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A remarkable fossiliferous mass flow deposit in the Eocene Eckfeld Maar (Germany)—sedimentological, taphonomical, and palaeoecological considerations

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Abstract The distal part of a mass flow deposit has been excavated across an area of 400 m² in the basal facies of the Eckfeld Maar. The high concentration and diversity of fossils in mainly excellent preservation (i.e. leaves, fruits/seeds, wood, molluscs, vertebrate teeth, and bones such as undeformed skulls) is unique and underline its outstanding importance concerning sedimentological, taxonomical, and palaeoecological aspects. Together with a subaerial landslide from the inner crater slope, shoreline deposits—previously acting as a highly effective taphonomic filter—were transported towards the central lake basin. Complex processes like erosion, flow turbulence, and subsequent turbidity currents produced a characteristic sedimentary sequence. The interpretation of sedimentological, taphonomical, and physiological leaf characters allows an insight into the thus preserved shore line environment and provides information on the surrounding vegetation. Embedded leaves from open stands and understorey indicate dynamic successions on rather steep and unstable inner slopes of the crater.

Keywords Mass flow · Turbidity current · Taphonomy · Flora and fauna · Leaf morphology · Palaeoecology · Eckfeld Maar

Introduction

In the Eifel area, nearly hundred ancient Maar lakes have been identified with the Eckfeld Maar being the oldest one

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(Fig. 1). Determinations using ⁴⁰Ar/³⁹Ar revealed an age of 44.3 Ma (Mertz et al. 2000), similar to those of other outstanding Eocene Fossil-Lagerstätten in Germany like Messel and Geiseltal. Since scientific excavations started in 1987, several thousand plant and animal macrofossils from about 150 families were recorded.

The fossil record comprises prokaryotes (Micklich and Wuttke 1988a; Wuttke and Radtke 1993, 1994; Zink and Püttmann 1994), algae (Wilde et al. 1993), rhizopods (Schiller 1999), sponges (Gruber 1994), terrestrial plants (Wilde and Frankenhäuser 1998), molluscs (Groh and Jungbluth 1994; Neubert 1995), insects (Wappler 2003), crustaceans (Gruber and Schäfer 2000) and vertebrates (Micklich and Wuttke 1988a, 1988b; Tobien 1990; Franzen 1993, 1994, 1998; Micklich 1994; Windolf 1994; Gröning and Brauckmann 1996).

A great number of tetrapod and plant taxa showing excellent preservation are reported from one mass flow deposit. Most of the Eckfeld mammal species are known exclusively from here. Terrigenous fossils in mass flow deposits (*sensu* Einsele 1991) are reported especially from the marine realm, but often are poorly preserved due to the oxidising sedimentary environment (e.g., Cjajic and Ercegovac 1997; Lucas et al. 2000; Matano 2002; Sachse 2004). For the present case the rapid transport of plant and animal remains into the anoxic water body below the chemocline and minimal deformation permitted excellent and unique preservation. In addition, the exploitation of this deposit during the past 15 years allows a detailed insight into both, its three-dimensional sedimentary structures and the distribution and preservation of the fossils (Fig. 2).

This paper combines previously published and unpublished results with the author's personal investigations as excavation supervisor during the years 2000–2003.

Methods

In search for fossils, the coarse-grained layers were broken by hand, while silty to clayey layers were split with knives. Screening of the remaining coarse material

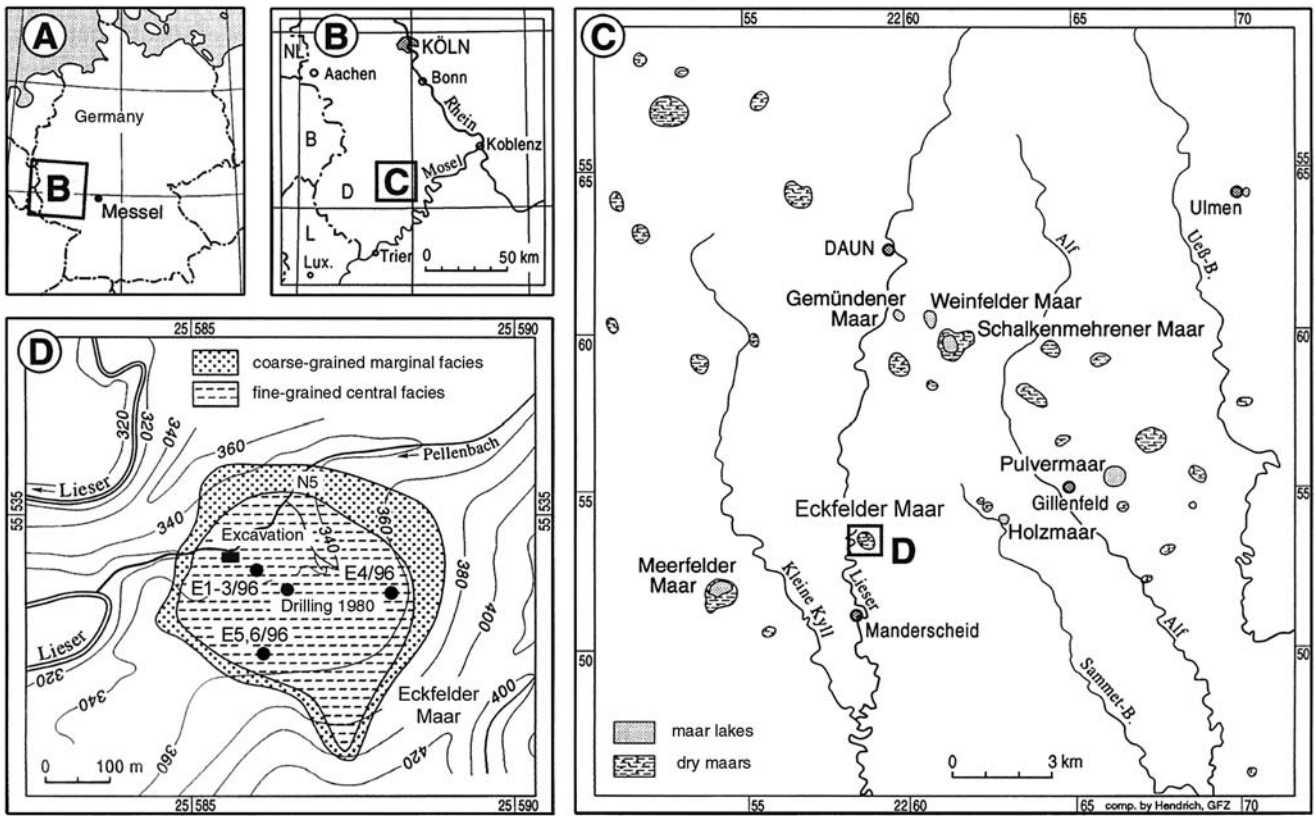


Fig. 1 a–c Location of the Eocene Eckfeld Maar. d Location of the excavation site within the basin facies. After Bullwinkel (2003)

revealed that hardly any fossils were overlooked during field work. In order to reconstruct the quantitative distribution, specimens were counted from the year 2000 onward

within areas measuring about 0.5 m². For most areas only semiquantitative observations were available from previous years. For this reason, distribution patterns of those years cannot be localised exactly and therefore are stippled and dotted in Fig. 2. Other possible sources of errors are faulted zones caused by subrecent landslides. However, in most cases careful observation enabled discrimination between sedimentologically-taphonomically and tectonically induced variations.

