL COBRE CANYON FORMATION, LATE PENNSYLVANIAN/EARLY PERMIAN, CHAMA BASIN, NEW MEXICO

Nonmarine siliciclastic red beds at the base of the Phanerozoic section across most of the Chama Basin of northern New Mexico are assigned to the Pennsylvanian-Permian Cutler Group. These strata are divided into two mappable lithostratigraphic units, the El Cobre Canyon and overlying Arroyo del Agua formations (Krainer and Lucas, 2001; Lucas and Krainer, 2005). The El Cobre Canyon Formation is up to 500 m of brown siltstone, sandstone and extraformational conglomerate of an ephemeral braided and anastomosed stream environment (Eberth and Miall, 1991) that overlies Proterozoic basement in the subsurface and is conformably overlain by the Arroyo del Agua Formation. Siltstone beds of the El Cobre Canyon Formation contain numerous rhizoliths (Fig. 2E-F) and comprise relatively thin, slope-forming units between multistoried sandstone beds that are arkosic, micaceous, coarse grained and trough crossbedded (Fig. 2A-C). *Scoyenia* traces are typical of horizontal bedded, mica-rich siltstones (Fig. 2 D). Complete bioturbation of the *Planolites montanus* type is rare.

The El Cobre Canyon Formation approximately corresponds to megasequence 1 of Eberth and Miall (1991). According to Eberth and Miall (1991), during deposition of megasequence 1 the climate was semi-arid, major channels were broad and shallow, interfluvial areas were frequently inundated by sheet floods and splays, and floodbasin ponds were relatively common. These sediments are devoid of coal, but do contain leaf floras dominated by seed ferns (DiMichele and Chaney, 2005).

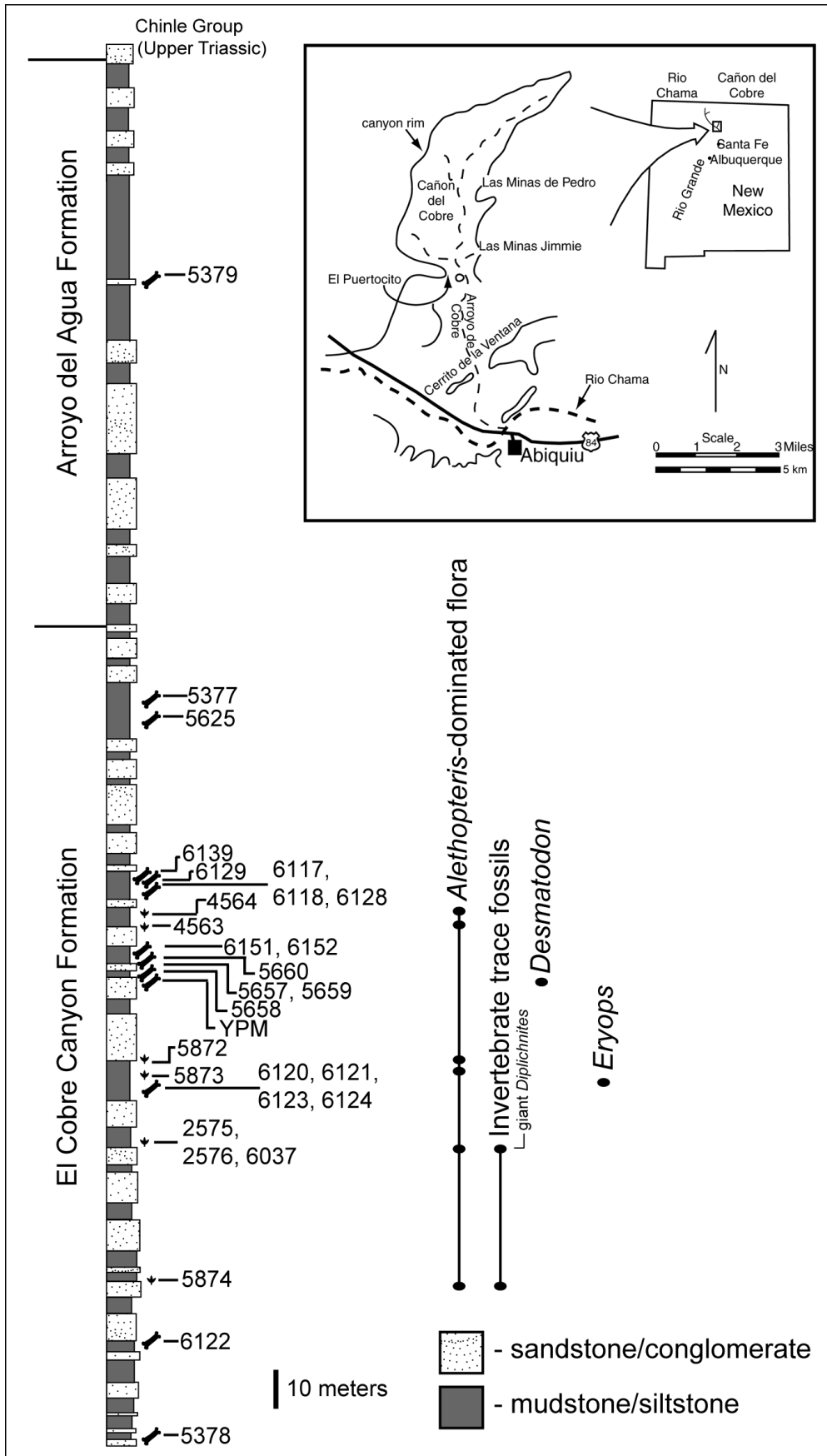


FIGURE 1. Location map of Cañon del Cobre in northern New Mexico and stratigraphy and fossil locality distribution (numbers are fossil localities of the New Mexico Museum of Natural History and Science) of the Upper Pennsylvanian and Early Permian strata in Cañon del Cobre (after Lucas et al., 2005b).

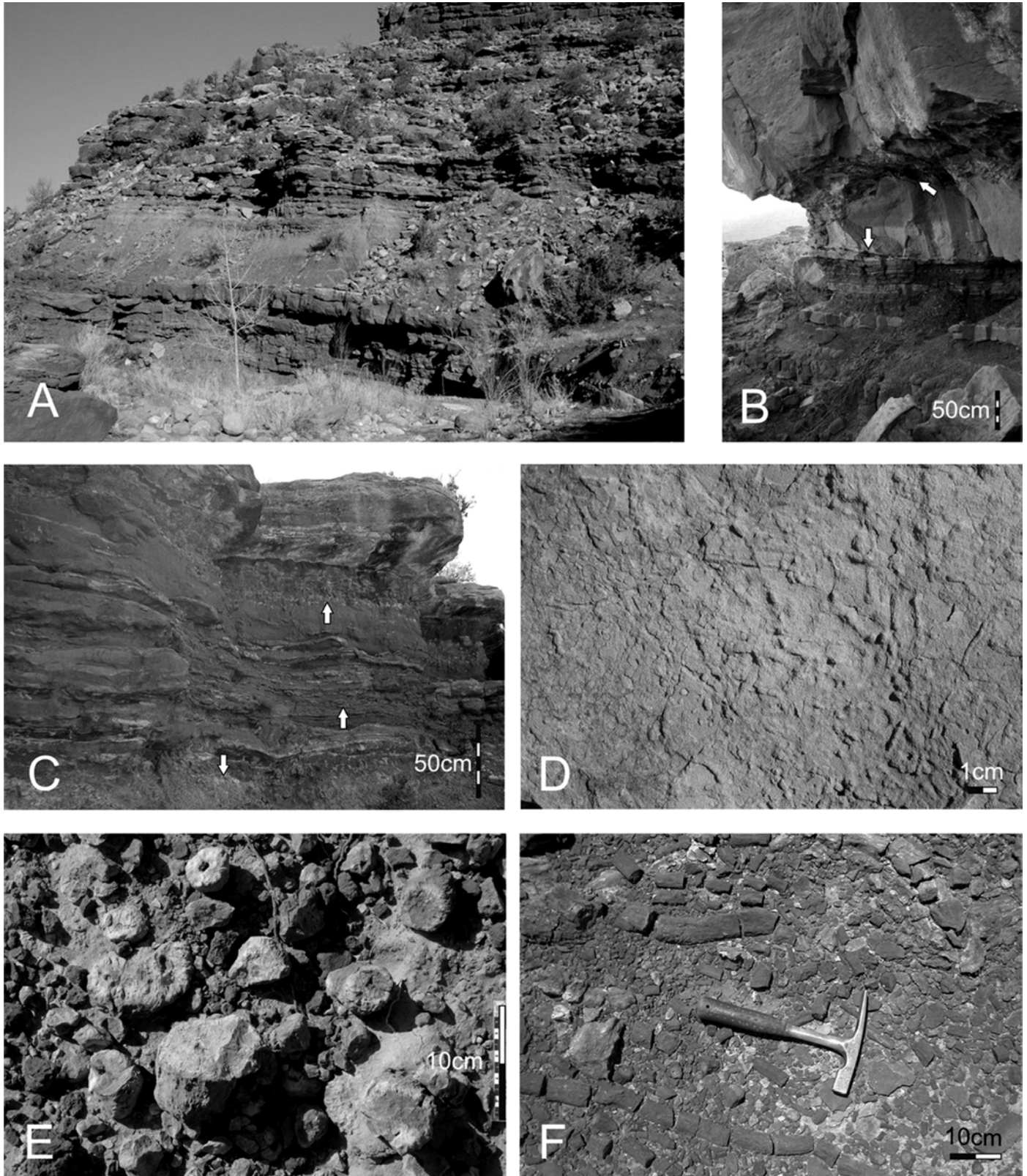


FIGURE 2. Facies pattern and facies-typical fossils of wet red beds of the El Cobre Canyon Formation (Late Pennsylvanian/Early Permian) in Cañon del Cobre. **A**, Typical alluvial plain multistoried sandstones and pedogenically-overprinted siltstones, which make up the whole profile of the formation. **B**, One of the rare, horizontal-bedded, shallow lacustrine mudstone and fine sandstone horizons, which is erosively overlain by trough-cross bedded channel sandstones; at channel bottoms are large mudstone intraclasts (arrows). **C**, Interbedding of lenticular sandstones of minor channels with overbank siltstones, covered by a major channel sandstone. Siltstones altered to calcic soil with bright red to whitish-bluish color mottling and horizons and layers of carbonate nodules. **D**, Fine sandstone with cf. *Scoyenia* burrows. **E**, Densely arranged vertical rhizoliths in siltstone. **F**, Horizontal rhizoliths weathered out from siltstone.

The age of the El Cobre Canyon Formation is Late Pennsylvanian-Early Permian (Lucas et al., 2005b; Lucas, 2006). Fossils from the lower part of the formation in the floor of Cañon del Cobre indicate a Late Pennsylvanian age: palynomorphs (Utting and Lucas, 2010, this volume), megafossil plants (*Alethopteris* flora: Smith et al., 1961; Fracasso, 1980; Hunt and Lucas, 1992; DiMichele and Chaney, 2005; DiMichele et al., 2010, this volume) and fossil vertebrates such as *Desmatodon* and *Limnoscelis* (Fracasso, 1980; Lucas et al., 2005b).

In general, the red-bed sequences of the El Cobre Canyon Formation belong to the type called “wet red beds” (Schneider et al., 2006; Roscher and Schneider, 2006). Wet red beds are characterized by the following litho- and biofacies markers, which are observable in fine clastics of overbank deposits in channel-sandstone-dominated alluvial plains as well as in fine, clastic-dominated floodplain deposits:

1. Horizontal, planar to weakly flaser bedded, fine sandy to clayey, often mica rich, red-brown to red siltstones with common *Scoyenia* burrows and/or completely bioturbated by *Planolites montanus* burrows (*Scoyenia* ichnofacies). In places, laminated siltstone and claystone of shallow pools and lakes (Fig. 2B) preserve traces of the *Mermia* ichnoguild.

2. Bed-scale, pedogenically overprinted, in situ micro-brecciation (mm- to cm-scale), pedogenic slickensides (vertisols) and color mottling.

3. In places, mm-thin, mainly horizontal arranged and branched root systems, preserved as red clay inundations or leached whitish.

4. Calcic soils of different maturity, ranging from mm- to dm-sized calcareous nodules and rhizoconcretions up to massive calcrete horizons (Fig. 2C, E, F).

5. Rarely, dm-thick lacustrine micritic limestones with ostracods, gastropods and characeans.

6. Channel sandstones and conglomerates that may be leached to bright reddish and whitish-greenish because of paleo-groundwater flow.

7. Rare desiccation cracks and raindrop imprints.

In contrast to the semiarid to arid dry red beds of playa and sabkha environments, wet red beds are indicative of a semihumid to semiarid climate with seasonal wet and dry conditions. Evaporation is higher than precipitation, allowing the formation of calcic soils. Seasonal high groundwater levels allow for sparse vegetation only, which is merely documented by the root structures. Above ground (surface) macro-remains are mainly rare or missing. In the paleo-equatorial belt, these kind of red beds were first widespread in the Westphalian D after the Westphalian C/D wet phase A of Roscher and Schneider (2006) and can be observed in all the succeeding dry phases up to the intensive aridization during the late Early Permian (Kungurian: cf. Roscher and Schneider, 2006, fig. 15a-b; Schneider et al., 2006), when they are increasingly replaced by playa red beds.

The El Cobre arthropleurid trackways (Lucas et al., 2005c) occur in the lower part of the exposed section of the El Cobre Canyon Formation on the top surface of a 13- to 15-cm-thick bed of mainly fine- to medium-, slightly coarse-grained, small scale trough-cross bedded to ripple laminated, micaceous, arkosic channel sandstone at NMMNH locality 6037 (Figs. 3-4). The channel sandstone is erosively cut into small scale, trough-cross bedded, dark reddish-brown-violet, fine-sandy siltstone and it is overlain by grayish-red, plant-bearing muddy siltstone beds with dm-wide fine sandstone lenses. The siltstone beds are indistinctly horizontal bedded; common cm-size hematitic nodules as well as roots point to a low pedogenic overprint. They can be regarded as an immature ferrallitic paleosol.

Two trails with the typical features of *Diplichnites cuithensis* were found (Hunt et al., 2004; Lucas et al., 2005c), both running nearly to the west about 5 m distant from one another. The best preserved track is stored now in the New Mexico Museum of Natural History and Science (NMMNH P-45287). It consists of two track rows of mostly crescentic imprints oriented perpendicular to the midline (Fig. 4B; for further details see Lucas et al., 2005c). Imprints are 5-7 cm wide and up

to 1.5 to 2 cm deep (Fig. 4C-E). The external width of the trackway is 32-38 cm. Based on the body width/length ratio of 3.6 to 4.4 (Kraus, 1993; Schneider and Werneburg, 1998), an *Arthropleura* of 1.37 to 1.67 m body length was the trail maker.

