NEW OBSERVATIONS AND INTERPRETATIONS OF THE ENIGMATIC POORLY KNOWN LATE PALEOZOIC *IRREGULARINA* BYKOVA, 1955

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Abstract Specimens of the enigmatic poorly known taxon *Irregularina* Bykova, usually classified as a parathuramminid foraminifer, occur in great abundances irregularly distributed within fine-grained wacke-/packstones, partly pressing against bioclasts. The aggregation of their numerous and variously shaped sparite-filled bodies within the sediment may resemble abiogenic fenestral fabrics. It is suggested that these organisms were sediment-dwelling (psammobiontic) forms being capable of stretching into sediment interstices. In *Amphipora* wackestones, *Irregularina* settles on amphiporids skeletons and cryptoendolithically penetrates the latter by completely mimicing the labyrinthic canal system. Given the wide range of intraspecific variation by adaptation of the dynamic shape, the high species diversity of *Irregularina* based on differences in morphology and size is challenged. The irregular shape with finger-like extensions interpreted as moveable pseudopodia (lobopodia) and the supposed ability to change the shape requires a primarily not calcified, flexible outer body membrane. Therefore *Irregularina* shares some similarities with modern giant amoeboid heterotrophic protists that may also exhibit a psammobiontic way of life. Another cross-reference is given to homeomorphic representatives of Mesozoic thaumatoporellaceans. The true biogenic nature of *Irregularina*, however, is still unsolved.

Keywords: Parathuramminida, incertae sedis, psammobionts, cryptoendoliths, protozoa

INTRODUCTION

Single chambered benthic foraminifera of the superfamily Parathuramminida (Mikhalevich, 1980; Loeblich & Tappan, 1987; Vachard et al., 2010) are one of the most important microfossil groups in Middle to Late Devonian shallow-water lagoonal limestones. The majority of these genera, species and subspecies were described by Russian micropaleontologists mainly from the Russian Platform, Urals and Tien Shan (e.g., Birina, 1948; Lipina, 1950; Vissarionova, 1950; Bykova, 1952; Reitlinger, 1954; Antropov, 1959; Chuvashov, 1965; Poyarkov, 1969; Petrova, 1981; Zadorozhnyy & Yuferev, 1984; Kulagina, 2013). The Russian papers had their focus on micropaleontology, i.e. systematics, and stratigraphic implications. However, only little to no attention was paid to microfacies, diversities, palaeoecology and palaeoenvironment. And, as common practice, the majority of taxa are poorly illustrated often only represented by its holotype specimen. Among the considerable number of erected taxa, one is the genus *Irregularina* Bykova, 1955 (type-species *I. karlensis* Vissarionova). Because of the ambiguous biogenic origin (animal *versus* plant), Vachard (1991, p. 259) treated *Irregularina* as a “pseudo-foraminifer” and the Parathuramminida in general as an artificial “morpho-order”. In the present contribution, specimens of *Irregularina* are described from the Middle Devonian of the Eifel, Germany, and the Upper Devonian of Moravia, Czech Republic (Fig. 1).

The studied material provides new observations of the enigmatic way of life of this poorly known taxon and also supplies new aspects of its possible biogenic nature. In addition, the evidenced high morphological variability permits us to discuss and critically comment the species inventory deduced from literature data.

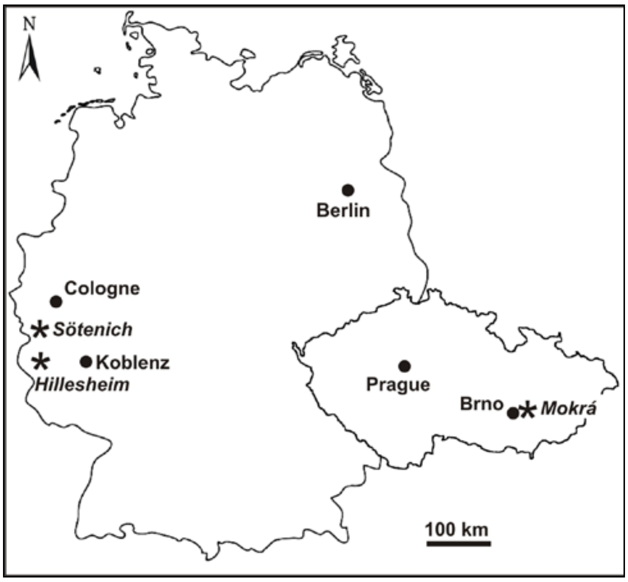

Fig. 1 - Map of Germany and the Czech Republic with the localites Sötenich, Hillesheim and Mokrá (stars).