The deposit and its inventory

Sedimentological description

Covering the entire 400 m² of the excavation site in the north-western part of the basin facies (Fig. 1d), the coarse-grained deposit of a mass flow previously named HT (Hauptturbidit; Lutz 1993), and T20 (Turbidit 20; Mingram 1994) is the most prominent one among many others within the Eckfeld Maar deposit. Its thickness exceeds 5 cm, locally reaching 25 cm and decreases from a narrow NW–SE directed ridge to 0.5 cm in the periphery (Fig. 2).

The vertical structure roughly fits into a schematic sequence for mass flow deposits of Bullwinkel (2003: 42) which he developed using petrographic and microfacies analyses on logs from the Eckfeld Maar. Since established classifications (e.g., Bouma 1962; Lowe 1982; Einsele

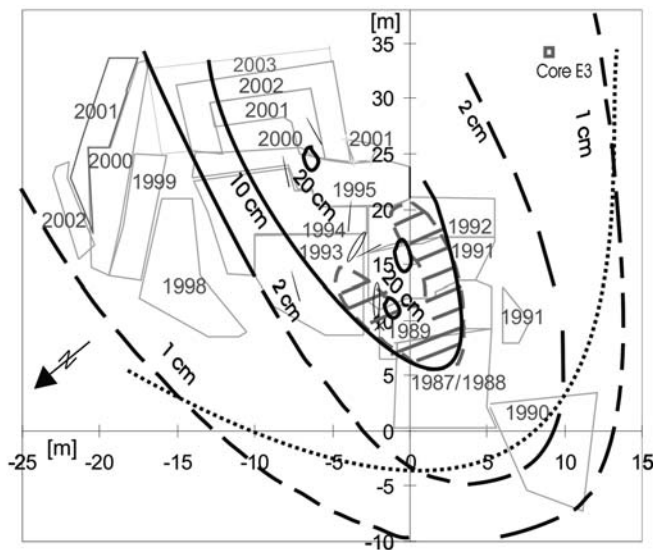


Fig. 2 Distribution of the mass flow deposit during the excavation campaigns 1987–2003. Thick black lines indicate isopachs (stippled when not proven). Presumed lateral expansion of the X division outlined by dotted line. Thin lines show alignment of large clasts (elongated ellipses) and tree trunks (dashes). A sickle-shaped greyish stippled area with particularly high concentrations of intraclasts are interpreted as the former flow front

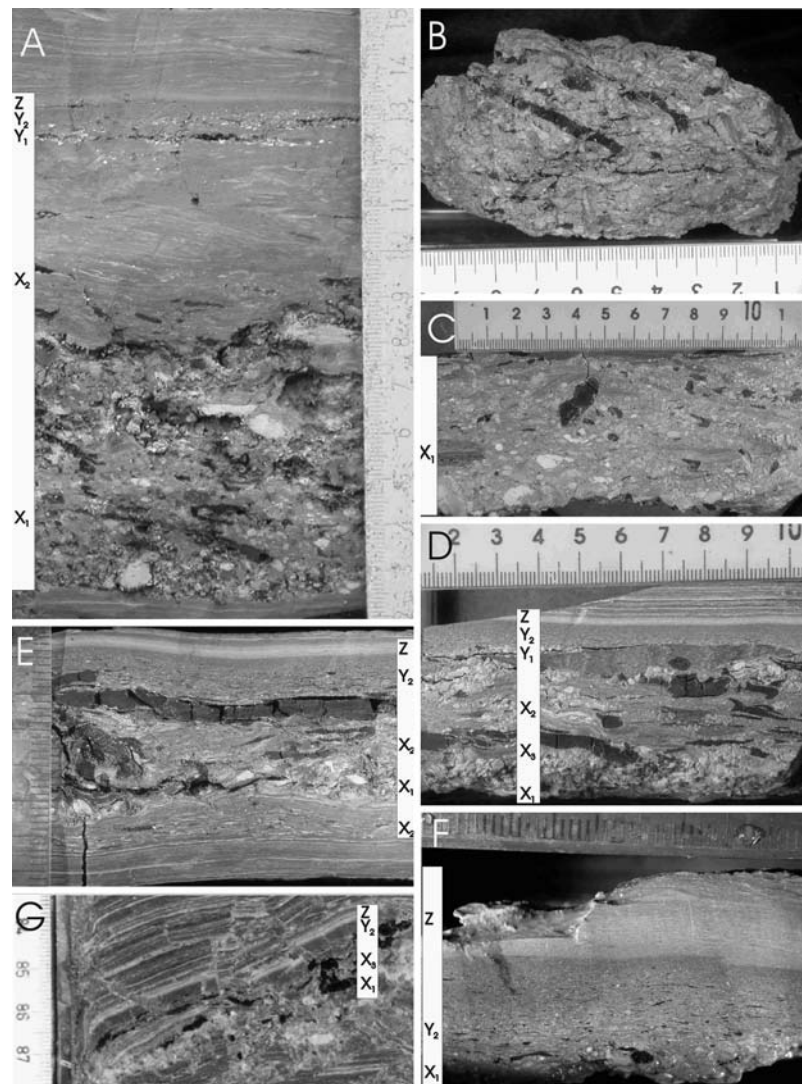


Fig. 3 Lateral variability within HT divisions: **a** Complete profile (X_1 , X_2 , Y_1 , Y_2 and Z divisions) with underlying uneroded beds and overlying disturbed resediments. Y_1 developed not as a continuous layer but represented by lenses embedded in Y_2 . Sample G2003/670-LS; **b** Arrangement of elongated woody fossils within X_1 subdivision. Oblique orientation in the upper part indicates turbulent flow above a shear plane, separating a laminar flow below with horizontal orientation. Sample G2003/669-LS; **c** X_1 subdivision. Partly rounded extraclasts (*light colours*) and minor components of intraclasts (*laminated*) and woody clasts (*black*) supported by a matrix. Sample G2003/666-LS; **d** X_2 subdivision with horizontally orientated wood fossils (X_3) and lenses of extraclasts. While X_2 and Y_2 are distinguished by their intraclast size, there is no such