The track-bearing sandstone horizon is interpreted as the result of lateral avulsion on the floodplain of minor side channels of a major channel in a braided river system. Larger conglomeratic channels are exposed 1.95 m above the track-bearing horizon (Fig. 3), which could easily be regarded as lateral equivalents of the minor channels. A part of the tracks is preserved as more than 2 cm deep, impressed, crescent-shaped undertracks, well visible where the higher parts of the sandstone with the surface, on which the animal walked, were weathered away (Fig. 4C-D). The remarkable depth of the tracks as well as the soft sediment deformation with indications of plastic to fluid behavior of the river sand during trackmaking indicate that the animal moved on wet sand (Fig. 4B-E). Identical observations were made on several other *Arthropleura* tracksites (see below). The sandstone is strongly carbonate cemented, which may indicate high primary porosity as a prerequisite for fluidization. Bright red to whitish colors and greenish patches (Fig. 4B-D) result from leaching by paleo-groundwater flow, which is responsible for the syngenetic to early diagenetic carbonate cementation as well.

About 15 m above the *Arthropleura* tracksite (NMMNH locality 6037), another NMMNH locality (6121) contained a well preserved *Eryops* skull together with bones of an embolomere, of the dissorophid *Platyhystrix* and pelycosaur in muddy sandstones (Lucas et al., 2005a; Werneburg et al., 2010, this volume).

A rare ichnofossil assemblage of the nonmarine Late Carboniferous was recently discovered at NMMNH locality 5874 about 35 m below the *Arthropleura* tracksite (Lucas and Lerner, 2010, this volume). The assemblage comes from a clastic lake-margin facies and consists of arthropod trackways (*Diplichnites* x *Diplopodichnus*, *Diplichnites gouldi*, cf. *Paleohelcura tridactyla*, *Protichnites* isp.), invertebrate grazing and feeding traces (*Gordia indianensis* and *Helminthoidichnites tenuis*), tetrapod footprints (*Batrachichnus salamandroides* and aff. *Amphisauropus* isp.) and fish swim traces (*Undichna* isp.) The numerically dominant ichnofossils are *Helminthoidichnites* and *Diplichnites*; the other ichnotaxa are represented by a few specimens. Overall, the wet red beds of the El Cobre Canyon Formation belong to the *Scoyenia* ichnofacies (cf. Buatois and Mángano, 2007) and it is composed of members of the *Diplichnites* and *Mermia* ichnoguilds, typical of floodplains and shallow lacustrine settings (Buatois et al., 1998; Buatois and Mángano, 2009).

LITHO- AND BIOFACIES OF THE ARTHROPLEURA OCCURRENCE IN THE MANEBACH FORMATION, EARLY ASSELIAN, THURINGIAN FOREST BASIN, GERMANY

The Thuringian Forest Basin (formerly SW-Saale basin), an approximately 40 to 60 km wide NW-SE oriented depression, is largely exposed in the horst structure of the Thuringian Forest Mountains in East Germany. The basin is situated at the northern border of the Variscan orogen above deeply-eroded Variscan methamorphites and granites. The Gzhelian/Asselian (Late Stephanian) to Guadalupian/Lopingian basin fill of about 6000 m thickness is subdivided into nine formations (Lützner et al., 2007). The coal-bearing (in the type area up to 180 m thick) completely gray Manebach Formation was deposited in a low-relief landscape by forested swamps, local lakes, and fine-clastic-dominated fluvial deposits rich in organic matter. Volcanic rocks in the Manebach Formation are restricted to mm to cm thick ash layers within lacustrine black shales. This formation is famous for its characteristic and well investigated Euramerican Stephanian/Lower Rotliegend (Gzhelian/Asselian) flora (e.g., Barthel, 2001, 2003-2008).

Based on both the lithofacies and fossil content the following sub-environments can be distinguished in the Manebach Formation (Figs. 5A, 6; for details see Schneider, 1996; Werneburg, 1997; Barthel, 2001, 2003-2008; Lützner, 2001):

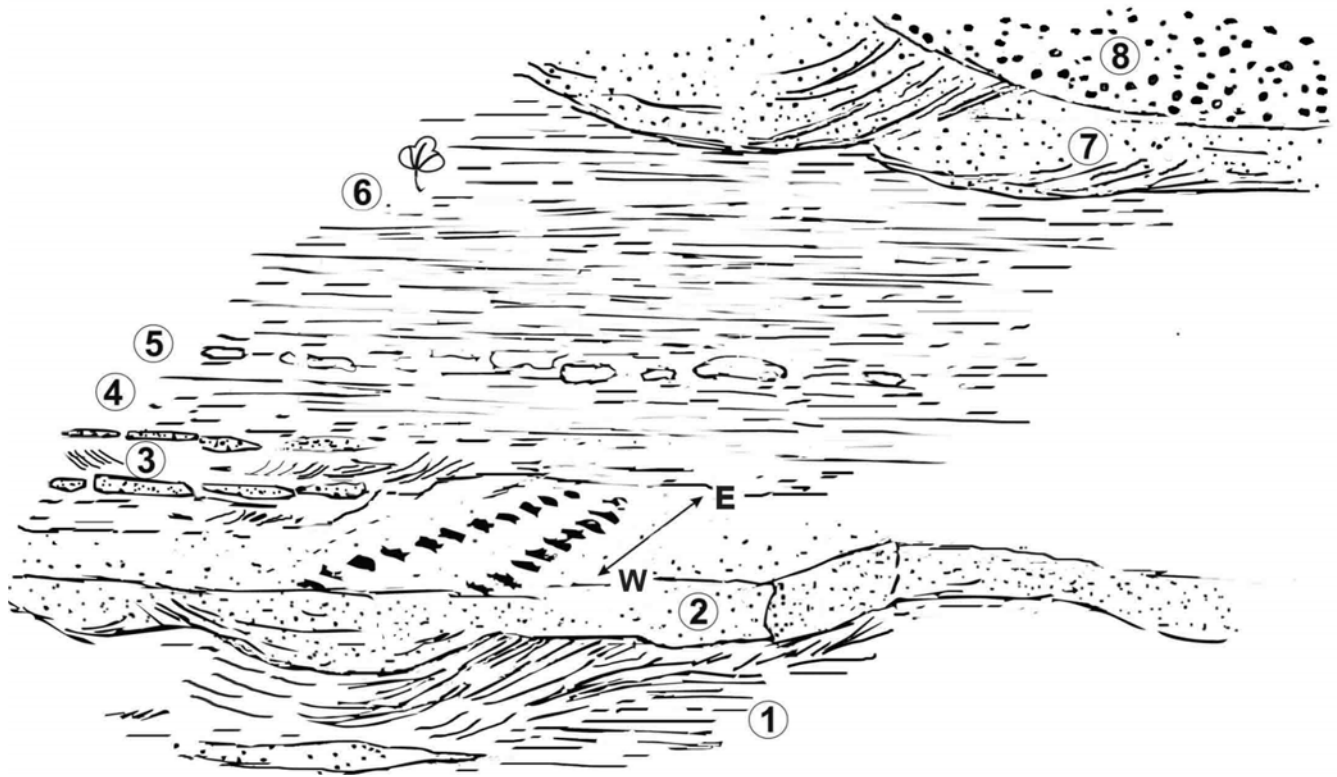


FIGURE 3. Sketch of the *Arthropleura* tracksite at NMMNH locality 6037 (compare Fig. 4) in alluvial plain deposits of the El Cobre Canyon Formation (Late Pennsylvanian/Early Permian) in Cañon del Cobre. 1, 30 cm thick (base not exposed), silty fine sandstone, dark reddish-brown-violet, mica rich, trough-cross bedded, intercalated with up-to-10-cm-thick lenticular fine sandstone. 2, 13-15 cm thick, bright red to whitish, fine- to medium-grained, small scale trough-cross bedded to ripple laminated, micaceous arkosic channel sandstone; at the top is the up-to-38-cm-wide *Diplichnites cuihensis* trail, NMMNH P-45287, extending W-E. 3, 45 cm thick, silty fine sandstone, mica rich, grayish-red-brown, small scale trough-cross bedded, and two intercalated, 5-cm-thick, discontinuous layers of fine-grained sandstone lenses. 4, 40 cm thick, silty fine sandstone, dark brown, structureless/massive. 5, 10 cm thick, silty fine sandstone, greenish leached (immature soil). 6, 100 cm thick, fine sandy siltstone, dark brown, at mm-scale indistinctly horizontal bedded, containing plant fragments as well as cm-size hematitic nodules, some with about 1 mm wide central root channels (tubes) (immature ferrallitic soil). 7, up to 45 cm thick, pebbly coarse channel sandstone, whitish, trough cross-bedded. 8, 70 cm thick (top eroded), fine conglomeratic coarse channel sandstone, dark brown, mainly rounded to sub-rounded quartz pebbles.

1. Medium- to coarse-grained, pebbly, trough cross-bedded channel sandstones; common are stem and strobili remains of *Calamites gigas*, twigs of meso- to xerophilous conifers (“walchians”) and skeletal remains of the eryopid amphibian *Onchiodon* (Fig. 5A) as well as isolated bones of a pelycosaur (?*Haptodus*) (Werneburg, 2007). In the immediate neighborhood of channels as well as in point bar sandstones and channel sandstones, *C. gigas* has been found buried in an upright position (Fig. 5E). At the Manebach localities, this unique succulent calamite forms (nearly) monotypic stands with about 1 m distance between the stems (Barthel and Rößler, 1996; Barthel, 2001).

2. Fine- to coarse-grained sheet sands generated during flood events as overbank and crevasse splay deposits; autochthonous *Calamites gigas* stands are present as well as allochthonous remains of meso- to xerophilous plants from different growth sites above the groundwater level, such as sand bars along river courses and from drier, elevated areas inside the basin and along the basin borders (callipterids, different conifers such as walchians, the coniferophyte *Dicranophyllum* and *Odontopteris lingulata*, etc.).

3. Fine, sandy siltstones to clayey floodplain siltstones deposited during waning stages of flood events with layers of species-rich parautochthonous (often well-preserved large fern fronds), hydro- to mesophilous plant remains, representative of the fern-pteridosperm-calamite vegetation of floodplain areas outside the peat-forming mires; *Arthropleura* remains are not rare.

4. Laminated claystones and siltstones of floodplain pools between the channels, with layers of *Anthraconaia* (Fig. 5D) in places

homogenized by bioturbation (*Pelecypodichnus*).

5. Rooted siltstones and claystones of very wet floodplains, and in places pure hydromorphic to subhydric cordaitalean root horizons of coal-forming forest mires. In the roof shales of seams, the autochthonous swamp forest communities are preserved; most common are *Psaronius* ferns with their fronds (*Pecopteris*, *Scoleopteris*) and pteridosperms, like *Odontopteris schlotheimii*, *Dicksonites pluckenettii*, *Taeniopteris jejuna*, different neuropterids and others, the hygrophilous *Calamites multiramis* and *C. undulatus* as well as the coal-forming cordaitaleans (Barthel, 2001); insect remains are present (mostly cockroaches).

6. Above the coal-seam-containing part of the profile there appear lacustrine, carbon-rich siltstones and claystones with the typical Early Permian palaeoniscid-xenacanthid-fish association of smaller lakes (Schneider et al., 2000). Branchiosaur amphibians are very rare; common lacustrine invertebrates are ostracods, and, in layers, conchostracans; the terrestrial biota is represented by diverse plant fragments and blattid insects (most common, as in many Euramerican lake sediments, is *Anthracoblattina*).

The Manebach locality has been sampled by private plant collectors and palaeobotanists for about 300(!) years (Barthel and Rößler, 1995). Collecting has focused on the plant-rich roof shales of the coal seams. *Arthropleura* and tetrapod skeletal remains were not discovered before the first paleontological research in the fluvial deposits of this profile commenced (Werneburg, 1987; Schneider and Werneburg, 1998). Obviously, they are restricted to those fluvial deposits and their depositional environments. From reconstructed leg length and the size of

