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Palaeoenvironments of the Eifelian dolomites with earliest tetrapod trackways (Holy Cross Mountains, Poland)

Marek Narkiewicz [a,*], Jacek Grabowski [a], Katarzyna Narkiewicz [a], Grzegorz Niedźwiedzki [b], Gregory J. Retallack [c], Piotr Szrek [a], David De Vleeschouwer [d]

[a] Polish Geological Institute-NRI, 00-975 Warszawa, Poland
[b] Department of Organismal Biology, Uppsala University, 752 36 Uppsala, Sweden
[c] Department of Geological Sciences, University of Oregon, Eugene, OR 97302, USA
[d] Earth System Sciences, Vrije Universiteit Brussel, B-1050 Brussels, Belgium

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ABSTRACT

The Eifelian dolomites in the Zachełmie Quarry (Holy Cross Mountains, Poland) contain trackways and tracks of tetrapods 390–391 Ma old, and thus the oldest known so far. The environments of the trackway-bearing beds have been investigated using sedimentological, palaeontological, geochemical and palaeomagnetic methods. The reconstructed tetrapod habitats comprised shallow-water lagoons separated from an open marine basin by sparsely vegetated islands and spits. The lagoonal waters were well-aerated and a few metres deep at most, undergoing periodic desiccation. The dolomitic sediments, primarily of microbial origin, formed in tropical waters of slightly modified marine composition. Oxygen isotope data obtained from the dolomicrites suggest water temperatures around 30 °C. The seasonal semi-arid to sub-humid climate, deduced from paleosol characteristics, was probably of a tropical monsoonal type. The degree of restriction of the lagoonal system evolved from relatively open, evaporation-dominated towards increasingly closed, freshwater influenced.
The detailed observations of the footprint-bearing beds, as well as the characteristics of the tracks, indicate that they were formed mostly under subaqueous conditions, by wading, walking on the bottom or swimming animals. Lack of tidal indicators in the restricted Zachełmie lagoons argues against previous concept that tidal flats served as a food source for the early tetrapods. Nor is a hypothesis of flooded woodlands confirmed as a habitat promoting the "fish-to-tetrapod" transition. We propose that functional limbs emerged among aqueous animals that acquired their locomotional capabilities in a shallow lagoonal water before attempting longer excursions on land.

1. Introduction

Discovery of the earliest tetrapod trackways in the Eifelian (early Middle Devonian) strata of the Zachełmie Quarry of Poland (Niedźwiedzki et al., 2010) radically changed the timing and evolutionary scenario of a fish-to-tetrapod transition (Janvier and Clément, 2010; Friedman and Brazeau, 2011; Clack, 2012). The palaeoenvironmental context of the Zachełmie tracks was tentatively interpreted as marginal marine, peritidal or lagoonal facies, based on preliminary sedimentological observations (Narkiewicz and Narkiewicz, 2010). This general interpretation prompted Niedźwiedzki et al. (2010) to put forward a hypothesis of intertidal mudflats as an optimum habitat for the early tetrapods, with its wealth of invertebrate organisms available for feeding (smorgasbord concept, Niedźwiedzki et al., 2010). Such a hypothesis was in opposition to a widely accepted idea of brackish to freshwater vegetated areas as a probable scenery of the tetrapod emergence (Clack, 2012), and the hypothesis of Retallack (2011) who proposed flooded woodlands as likely environments of a fish-to-tetrapod transition.

Lack of a well-constrained interpretation of the earliest tetrapod habitats renders further discussion on quadrupedality development and terrestrialization of vertebrates difficult. Therefore, the present study was planned in the aftermath of the Zachełmie discovery, to gain more detailed insight into palaeoenvironments of the track-bearing strata. Because no bone material has been found in association with the footprints so far, the palaeoecological interpretations can be based solely on the investigation of the tracks and their enclosing sediments. On the other hand, the nature of ichnological record excludes a possibility of redeposition and thus the present sedimentological and palaeoecological considerations can be directly referred to the habitats of the trackmakers. A range of various sedimentological, palaeontological, petrological and geophysical tools have been applied to interpret conditions in which the early tetrapod ichnorecord has been formed and preserved. The ultimate goal is to

* Corresponding author. Tel.: +48 22 459 2321.
E-mail address: marek.narkiewicz@pgi.gov.pl (M. Narkiewicz).

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constrain possible environmental conditions of the tetrapod emergence and quadrupedality development.

2. Regional and stratigraphic setting

The present study is based on a section exposed in the abandoned Zachełmie Quarry turned into a geological reserve in late 2010. The quarry is located in the northwestern Holy Cross Mountains (Fig. 1) in central Poland (50° 58′07.39″N; 20° 41′26.71″E). The outcropping Devonian strata, ca. 90 m thick, comprise the upper part of the Wojciechowice Formation and its contact with the overlying Kowala Formation (Fig. 2). The lower unit is composed of thin- to medium bedded, micritic dolomite mudstones and wackestones with a variable admixture of clayey material, interlayered with dolomitic marls and shales. The Kowala Formation typically includes pure, crystalline dolomites with amphiporoid biostromes (see Narkiewicz and Narkiewicz, 2010, for more details).

The measured section, described in detail below, comprises ca. 30 m thick strata attributable to the lower part of the Wojciechowice Formation, exposed mostly along the southern quarry-wall. Narkiewicz and Narkiewicz (2010) described a characteristic, almost monospecific conodont assemblage of the Lower–Middle Eifelian *costatus* Zone in the uppermost part of this section. Later conodont investigations (Narkiewicz, in press) furnished additional material from the basal part of the section, below the track-bearing interval. This constrains the age of the entire studied section to the *costatus* Zone, probably its lower part (Narkiewicz and Narkiewicz, in press). The age of the studied strata is 390–391 Ma according to the latest version of the Geological Time Scale (Becker et al., 2012) and the recent revision of the Devonian geochronology by De Vleeschouwer and Parnell (2014). This means that the tetrapod track-bearing beds are 4–5 myr younger than previously estimated, predating oldest known tetrapod body fossils by 14 myr (Narkiewicz and Narkiewicz, in press).

3. Materials and methods

Zachełmie Quarry is the only locality in the Holy Cross Mts. from which the earliest tetrapod trace fossils have been described so far. Other exposures displaying similar stratigraphic position and depositional characteristics are scarce and difficult to correlate with the studied section. The section was described in detail and sampled during 2010–2011. The macroscopic description was supplemented by sedimentological observations of ca. 50 hand samples. Several dozens of hand samples were independently collected to document invertebrate trace fossils (Niedźwiedzki et al., 2014). All the analytical investigations listed below have been carried out in the Polish Geological Institute-NRI in Warszawa, unless otherwise stated.

Microfacies study was based on 114 thin sections stained with the Evamy's solution in order to identify carbonate minerals. The microscopic observations were performed using petrographic Nikon SMZ 1000 binocular with attached digital Coolpix camera. Organic remains were additionally studied in insoluble residues from 10 dolomite samples, 1.5 to 5 kg each. The samples were crushed and dissolved in 15% formic acid. The obtained residues were then concentrated using heavy liquids, but microscopic examination embraced both heavy and light fractions. Moreover, 3 samples of grey-coloured dolomitic shale were processed for palynological contents.

Eighteen dolomite samples were investigated under scanning electron microscope Zeiss LEO (model 1430). The samples were chipped

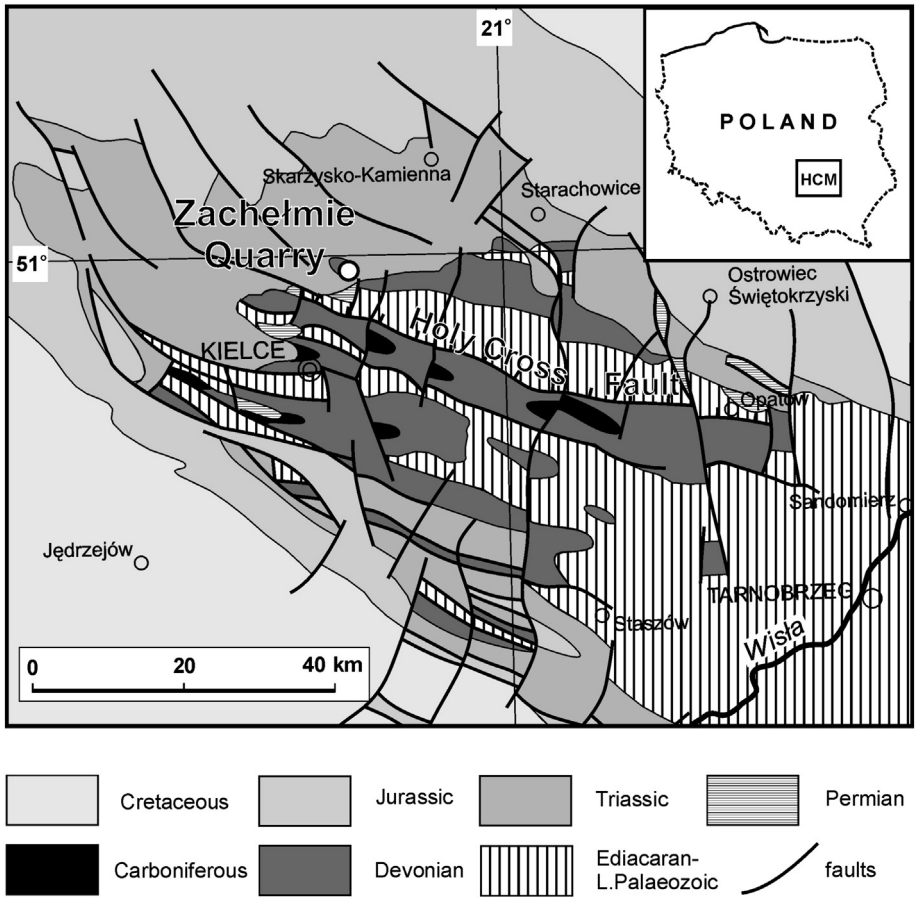

Fig. 1. Location of the Zachełmie Quarry in the Holy Cross Mountains (HCM) in southern Poland, on the background of the geological map without Cenozoic strata (after Dadlez et al., 2000, simplified).

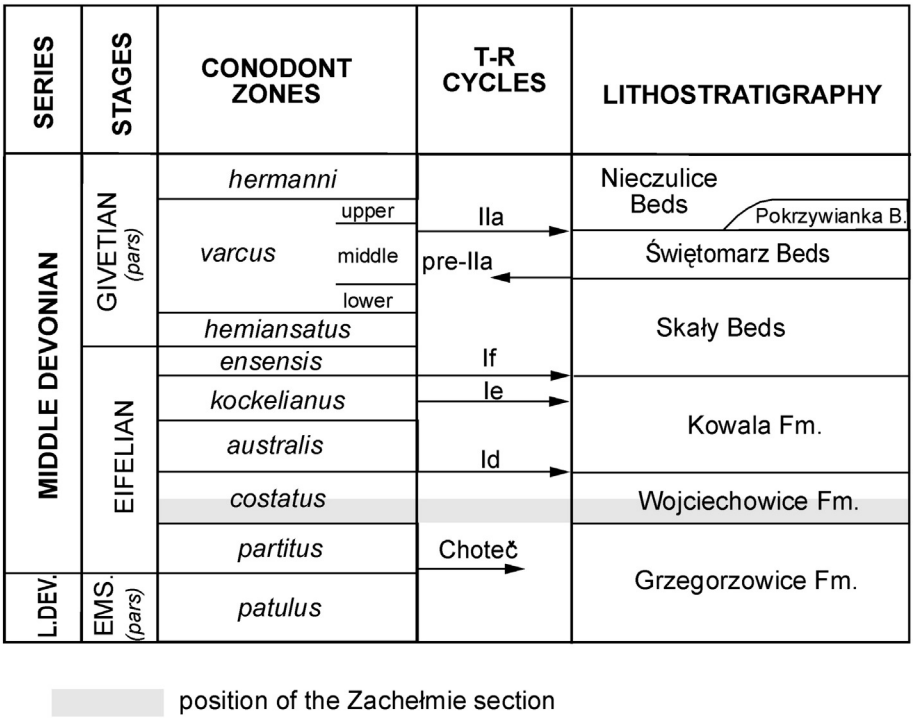

Fig. 2. Stratigraphic framework of the Eifelian in the northern part of the Holy Cross Mountains with indicated position of the studied Zachełmie section (partly after Narkiewicz and Narkiewicz, 2010).

off from the fresh rock surface and etched for a few seconds in 1 molar HCl. For several dozens of mineral grains a semi-quantitative elemental analysis was performed by means of energy-dispersive X-ray spectroscopy (EDS), using ISIS microprobe (Oxford Instruments Ltd.). The cathodoluminescence was examined in 12 polished thin sections using CCL 8200 mk3 equipment (Cambridge Image Technology Ltd.) coupled with polarization microscope Optiphot 2.

Ten samples of most common lithotypes were analysed by powder X-ray diffractometry (Phillips X'Pert PW 3020) to constrain the mineral composition of the studied sediments. The composition of a clay fraction was independently determined in oriented dry-air preparations treated with glycol and heated up to 550 °C.

The magnetic studies included field-profiling of a magnetic susceptibility (MS) with a 20–25 cm resolution, using portable SM30 equipment. In addition, various magnetic parameters were measured in laboratory in 35 hand samples taken in one-metre steps in the section (for methodological details — see Grabowski et al., in press). Major elemental composition of the samples was determined by X-ray fluorescence (Philips PW 2400 spectrometer; measurement uncertainty 10%) while trace and rare element components were determined by inductively coupled plasma mass spectrometry (ELAN DRC II, Perkin Elmer; extended measurement uncertainty 20%). Three reconnaissance samples were also analysed for organic carbon in Silesian University (Sosnowiec) using methodology described by Racka et al. (2010).