clear separation of Y_1 from X_1 due to the restricted lateral extension of the lens-shaped bodies. Sample G2003/664-LS; **e** X_2 subdivision enveloping a lens-shaped X_1 subdivision with interfingering fossils and intraclasts. Small extraclasts are scattered across the overlying X_2 subdivision. Sample G2003/668-LS; **f** Expanded thicknesses of Y_2 and Z divisions, here separated by load structures. While Y_2 is graded, a delicate darkening to the top, intraclast fragments and cross lamination indicate increasing and changing flow velocities for the Z division. There twigs and leaves described in the text are concentrated. Sample G2003/666-LS; **g** Peripheral section consisting of X_1 , X_3 , Y_2 and Z divisions. In Y_2 only the upper homogeneous part is present, while only the Z division reached its normal thickness. Photograph from core E3/8, depth 7.45 m

1991) do not fit to his principal observations he divided his sequences from base to top into three divisions: X, Y, and Z. These sequences are characterised by a decrease in grain size from dominantly sand and gravel in the X division to clay size in the Z division. Besides X divisions are matrix supported, while Y divisions are clast supported. Both may consist of two subdivisions, the lower (X_1 resp. Y_1) dominated by extraclasts, the upper (X_2 resp. Y_2) dominated by intraclasts (Fig. 3a). Extraclasts are derived from the surrounding Devonian sediments but occasionally include also

pyroclastic components (basaltic lapilli). Intraclasts are re-worked bituminous laminites previously deposited below the chemocline; some even have been identified as belonging to an original stratigraphical position at least 40 cm below (Lutz 1993). The size of these partly deformed and disc-shaped clasts may exceed some centimetres or even decimetres. Throughout the logs Bullwinkel (2003) observed the lack of single divisions within a sequence, explaining this by base-cut-out and top-cut-out *sensu* Piper and Stow (1991).

Own field observations indicate that this scheme is indeed applicable to the HT, but they have led to somewhat modified reconstruction of the flow event.

The coarse-grained basal X₁ division generally constitutes the main component of the deposit. It is characterised mainly by poorly sorted sand to gravel sized clasts supported by a silty matrix. Sorting and clast orientation locally changes within a few centimetres. On top of the X division the occurrence of large SE–NW orientated floating extraclasts exceeding 40 cm in their longest axis (e.g., Lutz 1993) and of whole trunks measuring up to 30 cm in diameter seems to indicate locally a reverse grading.

A lateral decrease of clast sizes becomes evident, where thickness of the entire deposit remains below 5 cm. The composition of intraclasts and fossils reflects a variety of biotic and abiotic sources (Fig. 3). Fossils frequently are pyritised internally (esp. spongiosa of larger bones) and often enclosed by siderite concretions or embedded in a diffuse siderite enriched yellowish matrix.

The X₂ subdivision is unusually thick in a sickle-shaped area in the NW of this deposit (Fig. 2), where it locally even completely replaces the X₁ subdivision. However, the X₂ subdivision generally constitutes about one third of the X division. In contrast to Bullwinkel's (2003) scheme, its relative position is highly variable (Fig. 3): It may occur above as well as below, or embedded as lenses within X₁ subdivision, or may be even missing completely.

In X₁ thousands of fossils have been found comprising bones of mammals (Fig. 4b, c), reptiles (Fig. 4d), and birds (e.g., well-preserved crania of *Propalaeotherium* spp.; Fig. 4a), isolated teeth of tetrapods, fish bones (Fig. 4i) and scales (Fig. 4h), mollusc steinkerns (Fig. 4j), phosphatised coprolites (Fig. 4f), wood, fruits and seeds (Fig. 4k), and even some leaf impressions (Fig. 4l). Thus far, the following families have been identified in this division:

- Angiosperms (Nyssaceae, Rutaceae, Mastixiaceae, Menispermaceae, Vitaceae, Anacardiaceae, Cyperaceae, Burseraceae, Sargentodoxaceae, Caprifoliaceae)
- Molluscs: gastropods (Viviparidae) and bivalves (Unionidae)
- Fishes (Amiidae, Lepisosteidae)
- Reptiles: crocodiles (Alligatoridae, Crocodylidae), turtles (Trionychidae, ? Dermatemydidae), lizards (Aniguidae)
- Birds (div. fam. indet.)
- Mammals: perissodactyls (Equidae, Palaeotheridae, Lophiodontidae), artiodactyls (Dichobunidae, Haplobunodontidae, Cebochoeridae, Diacodexidae), rodents (Paramyidae), ? carnivores, primates (Lemuridae).

These fossils are generally more or less randomly distributed in those parts of the X division, which exceed a thickness of 10 cm, while only small and light fossils (no steinkerns or large bones, but more than 500 seeds per m³) are found in the peripheral parts. In the outermost parts concentrations of wood fragments are distinguished as X₃ subdivision if they either locally replace extra- and intraclasts or constitute a layer on top of the X₂ subdivision. A typical slice of the X division measuring 0.5 m² × 5 cm,

rich in fossils yielded 60 seeds, 6 fish vertebrae, 7 mammal and reptile bones, 10 minor bone fragments, 15 fish scales, 2 coprolites of reptiles and 1 tooth (wood not counted).

The Y₁ subdivision occurs in lenses of various size and position within the profile (Fig. 3a), e.g., within the clayey Z division. Even when the Y₁ subdivision is absent, the overlying greyish Y₂ can easily be distinguished on the basis of its normal grading and texture which is characterised by tiny intraclasts and leaf fragments as well as few sand-sized extraclasts (Fig. 3f). At the excavation site the thickness varies between 0.7 cm and 2 cm within the central ridge decreasing to 0.3 cm in the periphery. Here, only the uppermost, nearly homogeneous part is present (Fig. 3g), due to a base-cut-out *sensu* Piper and Stow (1991). The transition to the overlying Z-division seems to be sharp for the naked eye, but proves to be gradual under the microscope (Bullwinkel 2003). At this transition occasionally land and flame structures may be observed (Fig. 3f).

The clayey Z division generally consists of a 2 mm thick couplet of whitish layers separated by a very thin dark layer (Fig. 3d-g). Especially on the central ridge its thickness may increase up to 1 cm. Even the dark layer in between may grow or disappear or even split up into several small discontinuous wavy layers, caused by slumping or erosion (Fig. 3f). In those areas leaves and twigs and small intraclasts of the same layer are concentrated. A gradual darkening indicates a coarsening upward to the top of the upper layer.