GEOLOGICAL FRAMEWORK

Eifel synclines, Eifel hills, Western Rhenish Slate Mountains, Germany

The limestone synclines of the Eifel hills (Eifeler Kalkmuldenzone) are part of the western Rhenish Slate Mountains within the Rhenohercynian fold-thrust belt of the European Variscides. Synclines are situated in a N-S trending, approx. 50 km wide, major depression of the Eifel nappe, the so-called Eifel North-South Zone (Oncken & Weber, 1995; Oncken et al., 2000; Franke, 2000). The Eifel North-South Zone covers mainly the lower and middle parts of the Devonian sedimentary record of the Ardennes-Eifel shelf developed at the

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southern margin of the Old Red Continent. In this allochthonous succession, the Lower Emsian siliciclastics are possibly the oldest known (Belka & Narkiewicz, 2008: p. 393). These molasse-like sediments are up-to kilometres thick and the transition to carbonate beds is in the Upper Emsian Heisdorf Formation. Carbonates containing a diverse reef-building fauna first occurred during the early Eifelian, followed by the widespread and intensive transgressive development of shallow water reef-bearing carbonates of Early to Middle Givetian ages. The Late Givetian to Early Frasnian platform is partly dolomitized. The Middle Frasnian has diverse facies, but argillaceous and black shales prevail in the youngest known parts of the succession (Late Frasnian and Early Famennian).

General large scale palaeogeographical models for the Devonian of the Rhenohercynian Belt in central Europe assume that shelf zonation parallels the SW-NE trending southern margin of the Old Red Continent (Krebs, 1974; Burchette, 1981). The Emsian–Givetian shelf and platform configuration in the context of the Eifel hills is still debated, but a ramp configuration with a southward deepening trend is most likely based on detailed facies studies (e.g., Utescher, 1992; Salerno, 2008), though different models exist with postulated structural highs controlling platform development and resulting in a E-W shelf zonation pattern (Struve, 1963; Faber et al., 1977). Samples studied herein stem from the Lower Givetian of the Sötenich Syncline (Scheidberg quarry south of Sötenich village, Urft River Valley, Rodert Formation, thin-section no. SB 16) and the Hillesheim Syncline (Korea quarry between Nohn and Üxheim villages, Ahbach Glen, Loogh Formation, thin-sections nos. Ko 1a, b) and represent shallow subtidal, lagoonal to peritidal facies types. *Irregularina* occurs within various lithologies including ostracod-tubular algal mudstones/wackestones, auloporoid floatstones [on the surface as well as in the calical tubes of cf. *Roemerolites tenuis* (Schlüter)] and intraclast-calcitarcha-bioclast wackestones/packstones with thrombolitic microbial fabric in some places (Fig. 2).

Sometimes, the bodies of *Irregularina* can be misidentified as growth cavities within irregularly growing thrombolitic microbial communities, especially when walls of *Irregularina* are diagenetically altered or mostly lacking. Some fenestral micritic facies types resembling, at first glance, loferitic intertidal fabrics can turn out to be formed by numerous *Irregularina* individuals, sometimes associated with reticulate peloidal patches of microbial origin. *Irregularina* with its spar-filled internal cavities are also frequently arranged in indistinct layers looking like sheet and prism cracks of loferite-type or related fenestral fabrics (Fig. 3).

Moravia, Czech Republic

Middle to Upper Devonian (Eifelian–Frasnian) limestones crop out mainly between the middle and north-eastern parts of Moravia, eastern part of the Czech Republic; the Moravian Karst outcrops N of Brno are the largest (Fig. 1). The total outcrop area, however, comprises only 2% of the entire 15,000 km^2 large limestone complex which spreads up to hundred kilometres farther towards the E and S in the subsurface structures (evidence from numerous boreholes and seismic surveys). The limestones are mainly shallow-water platform facies with banks, reefs and lagoonal deposits. The adjacent slope facies are less frequently preserved, being partly trimmed by major Variscan faults on the West and Carpathian-(Alpine) faults on the East, in addition, reduced along with the transverse, WNW–ESE fault displacements (Hladil, 2002; Geršl & Hladil, 2004; Bábek et al., 2007; Hladil et al., 2009). The parasequences of these limestones show a successive onlapping and then offlapping on the central crystalline highs, with the turning point around very late Middle Frasnian. In the very centre of such elevated blocks, a thinnest limestone occurs and also paleokarst structures and aeolian sediments are found (Bosák et al., 2002). The facies analysis of the "East Moravian platform complex" shows a predominance of *Amphipora* facies in lagoonal

