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ENDOLITHIC AND HYPOLITHIC SOIL-LIKE SYSTEMS: STRUCTURE AND COMPOSITION FROM THE MACRO- TO SUBMICRO-LEVELS

© 2016 N. S. Mergelov, I. G. Shorkunov, A. V. Dolgikh, V. A. Shishkov, E. P. Zazovskaya, V. O. Targulian, and S. V. Goryachkin

Institute of Geography, Russian Academy of Sciences, Staromonetniy lane, 29, Moscow 119017, Russia
e-mail: mergelov@igras.ru

The paper presents a detailed study on structure and composition of endolithic and hypolithic systems. The following issues are discussed: morphology at macro to submicro levels, biochemical weathering, formation of carbonates and oxalates in situ, migration of Fe compounds, and spatial patterns of endolithic systems. Endolithic and hypolithic systems have major features attributed to soils: (a) rock layer exposed to external abiogenic factors, (b) lithomatrix inhabited by living organisms which are synthesizing and decomposing organic matter, (c) as a result initial parent rock (lithomatrix) is transformed in situ by biogenic and abiogenic factors, the products of transformation are retained and/or removed, the vertical heterogenity is established in a form of microhorizons composing microprofile. Examined profiles of endolithic systems in granitoids of East Antarctica with high quartz content had clear eluvial-illuvial differentiation patterns. Similar patterns have been discovered in different landscapes from the Plateau Ozark in Missouri to the Table Mountain in South Africa.

Key words: soil-like body, endolith, hypolith, organo-mineral interactions.

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INTRODUCTION

Endolithic and hypolithic bio-abiotic systems are often not recognized as soil-like bodies. However, they could act as precursors to the more advanced soil formations or even the only steady state soil-like bodies if occur in regions with climatic extremes. In certain areas of hot and cold deserts or high mountains various external stresses inhibit development of biota on the rock surface. The organisms find their ecological niche inside the rocks (endolithic environment) or under the stone pavements (hypolithic environment) (Chan et al., 2012;

Pointing et al., 2012; Mergelov et al., 2012). The dominant autotrophic components of such ecosystems are cyanobacteria and green algae, mainly in the form of biofilms. They are capable of primary production under limited levels of light, for example in the subsurface layers of granite, gneiss and sandstone rocks, which contain translucent quartz and feldspars grains. Understanding the structure and processes in modern endolithic and hypolithic bio-abiotic systems is of fundamental importance, since they are possibly the closest modern analogues of protosoils that existed on our planet before the higher vascular plants with root systems established.

STRUCTURE AND PROPERTIES OF HYPO/ENDOLITHIC SYSTEMS

Morphological features of endolithic and hypolithic systems at different structural levels (Fig. 1) as well as the products of organo-mineral interactions are very similar. The common property of endolithic and hypolithic systems is that primary production, subsequent accumulation of organic matter, as well as the most intensive biomineral interactions occur not on the surface but inside the mineral matrix in cryptic biogenic horizon. Such climatic parameters as lack of moisture, UV–A and UV–B radiation and wind corrasion completely or partially inhibit the primary production and formation of organogenous horizons on the surface of hard rocks or loose mineral substrates. Climatic extremes are mitigated due to the lithogenic factor (shelter from wind and desiccation, quartz-feldspar filter of UV radiation, additional insolation heating of the surface): either in the porous rocks under the exfoliation plates (Fig. 1a, 1c) or in loose sediments under the stone pavements (Fig.1b, 1d). For instance, in the ice-free areas of East Antarctica these hidden habitats provide one of the most favourable conditions for the long-term organic matter preservation and in some cases even formation of prominent organogenous horizons. Important role plays simply the physical stability of the substrate in endolithic and hypolithic ecological niches which allow slow-growing cyanobacteria to develop (Makhalanyane et al., 2015).

In this part of the paper we present the case study of endolithic and hypolithic systems from the Larsemann Hills (69°24′S, 76°13′E) and Thala Hills (67°40′S, 45°20′E) oases in East Antarctica.