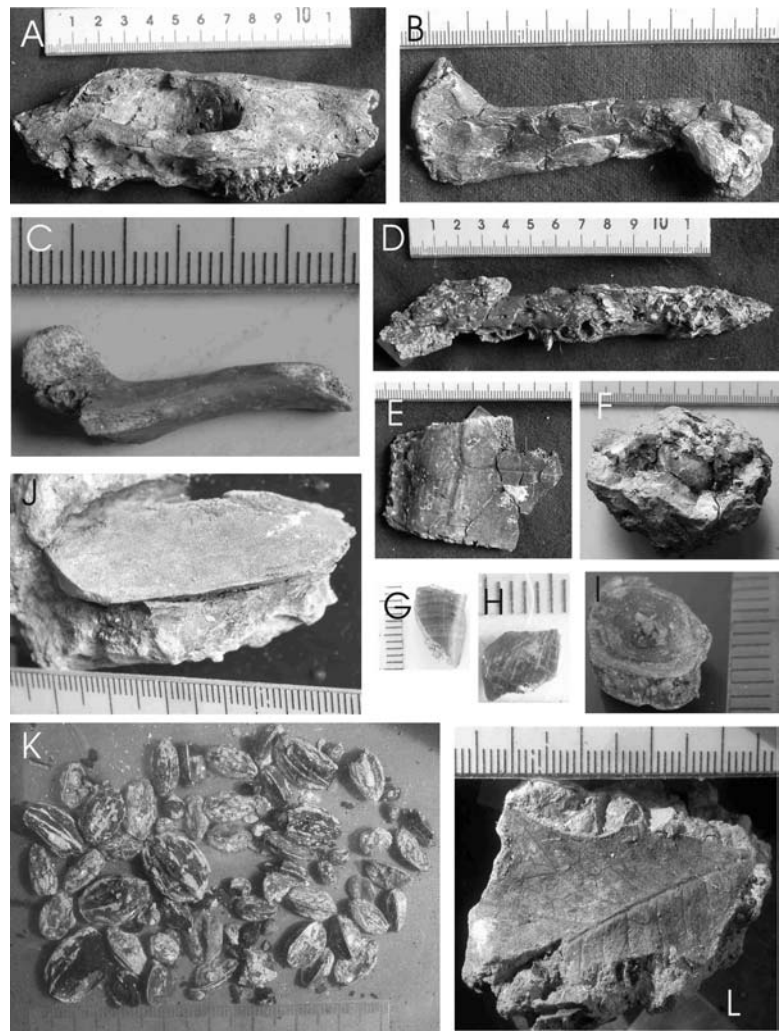
The Z-division is topped by a number of fine-grained intraclast turbidites characterised by discontinuous lamination *sensu* Cole and Picard (1975). On top of leaf-enriched patches of the Z division, slumping structures and erosive bases (Fig. 3f) but also leaves of the same type as below may be found within the lowermost centimetres.

Prominent leaf types of the Z division

Generally, the sediments of the Eckfeld Maar are dominated by laurophyllous, mostly entire-margined and black-coloured leaves, reflecting the subtropical zonal vegetation of this area. During field seasons 2000–2003 several slices measuring one or more square metres with high concentrations of excellently preserved leaves have been excavated from the Z division. Each of these is dominated by a single taxon. Apparently, whole branches were transported here since many leaves are still attached. Leaf types are prevailing here, which are very rare in the adjacent oil shales except for the Juglandaceae. Although minor amounts of entire-margined laurophyllous leaves are scattered in between, the following presentation focuses only on attached leaves or leaflet types, because they do not only allow an insight into the vegetation but also into the sedimentary history of the deposit.

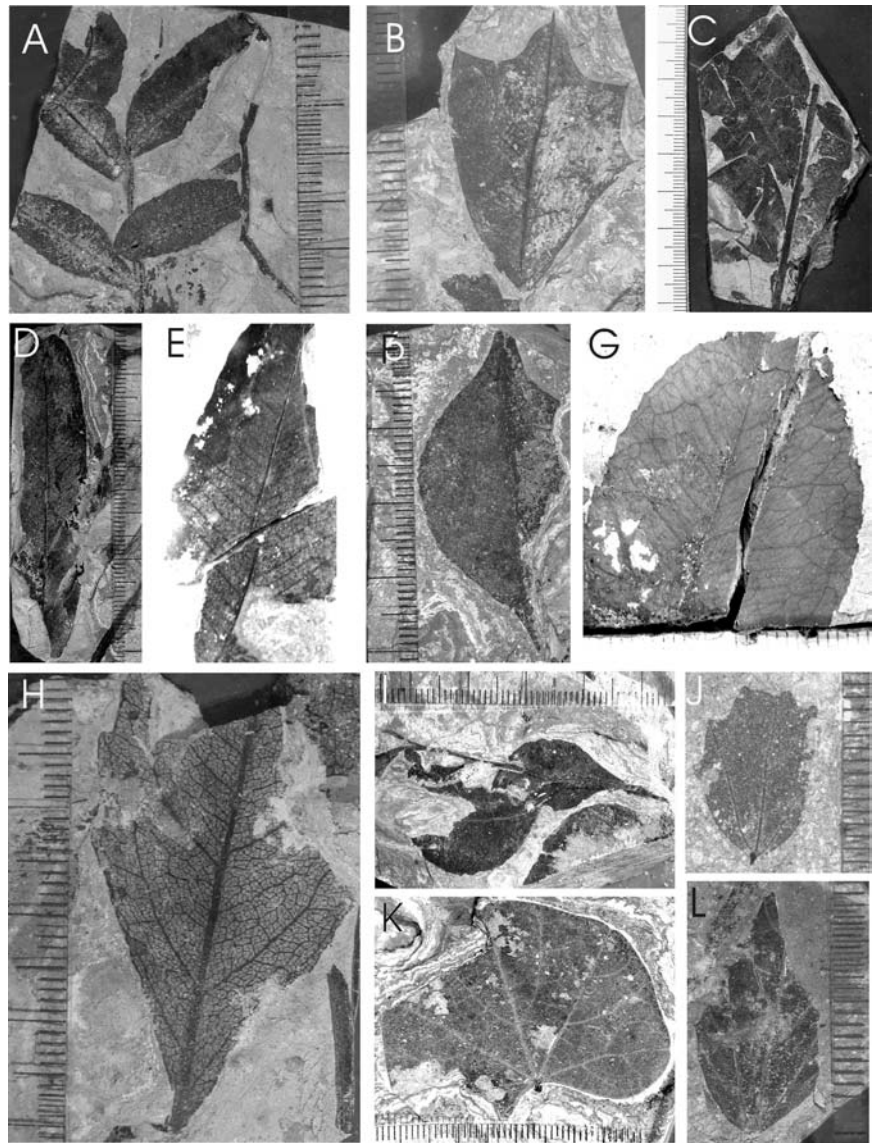
- Juglandaceae (Fig. 5a): Leaflets black, relatively thick. Lamina lanceolate to narrowly elliptic, with simple teeth. Venation craspedodromous to semicraspedodromous. These are the most prominent leaflets in Eckfeld,