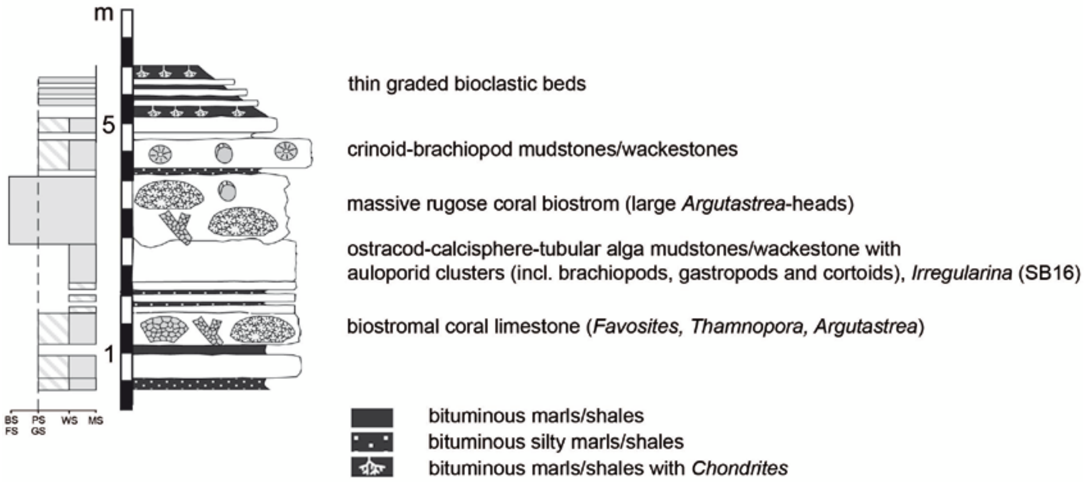

Fig. 2 - Occurrence of *Irregularina* in the uppermost part of the Lower Givetian succession (Rodert Formation) at the abandoned Scheidberg-quarry near Sötenich (Sötenich Syncline) with shallow marine lagoonal, partly restricted platform carbonates including coral biostromal units.

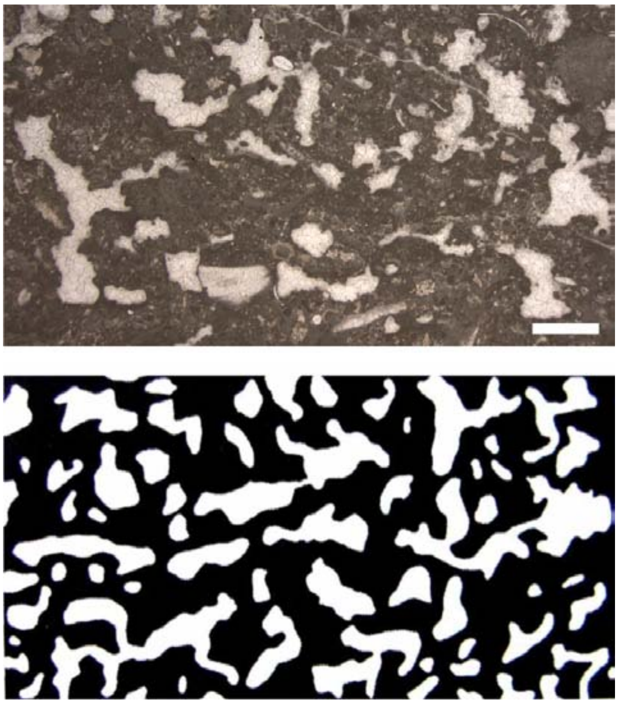

Fig. 3 - Above: Abundant *Irregularina* specimens within fine-grained sediment forming a fenestral fabric. Givetian of Hillesheim Syncline, thin-section KO 1b. Scale bar 1 mm. Below: Irregular laminoid type LF-B I fenestral fabric (Flügel, 2004: partly from Fig. 5.5). Without scale.

settings (Hladil, 2007a, b), but the overall facies diversity is much greater, changing both vertically and laterally (Hladil, 1994). Scattered occurrences of *Irregularina* are reported from the Givetian to Frasnian samples from the drilling cores on many places of Moravia (Zukalová, 2004) but we concentrated on rich populations found in the Mokrá western quarry, which is located 15 km ENE of Brno in the southernmost part of the Moravian Karst (Hladil et al., 2009, with references therein).