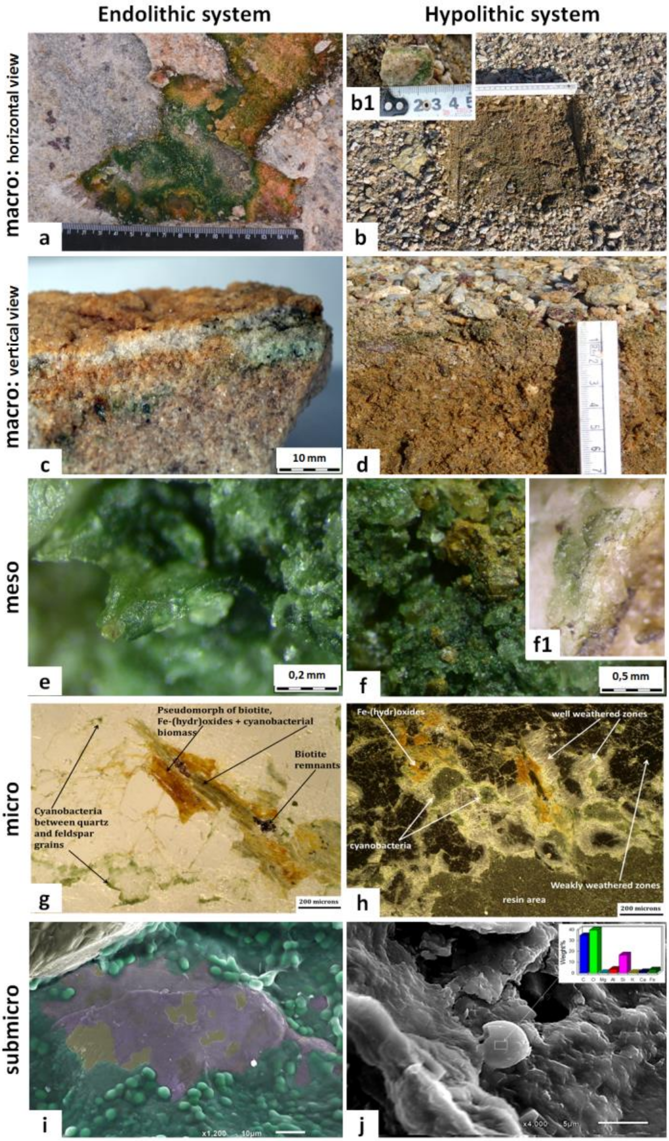

Fig. 1. Morphology of endolithic and hypolithic systems at different structural levels (on granites and gneisses in East Antarctica, explanations are given in the text).

Cryptic organogenous horizon. Living and dead biomass is arranged as a separate microhorizon within 1–2 cm from the surface in endolithic systems and 1–5 cm in hypolithic systems and covers mineral grains with biofilms up to tens und hundreds of microns thick. In case of hypolithic niche cyanobacteria dominated biofilms cover not only the underside of gravel pavement (Fig. 1, b1) but often also the few centimeters of mineral matrix in the sorted sandy bedding immediately under the pavement (Fig. 1d). Sometimes it leads to more prominent formations known as biological soil crust (Weber et al., 2016). However they are still located in the cryptic hypolithic refuge and inhabited by the same cyanobacteria based communities.

Cryptogamic and microbial complexes of organogenous horizon are often arranged in a specific form of subaerial biofilms firmly attached to the mineral grains. We identified biofilms at various structural levels: *meso* – Fig. 1e, 1f, *micro* – Fig. 1g, 1h, *submicro* – Fig. 1i, 1j). They consist of multiple cell assemblages embedded in an extracellular polymer matrix. Virtually every grain of quartz, feldspar, biotite, garnet is covered by a stratified film-like microecosystem comprising complexes of cyanobacteria, chlorophyta, fungi, heterotrophic bacteria, etc. Fig. 1e, f1 demonstrates dramatic degradation of euhedral quartz grains into the “licked” plate-like forms under the influence of cyanobacterial biofilms.

Biofilm capacity for mineral transformation is surprisingly high. For example, during cyanobacterial photosynthesis pH rises shortly and locally up to 9.0 that facilitate dissolution of quartz and subsequent deposition of amorphous silica glaze. Integrated pH measured by the standard soil method in a bulk sample indicates neutral reaction which is a misleading result and does not describe interaction of the biofilm with the mineral and specific geochemical shift at the micro scale. When interacting with the minerals biofilms contribute to the formation of new products – organo-mineral films, which we consider as *in situ* microproducts of biochemical weathering/pedogenesis. They could be identified mostly by advanced methods of scanning or transmission electron microscopy, microtomography, X-ray microanalysis, etc.