Fig. 4 Fossils of the X₁ subdivision: **a** Skull of *Propalaeotherium parvulus*, Equidae. Sample PW2000/163-LS; **b** Mammalian Humerus. Sample PW2003/177-LS; **c** Mammalian Femur. Sample PW1998/57-LS; **d** Mandible fragment, *Diplocynodon* sp. (Pomel 1807), Crocodylia. Sample PW2003/29-LS; **e** Armour plate, Testudinata. Sample PW2003/34-LS; **f** Phosphatised coprolite, Crocodylia. Sample PW2002/106-LS; **g** Isolated tooth of *Pristichampsus rollinatti* (Gray, 1831), Crocodylia. Sample PW2003/46-LS; **h** Fish scale, Atractosteidae. Sample PW2001/209-LS; **i** Fish vertebra, Amiidae. Sample PW2001/209-LS; **j** Steinkern, Unionidae. Note the dilution slot of the shell in between steinkern and surrounding matrix. Sample PWL2001/244-LS; **k** Fruits and seeds; **l** Leaf of *Pungiphyllum waltheri* (Frankenhäuser and Wilde 1995). Sample PB2003/1096-LS



- most closely resembling “types 1” and “2” of the four Juglandaceous types distinguished by Wilde (1989) at Messel. Wilde assigned these types to the Engelhardiidae, which are documented in Eckfeld by pollen, winged fruits, and leaves. Within the Z division several hundred leaves have been counted.
- *Pungiphyllum waltheri* (Frankenhäuser and Wilde 1995) (Figs. 4m and 5b): Leathery black or brownish-coloured leaves of variable size and shape. Some reddish coloured leaves occur as well and are considered here as being juvenile. Margin irregularly toothed to deeply lobed with acuminate to attenuate spines. Small sizes of stomata indicate xeromorphic character. Detailed investigations and comparisons by Frankenhäuser and Wilde (1995) did not allow further identification, since similar leaves occur in many different families. *Pungiphyllum* leaves are found throughout the exposed section, but only 15 out of 100 are from the Z division.
 - Type 1 leaves (Fig. 5c-e): Compound leaves with brownish-coloured leaflets up to 10 cm long. Shape narrow to very narrow elliptic. Venation eucamptodromous with densely-spaced secondaries. Affinity unknown. Several hundred leaflets and compound leaves were identified in the Z division as well as in laminated sediments 1 cm above. Only few are found in another layer, which is assumed to be a turbidite.
 - Type 2 leaves (Fig. 5f, g, i): Lamina brownish-coloured, small (up to 5 cm long) and broadly elliptic with cuneate base and acuminate apex (drip tip). Venation semicraspedodromous, secondaries widely spaced but frequently ramifying with densely spaced intersecondaries. Margin crenate to dentate with theoid glands *sensu* Hickey and Wolfe (1975). Affinity unknown. Out of several hundred leaves only few are not derived from the Z division.
 - Type 3 leaves (Fig. 5h): Thin brownish-coloured leaves with strongly variable shape. Length of lamina varies between 3 and about 12 cm, shape narrow to wide elliptic, irregularly rounded teeth with varying distance. Venation craspedodromous to semicraspedodromous. In gross morphology resembling various fossil taxa: “*Symplocos*” *hallengensis* described by Barthel and Rufflé (1976) which was later referred to the Theaceae as *Polyspora* by Rufflé (1993) and various species of *Sloanea* (Elaeocarpaceae) described by Kvaček et al. (2001). Some fruits closely resembling those of *Sloanea* have been found in the adjacent oil shales. However, com-

Fig. 5 Leaf types of the Z division; **a** Juglandaceae. Sample G2003/667-LS; **b** *Pungiphyllum waltheri* (Frankenhäuser and Wilde 1995). Sample PB2003/891-LS; **c** Type 1, Compound leaf. Sample PB2003/891-LS; **d** Type 1. Sample PB2003/192-LS; **e** Type 1. Sample PB2003/1097-LS, scale bar = 1 cm; **f** Type 2. Sample PB2003/219-LS; **g** Type 2. Sample PB2003/1098-LS; **h** Type 3. Sample PB2003/167-LS; **i** Type 2. Sample PB2003/504-LS; **j** Type 5. Sample PB2003/207-LS; **k** Type 4. Sample PB2003/884-LS; **l** Type 5. Sample PB2003/181-LS



pared with these taxa the cuticle is much less cutinised, stomata are less rounded, anticlinal walls are hardly visible. Similar leaves are present in extant taxa of various families like Symplocaceae, Euphorbiaceae, Actinidiaceae or Flacourtiaceae. Out of several hundred leaves only few are not from the Z division.

- Type 4 leaves (Fig. 5k): Brownish-coloured lamina rounded, 5 cm in diameter. Base actinodromous with seven primary veins. Margin entire, auriculate. Affinity unknown. So far five leaves are known from the Z division and one from the oil shales.
- Type 5 leaves (Fig. 5j, l): Reddish-coloured ovate lamina, 2–3 cm in diameter. Sclerophyllous leaves with protruding veins. Venation craspedodromous, with only few secondaries ending in small spines. In spite of their reddish colour the cuticle is thick, since veins of higher orders are not visible, in contrast to the former types. Affinity unknown. So far 20 out of ca. 80 leaves are from the Z division. Affinity unknown.