The stable isotope analyses were made on whole rock fragments split off from fresh rock surfaces carefully selected to avoid contamination by recent soil/plant material and mineral inhomogeneities (e.g. late mineralization, dedolomitization etc.). The oxygen and carbon isotopes in 88 samples were analysed in the Institute of Geological Sciences (Warszawa) using Delta+ spectrometer with the KIEL IV attachment. The samples were dissolved in orthophosphoric acid of 1.94 g/cm^3 density in temperature 70 °C. The analytic uncertainties based on long-term measurements of the NBS19 standard are 0.12 for O and 0.07 for C. All results are given as $\delta^{13}C$ and $\delta^{18}O$ relative to the V-PDB standard. For the oxygen data, the fractionation correction for dolomite was applied after Rosenbaum and Sheppard (1986).

4. Characteristics of the Zachełmie succession

The measured section consists of three subsections labelled EL, EM and EU (Fig. 3) separated by a few metres of inaccessible strata. The fourth section WE, located in the SW part of the quarry can be correlated with the middle part of the EM subsection by tracing characteristic paleosol beds (Narkiewicz and Retallack, 2014) and comparing MS logs (Grabowski et al., in press).

General lithology, distribution of depositional structures and biotic constituents allow the subdivision of the measured section into lower and upper complexes, separated by a sharp, erosional boundary running between the beds EM 65 and EM 66 (Fig. 4). The Lower Complex, with the tetrapod trackways, is characterized by a predominance of laminated dolomite mudstones and a considerable proportion of clayey-dolomitic shales. Typical are mud-cracked beds and various discontinuity surfaces, including erosional and/or associated with dolomitic paleosols. In contrast, the Upper Complex is typified by a more massive bedding and a common presence of dolomite wackestones. Bioturbation is commonly pervasive, leading to homogeneous and wavy-nodular structure, while in the Lower Complex it is rare and confined to single levels. Both complexes differ also in their micro- and macroscopic organic skeletal composition. Notably, the marine body fossils, including echinoderms, bryozoans, scolecodonts and conodonts occur almost exclusively in the Upper Complex (Fig. 3). The exception is the lower part of the EL subsection where a more diverse fossil assemblage has been found, including conodonts in particular.

The following description will be focused on the Lower Complex with a particular emphasis on the interval with the tetrapod ichnofauna.

4.1. Depositional cycles

The Lower Complex is composed of 14 or 15 cycles some decimetres to 2 metres thick, each displaying an ordered succession of lithologies and sedimentary structures (Fig. 5). Most cycles start with evenly bedded, parallel-laminated clayey-dolomitic shales or homogenous marly dolomudstones. These grade upwards into dolomudstones displaying

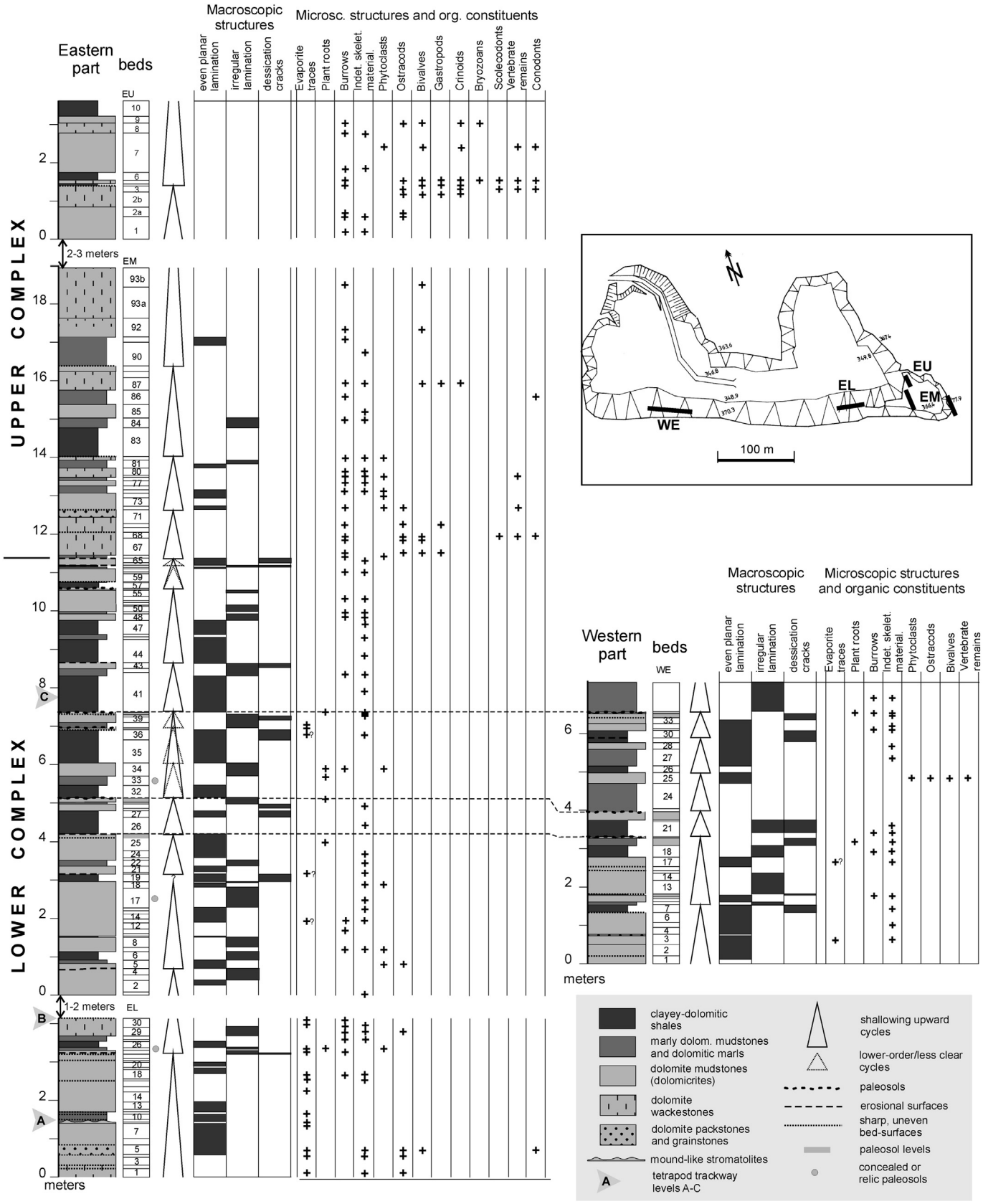

Fig. 3. Detailed graphic log of the studied section. Location of the subsections EL, EM, EU and WE is shown against the schematic plan of the Zachełmie Quarry in the inset.

discontinuous, wavy lamination. Bedding-planes reveal characteristically wrinkled lamination surfaces (see Niedźwiedzki et al., 2014, fig. 4f). Upper parts of the cycles commonly show desiccation phenomena exposed as polygonal mudcracks on several bedding planes in the quarry. Less common are small teepee structures associated with evaporite pseudomorphs (Narkiewicz and Retallack, 2014, fig. 5c). Macroscopically

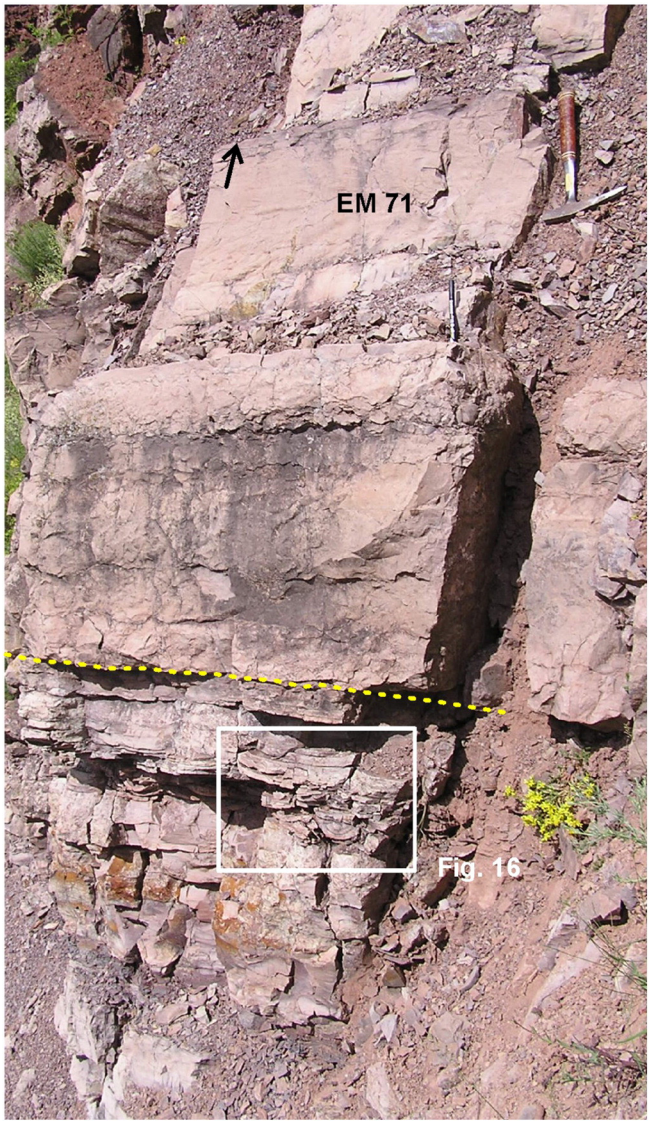

Fig. 4. Lower and upper complexes boundary marked as a broken yellow line in the EM subsection. Arrow points to the bed EM 71 top. Boxed fragment is enlarged in Fig. 16. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

visible traces of vanished evaporites can take a form of millimetre to centimetre-sized nodules of quartz and dolosparite (Fig. 6a) or compacted hopper halite casts in marly dolomudstones (Fig. 6c, also fig. 4e in: Niedźwiedzki et al., 2014). The cycles may display subordinate internal discontinuities that range from flat erosional surfaces to irregular bedding planes.

The cycle tops can be developed as sharp erosional surfaces truncating underlying mud-cracked beds. They are mostly planar or with a low-relief, and may be associated with local intraclasts (Fig. 6a). In other cases the mud-cracked laminites grade into homogenous to nodular beds topped by sharp undulating surfaces that may show a characteristic prismatic to pillow-like textures. The beds display strong internal deformation, presence of root traces and vertical peds, and are interpreted as weakly-developed dolomitic paleosols (Narkiewicz and Retallack, 2014). The lowermost cycle (EL subsection, Fig. 3) is topped by an irregularly laminated bed with domal stromatolites displaying low (up to 10 cm) relief (Fig. 6b) and characteristic cement-filled gas domes (Noffke et al., 2001).

The cycles, interpreted as a record of gradual shallowing and desiccation, are characterized by a distinct pattern of an upward decreasing MS (Grabowski et al., in press). This trend is ascribed to a general drop in terrigeneous clay admixture.

4.2. Microfacies

Microfacies study of the Lower Complex was based on observations of 88 thin sections. Overall, nine microfacies types have been distinguished based on sedimentary and early diagenetic structures and on inventory of organic constituents (summarized in Table 1). Fig. 7 shows distribution of particular types in the section whereas representative examples of the microfacies are illustrated in Fig. 8.

4.2.1. Microbial laminite (Lm)

Sub-millimetre lamination consists of alternating dark micritic, and brighter, finely-detrital laminae (Fig. 8a). The laminae may be irregular, wavy and tapering laterally. The detrital laminae are composed of peloids, small intraclasts (including rare blackened clasts – "black pebbles" of Strasser, 1984), and different indeterminable bioclasts – sparitic fragments, fibres, tubules and spheres. They also contain fine-grained quartz and their base may rest on a microerosional relief partly truncating underlying micritic laminae. Lamination may enclose small irregular or horizontal fenestral structures partly grading into lamination-parallel fractures. Lamination may be also disrupted by nearly vertical structures related to bioturbation or sediment degassing. The sets of laminae can be bounded by subordinate erosional surfaces. Evaporite relics, in a form of small pseudomorphs, are locally common.

Under SEM the dark laminae show a more uniform and finer-grained texture (≤ 10 μm) whereas the detrital ones are composed of larger grains, partly in decimicron range, and including quartz and layered aluminosilicates (Fig. 9a). The fine-grained dolomite may be locally recrystallized (Fig. 9b) but it nevertheless mostly retains its primary grained texture. The grains include oval or spheroidal particles that can be composed of sub-micron-sized crystallites. Such grains have been documented also in paleosols (Fig. 9c; see Narkiewicz and Retallack, 2014) and in other microfacies types (L, M and W, see below). Similar dolomite grains have been described from recent lagoonal microbialites in Brazil as *peloidal aggregates* (Spadafora et al., 2010) or *spheroidal clusters* (Sánchez-Román et al., 2009).

4.2.2. Disturbed microbial laminite (Lm(d))

This microfacies is characterized by a strong deformation of the above described microbial lamination (Fig. 8b). It differs from the latter type also in a relatively more common occurrence of blackened clasts, presence of root traces and relict phytoclasts. The deformation is either ductile, leading to a formation of microfolds or microthrusts, or may be brittle, resulting in fractures, in situ fragmentation and formation of local angular clasts. In transitional cases to the microfacies BC (see below) the sediment attains a partly brecciated appearance (as in the lower right corner of Fig. 8b). Locally, the detrital quartz admixture may be considerable.

4.2.3. Breccia/conglomerate (BC)

In most cases the BC microfacies is associated with paleosol beds. It includes intraclastic wackestones or packstones with poorly-sorted and rounded clasts composed of various lithologies: microbial laminites, mudstones, skeletal wackestones and microsparites. Clasts may show various in situ deformations: from local fracturing to plastic disturbance. Strong internal reworking may lead to homogenization of the sediment. Common are blackened clasts, root traces and phytoclasts. The SEM images reveal presence of dolomite grains in the range 1–10 μm, including spherical grains composed of sub-micron-sized crystallites (Fig. 9c). For a more detailed description see Narkiewicz and Retallack (2014).