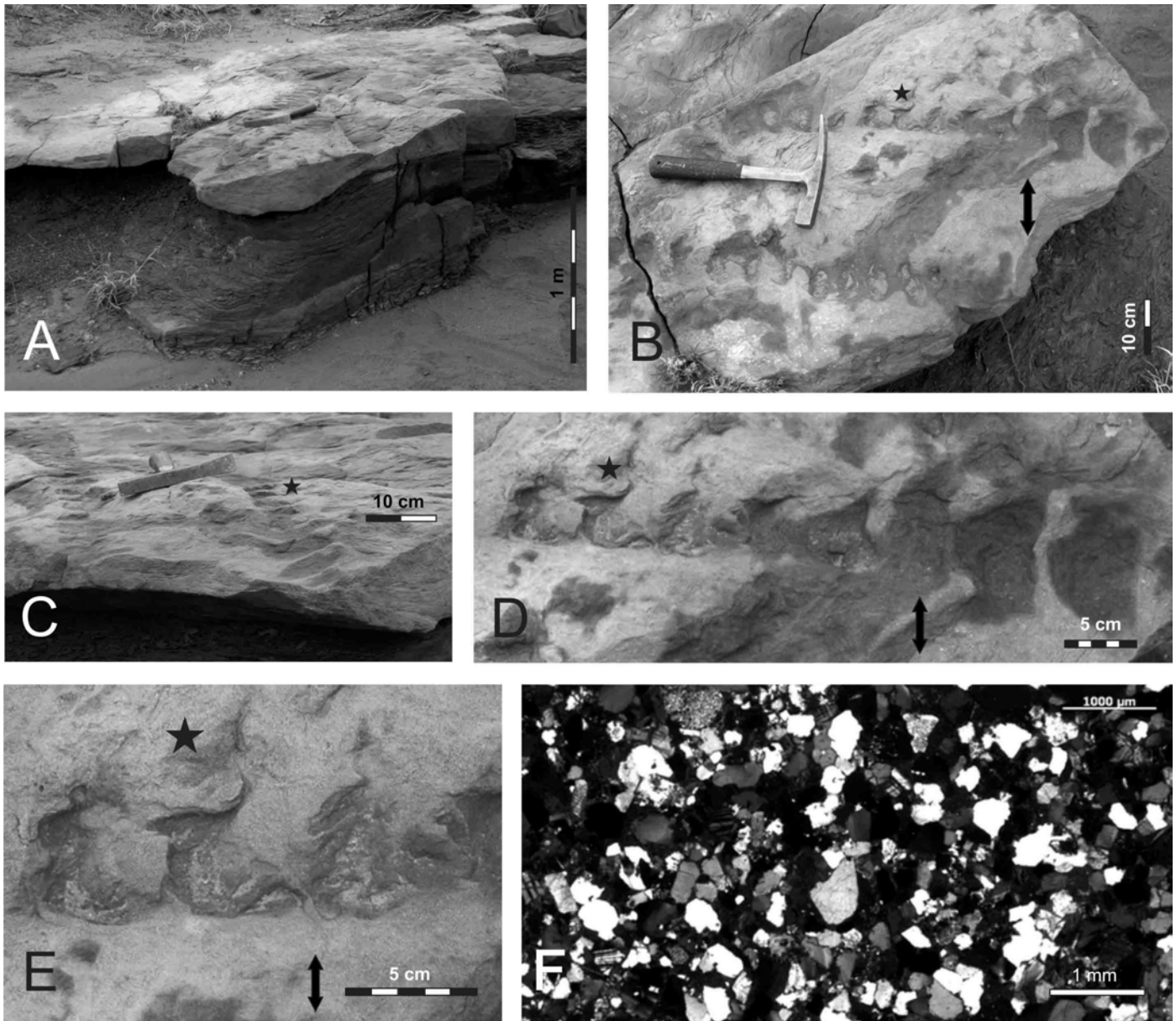


FIGURE 4. Overview of the *Arthropleura* tracksite, NMMNH locality 6037, and the preservation of *Diplichnites cuithensis* in alluvial plain deposits of the El Cobre Canyon Formation (Late Pennsylvanian/Early Permian) in Cañon del Cobre. **A**, *D. cuithensis* trail on top of a sandstone horizon originated from channel avulsion; both the trail-bearing, bright red to whitish channel sandstone and the dark reddish-brown, silty fine sandstone below are trough cross-bedded. **B**, Up to 38 cm wide *D. cuithensis* trail (NMMNH P-45287), which is weathered down to different levels of undertracks; the black star marks the track shown in figs. D and E, double arrow indicates the inside/outside orientation of the trail and tracks in figs. D and E. **C**, Deepest undertracks in front; tracks become shallower and sharper in outline in the direction of the hammer. **D**, Closeup of the upper track row in B; the transition from simple crescent undertracks (right) to increasingly shallow but more detailed tracks (left) is not caused just by the varying depth of modern erosion of the trail but also by the primary depth of imprints, which is 1.5 cm at the track marked by the black star and more than 2 cm (measured from the level of the modern erosion surface) for the track above the scale bar; the depth of undertracks obviously depends on changing wetness of the channel sand. **E**, Closeup of tracks in B (for orientation see black star); the form of the imprints indicates fluid behavior of the sand during trackmaking. **F**, Thin section of the track-bearing sandstone; grain size ranges from dominantly medium to fine sand with some coarse grains, mainly angular, mostly quartz followed by plagioclase, rare lithoclasts, strongly carbonate cemented; strong cementation point on high primary porosity and water fill, which was responsible for the fluid behavior of the still uncemented sand during trackmaking.

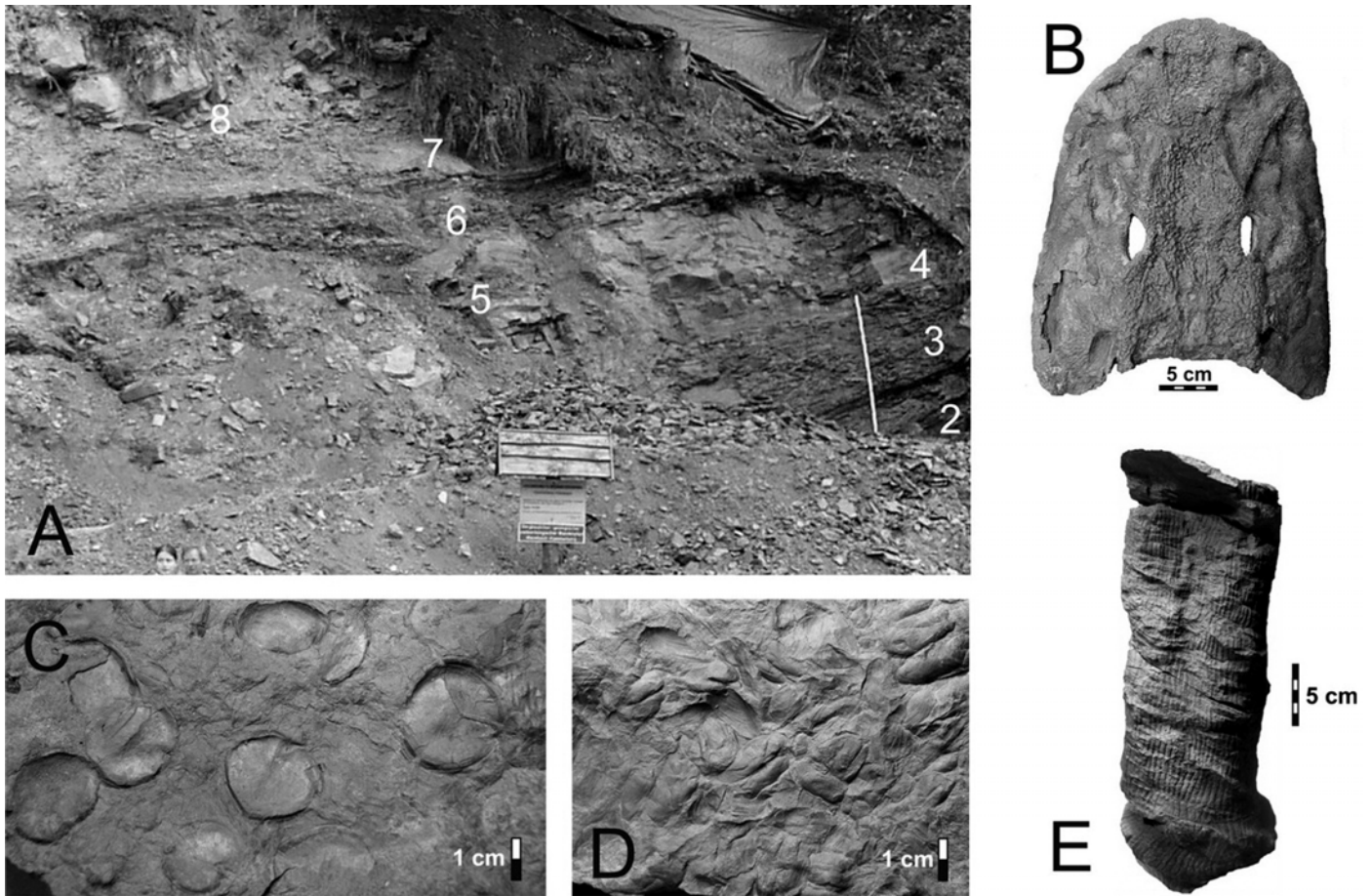


FIGURE 5. Exposure and fossil content of the Manebach Formation (Early Permian) at the type locality south of Manebach village, slope at the B4 road, Thuringian Mountains, Germany. **A**, Excavation site 2005; numbers 2 to 8 refer to the meter-scale in Figure 6; remains of the eryopid *Onchiodon thuringiensis* Werneburg, 2007 were found in the pebbly channel sandstones at 5; *Arthropleura* remains come from plant-bearing overbank siltstones between 7 and 8 as well as from loose blocks. **B**, ca. 30-cm-long skull of *Onchiodon thuringiensis*; NHMS-WP 2140a. **C**, *Cardiocarpus* fructifications washed together in fluvial fine sandstone; NHMS-WP 3310. **D**, Freshwater pelecypod *Anthraconaia* in floodplain pool siltstones; NHMS-WP 3350. **E**, Trunk base of *Calamites gigas* buried upright in fluvial sandstone; NHMS-WP 3407.

paratergites (“pleurites”), body lengths of 0.85 m to 2.25 m have been calculated for the individuals from Manebach. Based on the above characterized litho- and biofacies types, the biotope of *Arthropleura* and *Onchiodon* during Manebach time could be described as follows.

The Manebach Formation belongs to the Late Gzhelian/Early Asselian wet phase C of Roscher and Schneider (2006), which is represented, e.g., in the Saar-Nahe basin of western Germany, by the Breitenbach to Altenglan formations and in the French Massif Central by the Molloy and Igornay formations (Roscher and Schneider, 2006, fig. 15 a-b). Red sediment colors are almost completely absent; only in the alluvial fan conglomerates of the basin border facies do violet-colored coarse clastics appear in places. Characteristically, coarse channel clastics are of whitish-yellowish color, which is interpreted as the result of leaching by paleo-groundwater flows. This is supported by the presence of pale gray leached, primary dark violet to reddish brown rhyolite clasts of the fan and channel conglomerates (Lützner, 2001; Lützner et al., 2007). Lamination as an indication of seasonality is not really well expressed in the lake deposits. Therefore, nearly year-around high precipitation as well as high groundwater levels can be inferred. In this way, the Manebach Formation is climatically very close to the Westphalian C (Bolsovian) and early Westphalian D, from which most *Arthropleura* remains were discovered in Europe. Both *Arthropleura* and *Onchiodon* lived outside the swamp areas in a river landscape that was dominated by *Calamites gigas* stands along the river banks as well as by fern-pter-

idosperm-calamite vegetation on floodplain areas between river courses.

LITHO- AND BIOFACIES OF THE ARTHROPLEURA OCCURRENCE IN THE DÖHLEN FORMATION, EARLY ASSELIAN, DÖHLEN BASIN, GERMANY

This Late Pennsylvanian to Early Permian basin forms a small half graben of 22 km by 6 km with its primary extent in the Elbe zone, which is part of the NW-SE striking Elbe lineament (Schneider, 1994). The basement and the border of the basin are formed by different Variscan rock units such as the Meißner Intrusive Complex, metamorphosed and folded early Paleozoic sediments as well as the Ore Mountain (Erzgebirge) gneisses. Basin topology and the high number of clastic dikes (formed by paleo-earthquakes) indicate that basin development and tectonic activity along the Elbe zone were coeval. Preserved basin fill amounts to about 800 m of thickness and is subdivided into four fining-up megacycles or formations. In contrast to other Permocarboneous basins, pyroclastic rocks dominate, comprising up to 50% of the deposits of this basin (Schneider and Hoffmann, 2001). Generally, sedimentation and facies pattern are governed by higher subsidence along the main fault at the southwestern graben border as well as by strong volcano-tectonic activity, including strong seismicity.

The Döhlen Formation (as much as 100 m thick) comprises two, approximately 50-m-thick fining-up mesocycles. The mainly red-col-

ored basal conglomerates are overlain by gray sandstones and siltstones, locally with seams of carbonaceous shale. The second mesocycle consists of grayish to yellowish-white fluvial pebbly arkoses, pyroclastic rocks, and five seams of carbonaceous shale and coal beds up to 6 m, and locally 12 m, thick. As in the Manebach Formation of the Thuringian Forest basin, red beds are completely missing in the coal-bearing upper mesocycles. Primary dark violet rhyolite clasts of channel conglomerates are leached to pale gray. The presence of subaerial to subaquatically-deposited air fall pyroclastics and fluvially-reworked pyroclastics between the coal seams indicates that nearly continuous peat formation occasionally was interrupted by strong ash falls. These ash falls are responsible for in situ preservation of plant communities at their growth sites (Figs. 7F, 8; Barthel, 1976; Schneider and Barthel, 1997; Rößler and Barthel, 1998). Upright-standing (up to 3 m tall) calamite trunks at the tops of seams indicate that they were buried during catastrophic ash-fall events.

Because of the absence of surface outcrops, the lithofacies and biofacies pattern of the Döhlen Formation are known only from subsurface coal mining and well cores in the coal-seam-containing facies in front of the alluvial fans that frame the northeastern basin border. Generally, facies architectures are governed by volcanotectonic subsidence and regional ash falls. Characteristic are vertical and lateral changes between fluvial tuffitic pebbly arkoses, fine-grained ash tuffs and coarse-grained crystal tuffs, shallow lacustrine tuffitic pelites and marlstones as well as dirty coals and pure coals. Peat formation was interrupted several times by ash falls on the swamps, which form basin wide, cm-to-dm-thick pyroclastic layers (tonsteins) within the coal seams as well as the sharp upper boundaries of the main seams. The ash falls have buried plant communities in situ, often as monospecific stands (sinuses) (Figs. 7F, 8), and very often the trunks of calamites in upright position.

Based on lithofacies and fossil content the following sub-environments could be distinguished in the Döhlen Formation (for details see Schneider and Barthel, 1997; Rößler and Barthel, 1998; Schneider and Hoffmann, 2001):

1. Well-drained channel arkoses, sand flats of coarse grained tuffs/tuffites and elevations inside the mire bear monospecific, in situ stands of the xerophytic *Calamites gigas*, rarely together with single *C. undulatus*.

2. Inside the mire, pure stands of the hydrophilous to hygrophilous, peat-forming, rhizome-bearing *Calamites multiramis* (= *Calamites striata* in anatomical preservation) are present on wet organic substrates (mostly buried in upright position).

3. Hygrophilous forest swamp communities in permanently waterlogged areas with broad-leafed, coal-forming cordaitaleans and their typical roots (Fig. 7G-H), psaronaceous tree ferns, *Calamites multiramis*, *Sphenophyllum oblongifolium* and rare *Nemejcopteris feminaeformis* as well as other ferns; fluent lateral transitions into pure cordaitalean swamps as well as into *C. multiramis* stands.

4. Together with 3, locally monotonous scrambler communities (sinuses) of *S. oblongifolium* and *N. feminaeformis* in places with *Botryopteris*, *Dactylothea*, *Taeniopteris* and *Calamites multiramis*.

5. Mesophilous pteridosperm-fern-communities (open pioneer communities) of *Oligocarpia leptophylla*, *Senftenbergia*, *Dactylothea*, different pectopterid ferns and pteridosperms like *Dicksonites*, *Neuropteris* and *Barthelopteris*, and rarely, *Autunia* and *Subsigillaria brardii*, on well-drained elevated drier areas inside and at the borders of the swamps; the border facies of the swamp is characterized by shallow but wide fluvial channels filled with reworked pyroclastics.

6. Mesophilous to xerophilous conifers on slopes and hills surrounding the basin and possibly on well-drained elevations and swells inside the basin, too.

The articulated ventral part with sternites and legs of a reconstructed, approximately 0.85-m-long *Arthropleura* was found in a 6-cm-thick, slightly fluvially-reworked pyroclastic horizon. This horizon is situated at the top of a 0.6-m- to 0.8-m-thick, medium to coarse, air fall

crystal tuff that overlies with sharp contact and load casts the third coal seam in the mining field Bannewitz of the Döhlen basin. Both pyroclastic horizons contain the above-characterized mesophilous pteridosperm-fern community (sub-environment 5). Compared to the mining field Gittersee, 3.5 km away, the discovery horizon in the mining field Bannewitz was situated on an elevation generated by the ash falls, as shown by Schneider and Barthel (1997, fig. 3). Immediately overlying strata are 3-4 m of sandy tuffites containing tight *Calamites gigas* stands.