Discussion

The flow event

A close causal connection for all three divisions is obvious from their parallel flow direction and spatial distribution of thickness. Considerable lateral and vertical variation within subdivisions X_1 , X_2 and X_3 indicates that a turbulent flow was responsible for the deposition of the whole X division. However, following Fisher (1971) the occurrence of large horizontally orientated wood fragments and intraclasts may be interpreted as indicating laminar flow. In addition, large extraclasts of Devonian bedrock floating on top of the division in the flow centre are caused by matrix buoyant lift (Lowe 1982) or rafting (Mulder and Alexander 2001). As pointed out by Fisher (1983) and Mulder and Alexander (2001), temporal and spatial transitions between laminar and turbulent flows (Fig. 3b) are quite common and caused by variations, velocity, density, and thickness of the flow, as

well as cohesive forces, or bed roughness. Since turbulence and sorting enforces with decreasing flow thickness, only seeds, fish scales, and small bones have been found in the peripheral parts, while the distribution of most fossils within the central ridge is random. Despite the great number of studies concerning flow processes terminology is not standardised yet. For a detailed discussion see Mulder and Alexander (2001). Thus the X division of the HT has been described as debrite by Lutz (1993) and Mingram (1994), but as hyperconcentrated density flow by Bullwinkel (2003). Since field observations do not allow a definite distinction between both flow types, a more general term “mass flow” as used by Einsele (1991) is preferred here.

What caused a narrow tongue-shaped instead of a wide fan-shaped distribution in the X division (Fig. 2) cannot be ascertained since only a part of this layer has been excavated. Possibly the flow came to a sudden halt, thus preventing size dependent sorting and causing features like oblique deposition of oblong clasts. Thus the unusual concentration of fossils could be preserved.

Because of the low clay content and the overall flow behaviour it seems unlikely, that cohesive forces typical for clay-rich debris flows (Einsele 1991; Mulder and Alexander 2001) caused en-masse deposition.

Most probably, this main flow was channelled and possibly even stopped by a barrier on the lake floor, while finer grained sediments from the Y and Z division were partly transported beyond (Fig. 6). Such a barrier could have been caused by synsedimentary settling of the loose volcanoclastic filling below and by slump structures which commonly occur at the foot of slope of deep lakes (Hsü and Kelts 1985). Major slump structures measuring 1 m in thickness have been observed by the author at the excavation site about 2 m below the mass flow deposit. Synsedimentary folds accruing slightly above these slump structures are documented by Lutz (1993).

In addition, the presence of intraclasts may be explained by resuspension of sediment during the flow due to the relief in the lake floor. Hampton (1972) experimentally identified reverse shear layers along the flow front in which eroded intraclasts may be whirled up and redeposited in its rear as in our case (Fig. 6a). Smaller clasts would have been suspended in the associated turbidity current.

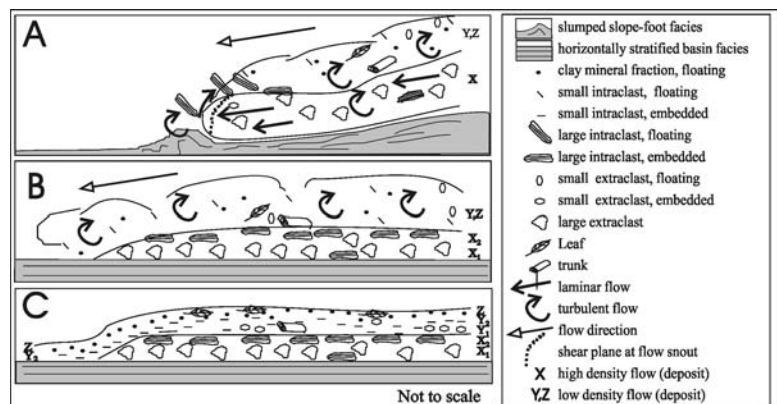
Other sources for intraclasts could be currents moving after the deposition of the mass flow and prior to the succeeding turbidity current. Because of numerous internal deformations of intraclasts (Fig. 3a), Bullwinkel (2003) even interpreted all of the X₂ subdivisions as deposits of subaqueous slumps and slides, triggered by the main flow on the slope. However, based on present field studies the frequently observed lens-shaped interfingering of the involved subdivisions rather points towards complex turbulences within a major flow. Thus intraclast deformation either occurred in the bedrock prior to the mass flow event or developed during erosion and entrainment of unconsolidated mud.

Therefore the sickle-shaped section in the western part of the excavation site dominated by the X₂ subdivision (Fig. 2) probably corresponds to the former flow front. A rapid slow down can best explain its conservation as well as the absence of erosion below the mass flow deposit throughout the excavation site, which is indicated by the continuous presence of a characteristic sequence of layers.

The marked decrease in clast size between X and Y division reflects a transition from mass flow to subsequent turbidity current deposition. Local embedding of extraclast lenses of the Y₁ subdivision within X₂ deposits (Fig. 3a, e), however, indicates that mass flow and turbidity current overlap in time. The slowing down of this current is documented by the gradual decrease of grain size throughout divisions Y₂ and Z. Beside possible secondary flows released at the lake shore, another source probably has been erosion during the mass flow along its front and back as described by Hampton (1972). However, the large number of attached leaves within the Z division is due to the incorporation of branches of trees suggesting an important subaerial component for the turbidity current.

The relief left after the mass flow had settled was determined by trunks and branches rising above the surface and generated minor turbulences locally causing higher sedimentation rates. In fact, in such places (Fig. 3f) attached leaves are more abundant than outside, where little sedimentation occurred. This mode of sediment distribution clearly suggests lateral current transport along the lake bottom rather than vertical settling from a chemo- or thermocline. Mingram (1994) proposed the segregation into a

Fig. 6 Reconstruction of flow and depositional processes during the subaqueous mass flow. **a** On the slope: Mass flow and associated turbulent cloud of a turbidity current fed by erosion along the flow front. **b**, **c** In the basin: Subsequent deposition of sediments from the mass flow (division X) and the turbidity current above (divisions Y, Z)



bottom current and an inter- resp. overflow for turbidity currents in Eckfeld based on the seemingly sharp boundaries between dark and light layers on a macroscopic scale. Instead, a temporal and local break-up of lake stratification caused by the mass flow as assumed by Lutz (1998) is confirmed.

Directly connected with this depositional sequence is a number of subsequent intraclast turbidites. An increase in flow velocity is already indicated by a gradual darkening within the top portion of the Z division. Above the Z division, layers with discontinuous even parallel stratification (*sensu* Cole and Picard 1975) characterize distal turbidites. The presence of leaves typical for the Z division in these overlying sediments indicate that the flow process had not yet completely ceased. Such waxing and waning might have been caused by either changing flow velocities due to an uneven relief or subsequent minor currents. Since frictional loss is practically negligible during turbidity current movement (Hsü and Kelts 1985) it even might have been reflected from the opposite lake shore as a kind of echoing.