4.2.4. Abiogenic laminite (L)

This microfacies type differs from the microbial laminite in displaying regular planar structure marked by changes in grain-size

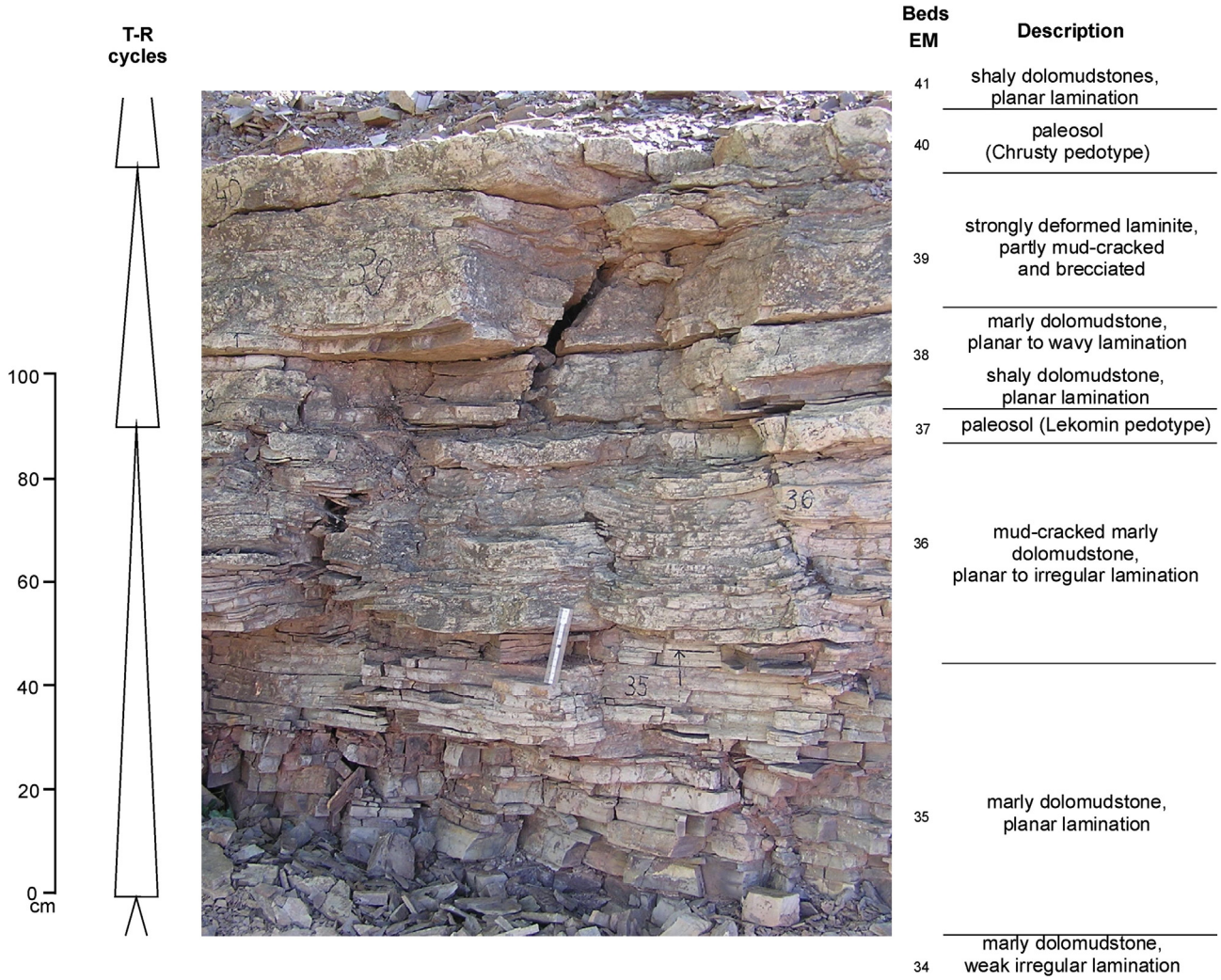

Fig. 5. Field details of two shallowing upward cycles capped by paleosols (cf. Narkiewicz and Retallack, 2014, for explanation of paleosol types).

and terrigeneous admixture (Fig. 8d). The millimetre to sub-millimetre laminae are mostly composed of alternating dolomite micrite/mudstone and fine-grained wackestone to grainstone. The latter commonly contains silt-sized grains of quartz and muscovite, and subordinate feldspars and apatite distinguished by a distinct cathodoluminescence. Coarser-grained laminae contain peloids and bioclasts represented by indeterminable fine skeletal detritus. Lamination may be very subtle in some cases, marked merely by alteration of slightly darker and brighter laminae in a dolomitic mudstone. In rare instances laminae become wavy or form thin small-scale cross-bedded sets. Subordinate erosional surfaces are frequent, while burrows with peloidal infill are less common.

4.2.5. Mixed microbial and abiogenic dolomite (Lm-L)

This microfacies is characterized by co-occurrence of sets of Lm- and L-type laminae in the same thin section. Microerosional surfaces are common, while deformed or disrupted laminae, large clasts (including blackened ones), phytoclasts and evidence of infaunal activity may be occasionally found (see Table 1).

4.2.6. Mudstone (M)

These are homogeneous dolomite and dolomite-terrigeneous muds with subordinate occurrence of wackestone or packstone laminae/zones in transitional examples to the L and Ws microfacies (see below). Common terrigenous admixture comprises quartz and muscovite silt, more rarely quartz sand grains. Bioturbation is rare, a few burrows may be filled with peloid material. Pseudomorphs after sulphate minerals may occur as nodules or dolospar-filled crystal-casts (Fig. 8e).

4.2.7. Skeletal wackestone (Ws)

Homogeneous, more or less bioturbated wackestones contain various skeletal remains, mostly indeterminable biosparitic fragments, more rarely ostracods, thin-shelled bivalves, phytoclasts and small ichthyoliths. The grains, mainly of arenite or fine rudite size, may also comprise peloids and intraclasts, including rare blackened clasts. Variable terrigeneous admixture consists mainly of quartz and muscovite silt and less common quartz sand. Bioturbation ranges from well-defined tubular, variously oriented burrows to thorough reworking. Rare evaporite traces include halite casts (Fig. 8f)

4.2.8. Nonskeletal wackestone (W)

Depending on the dominant grain components these are pelletal or intraclastic wackestones with a subordinate admixture of indeterminable skeletal detritus and rare phytoclasts. The grains are mainly in arenite to fine rudite size range. Structure is homogeneous due to common bioturbation evidenced as overall reworking or as partly retained outlines of tubular horizontal or oblique burrows. SEM observations confirm chaotic grained texture of the sediment (Fig. 9d).

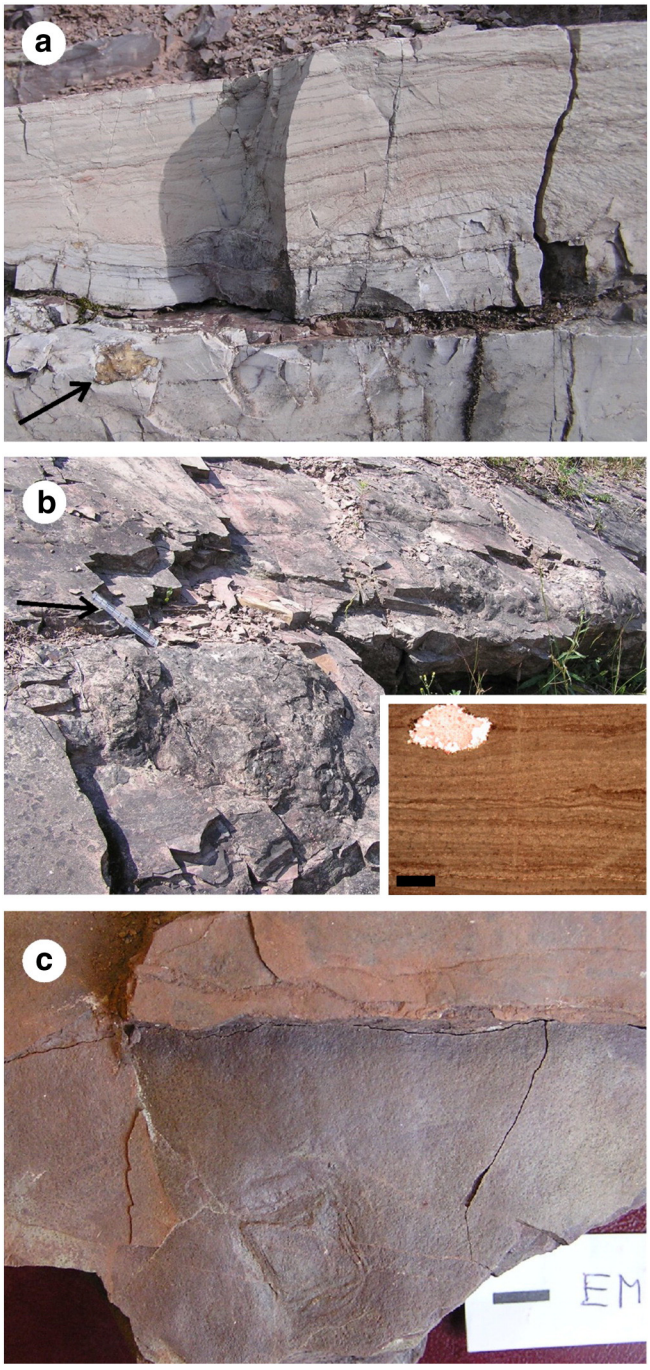

Fig. 6. Macroscopic features of the Lower Complex. (a) erosional surface developed above mud-cracked dolomite mudstone (bed EL 23), overlain by irregular laminite (arrow points to a dolosparitic sulphate pseudomorph), height of the view is ca. 15 cm; (b) level of mound-like stromatolites (bed EL 8); (arrowed ruler is ca. 12 cm long); the inset photo shows a microbial lamination in the stromatolite with a gas dome filled with quartz and dolomite cement (scale bar — 1 mm) (c) compacted halite cast on the bedding plane of a dolomitic marl (bed EM 38), scale bar — 1 cm.

4.2.9. Packstone (P)

These mostly homogeneous dolarenites with dolomicritic or microsparitic matrix can be ascribed to intraclastic-skeletal or peloidal packstones. Transitions to wackestones can be observed in varieties enriched in dolomitic mud. Poorly-sorted and -rounded intraclasts are composed of micrite. Skeletal material is mainly of fine, indeterminable type or, rarely, may include ostracod and bivalve remains. Sulphate pseudomorphs of euhedral crystals were found in some thin sections.

Distribution of the most characteristic microfacies types in the shallowing upward cycles is consistent with macrosopic observations (Fig. 7). Thus, variety L is found usually in the lower part of the cycles while Lm(d) and BC are confined to cycle tops developed as paleosols (Narkiewicz and Retallack, 2014). Microbial laminite (Lm) has a less regular distribution but in most cases occurs in middle to upper parts of the cycles. The wackestones may occur in different positions in the cycles.

4.3. Biota

The Lower Complex of the Zachełmie dolomites seems almost completely barren with respect to macroscopic body fossils, even on a closer field inspection. On the other hand, thin sections reveal ubiquitous fine skeletal material composed of indeterminable spheres, filaments or fibers in most of the microfacies types described above (Table 1). It may be speculated that these enigmatic remains represent strongly reworked algal/microbial material. Ostracods and phytoclasts are rare while bivalves and ichthyoliths have been found only exceptionally (Fig. 3).

Surprisingly rich fossil material has been obtained from the insoluble residues of the conodont sample in the lowermost part of the section (bed EL 5). In addition to conodonts (Narkiewicz, in press), the assemblage comprises numerous agglutinated foraminifers from the genus *Hyperammina* Brady 1878, and benthic ostracods ascribed to Palaeocopida and Podocopida. Moreover, single examples of mineralized lichens and vertebrate remains have been found. The latter are represented by poorly preserved undetermined remains belonging probably to placoderms and osteichthyan fishes. The ichthyoliths have been encountered also in a sample from the bed WE 25: a single scale that may be ascribed to a basal actinopterygian.

More abundant and diverse vertebrate remains have been obtained from the Upper Complex (subprofile EU). This mixed assemblage is composed of the remains of basal actinopterygians (Fig. 10A) and sarcopterygians (Onychodontiformes, Actinistia and Dipnomorpha; Fig. 10B). These are generally marine forms that could have been tolerant for brackish or fresh waters to some degree (Janvier, 1996; Long, 2011). Middle Devonian sarcopterygians lived primarily in near-shore marine environments and were active predators (especially in the case of Onychodontiformes). On the other hand, basal actinopterygians were mostly marine and probably pelagic forms.

Macroscopic plant fossils are very rare, poorly preserved and thus problematic. Also attempts to obtain palynomorphs from dolomitic shales gave mostly negative results. Only a single sample EM 6 furnished a few poorly preserved spores (genera *Anapiculatisporites*, *Apiculatisporites*, *Leiotriletes*, aff. *Retusotriletes*) and acritarchs (*Micrhystridium* sp.). The presence of plants is nevertheless evidenced, not only by phytoclasts seen in thin sections (Fig. 8c; Table 1), but also by root traces found in paleosols (Narkiewicz and Retallack, 2014). Based on paleosol development and associated structures the cited authors interpreted sparse vegetation as representing equivalents of the present herbaceous to small shrubby plants, depending on the advancement of pedogenic processes in particular paleosol types.