The occurrence of eryopids in the Döhlen Formation is demonstrated by the discovery of *Limnopus* tracks in pyroclastics between the first and second coal seams of the Döhlen Formation (Hausse, 1910, and later discoveries). The track-bearing horizons are cm-thick, silty to fine sandy pyroclastics with desiccation cracks. Additionally, in sediments just above the uppermost or first seam, which is about 6.5 m above the track-bearing horizon, the famous concentration of six skeletons of *Haptodus (Pantelosaurus) saxonicus* was discovered (Hausse, 1902; v. Huene 1925). Thus, *Arthropleura*, eryopids and haptodonts (pelycosaurs) can be regarded as quasi-contemporaneous in the above-characterized drier environments with hygro- to mesophilous plant communities of the coal-forming Döhlen Formation.

COMPARISON OF PARAUTOCHTHONOUS ARTHROPLEURA BODY REMAIN OCCURENCES AND AUTOCHTHONOUS TRAIL OCCURRENCES

The oldest true *Arthropleura* body fragments (legs, paratergites), which mark the oldest occurrence of this animal, are known from the Viséan (late Asbian to early Brigantian, Middle Mississippian) in the Hainichen basin of East Germany (Rößler and Schneider, 1997). Leg lengths of about 6 cm (Fig. 9A) indicate individuals of 18 cm body width and 0.8 m body length; lengths of up to 1 m are indicated by the size of the paratergites (Fig. 9B) (calculation based on Rolfe, 1969; Schneider and Werneburg, 1998), which is in good agreement with the body sizes calculated from tracks from the Viséan (see below). The *Arthropleura* remains occur together with other terrestrial arthropods such as arachnids (e.g., the phalangiotarbid *Bornatarbus mayasi* and the trigonotarbid *Aphantomartus areolatus*) and scorpionids as well as shark egg capsules of the *Fayolia* type. They are preserved in fluvial sandstones of an alluvial braid plain/floodplain environment with upright, buried stumps of arborescent lycopsids and sphenopsids of the *Archaeocalamites radiatus* type. These trees colonized channel banks, mires and open forested areas, the latter containing higher amounts of mesophilous plants (Schneider et al., 2005).

The next oldest record of *Arthropleura* body remains comes from the Westphalian A (Langsetian, Middle Bashkirian, Early Pennsylvanian) of the Ostrava-Karvina basin in the Czech Republic (Řehoř and Řehořová, 1972). In younger strata, the finds increase in abundance, with a maximum in the Westphalian C (Bolsovian) and D (Moscovian, Middle Pennsylvanian), which is caused simply by widespread coal-mining in deposits of this time slice in both Europe and North America (Hannibal, 1997). Guthörl (1936) counted 105 *Arthropleura* fragments in the Westphalian B and C (Duckmantian and Bolsovian) of the Saar basin (Guthörl, 1936, fig. 1 and p.189-195), which led him to the conclusion that this arthropod "is the most common animal fossil of the Saarbrücken beds."

The vast majority of these finds come from roof shales of coal seams, stored on the mine dumps. (Since the 1980s, a German private collector, Michael Thiele-Boucier [personal comm.], has sampled more than 100 *Arthropleura* remains from coal mine dumps of the Westphalian C and D in the Saar basin). Roof shales represent the silting-up of swamps by fluvial deposits in intracontinental basins and by tidalites in paralic basins (Gastaldo et al., 2004). Floras and faunas of roof shales are, therefore, a nearly indistinguishable admixture of terrestrial and aquatic organisms of swamps, floodplain environments and shallow marine en-

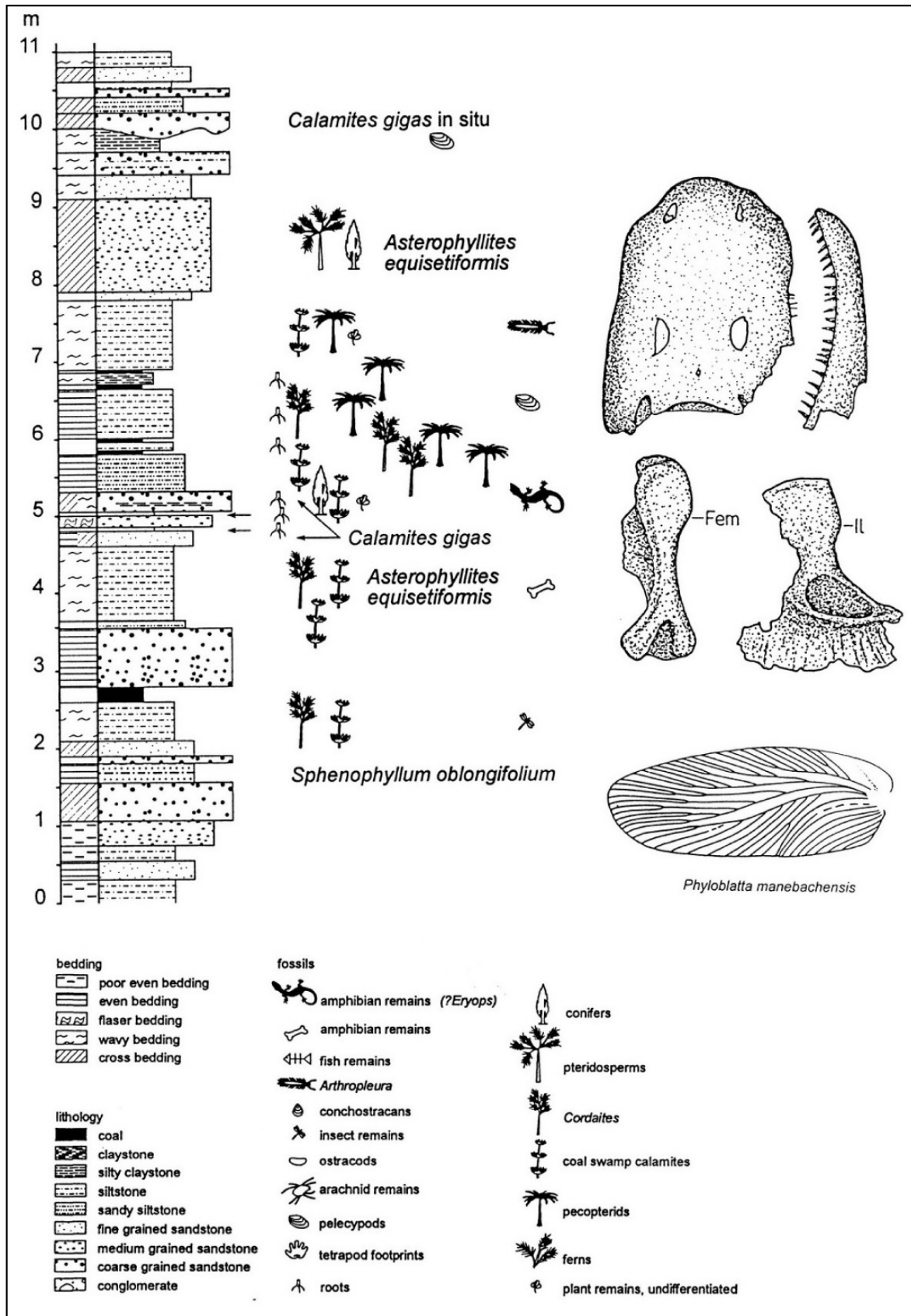


FIGURE 6. Sedimentology and fossil content of the Manebach Formation (Early Permian) at the type locality south of Manebach village, slope at the B4 road, Thuringian Mountains, Germany; excavation site 2005, compare Figure 5A. Channel lag deposits at profile-meter 5 contain calamite trunks as well as the *Onchiodon* remains – skull about 30 cm long with the lower jaw as well as femur (Fem) and ilium (Il) (from Gebhardt et al., 1995; completed after the 2005 excavation by Werneburg).

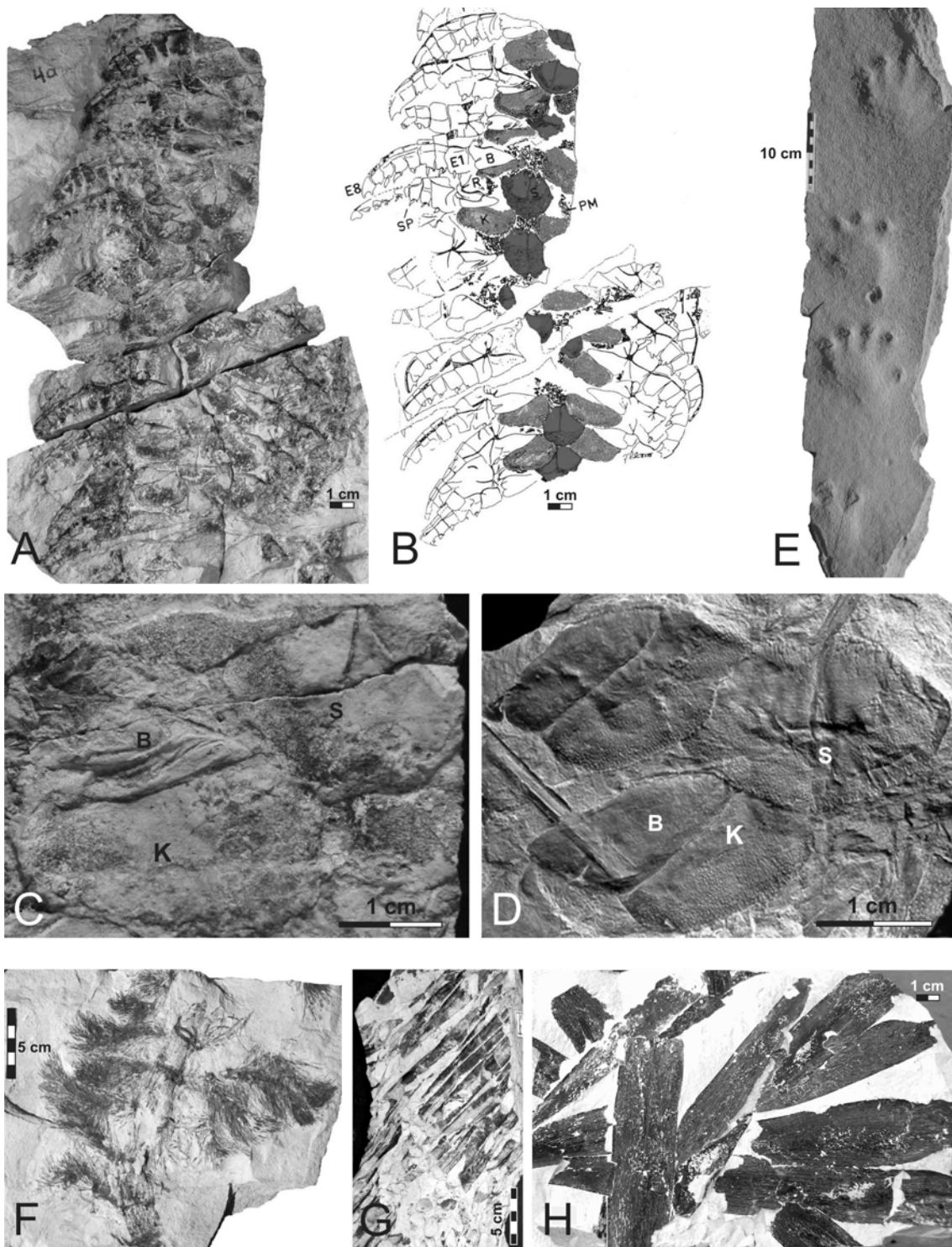


FIGURE 7. *Arthropleura* and selected fossils from the Döhlen Formation (Early Permian) of the Döhlen basin in Saxony, Germany; (D from the Saar basin, Germany, see below). **A-B**, *Arthropleura* in partially fluviially redeposited pyroclastics above the 3rd coal seam in the mining field Bannewitz-North of the Döhlen basin, ca. 24 cm long portion of ventral side showing the well preserved articulated limbs as well as the elements of the ventral exoskeleton, E1 – 1st limb segment, E8 – 8th (last) limb segment with the terminal claw, Sp – movable articulated unpaired spines at each limb segment, R – rosette plate, PM – ventral part of the flexible pleural membrane on which the sclerites S and K are fixed, S – sternites, K – K-plate, B – non-sclerotised B-element (?a kind of tracheal pocket); apodema of the limbs in black; FG Thümmel collection. **C**, Closeup from A, intensely wrinkled B-element and the strongly sclerotised undeformed sternite and K-plate; sternite and K-plate show on the outer (ventral) surface fine dimples with increasing density towards the posterior borders of these sclerites. **D**, Ventral sclerites; note the fine dimples on the outer surface of the sternite and the K-plate as in C and the smooth surface of the B-element apart from some dimples at the base only; early Westphalian D, pit 4 at Göttelborn, Saar basin, Germany; MTB 1215. **E**, *Limnopus*, tracks of an eryopid amphibian in pyroclastics between the 1st and 2nd coal seams of the Döhlen Formation; SSB. **F**, Apical portion of a *Calamites multiramis* shoot with *Annularia spinulosa* leaves, buried *in situ* by volcanic ash fall, pyroclastics above the 2nd coal seam, Döhlen Formation, Zauckerode; FG 15/98. **G**, Root horizon in fine-grained volcanic ashes with three-dimensionally preserved cordaitalean roots, Döhlen Formation, Zauckerode; FG 609. **H**, *Cordaites principalis*, pyroclastics above the 3rd coal seam, Döhlen Formation; private collection Hertl, Freital, Germany.