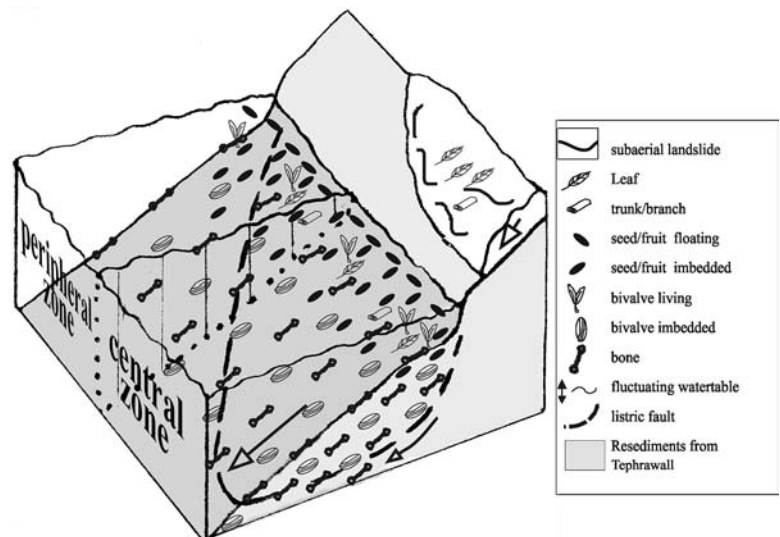
The lake shore as source area

The origin of the flow can be deduced from both, the fossil assemblage and its sedimentary structures. Numerous steinkerns of unionids indicate that the flow started in shallow water of the photic and oxygenised zone at a river bank or near the lake shore. Here most bivalves were already incorporated in situ in the sediment and filled post mortem with surrounding sediment (Groh and Jungbluth 1994). Based on some completely pyritised steinkerns Lutz and Neuffer (1994) concluded that some of them were still alive just prior to being transported into the anoxic basin. A lake shore source of the flow is supported by large amounts of vertebrae, teeth and scales of fishes (Amiidae, Lepisosteidae). Indeed, extant species of these families prefer plant-rich shallow-water zones of lakes and rivers (Micklich and Wuttke 1988b). Sediments of a

river discharging into the lake can be rejected as a possible source for several reasons:

- Based on geological and palaeotopographical evidence (Löhnertz 1994; Pirrung et al. 2003) the existence of a river inlet from the north is suggested. The flow, however, originated at the south-eastern lake border. Possibly the coarse-grained sediments of outcrop N5 (see Fig. 1d) at the inlet of today's Pellenbach may include river delta sediments within the marginal facies.
- High concentrations of various fossils are generally associated with different hydrodynamic regimes. The different groups are expected to be concentrated in separate river placers, and erosion and redeposition of the entire river bank will result in low instead of high fossil concentration.
- Sample checks of the bones indicate excellent preservation, although during transport or bank storage, signs of weathering should be visible (Hanson 1980).
- Unlike other fossils, seeds and fruits increase in concentration significantly from the centre towards the lateral but not towards the north-western distal parts of the deposit. These differences cannot exclusively explained by turbulent mixing processes, but rather reflect the original lake shore distribution (Fig. 7). It can be expected that, due to floating effects, well-preserved seeds are concentrated close to the shore line, especially in undisturbed marginal zones of the lake. Thus, seeds are mainly concentrated in the peripheral parts of the deposit. In contrast, the central shore zone incorporated in the flow should include the most distant area with low seed concentrations. Due to decay and refloating caused by wave action, older seeds would gradually disappear or become at least unrecognisable here. Therefore small areas in the central part of the mass flow deposit with higher concentrations should also reflect a near shore position which was only little affected by later turbulent mixing.
- The moderate rounding of most of the gravel found within the deposit may be due to subaerial abrasion by autolytic friction within the maar eruption clouds

Fig. 7 Assumed original position of the lake shore deposit involved in the mass flow at the moment of a lystric decollement, in combination with a subaerial landslide (white). It shows the distribution of fossils in the water column, along the lake bottom, and in the sediment (the latter one in a cross-section parallel to the flow direction). The *stippled line* indicates the boundary of the sediment prior to mass flow, while the *dotted line* separates peripheral and central zones



rather than river transport might have caused (V. Lorentz, Würzburg, personal communication). Such rounding has been observed by the author in shore sediments of the extant Pulver Maar far away from a potential river inlet.

In contrast, the accumulation of tetrapod bones seems to be multicausal. Abrasion of some teeth, especially from the lower jaw of a primate indicate predation (Franzen, pers. com). Possibly the great amount of phosphatised coprolites of crocodiles indicates a feeding place in the shore area. Due to desiccation fissures for similar specimens from the Fossil-Lagerstätte of Messel Teichmüller (1988) assumed a subaeric origin.

However, most of the bones at Eckfeld may be attributed to floating carcasses, which were drifted to the shore by wind (Lutz 1993), causing high bone concentrations there. The time required for the decomposition of bones (Hanson 1980; Aslan and Behrensmeyer 1996), as well as an in situ dissolution of most bivalve shells suggests several years of storage.

Unfortunately only few investigations (e.g., Wuttke 1988; Martin 1999) on taphonomical processes for tetrapod carcasses have been carried out on comparable environments providing a measure of possible sorting effects. The HT contains a striking number of equids: Thus far 15 crania, many mandibles, and post-cranial elements of three proto-horse species were found, while other mammals are represented only by few or even single specimens. This relation corresponds to the findings in the surrounding sediments where—with the exception of three bats—mammalian carcasses are represented only by six proto-horses. It is not clear yet, whether this is a reflection of a former predominance of equids within the catchment area or the result of taphonomical sorting. However, when comparing the concentration of bones in the flow deposit with the scarcity of carcasses in the surrounding sediments (one equid per 120 m², personal data), it becomes evident, that the lake shore was highly effective as a taphonomical filter for all carcasses, either derived from the lake shore or a tributary (Proto-Pellenbach).

As observed by the author at the extant Pulver Maar plant material of living trees (leaves, seeds, trunks) and carcasses accumulate and rot in knee-deep water along a gently sloping shore line at the foot of the deep slope. In between branches of living trees offer hiding-places to the fishes.

The surrounding vegetation

A plant taphocoenoses never reflects the complete spectrum of the flora within the catchment area of a depositional environment. Selection affecting the taxonomical composition within the fossil record has been demonstrated by many authors (e.g., Roth and Dilcher 1978; Spicer 1981; Ferguson 1985, 1995; Burnham 1994, 1997) and is caused by various factors including the amount of production and the location and habitat of the plants. Especially leaves from trees and shrubs growing near the water, in open stands, or

within the canopy are represented in the fossil record. In addition, there are various ways of mechanical and biological degradation of leaves during transport or exposure to oxic environments.