Scarce invertebrate ichnofossils from the Lower Complex have been described in detail by Niedźwiedzki et al. (2014). They occur in discrete levels separated by ichnofossil-barren intervals and were attributed to six ichnogenera (*Skolithos*, *Balanoglossites*, *Alcyonidiopsis*, *Spongeliomorpha*, *Gordia*, *Rhizocorallium*) and some problematic traces. The low-diversity assemblages consist predominantly of horizontal and inclined burrows attributable to arthropods, probably crustaceans. The ichnofauna shows overall affinities to an impoverished *Cruziana* ichnofacies.

4.4. Mineralogy and elemental composition

Thin-section study confirmed field observation that the carbonate component of the Zachełmie sediments is dolomite. Minor calcite

Table 1
Microfacies summary (Lower Complex).

Microfacies	Number of thin sections	Sedimentary and diagenetic structures					Organic structures			Organic components			
		Erosional surfaces	Blackened clasts	Irregular fenestrae	Evaporite traces	Clayey seams	Root traces	Thorough bioturbation	Burrows	Phytoclasts	Fine skeletal detritus	Ostracods	Bivalves
Microbial laminite	24	++	+	+++	++	+	−	++	+	−	+++	−	−
Disturbed microb. laminite	10	++	++	+++	+	+	++	+	−	+	+++	−	−
Breccia/conglomerate	9	−	+++	+	+	+++	+++	−	−	++	+++	−	−
Abiogenic laminite	9	+++	−	−	−	+	−	−	++	−	++	−	−
Mixed laminite	8	+++	++	++	−	++	−	++	−	+	+++	−	−
Mudstone	6	−	−	−	+	++	−	+	+	−	+	−	−
Skeletal wackestone	11	−	−	−	+	++	+	++	++	+	+++	+	+
Nonskeletal wackestone	6	−	+	−	+	++	−	+++	+++	+	+	−	−
Packstone	5	−	−	−	++	+	−	+	+	−	++	+	+

+++ abundant; ++ moderately common; + rare; − absent.

occurs either as a late vein-filling cement or a dedolomite related to a Permian–Triassic or recent weathering. Terrigeneous silt- and sand-size fraction contains mainly quartz and muscovite (observed in polarized light), minor feldspar and apatite (seen under CL microscope) and sericite (detected by EDS). Feldspars and traces of amphiboles were also detected by XRD analyses in the single sample EU 3 (Table 2). XRD data confirm considerable contribution of clay minerals, mainly illite and a less common chlorite. The measurements of the

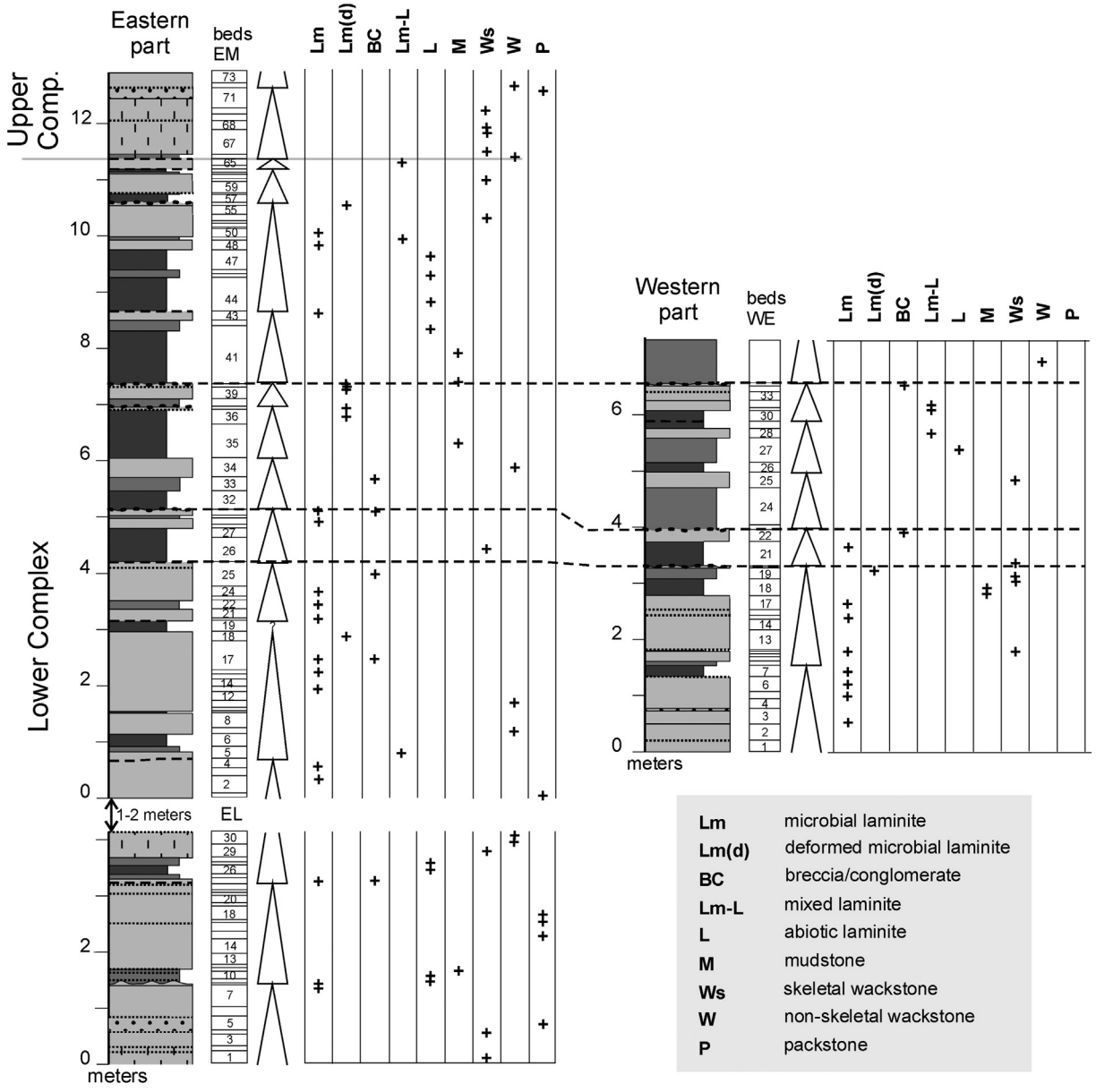

Fig. 7. Occurrence of microfacies types in the Lower Complex of the Zachełmie Quarry section. Other explanations — see Fig. 3.

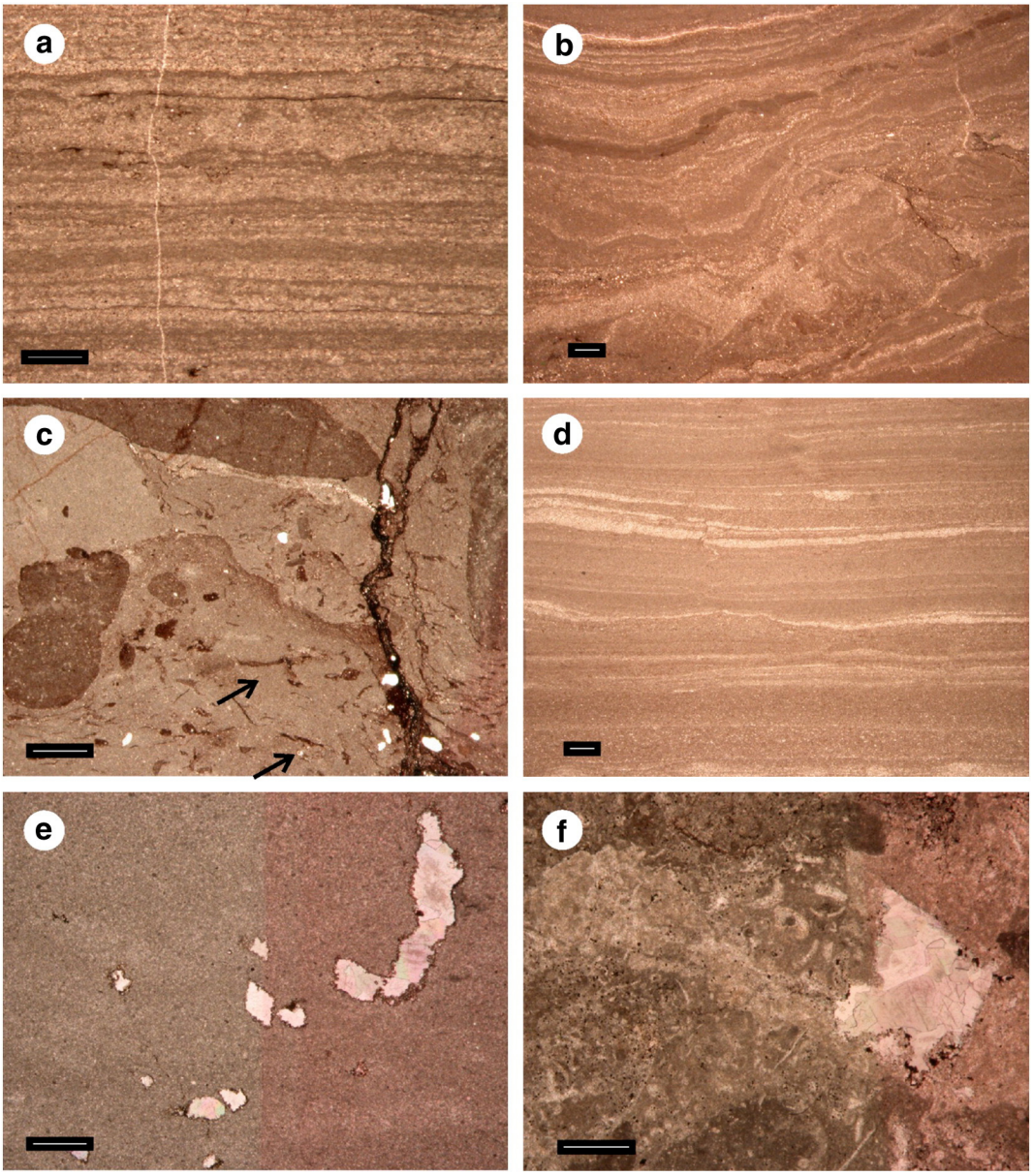

Fig. 8. Microfacies types in the Lower Complex (scale bar — 1 mm): (a) microbial laminite (bed EM 13); (b) disturbed microbial laminite (bed EM 40); (c) breccia/conglomerate (paleosol bed EL 25), note vertical root trace on the right, phytoclasts (arrowed), blackened clasts and single quartz sand grains; (d) abiotic laminite (bed EL 10); (e) mudstone with dolospar pseudomorphs after sulphates (bed EL 18); (f) skeletal wackestone (bed EL 5; note pseudomorph after halite crystal partly filled by dolomite spar).

crystallographic d_{104} parameter suggest deficit of calcium in a dolomite lattice (Lumsden, 1979). Dispersed late hematite mineralization is ubiquitous in the studied quarry and was identified as the main carrier of MS. Magnetite is subordinate and occurs mainly in the lowermost and uppermost parts of the section (Grabowski et al., in press).

The average values of the main-element composition for both complexes as well as for selected microfacies types are given in Table 3. The individual sample measurements are tabulated in Supplementary data (SD1) and the associated correlation coefficients are available in SD2.

High MgO and CaO content and a perfect correlation of both constituents reflect predominance of dolomite, while considerable SiO_2 and Al_2O_3 percentages (correlation coefficient $r = 0.962$) confirm importance of clay minerals as main terrigeneous components. TiO_2, Fe_2O_3 and K_2O are mainly associated with clays which is evidenced by their very good correlation with Al_2O_3 ($r > 0.9$; SD2). Nevertheless, some samples exhibit excess of Fe_2O_3 which may be explained by hematite mineralization and/or incorporation of Fe into the dolomite lattice. Most of trace elements are positively correlated with the clay admixture represented by Al_2O_3, with the exception of Cu, Sr, Cd, Ba (SD2). All REEs are strongly correlated with the Al_2O_3 content ($r \geq 0.8$), although for Nd, Sm and Th the correlation is weakest, while at the same time it is significant with P_2O_5 ($r > 0.7$).

In the case of uranium and phosphorus content, commonly regarded as reflecting palaeoredox conditions and palaeoproductivity (e.g. Jones and Manning, 1994; Tribovillard et al., 2006), their correlation with alumina is moderately good (0.64 and 0.76, respectively). This suggests that both elements are mainly of detrital origin although their authigenic formation cannot be excluded.