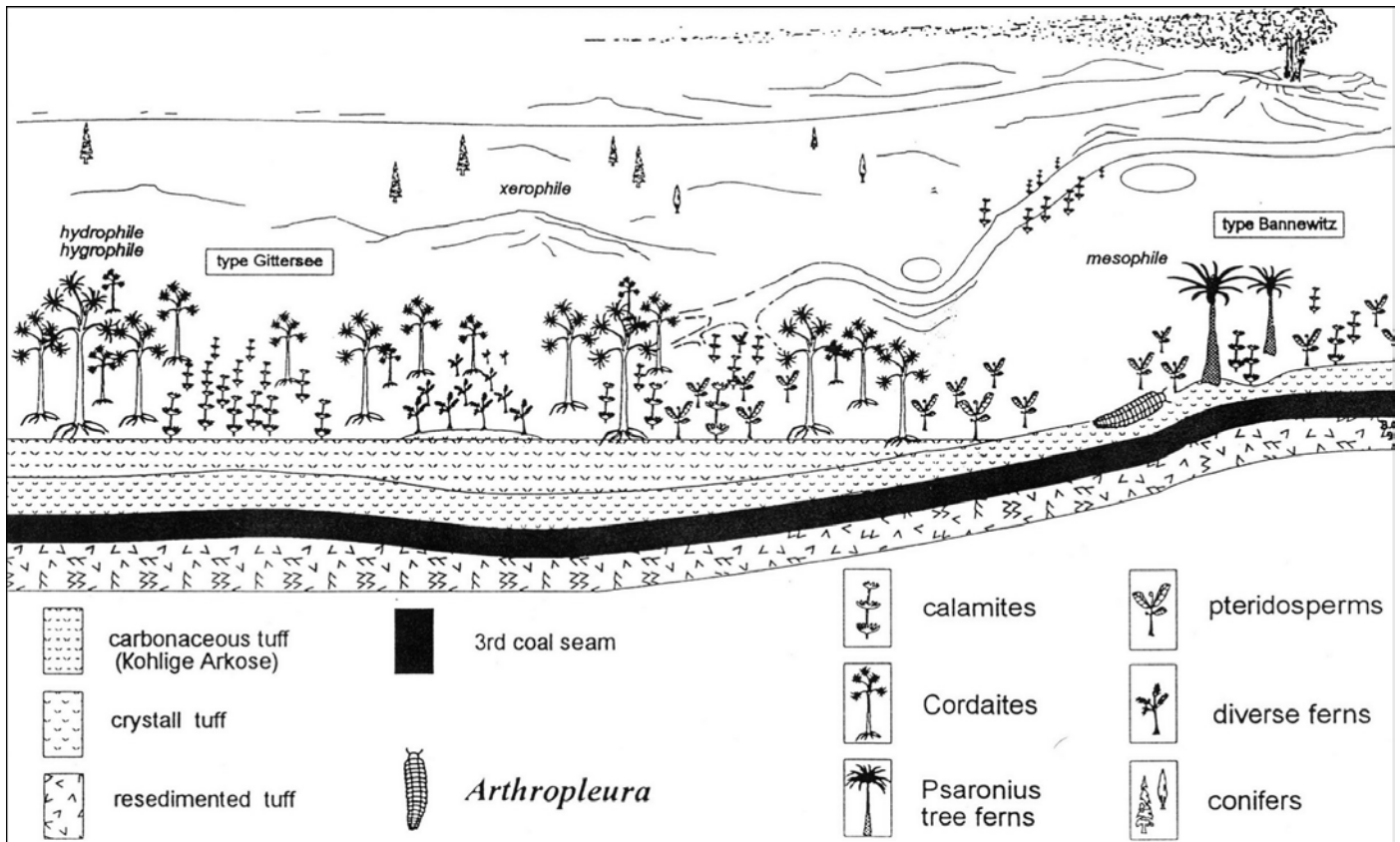


FIGURE 8. Reconstruction of the floral associations buried *in situ* above the 3rd coal seam of the Döhlen Formation (Early Permian) in the Döhlen basin based on plant collections from the mining fields Gittersee and Bannewitz (from Schneider and Barthel, 1997). The *Arthropleura* ventral side, shown in Figure 7A-C, comes from the mining field Bannewitz. Floras of the Gittersee type belong to the hygro- to hydrophile peat-forming communities of poorly-drained environments close to or below the groundwater level. The Bannewitz flora represents the pioneering mesophile associations on well-drained mineral stands above groundwater level. The open vegetation of comparable environments on sandy substrates of alluvial plains and deltaic settings seems to have been the preferred habitat of semi-adult and adult *Arthropleura*.

vironments. Additionally, roof shale samples from mine dumps lack sedimentological context. They are not suited to answer the question of the environmental preference of *Arthropleura*. As shown by Guthörl (1940) for the deep drilling Hangard No. 38 (see above), *Arthropleura* finds are as common in coal-seam-free alluvial plain deposits as they are in roof shales. This fits with the still scattered but nearly continuous records of *Arthropleura* tracks from the Namurian up to the Early Permian of Europe and North America in alluvial environments outside swamp areas. Those occurrences will be characterized in the following sections based on literature data and personal observations.

Strathclyde Group, Visean (Asbian, Mississippian), Fife, Scotland (Pearson, 1992)

The sediments of the Strathclyde Group of Fife are interpreted as deltaic in origin with occasional marine incursions. Nonmarine facies include channel sandstones and sheet-flood deposits, thin coals, seatearths, lagoonal mudstones and laminated siltstones and shales as well as red or black ironstones and dolomites with nonmarine bivalves. The track-bearing part of the section consists of meter-thick dark, organic-rich and often finely laminated mudstones and siltstones interspersed with ~ 1.5-m-thick, white, well-sorted, medium-grained channel-fill sandstones. The sandstones display multi-storied trough-cross bedded units with undulating surfaces and, in places, current ripples. Parts of the track-bearing sandstone bed are spotted with small mineralized rootlets; also present are poorly-preserved *Stigmara* root traces. Minimally, 13 individual trails occur, ranging in width between 18 and 30 (?46) cm; most of them

have a relatively narrow range between 21-24 cm. The longest preserved trail is 5 m, forming an S-bend. Some trails cross one another; at one place the sediment is pitted by deeply impressed, crescent-shaped and randomly oriented marks, which may represent hundreds of individual footfalls. Generally, individual tracks often appear crescent shaped and deeply impressed (1-2 cm estimated depth from the photographs in Pearson, 1992), comparable to the El Cobre trails. Not excluding the possibility that the trails are made by two or three individuals only, this mass occurrence of *Arthropleura* trails did not originate by chance. Animals of 0.80 m to 1.32 m body length (maximally ?2.11 m for the uncertain, 46 cm wide trail) were the trail makers.

Namurian Limestone Coal Group (Pendleian, Early Serpukhovian), Arran, Scotland (Briggs et al., 1979)

In general, the Limestone Coal Group was deposited in a proximal deltaic environment. The trail-bearing horizon is situated 6 mm below the top of a 6-m-thick white sandstone unit, which formed the roof of coal seams. The trail is preserved on the surface of a bedding plane of heterogeneous sandstone ranging in grain size from quartz arenite to fine sandstone and containing discontinuous layers of shale. Bedding structures indicate deposition in a variable low-velocity flow regime in a gradually silted-up fluvial channel. Root structures suggest that the vegetation was pencontemporaneous with the formation of the trail. A subaqueous origin of the trail is regarded as unlikely because of the clarity of the imprints in such a coarse lithology. The width of the trackway is 36 cm, suggesting a 1.6-m-long individual as the trackmaker.

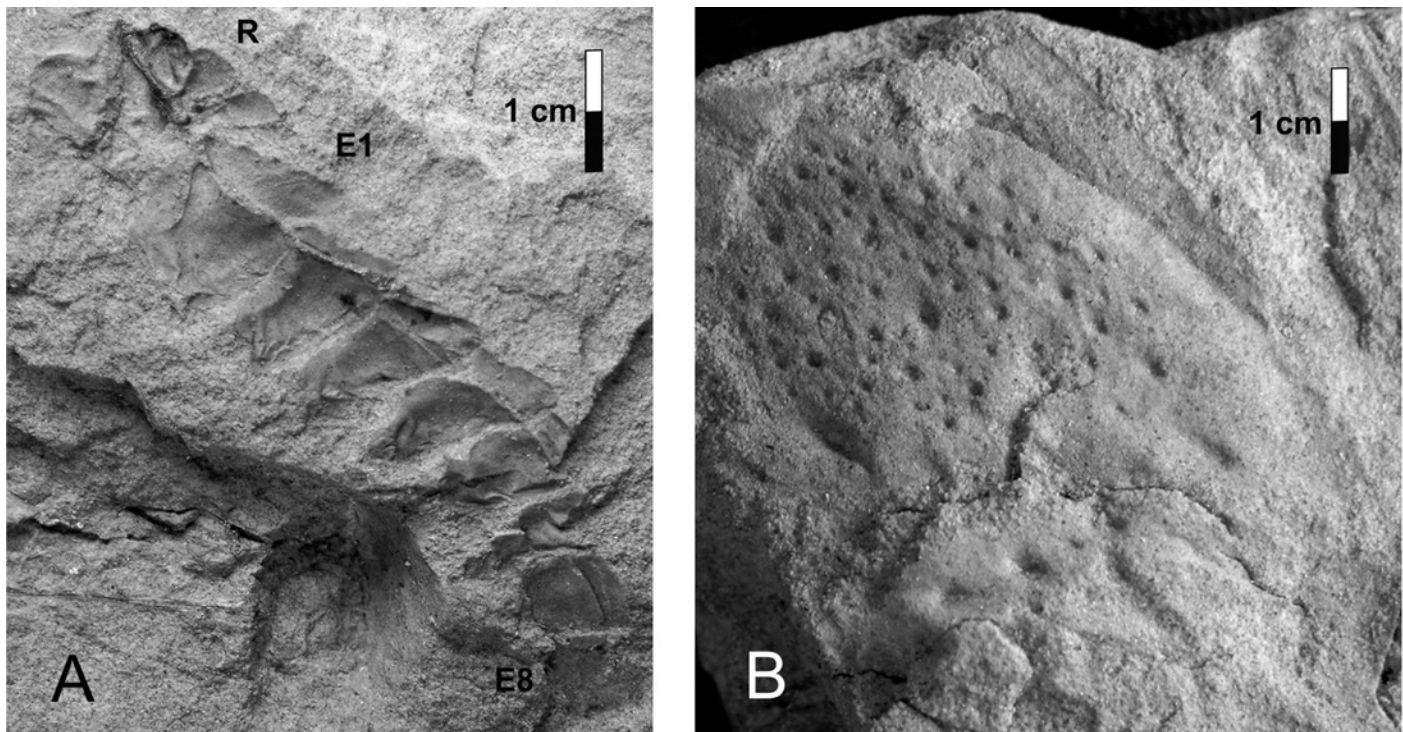


FIGURE 9. Oldest known *Arthropleura* remains, from the Viséan (late Asbian to early Brigantian, Middle Mississippian) in the Hainichen basin, Borna near Chemnitz, Germany (Rößler and Schneider, 1997). **A**, Counterpart of a nearly complete, 7.6 cm long limb, R – rosette plate, E1 – 1st limb segment, E8 – 8th (last) limb segment; MfNC F 439b. **B**, Counterpart of a fragmentary paratergite (“pleurite”) with the typical sculpture of *A. armata* from the Pennsylvanian; MfNC F 1125.

Little River Formation, Cumberland Group, ?Late Namurian to basal Westphalian, (?Kinderscoutian/Langsettian, Bashkirian, Early Pennsylvanian), Lower Cove, Nova Scotia, Canada (Calder et al., 2005)

The Little River Formation of the Lower Cumberland Group was deposited in the Cumberland sub-basin as part of the late Paleozoic Maritimes Basin complex of Atlantic Canada (Falcon-Lang et al., 2006). The formation consist of a wet red bed-succession dominated by mudrocks, which exhibit pervasive mottling from root traces and local pedogenic carbonate, with channel sandstone bodies typically 3-6 m thick. It represents the deposits of a well-drained alluvial plain dissected by shallow rivers characterized by flashy flow under a seasonally dry climate. Coals seams and brackish, marine-bivalve-bearing limestone beds, which are present in the overlying Joggins Formation, are missing. A 23 cm wide *Diplichnites cuithensis* is reported from inside a body of stacked channels by Calder et al. (2005). The tracemaker may have had a length of about 1 m. This is the stratigraphically oldest record of *Arthropleura* in wet red beds of seasonally dry environments.

Joggins Formation, Cumberland Group, Westphalian A (Langsettian; Bashkirian, Early Pennsylvanian), Joggins, Nova Scotia, Canada (Ferguson, 1966, 1975; Briggs et al., 1979; Falcon-Lang et al., 2006)

The Early Pennsylvanian Joggins Formation, containing the famous Joggins paleoecosystem, overlies the Little River Formation (see above). At that time, the Cumberland sub-basin was connected to the open sea during sea-level highstands, as indicated by brackish incursions, and was more restricted and intra-continental during sea-level lowstands (Falcon-Lang et al., 2006). The latter authors revised the fossil content of the Joggins Formation in a precise facies context, recognizing three main communities: open water brackish sea fossil assemblages (OW), poorly

drained coastal plain assemblages (pPDF) and the 31% of the Joggins Formation comprising well-drained alluvial plain red-bed assemblages (WDF). *Arthropleura* trails were reported from the last two assemblages. In the “grey mudstone with channel bodies facies” of the pPDF, a few *D. cuithensis* trails (Falcon-Lang et al., 2006) and *Dromillopus* microsauro trackways (Cotton et al., 1995) occur on top of some channel bodies.

The trails reported by Briggs et al. (1979) occur in the “red mudstone with channel bodies facies” of the WDF (Falcon-Lang, et al., 2006). This facies comprises red mudstone successions with scattered pedogenic carbonate nodules, sandstone sheets, and small, ribbon-like channel sandstone bodies. They contain common upright calamiteans, and a few upright lycopsids with attached *Stigmaria* roots. Plant assemblages are dominated by cordaitaleans (*Dadoxylon*, *Mesoxylon*, *Cordaites*, *Artisia*) as well as a few lycopsids and calamiteans. The trails occur in sheet sands thickening into a channel sand bed. Ranging in total width from 20 to 26 cm, they indicate an animal about 0.88 to 1.15 m long. The preservation of the largest trail, described as a paired series of regularly-spaced, oval depressions, elongate normal to the axis, resemble the preservation of the El Cobre trackways in wet sandstone. The smaller trail shows individual imprints, apparently arranged in closely spaced diagonals. These differences in preservation are explained by decreasing water content of the sediment, i.e., increased cohesiveness when the smaller trail was formed.

Tynemouth Creek Formation, Westphalian A to ?B (Langsettian - ?Duckmantian; Bashkirian/?Moscovian, Pennsylvanian), New Brunswick, Canada (Briggs et al., 1984)

The Tynemouth Creek Formation is regarded as partially coeval to the Joggins Formation of the late Paleozoic Maritimes Basin complex of Atlantic Canada (see above and Falcon-Lang, 2006). The formation is built up mainly of red siltstones, red and gray sandstones, and coarse

conglomerates in an overall coarsening upward sequence (Briggs et al., 1984). Rare freshwater limestones are locally present. The sedimentary environment is interpreted as a relatively dry alluvial fan environment characterized by periodic sheetfloods across an otherwise quiescent area of relatively slow deposition. Red/green mottled paleosols with slickensides and carbonate nodules are interpreted as vertisols of a seasonally dry climate (Falcon-Lang, 2006). The trail-bearing section consists of red, fine, slightly silty, tabular sandstones, interbedded with red and green siltstones. The up-to-2-m-thick sandstones are dominantly massive, but include planar and cross-laminated units. Upright buried calamite stems, up to 10 cm in diameter, are common.

The best-preserved trails occur at Gardner Creek in the top of a 40-cm-thick, fine sandstone with numerous *in situ* calamitaleans rooted in the 12-cm-thick siltstone horizon below. The fine sandstone grades up into a few mm of siltstone, and it is on this surface that the *Arthropleura* trail is preserved. The sandstones are interpreted as deposits of major sheet floods. The trail-bearing siltstone accumulated during the waning phase of the flood, and the trail was produced after subaerial emergence, when the *Arthropleura* was walking along a sinuous course through the calamite forest. The width of the trail in the straight part is 29.5 cm, suggesting an animal about 1.30 m long. Two further trails are mentioned in the top of channel sandbodies beneath overbank sediments at approximately the same stratigraphic level as the Gardner Creek trails. Their width of 27 cm and 30 cm implies similar large animals.