Organic matter components of the cryptic organogenous horizon stimulate biochemical weathering of silicate minerals and are involved in the new minerals formation, as well as the structuring of weathered mineral fine earth. Such functions of cryptic hypo- or endolithic organogenous horizon make it similar to the “classical” surface soil organogenous horizons. In 40 samples examined, the total organic carbon content varies from 0.1 to 10%, nitrogen – 0.01 to 1%. Organic matter show almost no or very slight degree of humification.

We observed that individual cells in the hypo/endolithic systems are partially fossilized (Fig. 1j). Extracellular polymeric matrix is also often exposed to mineralization. The main mineral component, which stabilizes organo-mineral films is silicon. They also include the following elements: C (50%), O, Al, Fe, K, Ca, Na, Mg. Evidently, such films are the result of interaction between biofilms and primary minerals and reflect elemental composition of both components.

Specific *in situ* products of weathering / pedogenesis that contain carbon in organic or inorganic form are frequently encountered in the interior of endolithic or hypolithic system. Among them are carbonates which accumulate on an external surface of cyanobacterial biofilms (Fig. 2a); crystals of carbonates could also be found embedded in the cyanobacterial extracellular polymeric substances (Fig. 2b).

Recent studies widely confirm possibility of carbonates precipitation by cyanobacteria. Two mechanisms are involved: $CaCO_3$ crystals precipitation on the cell surface layer and extracellular sheath calcification *in situ* promoted by pH rise due to CO_2 depletion and OH^- increase during photosynthesis (Dupraz et al., 2009; Fundamentals of Geobiology, 2012). Common features of cryptic organogenous horizon and its vicinities are the oxalate crystals produced when exudates of endolithic fungi including oxalic acid and its derivates react with silicates and/or non-silicate Fe compounds (Fig. 2c, 2d). The main sources of cations stabilizing oxalate and carbonate ions could be the feldspars. New born oxalates and carbonates are the products of pure *in situ* bio-mineral interactions, thus may also be considered as a proper pedogenic attribute.

ELUVIAL-ILLUVIAL PATTERN OF ENDOLITHIC SYSTEMS

Functioning of endolithic community in the interior of massive crystalline rocks in some cases results in the formation of eluvial-illuvial differentiated microprofiles (Fig. 3).

Previous X-ray microtomography data (Mergelov et al., 2016) have shown that subaerial segment of granitoids with endolithic systems in the oases of East Antarctica has mineral skeleton, which is permeable

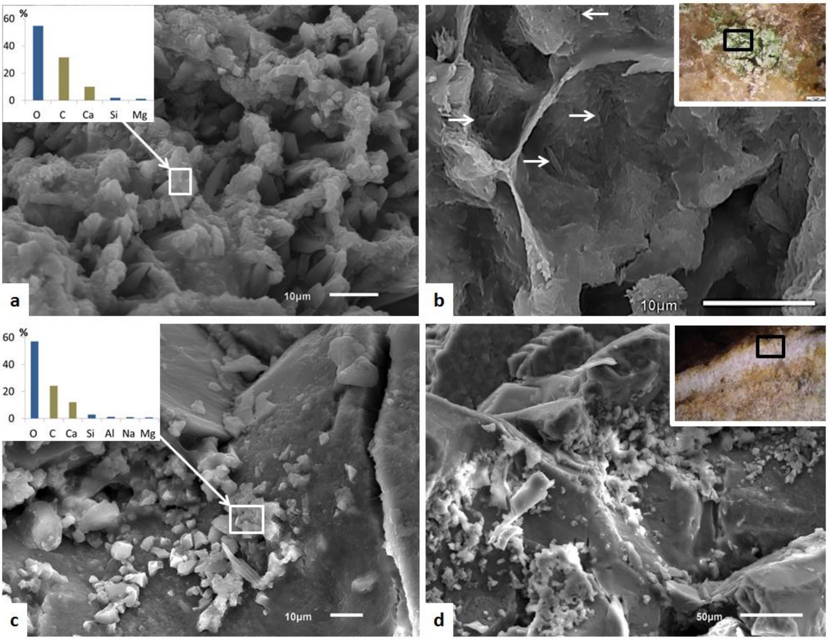

Fig. 2. Specific *in situ* products of endolithic weathering and pedogenesis. a – carbonates on an exterior of cyanobacterial biofilm; b – carbonates formed within cyanobacterial extracellular polymeric substances (pointed by arrows); c, d – oxalates in bleached eluvial horizon (from Mergelov et al., 2016).