With regard to the microfacies, the highest percentage of terrigenous elements and relatively low carbonate content are observed in the BC type characterizing the paleosols (Narkiewicz and Retallack, 2014). These are accompanied by increased levels of Fe and trace metals, except for Cu, and by much higher levels of REEs. In contrast, the lowermost values of SiO_2 or Al_2O_3 and associated trace and REE elements, have been found in wackestones (types W and Ws — Table 3). The values for microbial laminites are also below the mean for the

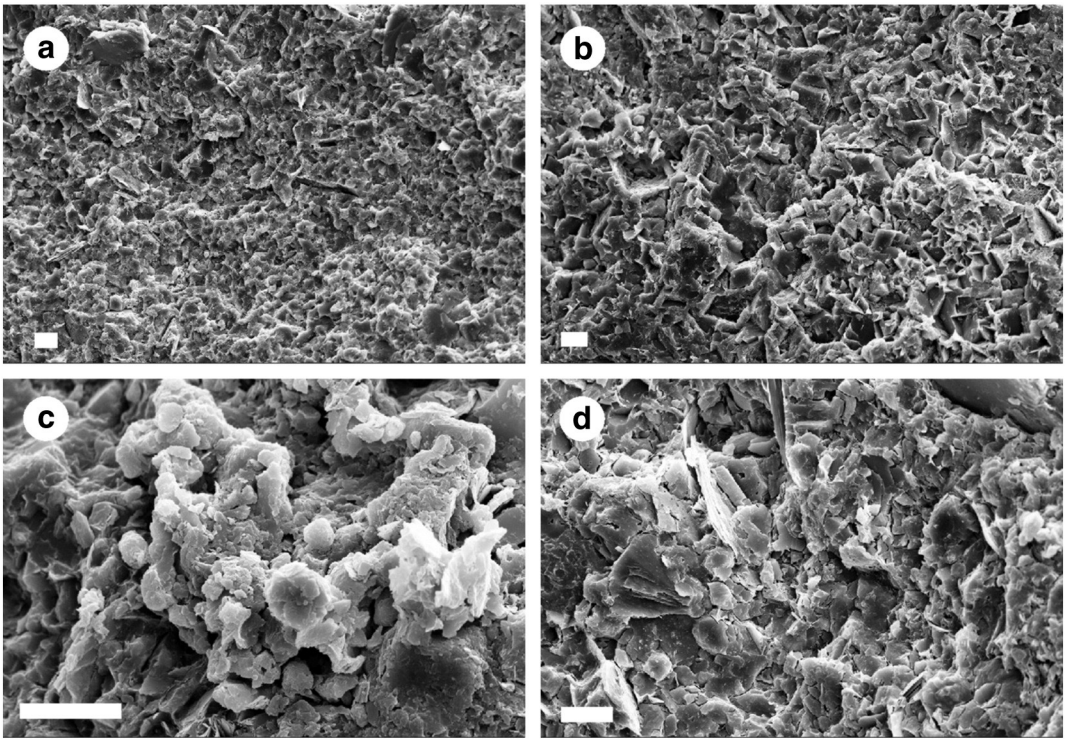

Fig. 9. SEM microphotographs (scale bar — 10 μm): (a) microbial laminite, upper half — detrital lamina, lower half — microbial micrite (bed WE 21); (b) microbial laminite, partly recrystallized (bed EM 43, note rhombohedral habit of some dolomite grains); (c) paleosol level, note compound dolomite spherules of a presumable microbial origin (bed WE 20); (d) bioturbated wackestone of the trackway-bearing level C, note poorly-sorted grains and chaotically oriented plates of layered aluminosilicates.

Lower Complex, while their carbonate content appears the highest when compared to other microfacies types. The second most terrigeneous microfacies after the BC type are the abiotic laminites displaying maximum REE contents as well.

The TOC percent has been determined in a few samples that represent lithologies most promising with respect to their elevated organic carbon content, namely from the beds EM 57, EL 26 (clayey-dolomitic shales) and EL 8 (domal stromatolite). Nevertheless, the measured TOC values appeared very low, i.e. 0.16, 0.09 and 0.09%, respectively, while the carbonate content was 46.41, 59.27 and 97.39%, and total sulphur did not exceed 0.002%.

4.5. Stable isotopes

Average oxygen and carbon isotope data for the studied dolomites are given in Table 4, whereas the $\delta^{18}O$ and $\delta^{13}C$ distribution in the section is illustrated in Fig. 11. The mean oxygen isotopic composition is similar for both complexes (ca. −2.6‰) although the range of

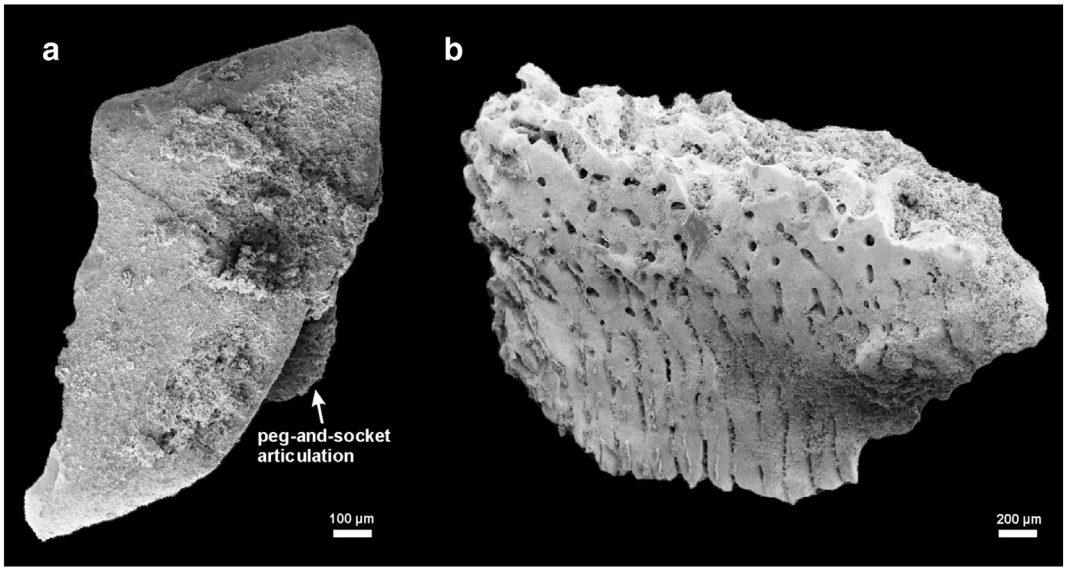

Fig. 10. Vertebrate remains: (a) actinopterygian palaeonisciform scale with a well-visible peg-and-socket articulation (bed WE 25); (b) abraded sarcopterygian (porolepiform?) scale (bed EL 5).

Table 2
Mineral composition and dolomite stoichiometry as determined by XRD method.

Bed number	Mineral composition					d104 (dolomite)	mol.% CaCO3 (dolomite)
	Dolomite	Quartz	Feldspars	Illite	Chlorite		
EL 9	X	X		X		2.8720	45.33
EL 26	X	X		X	X	2.8632	42.40
EM 31	X	X	X	X	X	2.8700	44.67
EM 40	X	X	X	X	X	2.8659	43.30
EM 83	X	X		X	X	2.8741	46.03
EM 86	X	X		X		2.8779	47.30
EU 3	X	X		X		2.8845	49.50
WE 20 (Z-1)	X	X	X	X	X	2.8800	48.00
WE 19 (Z-2)	X	X		X	X	2.8856	49.87
WE 18 (Z-6)	X	X		X		2.8791	47.70

Table 3
Main element composition of the Zachełmie dolomites.

Samples	n	SiO_2	TiO_2	Al_2O_3	Fe_2O_3	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5
		mean (%)									
Upper Complex	10	10.97	0.15	2.96	1.75	0.10	16.01	23.12	0.16	1.11	0.03
Lower Complex[a]	20	8.08	0.11	2.15	1.30	0.07	17.54	24.94	0.16	0.82	0.03
All samples	36	10.39	0.15	2.93	1.62	0.08	16.54	23.49	0.16	1.11	0.03
Abiotic laminites	4	10.84	0.17	3.14	1.58	0.06	17.01	24.00	0.17	1.18	0.03
Microbial laminites	4	7.48	0.09	1.79	1.10	0.07	18.14	25.78	0.16	0.66	0.02
Wackestones	4	5.26	0.07	1.34	1.06	0.06	16.81	24.24	0.15	0.50	0.02

[a] Without WE samples

measurements is wider for the lower one. It may be seen that $\delta^{18}O$ attains the minimum values in the lower and upper parts of the Lower Complex while the maximum values fall in the middle part, near the bed EM 26. The lower part of the Lower Complex is characterized by maximum $\delta^{13}C$ signatures with a narrow range between −0.5 and +0.5‰. The trend towards the lower values characterizing the Upper Complex (ca. −2‰) appears lower in the section, from the bed EM 25 upwards, with two positive excursions near the beds EM 50 and 93a. With respect to the correlation of the oxygen and carbon isotope signatures, the section may be subdivided into three parts. The lower and upper parts show reciprocal or uncorrelated $\delta^{18}O$ and $\delta^{13}C$ distribution, while the middle part, from the bed EM 12 upwards, to the Lower Complex top, is characterized by their covariance (Fig. 11).

The mean oxygen and carbon isotopic values for particular microfacies types given in Table 5 may not be fully representative as the numbers of analyses are low. Nevertheless it seems significant that there are no distinct differences between the microfacies, particularly for $\delta^{18}O$. Relatively low $\delta^{18}O$ and high $\delta^{13}C$ values are characteristic for packstones (P) and nonskeletal wackestones (W). It may be noted that microbial laminites (Lm) display mean $\delta^{18}O$ value similar to the average for the Lower Complex.

Table 4
Summary of carbon and oxygen isotopic characteristics of the Zachełmie dolomites.

Isotope indices	Value	Lower Complex (n = 60)	Upper Complex (n = 28)	Total (n = 88)
$\delta^{13}C$ (‰)	Min.	−2.27	−2.38	−2.38
	Max.	0.65	−0.05	0.65
	Mean	−0.63	−1.81	−1.00
$\delta^{18}O$ (‰)	Min.	−4.94	−3.04	−4.94
	Max.	−1.23	−2.01	−1.23
	Mean	−2.60	−2.59	−2.59

4.6. Trackway levels

Trackways and separate tracks were found in situ, in the levels A–C localized in Fig. 3, and in loose blocks from the scree close to exposed levels A and B. Morphological details of footprints and their preservation state are described by Niedźwiedzki et al. (2010; Supplementary information). The in situ footprints generally have more or less circular or oval outlines without or with only weakly marked digit impressions. No body drag is observed whereas displacement rims (substrate marginally uplifted under the weight of an animal) may be present in Level B (Suppl. Inf., figs. 11–12), and (rarely) A tracks (Suppl. Inf., figs. 14–15).

All three trackway-bearing levels occur in lower or middle parts of the shallowing upward cycles, in laminites or homogeneous muds lacking evidence of a subaerial exposure. The Level A trackways were found on the upper plane of the bed EL 9 composed of marly abiotic laminite (Fig. 12a). The sediment fills the relief of the upper part of the underlying bed composed of domal stromatolites (Fig. 6b) and consequently its thickness varies between 2 and 8 cm. Coarser-detrital laminae contain peloids and silt-size grains of quartz, muscovite, rare feldspars and apatite. The SEM images display weakly directional arrangement of layered aluminosilicates and dolomite grains, partly spheroidal, of diameter less then 10 μm. $\delta^{13}C$ and $\delta^{18}O$ values are −0.41 and −2.72‰, respectively, typical for the EL subsection.

Footprints of Level B are developed on the upper plane of the bed EL 30 composed of a homogeneous dolomite mudstone to fine wackestone 22 cm thick, with characteristic millimetre to centimetre-sized white nodules and idiotopic pseudomorphs (Fig. 13a). The microscopic observations show that these are composed of saddle dolomite and minor quartz, and are interpreted as pseudomorphs after sulphates, most probably anhydrite. They are embedded in pelbiomicritic matrix with fine terrigeneous sand and silt, and minor indeterminable bioclasts admixture. Bioturbation is partly irregular or expressed as nearly horizontal burrows (Fig. 13b). Under SEM the dolomite is mainly composed of poorly-sorted, chaotically arranged dolomite grains, mostly in the size range 5–20 μm, and including both idiotopic (recrystallized) as well as

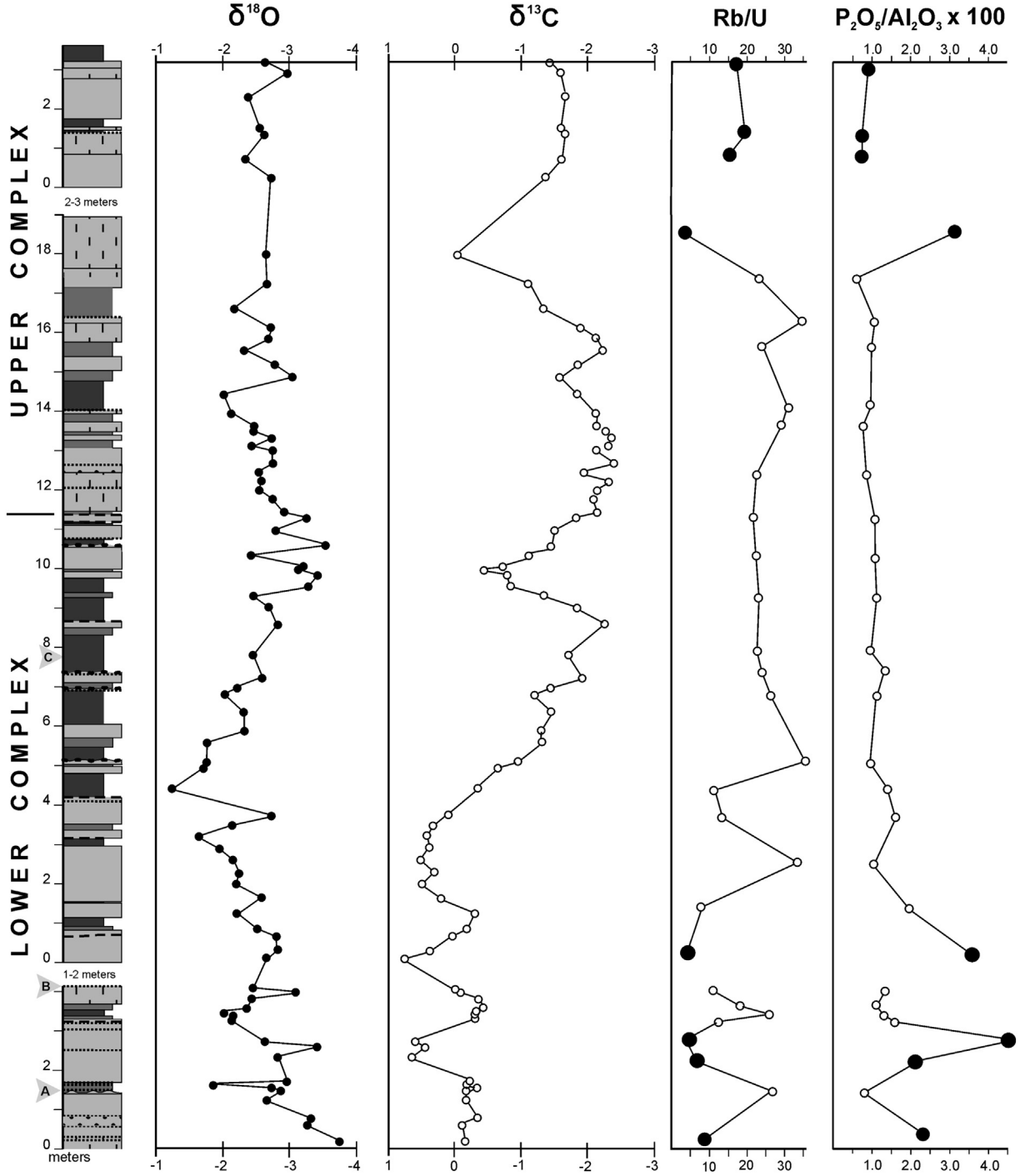

Fig. 11. Vertical distribution of stable C and O isotope values and selected elemental indices in the Zachełmie section. The Rb/U and P2O5/Al2O3 × 100 values after Grabowski et al. (in press), black circles — samples containing magnetite.

spheroidal grains. Two isotope samples, from the upper and lower parts of the bed show slightly different $\delta^{18}O$ values (−2.44 vs. −3.07‰), while $\delta^{13}C$ is similar (−0.02 and −0.11‰, respectively).