Cumberland Group, Westphalian B-C (Duckmantian-Bolsovian; Moscovian, Middle Pennsylvanian), Smith Point and Pugwash, Cumberland County, Nova Scotia, Canada (Ryan, 1986)

The Westphalian Cumberland Group of Cumberland County consists, according to Ryan (1986), of continental gray to red-gray calcareous mud-chip conglomerate, coarse- to fine-grained sandstone, siltstone and mudstone with minor amounts of coal, limestone and shale. Sandstones and conglomerates are trough cross-stratified and were deposited in low sinuosity streams. At Smith Point, 25 trails were found on two different surfaces that are separated by a 1.3-m-thick, cross-stratified, medium-grained sandstone. Crossover of trails is common; up to 300 degrees of bending is observed. The average width of the trails on the upper bedding surface is 37 cm, and it is 32 cm on the lower bedding surface, which gives a body length of 1.63 and 1.40 m, respectively, for the producer. The tracks are closely spaced, about 24 per meter; maximum depth of the tracks is 3 cm. At the Pugwash locality, 12 trails preserved mainly as undertracks were found. The trail width is approximately 38 to 41 cm; depth of tracks varies between 2 and 3 cm. The length of the trail-producing *Arthropleura* is calculated as about 1.8 m.

At both localities, the tracks occur in pebbly arkosic sandstones that are overlain by thin veneers of mudstone, preserved on some of the trail surfaces. The depositional environment is interpreted as mid-channel dunes prograding during flood stages, which were subsequently subaerially exposed as channel bars during a dry period, in which the trails were produced.

Stull Shale Member, Kanwaka Formation, Shawnee Group, Virgilian (Gzhelian, Late Pennsylvanian), Waverly, Eastern Kansas (Mángano et al., 2002)

The Stull Shale Member of the Forest City basin in eastern Kansas represents tidal flat deposits along a microtidal shoreline directly connected with the open sea. The arthropleurid tracks occur at the top of a 30-cm-thick, medium- to fine-grained channelized sandstone body 66 m wide, which cuts erosively into an intertidal runoff channel. Both channel bodies are encased by progressively shallowing intertidal mixed-to mudflat deposits. The track-bearing sandstone is interpreted as a channel fill in a coastal fluvial system. The width of the trackways is 23.3 to 30.2 cm, which indicates body lengths of about 1 to 1.3 m. The preservation style resembles very closely the El Cobre trackways with

closely spaced, elongated and sigmoidal imprints oriented normal to the axis of the trackway. Details of the imprints are not preserved because of the superimposition of imprints and soft-sediment deformation, which is visible in figure 32C of Mángano et al. (2002). Obviously, the sandy sediment was wet and plastically deformable when the animal was walking on it, as was the case with the El Cobre trackway.

Lower Conemaugh Formation, Virgilian (Gzhelian, Late Pennsylvanian), Boyd County, Kentucky (Martino and Greb, 2009)

The lower Conemaugh Formation of the Appalachian basin in Kentucky is regarded as an equivalent of the Glenshaw Formation of the Conemaugh Group in neighboring West Virginia, which consists predominantly of coastal plain fluvial sandstones and red to olive mudrocks deposited in a tropical flood-basin setting. Martino and Greb (2009) reported new direct evidence for the co-occurrence of *Arthropleura* with eryopid amphibians, indicated by the tracks of both on one-and-the-same bedding surface from the lower Conemaugh Formation, 6.5 m below the marine Ames Limestone. The roof shales of the Ames Limestone can be directly correlated with the early Stephanian of Central Europe based on fossil insects (Schneider and Werneburg, 2006). The tracks were found in float from a roadcut.

The trackways were derived from a 4-m-thick interbedded sandstone and shale interval 4.3 m below the base of the Harlem coal. The tracks are preserved as convex hyporeliefs in fine to very fine sandstone that is interbedded with silty shale. They were mainly produced on top of the silty shale. In one case (specimen PC-6 of Martino and Greb, 2009, p. 142, fig. 4), an *Arthropleura* trail is preserved as undertracks in the sandstone together with a *Limnopus* manus cast (?undertrack). The track-bearing sandstones occur as three broad, thin sheets and a small channel fill. This, together with graded bedding, parallel and current ripple cross lamination and desiccation cracks leads to the interpretation of crevasse splay deposits. Besides sparse root traces, no plant remains were reported. The Pittsburgh red shale, which directly underlies the trackway interval, is indicative of the climate conditions during deposition. These red beds consist of regionally-developed calcic vertisols, which classify them as wet red beds in a seasonal dry/wet semihumid to semiarid climate (see above and Greb et al., 2006). Open woodland vegetation is assumed. Based on the width of the *Arthropleura* tracks of 20 and 30 cm, we infer a body length of the tracemaker of 0.88 m for one of the tracks and 1.32 m for two other tracks. The *Limnopus* traces consist of 75 to 80 mm long pes and 53? to 57 mm wide manus imprints. An additional tracksite from the Conemaugh Group, Casselman Formation, in Cambria County, Pennsylvania, was briefly reported by Marks et al. (1998). The 15 cm wide by 3 m long trackway resembles *D. cuithensis* as far as can be determined from the published photographs.

Montceau-les-Mines, latest Stephanian C/earliest Autunian (Asselian, Cisuralian, Early Permian), French Massif Central (Briggs, 1986; Briggs and Almond, 1994)

The Blanzly-Montceau basin is one of the typical Late Pennsylvanian/Early Permian continental coal basins of the French Massif Central. It is famous for its fossiliferous nodules similar to Mazon Creek in Illinois. Arthropleurid trails were found in a unit of alternating pale gray mudstone and fine sandstones at the level of the first coal seam of the Assise de Montceau (Langiaux, 1984). The trails are preserved at the top of whitish-gray, silty, fine sandstone that contains numerous plant fragments (Fig. 10C; Briggs, 1986). The width of the trail of 10.8 cm indicates a length of the producing arthropleurid of 0.47 m. About 15 m above the trail-bearing level, three-dimensionally preserved tiny arthropleurids of 2.7 to 4.5 cm length have been found in sideritic nodules (Fig. 10A-B; Secretan, 1980; Almond, 1985; Briggs and Almond, 1994). The width of these dwarf arthropleurids ranges from 1.1 to 1.7 cm. They differ from the smallest true *Arthropleura* (*A. moyseyi* Calman,

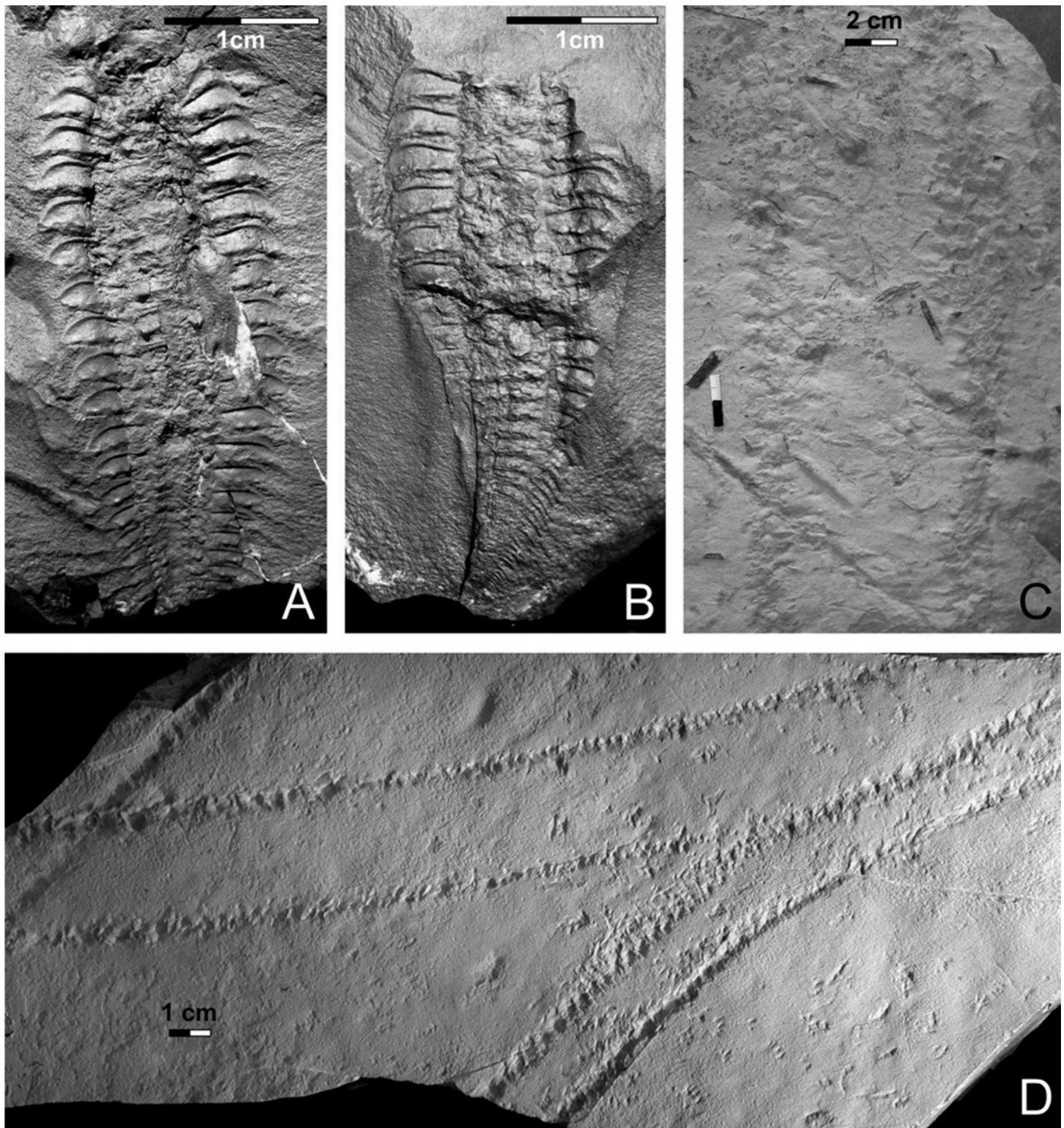


FIGURE 10. The tiny arthropleuroids of Montceau-les Mines, France, and trails of juvenile arthropleuroids from Flechting High, Germany. **A-B**, Two approximately 1.6 to 1.7 cm wide, three-dimensional arthropleuroids preserved in sideritic nodules, Assise de Montceau, latest Stephanian C/earliest Autunian (Asselian, Cisuralian, Early Permian), Montceau-les-Mines, French Massif Central; **A**, 3.7 cm long natural cast of the ventral (inner) side of the lateral paratergites and the dorsal side of the body as well as two incomplete ventral molds of sytergites that are about half of the length of the specimen; anteriormost plate of the ventral mold of a collum or cephalic shield (cf. Briggs and Almond, 1994; Kraus et al., 2003); MHNA 002122b. **B**, 3.6 cm long natural cast of the ventral (inner) side of the lateral paratergites and the dorsal side of the body as well as on the right distal side of the specimen imprints and counterprints of closely arranged limbs; note the strongly tapered posterior region of the trunk; MHNA 002123b. **C-D**, *D. cuihensis* trails of juvenile *Arthropleura* preserved as convex hyporelief in silty-clayey pyroclastics, Eiche Member, Altmark Subgroup, Stephanian ?C (Late Pennsylvanian/Early Permian, Ghzelian/Asselian), Flechting High, Germany (see Walter and Gatzsch, 1988); lower trail 2.0 to 2.2 cm wide; note the faint striae (especially in the bent part of the trail) made by the movable spines of the limbs during forward stroke; this trail was made in wet plastic mud; upper trail 3.2 cm wide; tracks have a lesser width despite the larger trail width and show more distinct limb end claw imprints of repeated foot falls; this trail was possibly made in a somewhat drier substrate; note the very common small cf. *Batrachichnus* tetrapod tracks; FG 607.

1915) of about 6 cm body length by a distally very strong, tapering body and possible diplopody (Briggs and Almond, 1994) as well as very long and thin, spike-like sculpture cones on the paratergites (JWS, personal observation on silicon rubber casts). They may belong to *Arthropleura* or represent a new minute form of arthropleurid — for discussion see Briggs and Almond (1994) and below.

The depositional environment is described as a fault-bounded graben with rapid lateral and vertical transitions of alluvial fan deposits, debris flows and braided river clastics interfingering with palustrine (locally up to 40 m thick coal seams!) and lacustrine sediments. Siltstones, intercalated into the first coal seam have yielded a diverse tetrapod track association (Langiaux, 1984; Gand, 1994), produced mainly by temnospondyl amphibians (e.g., *Batrachichnus*, *Limnopus*) and pelycosaurs (*Dimetropus*). The fossiliferous nodules and track-bearing Assise de Montceau is commonly attributed to the Stephanian B/C based on macroflora. Spiloblattinid cockroach wings indicate a latest Stephanian C/earliest Autunian, i.e., Early Permian (Asselian) age (Schneider and Werneburg, in prep.). A transitional Stephanian/Autunian age had been advocated by Doubringer (1994) based on palynomorphs, but was never taken into account.

Eiche Member, Altmark Subgroup, Stephanian ?C (Late Pennsylvanian/Early Permian, Gzhelian/Asselian), Flechting High, northeast Germany (Walter and Gaitzsch, 1988)

The Eiche Member is exposed at the top of subeffusive basaltic volcanites situated near the base of the Late Pennsylvanian/Early Permian Altmark Volcanite Complex of northeast Germany (Gaitzsch et al., 1995). It consists mainly of about 10 m of light-gray fluvial sandstones at the base followed by several meters of fine ash tuffs covered by debris flow fanglomerates with an ignimbrite at the top. The track-bearing unit is composed of (?water laid) grayish-green air fall tuffs as well as fluvially reworked and lacustrine, redeposited fine ash tuffs. Shallow channels with trough-cross bedding have a lateral width of only about one meter. Sedimentation took place under low energy conditions from suspension as indicated by the silty grain size and normal grading. Raindrop marks, shallow wave ripples and rare “anthracosian” (?*Anthraconaia*) imprints as well as *Pelecypodichnus* traces indicate the presence of shallow pools. The track-bearing layers are horizontally bedded at a 1 to 2 cm scale. Tens of arthropleurid trails per square meter are preserved on the bedding planes, in places as undertracks. Crossover and bending is common (Fig. 10D).