for the dissolved weathering products. Scanning electron microscopy (SEM) combined with microtomography data revealed the "pockets" with biofilms and weathering products such as silt and iron (hydr)oxides inside and under exfoliation plates. Weathered "pockets" were connected by the thin subvertical fissures rising up to the day surface. Fissures network also connects the bright iron depleted areas with lower zones with a high iron content and ferrugination loci on the day surface.

We suggest that the fractures network serves as a transport system for the elements transfer in the interior of the upper 1–2 cm of granitoid that makes eluvial-illuvial differentiation possible. In particular, upward migration of iron in dissolved form to the day surface where it is immobilized at the oxidative geochemical barrier. Mobilization/deposition of Fe compounds can occur in rare events of moistening

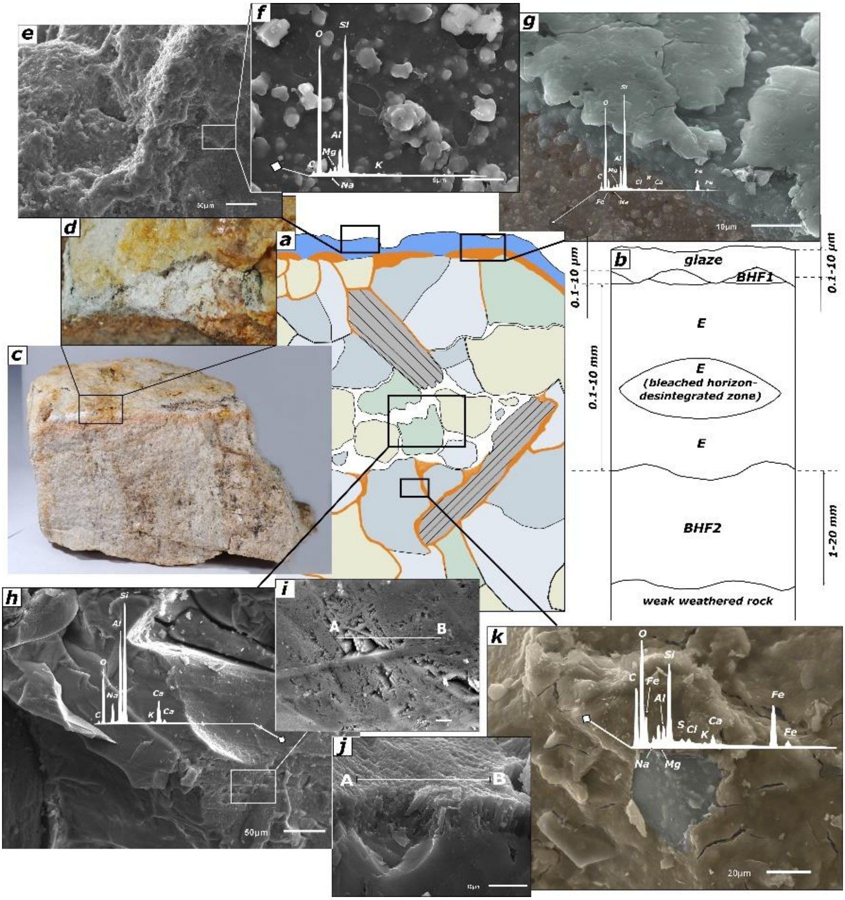

Fig. 3. Eluvial-illuvial differentiation in endolithic system: model and structural units.

a) structural units of the cross section, where:

- quartz grains *- amphibole grains* *- silica glaze*

- feldspar grains *- biotite grains* *- BHF microhorizons*

b) vertical stratification (for convenience the indexes of horizons in this model are given by the analogy with stratification of podzols, however we do understand all contentious issues of applying horizon indexes designed for classification of common soils to such specific objects);

c) subvertical artificial stone chip of original rock with endolithic microprofile (reflected light, 5000 K);

d) microprofile at the natural surface: translucent glaze and yellow to red-brown upper “BHF” microhorizon; artificial subhorizontal chip: bleached microhorizon, protolichen crust under exfoliation plate; fragment of cyanobacteria colonies (reflected light, 5000 K);
e) microprofile at the natural surface, a general view of the glaze: mottled uneven texture, closed micropores, dehydration cracks (SEM image, secondary electrons);
f) fragment of the glaze surface: nanometer scale ($n \times 10^9$–$n \times 10^8$ m) laminated film of amorphous silica with included associates of clay minerals (SEM image, secondary electrons, spectrum – here and after X-ray microanalyzer);
g) fragment of the natural glaze stratification: blue tones underline amorphous silicate layers, dull yellow allocate silicate layer with a high content of iron in the micro- and nano depressions – top “BHF” microhorizon (toned image, SEM, secondary electrons);
h) artificial chip through bright eluvial microhorizon: feldspar grain (center of the image and part of the first quarter), natural cavernous surface of feldspar grains – albite-anorthite series (center and fourth quarter of the image), natural rounded, cavernous surface of quartz grains (the edge of the first and third quarters – SEM, secondary electrons);
i) fragment of cavernous feldspar surface (albite-anorthite series) in the plan; AB – the direction of chip (SEM, secondary electrons);
j) artificial chip on grain perpendicular to the surface: the cavernous profile in feldspar; AB – the direction of chip (SEM, secondary electrons);
k) natural quartz grain surface in the lower “BHF” microhorizon: a thin film of amorphous silicate on the surface of grain (gray tone) overlain by a thick (1–4 microns) amorphous silicate film of complex composition with a high content of iron and carbon (dull reddish-brown tone) – toned image, SEM, secondary electrons.

and subsequent desiccation of granitoids surface in Antarctica. This process leads to a unique result – microprofiles morphologically and functionally resembling the structure of Podzols (Spodosols) are formed in granitoids (massive-crystalline rocks). However, these profiles are two to three orders of magnitude less thick than in “classical” Podzols on loose sediments.

Eluvial-illuvial differentiated microprofiles in hard rocks of various landscapes. A common hypothesis that endolithic systems are exclusively confined to extreme environmental conditions, apparently needs to be adjusted. We have found that as a result of the functioning of endolithic and epi-endolithic systems with microscopic fungi, actinomycetes, cyanobacteria and (proto) lichens on quartzite and iron sandstones in different natural environments eluvial-illuvial differentiation also occurs in the top subsurface layer of the rocks (1–5 cm). Profiles are primarily differentiated by Fe and organic matter. Bright eluvial zones are formed and microprofiles of soil-like bodies are established, similar to macroprofiles of common Podzols (Spodosols). Eluvial-illuvial differentiated microprofiles in hard rocks were discovered in such not extreme, and conducive to the development of epilithic or ground vegetation conditions, as forests and prairies of Missouri (in the Early Paleozoic light sandstone of Plateau Ozark) or fynbos landscapes of South Africa (in the Middle Paleozoic sandstones and quartzites of the Cape Fold Mountains) (Fig. 4).

The most striking example – universal formation of the bright eluvial layer (2–10 mm) under epilithic-endolithic lichen communities in the sandstones of the Table Mountain in South Africa. Formation of bleached eluvial horizon explains a light gray color of rock outcrops surface on the Table Mountain, which is originally (outside the endolithic weathering zone) composed of pale yellow and red sandstones.

As well as formation of "classical" Podzols, which are widely distributed in the world and are in general united by a common process, the formation of bright eluvial horizons in hard rocks occurs due to a similar mechanism in a variety of natural environments. Migration of elements through micro fissures network between the various components of endolithic and epilithic-endolithic systems plays the major role in formation of eluvial zones in the subsurface rock interior. One of the possible mechanisms involved is the "nutrient pump" operating between mycobiont and phycobiont of endolithic (proto)lichen. Redistribution of weathering products may also occur under gravitational and moisture-desiccation gradients after rock wetting by precipitation and subsequent evaporation of moisture from the pore space. A proper ecological explanation why organisms continue to occupy endolithic environment in rather favourable conditions just as they do in habitats exposed to climatic extremes is still has to be given.