Level C trackway is associated with thin-bedded marly dolomites. In the thin section, the uppermost part of the bed is composed of abiotic laminae disturbed by nearly vertical fractures suggestive of early-cemented sediment (Fig. 12b). Lower, the bed is formed of bioturbated biopelmicrite with indeterminable bioclasts, and a considerable quartz and muscovite silt admixture. Under the SEM the sediment is composed of poorly-sorted grains of dolomite (including spheroidal ones) and a terrigeneous silt (Fig. 9d). While $\delta^{18}O$ value (−2.48‰) is close to the mean for the middle part of the section, $\delta^{13}C$ is rather low (−1.66‰).

The loose block specimens partly exhibit irregular footprint outlines without distinct digit imprints. The sediment, composed i.a. of microbial laminite (Fig. 14a–b) is apparently plastically deformed, with diapire-like deformations of underlying shaly dolomite. The bed which furnished exceptionally "crispy" footprints with preserved digit outlines (Niedźwiedzki et al., 2010, fig. 4) is composed of a microbial laminite, with a characteristic wrinkled surface (Fig. 14c). The latter resembles *Kinneyia* — structure formed as an impression of a compact microbial mat on the underlying loose sediment (Porada and Bouougri, 2007). Apparently, in this case only the thin uppermost part of the sediment was unconsolidated, whereas overall the substrate attained a high degree of cohesion sufficient to produce well-defined footprints.

Table 5
Carbon and oxygen isotopic characteristics of microfacies types in the Lower Complex.

Microfacies	n	$\delta^{13}C$ (‰)			$\delta^{18}O$ (‰)		
		Mean	Min.	Max.	Mean	Min.	Max.
Lm	13	−0.24	−2.23	0.4	−2.58	−3.47	−1.65
Lm(d)	8	−1.23	−1.98	0.32	−2.49	−3.56	−1.90
BC	5	−0.54	−1.34	0.42	−1.98	−2.14	−1.74
LM-L	5	−1.37	−2.27	−0.20	−3.56	−4.94	−2.50
L	7	−0.79	−1.78	−0.22	−2.49	−3.32	−1.87
M	4	−0.96	−1.68	−0.31	−2.41	−3.00	−1.95
Ws	7	−0.59	−1.47	−0.19	−2.54	−3.71	−1.23
W	6	−0.55	−1.66	0.18	−2.95	−3.07	−2.22
P	5	−0.32	−0.42	0.65	−2.76	−3.42	−2.61
Total	60	−0.63	−2.27	0.65	−2.60	−4.94	−1.23

5. Palaeoenvironmental interpretation and discussion

5.1. General controls on facies development

During the Eifelian the northern part of the Holy Cross Mountains was located between the subsiding shallow-marine basin in the north and a vast carbonate platform with a shallow-water dolomitic-marly sedimentation in the south (Fig. 15; Narkiewicz et al., 2011). The boundary between both areas was controlled by the deep-seated and long-lived tectonic zone — the Holy Cross Fault (Lamarche et al., 2003; Narkiewicz, 2007). Its surface expression in the Eifelian can be envisaged as a linear belt of transitional facies with changing influence of restricted marine conditions propagated from the south, and open marine facies encroaching from the north. The former conditions prevailed during the Lower Complex deposition, and will be a subject of a detailed interpretation below. Open marine deposition of the Upper Complex strata is evidenced by the presence of bioturbated carbonate muds with benthic marine skeletal material, and lacking microbial sediments, desiccation structures and palaeosol levels.

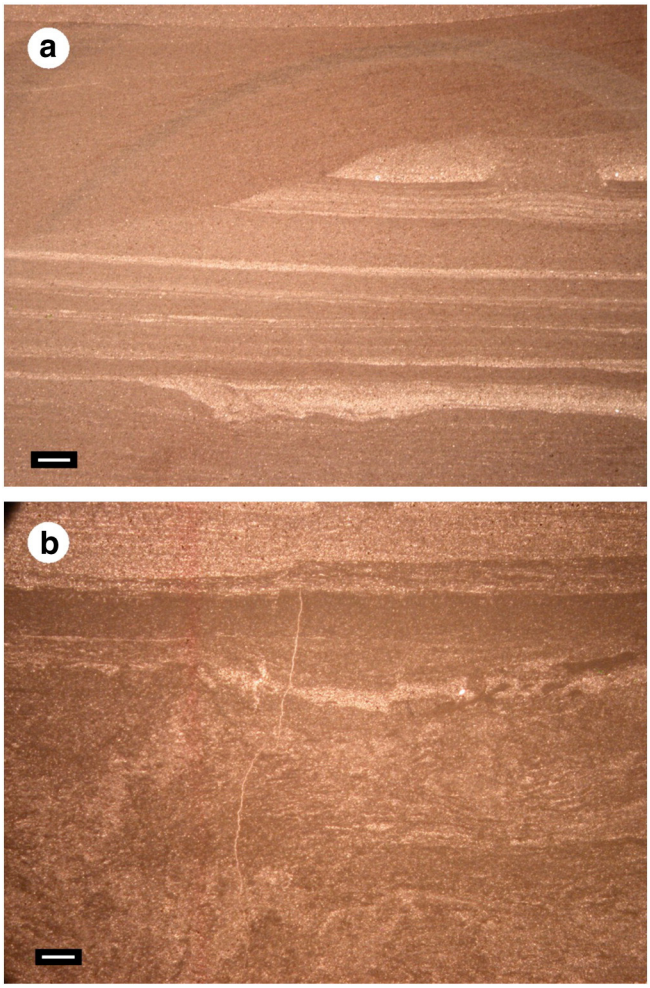

Fig. 12. Thin-section images of the track-bearing levels A (a) and C (b). (a) abiotic laminite with a minor scour-and-fill structure (bed EL 9); (b) fractured abiotic laminite overlying bioturbated biopelmicrite. Scale bar — 1 mm.

The sharp boundary between the upper and lower complexes truncates underlying mud-cracked laminite and it is overlain by a poorly-sorted intraclastic wackestone (Fig. 4). This distinct deepening event does not correspond to any of the eustatic transgressions known from the Middle Devonian (Fig. 2; Becker et al., 2012). At the same time, its tectonic controls are strongly suggested by a general palaeotectonic context of the southern, fault-controlled flank of the Łysogóry-Radom Basin (Fig. 15). Such an interpretation is further supported by sedimentological evidence found just below the erosional truncation. The thin EM 63 bed, is composed of flat-topped lenticular structures, up to 5 cm thick and 10 cm wide, and showing internally contorted laminae. The structures are hardly comparable to desiccation polygons like those seen in the Bed EM 65, 10 cm above (Fig. 16). In contrast, they resemble "dish structures" (e.g. Montenat and Barrier, 2007), forming due to seismically-induced hydroplastic deformations of a soft sediment (Ettensohn et al., 2011). According to Alfaro et al. (2010), who illustrated similar but larger-scale structures from lacustrine facies, the size of particular lenses or pillows depends on the type and thickness of a deformed sediment. In the Zachełmie example the thin unconsolidated mud layer was underlain most probably by a more cohesive sediment which caused a relatively small-scale deformation. In conclusion, it is here interpreted that the seismite level of the bed EM 63 was related to an earthquake heralding major block-faulting event that led to a marine incursion and the onset of the Upper Complex deposition.

In view of the above considerations it is tempting to apply tectonic explanation also for metre-scale depositional cyclicity observed in both complexes. The subaerial erosional or paleosol character of the upper cycle boundaries is an evidence of a forced regression (Posamentier et al., 1992) and thus allocyclicity related to an external factor (Schlager, 1993). Although synsedimentary tectonism could have been active, its significance as a main control on the cyclicity is hardly demonstrable. The seismite bed described above appears unique in the Zachełmie Quarry section. Moreover, a rather regular cyclic pattern (Fig. 3) argues against tectonic factors and is suggestive of eustatic, probably astronomically controlled cyclicity. Indeed, the time-series analysis of the MS signal demonstrates the presence of 1.67 m thick cycles and the higher order 11 m thick cycles (Grabowski et al., in press). After discussing different options in the framework of time-constraints available, Grabowski et al. (in press) concluded that the former cycles, of ca. 20 kyr duration, may be precession-driven while the latter may correspond to 100-kyr short eccentricity cycles.

Zachełmie dolomites have been deposited far from eroded continental areas (Fig. 15) which limits presumed availability of local, primarily

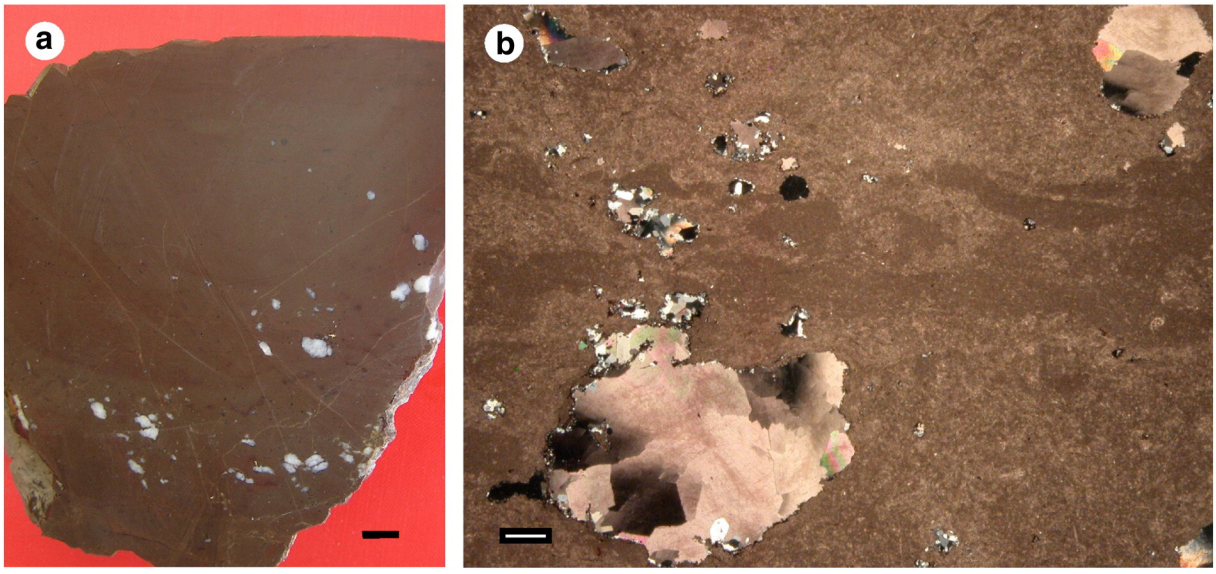

Fig. 13. Track-bearing level B (bed EL 30): (a) perpendicular cross-section of the uppermost part of the bed with small white nodules — dolomite and quartz pseudomorphs after sulphates (scale bar — 1 cm); (b) thin-section image (crossed nicols) showing bioturbated structure of the pelbiomicritic matrix, and saddle dolomite and minor quartz composing sulphate pseudomorphs (scale bar — 1 mm).

fluvial sources of a clastic material. Thus, the most probable supply mechanism of a majority of the terrigeneous silt is an eolian transport from distant land areas (e.g. Mazury Land in the north) via monsoonal wind systems interpreted for this part of Euramerican continent (De Vleeschouwer et al., 2012).

5.2. Palaeoenvironmental conditions

5.2.1. Water temperature

Preliminary interpretations of the Middle Devonian syndepositional dolomicrites from the Holy Cross Mountains indicated palaeotemperatures of dolomite-precipitating fluids in the range 25 to 45 °C, consistent with surface temperatures in the Devonian tropics (Narkiewicz, 2009). The estimates were based on a relationship between the temperature, $\delta^{18}O_{dol}$ and $\delta^{18}O_{water}$ given by Land (1983, fig. 5), and assuming the Middle Devonian marine values of $\delta^{18}O_{water}$ ranging from −1 to −3‰ (SMOW) (van Geldern et al., 2006).