Because of their small size, ranging from 2.0 to 4.0 cm width, the trails have been described as *Diplichnites minimus* Walter and Gaitzsch, 1988. Apart from bundles of striae situated in front of the single tracks in both track rows of some trails (Fig. 10D, lower track) no real differences exist when compared to *D. cuiithensis*. The striae result from the spines on the limb segments during forward stroke. Therefore, *D. minimus* should be regarded as a junior subjective synonym of *D. cuiithensis*. Based on the width of the trails, a length of 8.8 to 17.6 cm of the trailmakers can be calculated. This corresponds well to the smallest known, unquestionable *Arthropleura* (*A. moyseyi* Calman, 1915) with a body length of about 6 cm. There are no indications of the strong posterior tapering of the body as observed for the tiny “juvenile” arthropleurids from Montceau-les-Mines (see Briggs and Almond, 1994, figs. 1 and 2; here Fig. 10D). As discussed by Briggs and Almond (1994), the posterior tapering of the trunk and the closely-spaced rear limbs on either side should result in a trail in which the imprints occupy over 50% of the total width. The trail width of these small forms should be about 1.6 cm, corresponding to the largest width in the middle part of the body. This is very close to the smallest trails of 2 cm width from the Eiche Member. But, the trails from this member do not show any indication of a trailmaker with a posteriorly tapering body – they display the normal picture of two rows of tracks, as do the larger *D. cuiithensis*. It is therefore very unlikely that the minute arthropleurids from Montceau-les-Mines be-

long to the same *Arthropleura* species as the *D. cuiithensis* trail makers. The only way to produce trails of *D. cuiithensis* type by the tiny Montceau-les-Mines arthropleurids would be if the posteriormost limbs were held clear of the ground (Briggs and Almond, 1994, p.132).

The Eiche Member *D. cuiithensis* occur on different bedding planes. In places, normal surface trails (epichnia) are crossed by undertracks of trails produced later after a new layer of sediment was laid down. They are commonly associated with small cf. *Batrachichnus* trails of 3 to 7 mm track length (Fig. 10D). The wide range of preservation forms of the arthropod and tetrapod trails indicate different amounts of wetness of the substrate, ranging from possibly thin water cover over muddy to nearly stiff. Sparse remains of macroflora, mainly calamite trunks (up to 5 cm diameter) and *Annularia* leaves as well as rare fern leaves, indicate scattered vegetation in surrounding areas of small ponds. The high frequency of arthropleurid trails (laterally and vertically) and in places the common association with trails of small tetrapods demonstrates that this environment was settled by juveniles of *Arthropleura*. The lack of larger trails may indicate a different biotope preference of juveniles and adults.

Pictou Group, Upper Red Beds, Early Permian (Cisuralian), Cape John, Pictou County, Nova Scotia, Canada (Ryan, 1986)

The Early Permian Upper Red Beds, now called the Cape John Formation (Ryan et al., 1991), of the Pictou Group are composed of fluvial cycles of red to gray conglomerates and arkosic sandstones as well as siltstones and mudstones. The trail-bearing pebbly arkosic sandstones are interpreted as anastomosing river deposits, with sediment transport and accumulation primarily as the result of dune progradation at channel bottoms. At Cape John, on the northern coast of Nova Scotia, three trails were found, and two of them cross each other. The width of the trails is on average 47 cm, giving a body length of the arthropleurid of about 2.07 m. They are preserved as two parallel rows of tracks, each 13 cm wide, elongate and nearly normal to the trail axis with 28 tracks per meter. The depth of the tracks is about 1.3 cm.

In the Cape John Formation as well, about 8 km southwest of the Cape John *Arthropleura* tracksite, a spectacular tetrapod tracksite together with in-situ stumps of a walcian conifer forest is exposed at Brule Harbour, Colchester County (Van Allen et al., 2005). The tetrapod tracks represent a typical cosmopolitan Euramerican association with strong European affinity, consisting of *Limnopus*, *Amphisauropus*, *Dimetropus*, *Varanopus* and *Dromopus* and others. Absolutely dominant is *Limnopus*, followed closely by *Amphisauropus*. Provisionally determined invertebrate traces, as *Gordia*, *Beaconichnus*, and *Onisciodichnus*, are typical representatives of the shallow freshwater *Mermia* ichnoguild of the *Scoyenia* ichnofacies, an interpretation that is strongly supported by the co-occurrence with the ostracod *Carbonita* and leaiaid conchostracans. Besides *Paleohelcura*, no arthropod walking trails are reported. Most tetrapod tracks are preserved in thin, silty sandstone beds commonly draped by very thin mud layers. Desiccation cracks are typical. The depositional environment of the Brule Harbour tetrapod tracksite is described as an abandoned distributary channel hollow that was repeatedly flooded and exposed. Red beds of Prince Edward Island, adjacent and contiguous to Brule Harbour, have yielded skeletal remains of eryopid and brachyopoid amphibians and the reptiliomorphs *Seymouria* and *Diadectes* as well as of different pelycosaurs (Van Allen et al., 2005).

THE HABITAT PREFERENCE OF ARTHROPLEURA

Based on the foregoing, *Arthropleura* trail-bearing paleoenvironments can be characterized as follows:

1. Arthropleurid trails of dm width are preferably preserved both in nearshore transitional terrestrial/marine deltaic and tidal flat sediments as well as in intracontinental river braid plains on sandflats and on bedding planes at the top of channel sandstones. Smaller trails up to about 5 cm wide are preserved in silty mud of temporary pools.

2. As a prerequisite for the preservation of tracks, the substrate must be wet (of course) when the animal was walking on it; some of the trails show indications of plastic deformation/fluidization of the sand and mud caused by deeply impressed tracks (Fig. 4D-E).

3. Vegetation of the tracksites is scattered, consisting mainly of calamitaleans, and during the Westphalian, additionally of arborescent lycopsids, as indicated by their upright buried stumps and *Stigmaria* rhizomes/rootlets.

4. Associated with the track-bearing sandstones in coastal marine environments are gray lagoonal and fluvial overbank mudstones and siltstones, more or less rooted. Additionally, tracks are present since the middle Westphalian in alluvial plain and floodplain red siltstones and mudstones of wet red-bed facies type in continental settings.

5. In rare cases only, coal seams or swamp deposits are associated with the *Arthropleura* track-bearing facies architectures.

6. The most common tetrapods in those settings are terrestrially-adapted eryopid amphibians (Figs. 5B, 7E) and pelycosaurid reptiles.

The first question to be answered is: do the trail occurrences reflect the biotope preference of the trail makers or is it biased by sampling or by preservation potential? Of course, the discovery of large trails of 20 cm and more width and several meters long, and the chance to recognize them as trails, obviously depends on the dimensions of the exposed bedding planes. They are largest in areas of high recent erosional rates such as at modern sea coasts and in sandstone quarries. There, the fine clastics covering track-bearing sandstones are quickly eroded on large surfaces or – in the case of the quarries – removed. This is clearly shown, for example, in the case of the tracksites along modern coasts of Scotland, by the exceptional exposures along the coast of Nova Scotia and by the channel sandstones exposed in the modern, non-vegetated and seasonally dry river bed of Cañon del Cobre as well. The apparent absence of these large trails in Central Europe, where *Arthropleura* body remains are very common, is simply caused by the lack of such large exposure surfaces in upper Paleozoic fluvial sandstone units.

The preservation potential for animal tracks (invertebrates and vertebrates as well) is generally highest in fine clastics of river floodplains and playas (e.g., Haubold and Katzung, 1978; Haubold and Lucas, 2001; Voigt, 2005; Lucas, 2005). Tetrapod tracks are very common on floodplain mudflats and around temporary pools on floodplains that became dry after floods. But, those tetrapod track-bearing sediments have not delivered any associated arthropleurid tracks on the same bedding planes. Even so, they are broadly contemporaneous with *Arthropleura* tracksites, as in the case of Cañon del Cobre (Lucas and Lerner, 2010) and the case of the spectacular tetrapod tracksite of Brule Harbor, Nova Scotia (Van Allen et al., 2005). The only two exceptions are the *Limnopus* tracks together with 20 to 30 cm wide *Arthropleura* trails in the Upper Pennsylvanian of Kentucky (Martino and Greb, 2009; see above) as well as the minute *Batrachichnus* tracks together with 2-4 cm wide *Arthropleura* trails in the Upper Pennsylvanian/Lower Permian of the Flechting High, Germany (Walter and Gaitzsch, 1988; see above).

As shown before, the vast majority of *Arthropleura* trails are preserved in sandy substrates. Additionally, those trails are observed (depending on exposure conditions) mostly as mass occurrences (e.g., up to 25 trails at Smith Point, Nova Scotia – see above). Besides the above cited 10 cm wide Montceau-les-Mines trail and the small Flechting High trails, the width of the trails has a range of 18 to 47 cm, which indicates body lengths ranging from about 0.80 to 2 m. The variety of body lengths for particular sites, calculated from the width of the trails (e.g., Fife, Scotland: 18-30 cm; Kentucky 20-30 cm; see above), indicates animals of different growth stages as tracemakers (despite variations in trail width caused by locomotory behavior).

This leads to the conclusion that arthropleurids avoided muddy substrates, except for early juveniles of up to about 0.15 m body length, as at Flechting High (Fig. 10D). The preservation in sandy substrates begins by about 0.8 m body length. This may be caused simply by the fact that only animals of this size were heavy enough to leave tracks in

wet sands. Alternatively, the absence of tracks produced by arthropleurids larger than 0.18 m in the mass occurrence at Flechting High may indicate different habitat preferences of juveniles and adults. Nevertheless, it could be stated that arthropleurids, starting no later than 0.8 m body length, walked preferably on sandy substrates. This confirms Mángano et al. (2002), who described the depositional environment of *D. cuithensis* as “typical subaerial, commonly exposed fluvial bars, silted channels, and desiccated sheetflood deposits.” More generally, the preferred habitat of adult arthropleurids could be characterized as loosely vegetated sandy areas in open river landscapes under a year-round wet climate in coastal environments to seasonally wet, semihumid climates in continental settings. As indicated by skeletal remains and tracks, the most common tetrapods in these habitats since the start of the Late Pennsylvanian were eryopid amphibians and pelycosaurid reptiles (haptodonts).

IMPLICATIONS FOR THE PALEOBIOLOGY OF ARTHROPLEURA

The most frequently discussed issues concerning the anatomy and physiology of *Arthropleura* concern the up-to-now-missing structures of the head, especially the mandibles and the missing respiratory organs as well as the arrangement of the limbs (Brauckmann et al., 1997; Kraus and Brauckmann, 2003). Kraus and Brauckmann (2003) and Kraus (2005) discussed the phylogenetic relationships of *Arthropleura* as well as the anatomy and biology of this animal based on the reinvestigation of the tiny Montceau-les-Mines arthropleurids, the holotype of *A. moyseyi*, the large, well-preserved, so-called Maybach-specimen (Guthörl 1935; Hahn et al., 1986), and the *Arthropleura* ventral side from the Döhlen basin (Schneider and Barthel, 1997) as well as several new body fragments, including a presumed cephalic shield and presumed head capsules, from the Saar basin. Some of their observations and inferences as well as those of other authors will be discussed here with regard to our conclusions on the paleobiology of *Arthropleura*.

As shown by Schneider and Barthel (1997), based on a well-preserved, 42-cm-long part of a ventral side with about 25 limb segments, there are no indications that succeeding pairs of legs form groups of two pairs. In contrast, the legs had an almost regular arrangement (their pl. 7; here Fig. 7A-B). Whether or not one pair of legs corresponds to one of the dorsal syntergites still remains open (cf. Schneider and Barthel, 1979, fig. 5). Diplopody, as shown by the tiny Montceau-les-Mines specimens (Briggs and Almond, 1994), can be excluded for *Arthropleura* of more than 80 cm body length. A change from diplopody in early juvenile stages to a regular arrangement of single limb pairs in late juvenile and adult stages can also be excluded. Therefore, the inferences of Briggs et al. (1979) regarding the interpretation of *Arthropleura* traces still appear to be correct. However, the assumption of Kraus (2005) that the tiny Montceau-les-Mines arthropleurids are early juveniles of the giant *Arthropleura* as well as his conclusions on phylogenetic relationships to the Penicillata clade of Diplopoda are not well supported.

The respiratory structures of *Arthropleura* remain unknown. Rolfe and Ingham (1967) and Rolfe (1985) argued that the K- and B-plates may have covered a respiratory chamber. Schneider and Barthel (1997) have shown that the K-plate was as strongly sclerotised as is the sternite plate (Fig. 7A-C). Unlike the K-plates and the sternites, the so called B-“plates” are often wrinkled (Schneider and Barthel, 1997, pl. 8, figs. 1-3; here Fig. 7C). Possibly, this B-element, which is situated close to the base of each walking limb and linked to apodema, had a respiratory function as a kind of tracheal pocket. The “spongy internal structures” (Kraus and Brauckmann, 2003, p. 47) of K-plates are fine dimples on the outer surface, which give the inner surface a verrucose appearance. Not only the K-plate shows this structures but the sternites do, too (Fig. 7D), both dorsally and ventrally. Similar pits are situated on parts of the posterior surfaces of the limbs. Remarkably, the B-elements show only very weak pits on their median ends (Fig. 7D). A semiaquatic life and “plastron-breathing via series of paired ventral K-plates” (ibid, p. 48)