CONCLUSION

Endolithic and hypolithic systems have major features attributed to soils: (a) rock layer exposed to external abiogenic factors, (b) lithomatrix inhabited by living organisms which are synthesizing and

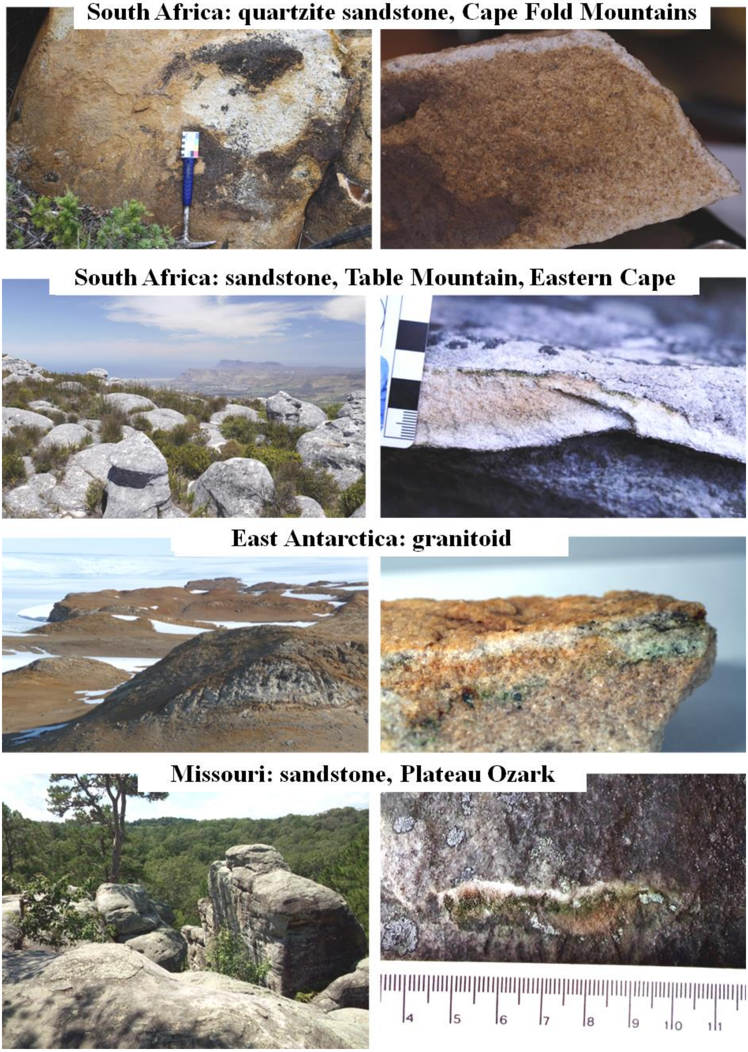

Fig. 4. Eluvial-illuvial pattern in endolithic systems of various landscapes.

decomposing organic matter, (c) as a result initial parent rock (lithomatrix) is transformed *in situ* by biogenic and abiogenic factors, the products of transformation are retained and/or removed, the vertical heterogenity is established in a form of microhorizons composing microprofile.

Crucial features of such soil-like systems: (a) the hotspot of biota-to-rock interactions is located not on the surface as in common soil but inside the mineral matrix under exfoliation plate or stone pavement, (b) major products of endolithic and hypolithic rock transformation are the silty-sandy fine earth and abundant organo-mineral films of various composition.

The study of endolithic weathering front with the approaches of soil science showed that microprofiles established in hard rocks morphologically and functionally are very similar to a common soil. Different horizons of this body are connected with the fracture network, which serves as a transport system for elements transfer. It leads to a unique result – the soil-like pattern is established inside the massive-crystalline rock.

The profiles being examined have clear eluvial-illuvial differentiation patterns similar to macroprofile of a common Podzol (Spodosol) on loose substrates. Due to the nature of the substrate (massive crystalline rock), position in the landscape (rock outcrops) and in some cases bioclimatic extremes the thickness of profiles and horizons are one to three orders of magnitude less than in common Podzols.

The eluvial-illuvial pattern in endolithic systems has been discovered in completely different landscapes from Antarctica to South Africa.

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