Present estimates, based on much larger database, are using a new palaeothermometer for dolomite, established by Vasconcelos et al (2005). Factor of fractionation between fluid and dolomite was calculated for the mean $\delta^{18}O_{dol}$ value −2,6‰ (Table 4) and assuming the $\delta^{18}O_{water}$ values for the Eifelian seawater between −1 to −3‰. The calculated palaeotemperature is 27.3 °C for the heavier, and 37.2 °C for the lighter $\delta^{18}O_{water}$ values, respectively. The value around 30 °C (and thus heavier oxygen signature for the Eifelian seawater) is preferred here as it is better supported by the interpretation by van Geldern et al. (2006). The palaeotemperature estimate seems more representative for the depositional environment of the Upper Complex which displays relatively constant $\delta^{18}O_{dol}$ values (Fig. 11). Moreover, normal marine conditions evidenced by biotic assemblages, suggest lack of salinity fluctuations, and thus seawater composition close to average. Nevertheless, the interpretation of prevailing tropical temperature conditions can be extrapolated over the Eifelian Zachełmie environments in general, including the Lower Complex facies as well.

5.2.2. Salinity

The isotopic signatures of the dolomites attest to the presence of fluids with a composition close to an Eifelian seawater, particularly during deposition of the Upper Complex dolomites. The oxygen isotopic composition of dolomitizing fluids can be quantitatively assessed for the Lower Complex using the relationship proposed by Vasconcelos et al. (2005) and assuming previously calculated palaeotemperature of 30 °C. The range of $\delta^{18}O_{dol}$ values in the Lower Complex is from ca. −3.5‰ in the lowermost and uppermost parts to a maximum −1.5‰ in the middle part. Assuming these values, the $\delta^{18}O_{water}$ increased from −3.03 to 0.48‰ and then returned to −3.03‰. Such evolution can be explained by a progressive evaporative concentration of hyposaline marine waters towards hypersalinity, followed by a return to slightly brackish conditions. Such trend is consistent with the occurrence of evaporite relics in the lower part, while their later disappearance may correspond to a prevalence of less saline waters. It must be stressed, however, that the presence of marine fossils in the lowermost part of the section (see Section 4.3) considerably limits minimum range of possible salinities. In that case modified seawater had salinities not far from typical marine values. The onset of the open marine sedimentation of the Upper Complex dolomites is recorded by an increase of $\delta^{18}O_{dol}$ by ca. 1‰ connected with the encroachment of a fully marine water.

The above salinity trends could have been punctuated by short-term fluctuations suggested by a widespread evidence of desiccation, particularly in the upper parts of the shallowing upward cycles. Also, the episodic development of impoverished infaunal assemblages was most probably controlled by fluctuating salinity conditions (Niedźwiedzki et al., 2014).

5.2.3. Redox conditions

Prevalence of well-aerated environments characterizing deposition of the Zachełmie dolomites is corroborated by the occurrence of subaerial exposure surfaces with paleosols, low TOC values, and a poor preservation of organic matter, plant material included. Rb/U and P_2O_5/Al_2O_3 ratios in most of the samples, particularly in the middle part of the section (Fig. 11), also suggest relatively higher oxygenation (positive Rb/U plateau) and lower organic productivity (low P_2O_5/Al_2O_3 ratio) (Grabowski et al., in press). The lower and upper intervals of higher redox and productivity variations, and at the same time magnetite-bearing, may reflect relatively less-aerated conditions (Grabowski et al., in press). The enrichment of the Upper Complex in light carbon isotope of organic origin, also probably related to relatively more reducing conditions.

The paucity of a skeletal vertebrate material in the Zachełmie section may be related to the well-aerated environment and an abundance of microbial cultures, two main factors responsible for a poor preservation of bones in general (Turner-Walker, 2008). Notably, the vertebrate remains were found mainly in the marine deposits overlying the track-bearing strata and characterized by relatively less oxic conditions.

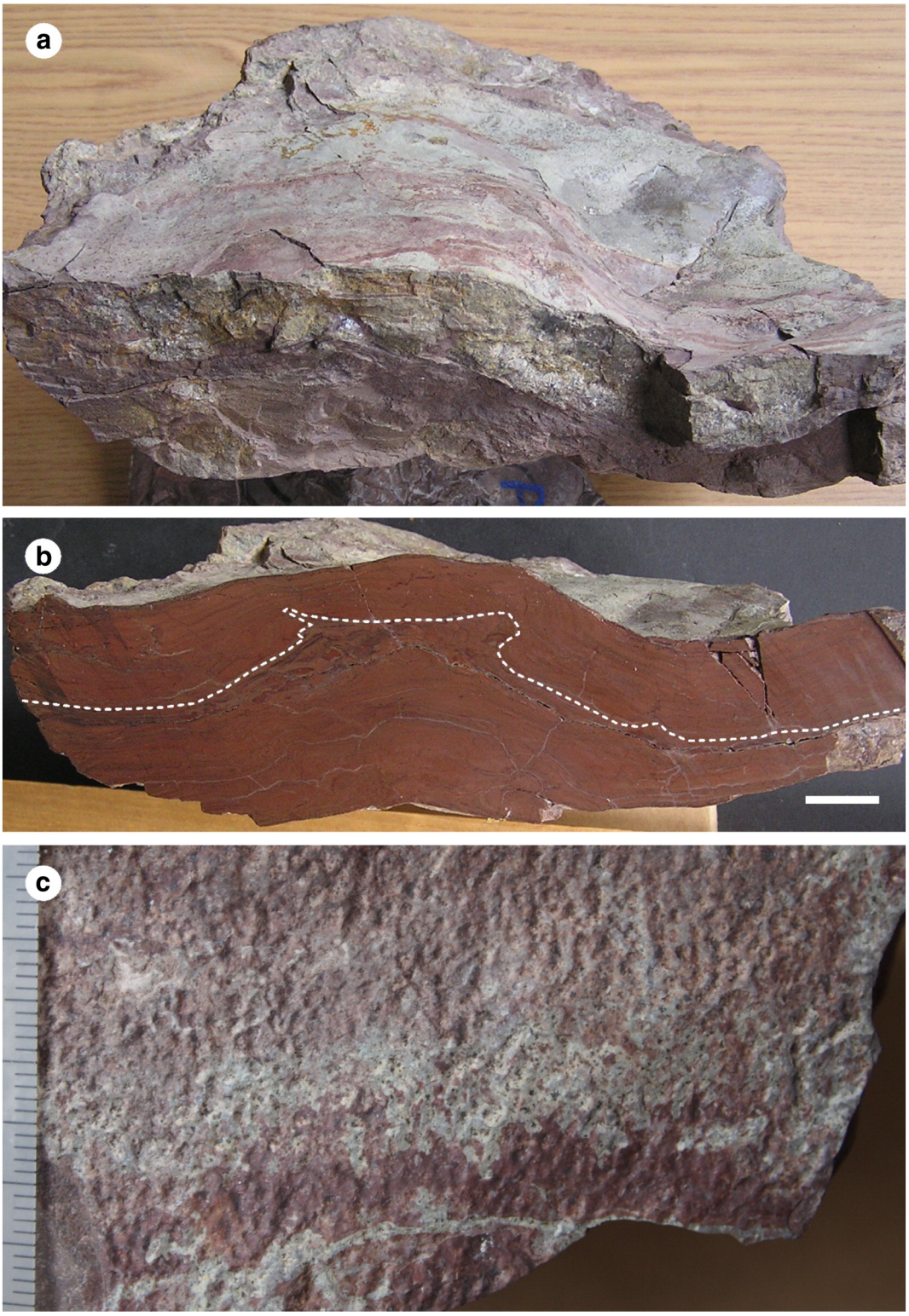

Fig. 14. Loose blocks from the track-bearing interval: (a–b) fragment of the footprint showing plastic deformation of the upper microbial laminite layer and the diapire-like deformations of underlying shaly dolomite marked by a white broken like (cf. Niedźwiedzki et al., 2010; Suppl. Inf., fig. 19), scale bar — 2 cm; (c) bedding plane of the bed with best-preserved footprints (cf. Niedźwiedzki et al., 2010, fig. 4) showing wrinkled surface of the microbial laminite, scale in millimetres.

5.2.4. Climate

The tropical climatic conditions are suggested by the high (around 30 °C) palaeotemperatures of surface marine-related fluids in which early dolomite formation proceeded (see above). This is in agreement with the palaeolatitude around 15° S which may be inferred from the global palaeocontinental reconstruction (Fig. 15). The features of paleosols seem to indicate a seasonal variability under generally semi-arid to sub-humid conditions. The pedological processes were influenced by a development of sparse vegetation composed of low stands of early land plants, including herbaceous plants, fen and shrub-carr

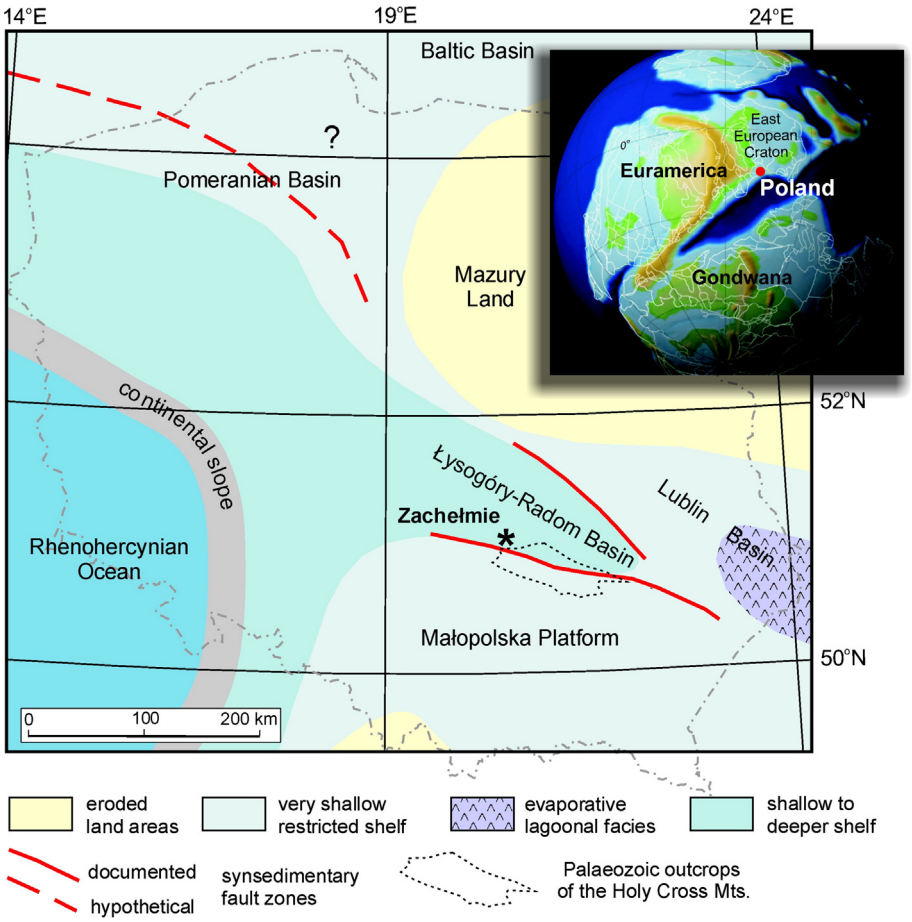

Fig. 15. Palaeogeographic setting of the Zachełmie locality shown against the present geographical coordinates of Poland (from Narkiewicz and Retallack, 2014, modified), and in the global palaeogeographic framework of the Eifelian (after Scotese, 2002, PALEOMAP Project).

with periphyton developing during wetter periods (Narkiewicz and Retallack, 2014). The palaeogeographic setting (Fig. 15) is consistent with the presence of a tropical climate with a prevailing monsoonal regime (De Vleeschouwer et al., 2012). Tropical monsoonal climate could have promoted short-term salinity changes superimposed on the above outlined trends (Section 5.2.2).

Fig. 16. Details of the bed EM 63 in the uppermost part of the Lower Complex (see Fig. 4). Note plastic deformations of laminae in the small pillow structure above the pencil (length — 15 cm). Compare bed EM 65 in the uppermost part, composed of a mud-cracked laminite.

5.2.5. Topography and hydrological regime

The pattern of shallowing upward cycles in the Lower Complex described above (Section 4.1) reflects desiccation and subaerial exposure cyclically occurring in a very shallow-water environment. Even during deposition of the transgressive abiotic laminites the water depths most probably did not exceed a few metres. Although quiet-water conditions prevailed, waters seem to have been stirred by waves and currents to such a degree that no salinity stratification and associated bottom-water anoxia would have been permanently developed. The poor biotic assemblages dominated by microbes and ?algae point to a lack of direct connections with open sea environments, such as those characterizing the Upper Complex facies.

Narkiewicz and Retallack (2014) estimated duration of pedogenic processes as several hundred to a few thousand years at most. However, given a considerable degree of an overall restriction, there may have existed more permanent low-relief areas separating lagoons from an open marine basin to the north. Such elevated zones of a coastal deflation (Narkiewicz and Retallack, 2014), could have been a source of eolian dolomitic silt for the adjoining lagoons.

Inferred physical separation of the Lower Complex lagoonal facies from open marine conditions is consistent with a lack of any sedimentary structures typical for a tidal regime. Neither tidal channels, nor smaller diagnostic structures like flaser-lenticular bedding or herringbone cross-stratification have been found. Also, subtidal marine skeletal accumulations or at least intense bioturbation is lacking in the transgressive parts of the cycles where they should be particularly expected in a tidal setting (Pratt et al., 1992). The tideless regime may have been partly related to a general palaeogeographic configuration of the adjoining marine basin (Fig. 15).