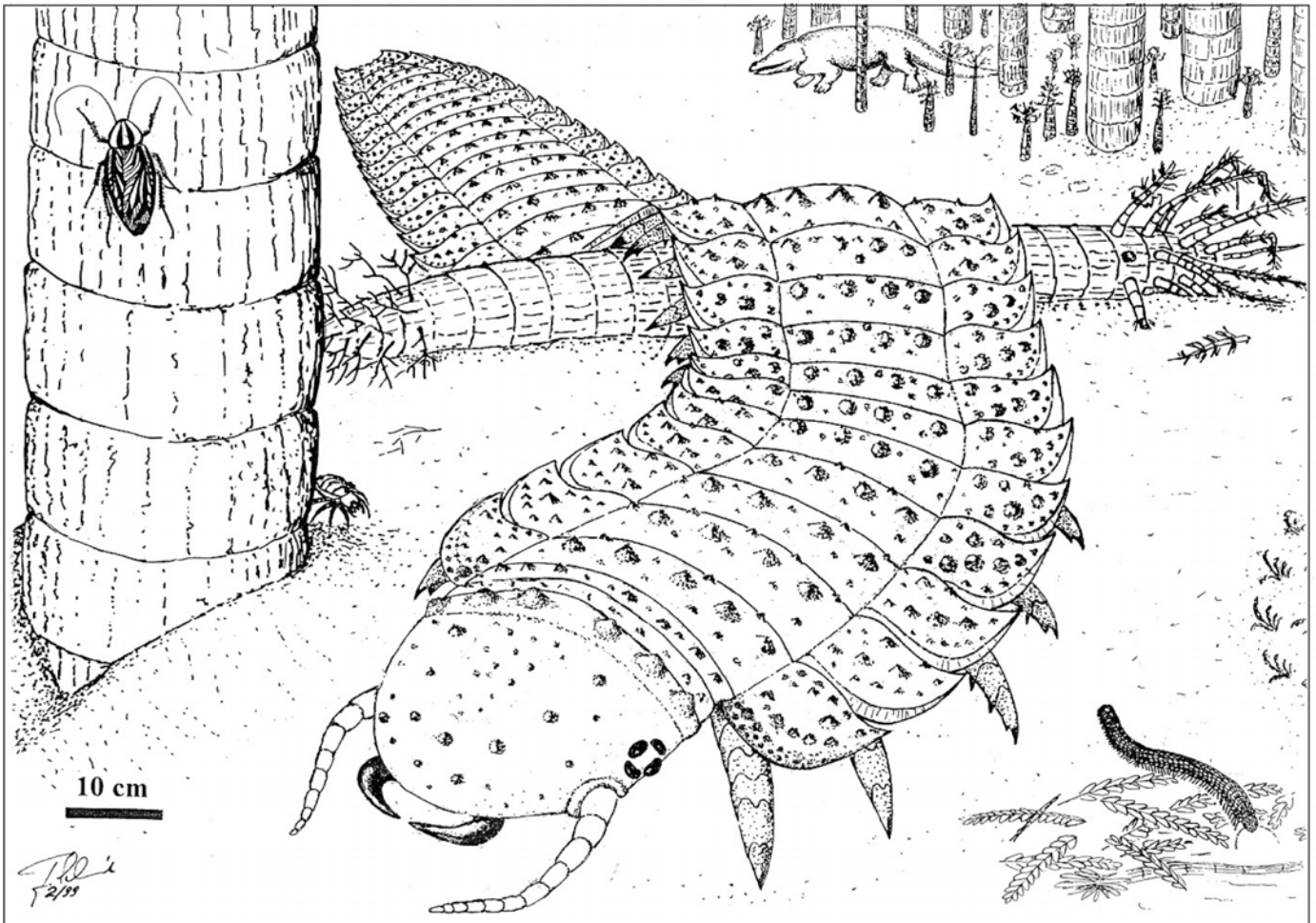


FIGURE 11. Reconstruction of the *Arthropleura* habitat in well-drained areas of alluvial environments with calamitaleans stands (here *Calamites gigas*) under ever wet humid to seasonally dry semihumid climate conditions; in the background an eryopid amphibian, often associated with arthropleurids as indicated by tracks and/or skeletal remains of both animals (modified after Schneider and Werneburg, 1998, fig. 15).

can be excluded because of the nature of the K-plates and the definite subaerial habitats indicated by the above discussed trails of late juveniles and adults. However, it cannot be excluded that a part of the small Flechting High trails was produced under thin water cover, but this is irrelevant to the mode of respiration.

Kraus and Brauckmann (2003) interpreted *Arthropleura* as a thin-skinned, caterpillar-like animal, stabilized by means of antagonistic hydraulics of body fluids only. This interpretation is based on fern leaves and other plant fragments impressed from below through paraterga (ibid, fig. 6). This interpretation has to be handled with care, because most if not all *Arthropleura* remains are exuvians. They exhibit unquestionably thin cuticles – but this could be simply a result of resorption processes during ecdysis. The common preservation of arthropleurid trails with up to 3 cm deep impressions of the limbs as well as the commonly deep undertracks in wet sand indicate a heavy animal with a well sclerotised exoskeleton similar to functionally comparable modern counterparts such as some chilopods (scolopenders).

A herbivorous diet of *Arthropleura* seemed to be demonstrated by the description of gut contents by Rolfe and Ingham (1967). Kraus (2005, p. 18-20) has reinvestigated this specimen with the result that “the wooden parts were accidentally fossilized together with the *Arthropleura* specimen and do not constitute any gut content.” However, assuming that *Arthropleura* was a penicillate diplodod, Kraus (2005, p. 20) concluded in a perfectly circular argument that *Arthropleura* was herbivorous, as are (nearly) all diplodods. The gigantism of arthropleurids

should therefore be “an evolutionary answer to the availability of an unusually plentiful food niche: masses of spores and pteridosperm pollen, perhaps also prothallia.” However, feeding on spores and pollen appears unlikely for an animal of this size, even if they are concentrated in lacustrine deposits such as cannel coals. If *Arthropleura* had used this nutrient source, lakeshores should have been most frequented by this animal. Again, this is very improbable because *Arthropleura* remains are completely missing in lake deposits thus far (see Hannibal, 1997, for the supposed occurrence in the lacustrine black shales of Linton, Ohio).

Alternatively, fructifications, megasporophylls and cm-size seeds (ovules) such as *Cardiocarpus* and *Trigonocarpus* could have been an energy-rich food for large arthropods. The question is whether or not this food source was available year-round. The production of fructifications and seeds could have been very seasonal as the climate became increasingly seasonal after the late Westphalian (Late Moscovian). Sporadic mass occurrences of gymnosperm seeds such as *Samaropsis* and *Cardiocarpus* in distinct layers (as in the Manebach *Arthropleura* locality – see Barthel, 2001; here Fig. 5C), are interpreted here as the result of seasonal seed production and taphonomic effects (washed together). Assumed carnivory and interpretation of *Arthropleura* as a chilopod in Barthel and Schneider (1997) is simply an incorrect citation by Kraus (2005, p. 20). Barthel and Schneider (1997, p. 198) solely compared functionally the construction of the ventral side of *Arthropleura* with chilopods but did not do so in terms of any phylogenetic relationship. Nevertheless, it could not be excluded that *Arthropleura* was predatory

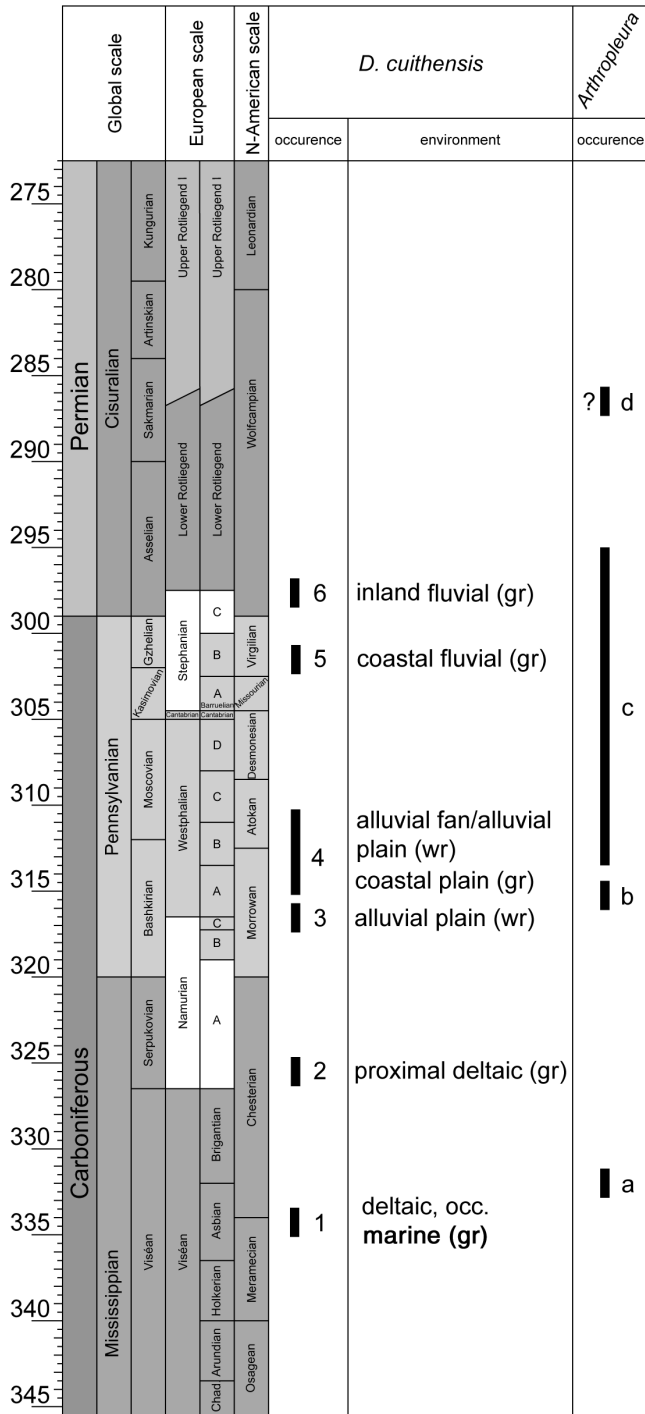


FIGURE 12. Stratigraphic distribution of the arthropleurid track *Diplichmites cuithensis* (1-6) in different environments (gr – gray facies, wr – wet red beds) and the occurrence of *Arthropleura* body remains (a – ?d). Occurrences of *D. cuithensis*: 1 - Visean (Asbian, Mississippian), Fife, Scotland (Pearson, 1992); 2 - Namurian (Pendleian, Early Serpukhovian), Arran, Scotland (Briggs et al., 1979); 3 - ?Late Namurian to basal Westphalian (?Kinderscoutian/Langsettian, Bashkirian, Early Pennsylvanian), Nova Scotia (Calder et al., 2005); 4 - Westphalian A (Langsettian; Bashkirian, Early Pennsylvanian), Nova Scotia (Ferguson, 1966, 1975; Briggs et al., 1979; Falcon-Lang et al., 2006); Westphalian A to ?B (Langsettian-?Duckmantian; Bashkirian/?Moscovian, Pennsylvanian), New Brunswick (Briggs et al., 1984); Westphalian B-C (Duckmantian-Bolsovian; Moscovian, Middle Pennsylvanian), Nova Scotia (Ryan, 1986); 5 - Virgilian (Gzhelian, Late Pennsylvanian), eastern Kansas (Mángano et al., 2002); Virgilian (Gzhelian, Late Pennsylvanian), Kentucky (Martino and Greb, 2009); Virgilian (Late Pennsylvanian), New Mexico (Lucas et al., 2005c); 6 - latest Stephanian C/earliest Autunian (Asselian, Cisuralian, Early Permian), French Massif Central (Briggs, 1986; Briggs and Almond 1994); Stephanian ?C (Late Pennsylvanian/Early Permian, Gzhelian/Asselian), Northeast Germany (Walter and Gaitzsch, 1988); Early Permian (Cisuralian), Cape John, Pictou County, Nova Scotia, Canada (Ryan, 1986). Occurrences of *Arthropleura* body remains: a - Visean (late Asbian to early Brigantian, Middle Mississippian), Hainichen basin, Germany (Rössler and Schneider, 1997); b - Westphalian A (Langsettian, Middle Bashkirian, Early Pennsylvanian), Ostrava-Karvina basin, Czech Republic (Rehoř and Rehořova, 1972); c - Westphalian B (Bashkirian, Pennsylvanian) to Lower Rotliegend (Early Asselian, Cisuralian) of the European basins (e.g., Hahn et al., 1986; for the youngest occurrences in the Permian (see Schneider and Barthel, 1997; Schneider and Werneburg, 1998); in North America (Hannibal, 1997): Lower Conemaugh, ?Missourian, Kasimovian, Ohio; Desmoinesian, Moscovian, Pennsylvania; Desmoinesian, Moscovian, Mazon Creek, Illinois; Springhill, Atokan, Bashkirian/Moscovian, Nova Scotia; d - upper Lower Rotliegend (Sakmarian, Cisuralian), Döhlen basin, Germany, large chitinous cuticle fragments that may belong to *Arthropleura* (Schneider and Barthel, 1997).

Rotliegend (LOD = ?LAD; Asselian) (Rössler and Schneider, 1997; Schneider and Barthel, 1997; Schneider and Werneburg, 1998). Trails are as common in the gray facies as in the facies of wet red beds. Preferred habitats of semi-adults and adults were open-vegetated river landscapes. They co-occurred in these habitats since the Late Pennsylvanian with semi-aquatic eryopid amphibians and terrestrial pelycosaur reptilians. But, the large size of 1 m to more than 2 m length in adult stages of *Arthropleura* protected it for a long time against natural enemies. Why did it suddenly become extinct in the Early Permian?

The changes from arborescent lycopsid- to tree fern- and cordaitalean-dominated wetlands during the Pennsylvanian through the Early Permian (Kerp, 2000; DiMichele et al., 2001, 2009; Falcon-Lang, 2004, Pfefferkorn, 2008) had no influence on *Arthropleura* as shown by the occurrences of (parautochthonous) body remains in the cordaitalean-dominated mires of the Early Permian in the Döhlen basin and Thuringian Forest basin of Germany (Schneider and Barthel, 1997; Schneider and Werneburg, 1998). Obviously, *Arthropleura* was not conditioned to any particular kind of mire and wetland vegetation.

It thus seems more likely that environmental changes driven by broadscale climate developments may have been one of the causes of the disappearance of *Arthropleura*. The last known occurrence of *Arthropleura* is in the “wet phase C” of Roscher and Schneider (2006) around the Gzhelian/Asselian transition. As shown by them, during the cyclically increasing aridization towards the Late Permian, each wet phase was drier than the preceding one. Wet phase C represents the last extensive gray facies with coal formation in most of the European basins (Roscher and Schneider, 2006, fig. 51a-b). The wet red beds of the foregoing dry phase of the Stephanian B to early C (Early Gzhelian) as well as of the succeeding dry phase around the Middle Asselian are characterized by common calcic soils and calcretes. *Arthropleura* had been adapted to these seasonally dry environments since the Early Westphalian (see above, Little River Formation, Nova Scotia).

and could overcome tetrapods as large as itself, as is the case with modern predatory chilopods such as *Scolopendra*. It can be speculated only that arthropods such as the eryopids, which lived in the same environment, could have easily been preyed upon by this giant arthropod. However, the problem of diet remains open as long as mouthparts or true gut contents of *Arthropleura* have not been found.

CONCLUSIONS

Well adapted to alluvial environments of every wet humid to seasonal dry semihumid climates, *Arthropleura* was a common member of the late Paleozoic continental biota of the paleo-equatorial biomes for more than 35 Ma, from the Early Carboniferous Late Visean (FOD; Middle Mississippian, Asbian/Brigantian) up to the Early Permian Lower

But, the intensity of seasonality increased as is indicated by intensely laminated (varved) lake sediments, which are very typical of all perennial lakes in the European basins after wet phase C (Clausing and Boy, 2000; Roscher and Schneider, 2006). Intensified seasonal dryness might have contributed to the demise of *Arthropleura*. Local populations may only have survived up to wet phase D in the Sakmarian, if the up to 2 cm size cuticle fragments, described from the Döhlen basin by Schneider and Barthel (1997, p. 200, pl. 9, figs. 1 and 2), belong to this animal. Possibly, the Döhlen basin during wet phase D was one of the “wet spots,” shrinking refuges of a formerly widespread wetland biota (DiMichele et al., 2006). Increasingly critical prey-predator relationships between *Arthropleura* and terrestrially-adapted amphibians and reptiles may have been an additional trigger to the demise of this giant animal, which was the largest terrestrial arthropod of earth history.

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