The studied material is from micritic *Amphipora* limestone of the Macocha Formation, specifically the "Hostĕnice facies" (Rez et al., 2011). The illustrated specimens are from the sample Mok 42.5 m (Geršl & Hladil, 2004: Fig. 5) which possibly belongs to the Middle Frasnian *Palmatolepis punctata* Zone (Fig. 4).

The microfacies is represented by wacke-/packstones that deposited in a low energy (mostly calm water) environment of shallow and very inner parts of a gently inclined ramp where numerous *Amphipora* skeletons and specimens of *Irregularina* occur together. The latter are sparsely distributed in the micritic matrix exhibiting many specimens attaching to the outer surface of the amphiporid skeletons (epiliths) and many pervade cryptoendolithically the host tissues.

MICROPALEONTOLOGY

Description of *Irregularina*

As we are dealing with different microfacies types along with differences in the overall appearance and distribution in the sediment, the description is split up for the material from Germany and the Czech Republic. *Irregularina* can to some extent be compared with lobose amoeboid-like protists as treated in the chapter following the description. For systematic classifications of Rhizaria, Amoebozoa and closely related groups see for instance the online wiki Palaeos (2012), Adl et al. (2005), Smirnov (2008, 2011) or Pawlowski & Burki (2009).

? Supergroup Amoebozoa Lühe, 1913, emend Cavalier-Smith, 1998
Genus *Irregularina* Bykova, 1955

Remarks. *Irregularina* was created by Vissarionova in 1950 (Tab. 1). According to Loeblich & Tappan (1987: p. 192), however, the name is not available under the regulations of the International Code of Zoological nomenclature (3rd version of ICZN, 1985, article 13.3) as no type was designated. In fact, Vissarionova introduced three new species of the new genus *Irregularina*, *I. karlensis*, *I. cardiformis* and *I. morpha* (in order of the original description) without fixing a type species. In such cases, article 69 of the ICZN (4th version, Ride et al., 1999) regulates in which ways the usage of the generic name can be conserved. In 1955, Bykova introduced the two further species *I. tcheslavkaensis* and *I. intermedia* (see Table 1). In this work (page 21), Bykova as first revising author designated *I. karlensis* as genotype (= type species) thus validating the genus (ICZN, article 69.1). Diagnoses of *Irregularina* were provided by Vissarionova (1950), Poyarkov (1969), Loeblich & Tappan (1987) and Vachard (1994) (Tab. 2). Note that Poyarkov (1969) stressed the presence of numerous apertures as characteristic of *Irregularina.* Consequently, specimens without apertures should belong to other taxa. Such a sharp discrimination is in so far problematic as representatives of *Irregularina* were described from random thin-sections.

Vdovenko et al. (1993) were considerably narrowing the content of *Irregularina* to three species, where one of them is the type species *I. karlensis* but two other remain unnamed, possibly equal to the species originally described by Vissarionova in the year 1950, *I. cardiformis* and *I. morpha*. The diagnosis of the genus *Irregularina* Vissarionova was reduced to the forms which possess tests of irregularly angular shapes and exhibiting numerous apertures which occur at the ends of tubular or papillary protrusions. This definition differs from Poyarkov (1969), remarking that these protrusions may also be absent so that the apertures may occur also directly in the wall of the test. In spite of an evident effort of Vdovenko et al. (1993) to separate and clarify all the diagnoses of the genera in the family Parathuramminidae, the systematic redescription (or discussion) of *Irregularina* described and published between the years 1950 and 1993 was not involved in their overall revision.

In the literature, the stratigraphic range of *Irregularina* is indicated as Middle Devonian (Givetian, possibly even Eifelian) to Lower Carboniferous (Tournaisian) by Vachard (1994). Most “species” were described from the Frasnian (Tab. 2).