In spite of the interpreted physical separation of the Zachełmie lagoonal environment, the marine affinity of dolomite-forming fluids, suggested by their inferred isotopic composition, implies the existence of discontinuous and/or permeable barriers separating lagoons from an open sea. Occasionally, the marine connections may have been more direct, as e.g. during deposition of the lowermost cycle with a more diverse faunal assemblage (Fig. 3). The degree of separation from the external hydrological influence may be assessed using the relationship between oxygen and carbon isotope signatures of authigenic carbonates. This question has been addressed by Li and Ku (1997) for lacustrine environments which may serve as an analogue or approximation of semi-closed lagoons. The cited authors found that over time scale of 5 ky or more the covariance of $\delta^{13}C$–$\delta^{18}O$ is a reliable indicator of a hydrological closure, while a lack of correlation supports hydrologically open environment. Their conclusions have been confirmed by the study of microbial dolomites in a recent Canadian lake (Last et al., 2012).

Comparison of vertical/temporal trends of the isotopic signatures measured in the Lower Complex (Fig. 11) reveals two distinct intervals. The lower one (up to the bed EM 12) is characterized by uncorrelated or reciprocal isotopic values. This interval probably represents partly open hydrological regime, with a more pronounced influence of marine waters, as evidenced by the presence of marine fauna (lowermost part) and evaporite relics. Thus, the progressive evaporative concentration of hyposaline marine waters (see above Section 5.2.2) proceeded in a relatively hydrologically open system. In contrast, the upper part of the complex (perhaps except its topmost interval) displays $\delta^{13}C$–$\delta^{18}O$ covariance of generally decreasing isotopic signatures. This trend can be interpreted as a hydrologically closed system with an importance of a freshwater dilution increasing at the expense of evaporation.

The more depleted $\delta^{13}C$ values prevailing in the upper part of the Lower Complex may thus reflect primarily the degree of restriction as interpreted above. On the other hand the decreased $\delta^{13}C$ signatures in the Upper Complex when compared to the lower half of the Lower Complex may be explained by a higher contribution of a light organic carbon in marine sediments. The other possibility is that they reflect some external regional or even secular factors. For example, van Geldern et al. (2006) documented the secular $\delta^{13}C$ shift on the order of 2‰ for the *costatus* Zone of the Eifelian, based on well-preserved brachiopod shell material.

5.3. Dolomite origin

Zachełmie dolomites, with their perfectly preserved depositional textures and intraclasts made of early lithified dolomitic sediment, seem to fall in a general category of syndepositional or eogenetic dolomites. Such dolomitic sediments have been described from different modern environments, including supratidal sabkhas, inland lakes, coastal lagoons and deeper anoxic basins (e.g. Warren, 2000; Machel, 2003; Meister et al., 2013). Recently, the microbial dolomite model has been proposed to explain dolomite formation due to bacterially-mediated precipitation (Vasconcelos et al., 1995; Vasconcelos and McKenzie, 1997; Sánchez-Román et al., 2009). This model has been applied to a dolomite presently forming in laminated bottom sediments of a shallow coastal Vermelha Lagoon in Brazil (Vasconcelos and McKenzie, 1997; van Lith et al., 2003).

Characteristic sediment texture of the irregular laminites (microfacies Lm) argues for the microbial model of their formation (compare similar fossil examples described by Perri and Tucker, 2007; You et al., 2013). Other arguments in favour of the Brazilian Vermelha model include partly preserved micron-sized complex dolomite globules seen under SEM, evidence of early lithification in a form of e.g. frequent intraformational truncation surfaces, and a relative paucity of evaporites (cf. Sánchez-Román et al., 2009; Spadafora et al., 2010). The $\delta^{18}O$ values correspond to precipitates from a Middle Devonian sea water at tropical surface temperatures (see above) which supports a marine source of dolomitizing fluids. This is again consistent with the Brazilian model in which marine waters percolate through permeable coastal barriers. In addition, an average temperature 30 °C estimated for the Zachełmie dolomite-forming fluids compares well with the average monthly temperature 28 °C of the Vermelha lagoon water (Vasconcelos et al., 2005). In general, climatic conditions inferred for the studied palaeoenvironments agree fairly well with the present climate of the Brasilian coast in the Rio de Janeiro area, which may be partly due to a similar (palaeo)latitude (15° S vs. 22° S).

The presence of a uniform grained texture seen under SEM, as well as a similar stable isotopic composition in all the described microfacies (Table 5) speak in favour of a common source of the dolomite. It is thus conceivable that the microbial laminites represented the "dolomite factory" supplying adjacent depositional settings and related microfacies types through redistribution of dolomite grains. This may be particularly true for the abiotic laminites with their sedimentary structures evidencing transport by low-energy currents. Notably, presence of the mixed Lm-L microfacies attests to a close spatial and genetic relationship of microbial and abiotic laminites. This microfacies probably records periods of intermittent influence of higher-energy regime leading to a reworking of microbial sediments and redeposition of dolomite grains. Narkiewicz and Retallack (2014) demonstrated that the paleosols are mostly composed of reworked dolomite grains with only a slight addition of authigenic dolomite. The homogeneous mudstone and wackestone intercalations also consist predominantly of detrital dolomite silt reworked by infaunal activity in relatively deeper portions of a lagoon.

Recently, Krause et al. (2012) documented a Mg-rich dolomite forming due to activity of sulphate-reducing bacteria under normal marine salinity. This could explain lattice parameters of the Zachełmie dolomite which probably reflect Ca deficit in favour of Mg (Table 2). As the deficit of Ca in a dolomite lattice may also reflect excess Fe^{2+} (Runnells, 1970), this problem requires more detailed geochemical studies.

6. Early tetrapod habitats: discussion and implications

Fig. 17 reconstructs depositional environments composing habitats of early tetrapods in the Zachełmie area. In particular, it shows overall relationship of a near-shore shallow-marine part of the Łysogóry Basin in the north and the barrier-lagoonal system marking the Małopolska Platform margin in the south. Typical for the latter system was a coexistence of protected shallow lagoons and sparsely vegetated, more or less ephemeral, flat emergent islands and spits. The lagoons were topographically separated from the influence of open sea conditions but, at the same time sourced by percolating marine waters.

The detailed sedimentological analysis of the trackway-bearing levels A–C (Section 4.6) revealed that their substrates are composed of shallow lagoonal dolomitic muds and silts deposited in an aqueous environment, without indications of a subaerial exposure. Apparently the animals were at least partly submerged while walking on a muddy substrate. Partial buoyancy and/or underwater bottom-walking may explain lack of a tail or belly drag (Petti et al., 2014). Aqueous conditions are consistent with poorly preserved outlines of footprints that were left in semi-consolidated bottom sediments. Niedźwiedzki et al. (2010) interpreted a single footprint from the Level A as "an aquatic print where a swimming tetrapod has used a single limb to kick against the substrate". Similar explanation of a swimming/floating animal may be applied to the trackway from the Level C (cf. fig. 17 in Niedźwiedzki et al., 2010, Suppl. Inf.). Analogous swim tracks of subrecent hippos have been described by Bennett et al. (2014).

The well-preserved "crisp" prints with clearly outlined digits, found as isolated specimens in a scree, may have been left by tetrapods walking on microbially-laminated muds that were better consolidated than those composing substrates of the levels A–C. The microbial laminites generally form upper parts of the shallowing upward cycles, and it is

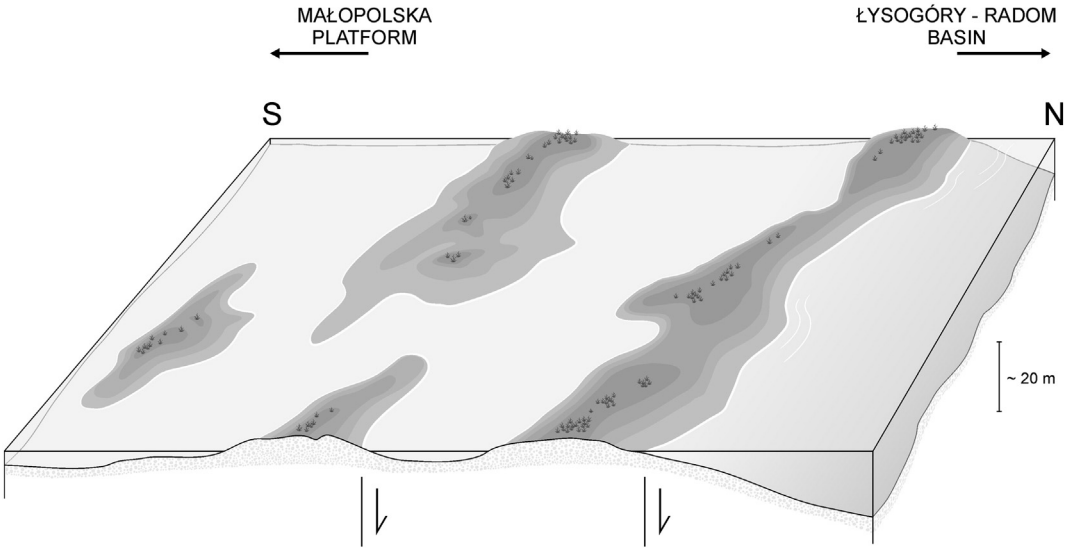

Fig. 17. Schematic interpretation of depositional environments of the Zachełmie dolomites.

plausible that they were intermittently exposed. Nevertheless, absence of an in situ evidence of footprints developed on mud-cracked substrates or on paleosols does not allow a direct inference that the animals were capable of striding across exposed mudflats or vegetated topographic elevations. The rare findings of such subaerial footprints may be related to their poor preservation potential when compared to the subaqueous tracks. On the other hand, the relative rarity of the "crisp" footprints may suggest that shallow-water-bodies were more frequently visited, and thus more natural habitat of the earliest tetrapods. If true, this would support the hypothesis that quadrupedality developed among aqueous animals which exercised their locomotional capabilities in a shallow lagoonal water before attempting longer excursions on land ("limbs before terrestriality" scenario; Pierce et al., 2013).

Niedźwiedzki et al. (2010) hypothesized that the intertidal zone could have been an appropriate habitat providing "a ready food source of stranded marine animals on a twice-daily basis, in the immediate vicinity of the sea" (see also Clack, 2012). Moreover, in the recent paper, Balbus (in press) argued that the Devonian was a period of an exceptionally large tidal range accompanying tidal modulation. He proposed that abundance of ephemeral isolated tidal pools provided optimum conditions for a quadrupedal locomotion development among specialized fishes, thus similar as in the classical drying-pool hypothesis of Romer (see Romer, 1958). If these two factors, i.e. food availability and advantageous coastal topography acted in concert they could have exerted a considerable evolutionary pressure towards development of functional limbs. However, as stressed by Retallack (2011), a general paucity of invertebrate fossils in the track-bearing strata argues against the smorgasbord hypothesis proposed by Niedźwiedzki et al. (2010). Moreover, in view of the present evidence, the Zachełmie track-bearing dolomites were formed in lagoons topographically separated from an open sea, and consequently lacking any evidence of a tidal regime.

The hypothesis preferred by Retallack (2011) envisaged flooded woodlands as an optimum habitat for the earliest tetrapods, those from Zachełmie included. A key component of this hypothesis is use of limbs in flood waters ponded by woody vegetation so that water depths were less than a body height. The diet of these large (up to 2.5 m in length) carnivores was envisaged as small fish corralled and large fish stranded by shallow water. Such interpretation based on observations of Devonian floodplains of New York, USA, is however at odds with our observations which did not confirm the presence of a woodland-type vegetation in the Zachełmie habitats. Nevertheless, coastal lagoons subject to periodic evaporation and restriction, as envisaged for Zachełmie, would have presented a similar combination of shallowing ponds and flats to that of floodplains. A large lagoonal system would also include deeper ponds as dry season refuges from the even larger predatory fish of the open sea.

7. Conclusions

The depositional environment of the lower, tetrapod track-bearing complex in the Zachełmie Quarry comprised a system of very shallow restricted muddy dolomitic lagoons surrounded by flat, sparsely vegetated islands and spits. The Upper Complex represents shallow-marine bioturbated carbonate muds onlapping the lagoonal system due to block downfaulting of marginal zone of the tectonically-controlled depocentre — the Łysogóry Radom Basin to the north.

The Lower Complex comprises 14–15 shallowing upward cycles topped by erosional and/or paleosol levels. The primary source of dolomitic sediment were laminated, partly mud-cracked, microbial muds whose closest modern analogues have been described from the coastal Brazilian Vermelha Lagoon (Vasconcelos and McKenzie, 1997). The reworked and redistributed dolomite grains are, in addition to eolian terrigeneous silt admixture, the main component of other sediments, including basal abiotic laminites, homogeneous mudstones and wackestones, and capping paleosols.

The lagoons were supplied with a marine water but morphological barriers and salinity fluctuations generally excluded benthic fauna development. Topographical separation from an open sea was also responsible for the protected environment lacking any sedimentary attributes of a tidal regime. Thus, the tidal-flat model postulated as a likely habitat of early tetrapod emergence (Niedźwiedzki et al., 2010; Balbus, in press) fails for Zachełmie. The woodland hypothesis for tetrapod evolution (Retallack, 2011) is not applicable as well, because there is no evidence of woodland vegetation from fossils or paleosols.

The in situ trackways and most of the isolated footprints from the loose blocks have been formed in a very shallow aqueous environment decimeters to a few metres deep. The animals were most probably swimming or wading on a soft or moderately cohesive muddy substrate. Only some best-preserved "crisp" footprints with digits, found on microbial sediments, could have been formed under subaerial conditions. Although the terrestrial environments, such as sparsely vegetated low-relief islands and spits, cannot be excluded from the range of

early tetrapod habitats, the collected data support their primarily aquatic mode of life. This refers also to their probable diet comprising most probably fishes and, possibly, tetrapod compatriots (Clack, 2012). Thus, similar to the intertidal and woodland concepts the proposed lagoonal model of a quadrupedality development draws upon the utility of limbs in acquiring corralled and stranded prey within aquatic habitats that are extremely shallow, sometimes less than a body height.

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