The predominant vegetation in comparable subtropical environments are evergreen forests with entire-margined laurophyllous leaves, which in fact predominate in the Eckfeld sediments. In this context, the leaves illustrated in Fig. 5 are uncommon within the Eckfeld flora and—except for the Juglandaceae—rarely occur outside the Z division, documenting the uniqueness of this horizon.

Considering aspects of functional morphology these exceptional leaves may allow an insight into the structure of remote parts of the surrounding forest. In the past these aspects have often been misinterpreted (e.g., leguminous leaflets as indicators for dry climates), and considered without reference to sedimentological and taphonomical evidence.

One prominent feature is the large number of leaves with thin lamina.

These leaves or leaflets were not adapted to direct exposure to sunlight (e.g., Ashton and Berlyn 1992), and thus required habitats in the shady and humid understorey or subcanopy. Here they followed different strategies under similar environmental conditions.

Thin leaves with toothed and/or lobed margins and with high stomatal density as found in type 3 may react with rapid growth to forest clearings due to their higher transpiration and better nutrient supply (Givnish 1979, 1984; Fahn and Cutler 1992).

A similar ecological adaptation may be assumed for the thin entire-margined leaflets of type 1. Givnish (1979) pointed out that such compound leaves—often deciduous—occur in tropical forests with frequently disturbed canopies. Since in compound leaves the growth of parenchyma in the rachis is more economical than the production of woody tissue, they are considered as ideal throw away branches for light favouring plants, whose lower branches become useless due to rapid overgrowth.

Other leaf types characteristic for the canopy have drip tips (here: type 2) “facilitating the more rapid growth and maturation of the leaf, thereby limiting the period of vulnerability to herbivory in unstable forests” (Baker-Brosch and Peet 1997).

The thick leaflets of Juglandaceae and their frequent distribution in the sediment indicate exposure to sun in the canopy and along the shoreline of the lake or a river bank. Here compound leaves may be advantageous, due to their adaptable surface area, e.g., by enrolling as protection against desiccation or herbivory, as well as their low cost regrowth (Givnish 1979).

The auriculate base of type 4 (Fig. 5k) might indicate an affinity to climbers since a convergent evolution of such leaf morphology is typical in this group (Richards 1964; Givnish and Vermeij 1976).

A completely different strategy is here assumed for the leaves of *Pungiphyllum waltheri*. Their leathery form (Fig. 4l) and small stomata indicate a scleromorphic character. Therefore their regular, but not frequent occurrence

supports the temporally and spatially limited existence of relatively dry stands in open areas since sclerophyllous leaves of exposed stands would be easily transported by wind and thus well represented in the sediment (e.g., Roth and Dilcher 1978). The presence of spinose teeth is considered as an advantage in defence against mammalian herbivory in small evergreen woody plants (Givnish 1979). Frankenhäuser and Wilde (1995) suggested that *Pungiphyllum* was a pioneer plant on unstable slopes of the inner crater. There the shallow soils are favourable for the growth of scleromorphic plants (e.g., Specht 1969).

A similar even more xeromorphic nature can be assumed for the leaves of type 5, due to their small size, thick lamina with protruding veins ending in spines as well as a similar distribution in the sediment.

An understanding of the diagenetic processes responsible for the observed differences in leaf colours may eventually reveal additional ecological information independent of taxonomy. On recently exposed leaves differences in colour are observed between species due to interspecific differences within the cuticles or wax layers but also

within the species *Pungiphyllum*—possibly reflecting adolescence levels. However, the fragility of reddish colours is indicated by a darkening after some minutes of subaerial exposure.

Summarising these observations a scenario for the vegetation as shown in Fig. 8 may be assumed. In general, forests are considered as dynamic mosaics of vegetation patches produced by disturbances and influenced by different abiotic and biotic conditions (e.g., Martínez-Ramos et al. 1989). In our case occasional landslides produced clearings, which allowed a close vicinity of open vegetation with pioneering plants and dense forest. This may explain some differences in the flora of the otherwise closely resembling Messel lake deposit. There sclerophyllous taxa like *Pungiphyllum*, and the above described brownish leaf types have not been found yet, indicating more stable and gentle crater slopes with deeper soils as supposed by Wilde and Frankenhäuser (1998).

Conclusions

Not many localities combine both: highly diverse fossil plants and animals in excellent preservation. Here, the vast majority of Eckfeld's tetrapod records known so far and leaves from various plant communities, which otherwise are hardly represented in the fossil record, are combined in a single layer. Thus this deposit demonstrates the enormous filtering effect of the lake shore, which has been overcome for a single moment. This unique taphocoenosis was caused by three successive events:

1. A high concentration of fossils partly allochthonous and wind driven accumulated at the south-eastern lake shore.
2. Untied from the shoreline a mass flow associated with less dense turbidity currents moved along the lake bottom of the basin centre transporting the fossils directly into the anoxic environment. Beside the fossils mentioned above branches of trees, shrubs, and/or vines of at least seven different species were transported from their original stands to the shore by a subaerial landslide. Due to facies interfingering and thus close temporal connection it remains unclear, whether the landslide triggered the mass flow or vice versa. Excessive rainfall, earthquakes, gradual eroding of the shore line or rapidly fluctuating water table as observed by Büchel (personal communication) in modern maar lakes of Indonesia may have been responsible.
3. Probably stopped by an uneven lake bottom the mass flow rapidly settled. Thus the original fossil concentration was preserved and its scattering along the lake bottom prevented. In addition, the flow also provided an excellent sedimentary matrix: sand and gravel prevented compaction while silty clay preserved the delicate leaves.

This sequence essentially corresponds to the generalised scheme of Bullwinkel (2003), although partly deviating sedimentary structures lead to a modified interpretation. However, experimental investigations on the behaviour of



Fig. 8 Landslide in 1999 at the Ranu Lading Maar lake, Java, Indonesia, creating a transverse section through dense forest and open shrub vegetation. Photo kindly provided by: Arbeitsgruppe Angewandte Geologie (Prof. G. Büchel), Institut für Geowissenschaften, Friedrich Schiller-Universität Jena

mass flows containing such a variety of fossils, extra-, and intraclasts are still lacking to explain facies changes like those documented here.

In addition to sedimentological and taphonomical evidence, physiological characters of leaves are used for palaeoecological interpretation of the structure of the adjacent forest. At least two tree layers were developed in densely populated forests, while partly scleromorphic shrubs characterised secondary growth in clearings and patches disturbed by landslides. Since only a part of the deposit has been excavated yet, our knowledge concerning the record of animals and plants and their palaeoecological significance may be considerably expanded by further excavations.

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