Irregularina sp.
Figs. 3a, 5-9, 10b, 11

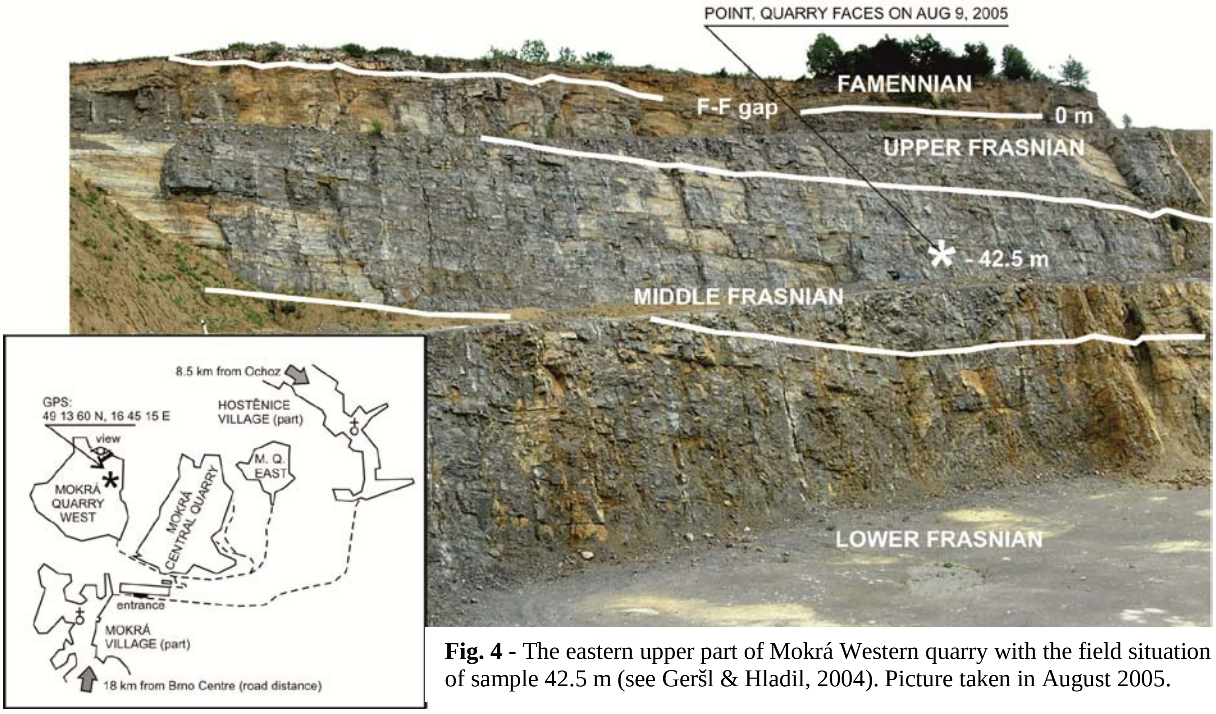

Fig. 4 - The eastern upper part of Mokrá Western quarry with the field situation of sample 42.5 m (see Geršl & Hladil, 2004). Picture taken in August 2005.

Table 1. Diagnoses of *Irregularina* according to various authors.

Author	Diagnosis
Vissarionova (1950: p. 35, translated from Russian)	Test free, irregularly shaped, often angular. Protuberances, possibly, are related to apertures. The wall is dark grey coloured, sometimes differentiated, with two layers (outer layer is bright).
Bykova (1955: p. 21, translated from Russian)	Test consists of one chamber, or occasionally is divided by constrictions into segments resembling the chambers; being usually asymmetric, of irregular shape. In some of the species, the tests possess protuberances ending with apertures. These can occur at the top of apertural nozzles, where their number is indistinct and remains undetermined, or the apertures can be present directly in the wall of the test. The test is calcareous, porous, and the wall seen in thin sections is dark, fine granular.
Loeblich and Tappan (1987: p. 192)	Test free, a single irregular chamber; wall calcareous, perforate, single layered; apertures at the end of necklike projections.
Vachard (1994: p. 34, Translated from French)	Test free (?), unilocular, irregular angular. Numerous apertures, located at the extremities of tubular or wavy prolongations. Wall calcareous, thin, dark, microgranular, homogeneous.

Description of the Eifel specimens

The specimens occur in great abundances in otherwise poorly fossilized wackestones (Figs. 3a, 5a) or in wacke-/floatstones with common calcitic tubes of auloporoids. Here they attach on the surface as well as occur cryptoendolithically in the calical tubes of cf. *Roemerolites tenuis* (Fig. 5f). Generally, *Irregularina* occurs irregularly distributed within the fine-grained matrix. Elongated specimens may show a weak subparallel orientation to each other. It assumes a variety of shapes, ranging from almost spherical to oval, bilobed, multilobed or flattened, with or without extensions/protuberances etc. The morphology mostly comprises an irregular swollen body (with or without constrictions) from which individual prolongations (= apertural nozzles or necks in the sense of Vissarionova 1950) may arise. The so-called foraminiferal apertures (= openings towards the exterior) are interpreted here as a breakage of these prolongations (see discussion). In exceptional cases these nozzles give rise to another body (Fig. 9b). Besides prominent constrictions that may be also absent, there are also small-scale protuberances and/or indentations. The chamber and the prolongations are surrounded by a thin micritic wall (Fig. 6a, e) that is poorly visible (if ever) in dark micritic matrix sediment.

Pores are not detectable. In some specimens, the chambers are surrounded by an irregular thick layer (or halo) of dark homogeneous micrite (Figs. 6f, 7g). The interior is usually filled with sparite. Some specimens exhibit geopetal fillings of light grey microspar, most

Tabel 2. Critical inventory of *Irregularina* according to the morphological concept and interpretations presented in this paper.

species/author/year	illustrations original work	type-level	remarks - interpretation
I. karlensis Vissarionova, 1950	1	Givetian of Bashkortostan, Russian Federation	type-species, figured by one single drawing (presumably a longitudinal section) so that nothing is known about its intraspecific variability. See also comments for *I. cardiformis* and *I. morpha*
I. cardiformis Vissarionova, 1950	1	Givetian of Bashkortostan, Russian Federation	possible transverse section of *I. karlensis*, or belonging to *Bisphaera*
I. morpha Vissarionova, 1950	1	Givetian of Bashkortostan, Russian Federation	possible oblique section of *I. karlensis*
I. nodosa (Antropov, 1950)	2	Middle to Upper of Frasnian Tatarstan, Russian Federation	poor illustrations, most likely identical to *I. karlensis*, respectively a specimen with irregular "wall thickness" probably aroused by sediment particles fixed to the external surface. Otherwise, could also represent a clast with a micritic rim.
I.? horrida Reitlinger, 1954	1	Lowermost Frasnian in Kirov Region (Russian Platform), Russian Federation	considered an attached specimen of *I. karlensis.* Note that all 3 species described by Reitlinger are from the Frasnian of the same borehole Kotelnich.
I. lobata Reitlinger, 1954	6	Middle Frasnian in Kirov Region, Russian Federation	no irregular outline, no apertures. Considered not a representative of *Irregularina*, *Bisphaera* in the sense of Palaeozoic workers!
I. obscura Reitlinger, 1954	1	Lowermost Frasnian in Kirov Region, Russian Federation	no irregular outline, no apertures. Considered not a representative of *Irregularina*, *Bisphaera* in the sense of Palaeozoic workers!
I. stellaeformis (Grozdilova & Lebedeva, 1954)	1	Upper Famennian of Perm Region, Russian Federation	not a representative of *Irregularina* as indicated by Poyarkov (1969: p. 95); should stay within the genus *Parathurammina* as in the original description.
I. intermedia Bykova, 1955	3	Givetian to Famennian of Bashkortostan and Tatarstan, Russian Federation	identical to the forms described by Reitlinger (1954) as *I. lobata* not mentioned in the comparisons by Bykova (1955). Note that both *I. intermedia* and *I. tcheslavkensis* come from the same locality and nearby beds
I. tcheslavkensis Bykova, 1955	3	Givetian to Famennian on western and southern slopes of Urals, Russian Federation	
I. subvasta (Bykova, 1955)	2	Frasnian on western slopes of Urals and in Tatarstan, Russian Federation	Originally described as a species of *Parathurammina*. Bykova noted the great abundance in the studied samples. The small size (0.16 to 0.21 mm), rather regular rounded outline with "apertural nozzles" radiating in all directions makes it very unlikely that this taxon belongs to *Irregularina*.
I. granda Kuznetsov & Miklukho-Maklai, 1955	-	Givetian–Frasnian, Upper Svaneti in NW Georgia	nomen nudem; just mentioned as I. granda M.-Maklay sp. nov. without description or illustration
I. longa Konoplina, 1959	3	Frasnian of Western Ukraine	Holotype (pl. 3, Fig. 1) refers to an undefinite micritic tube not matching the diagnosis of *Irregularina*. Other two illustrations might belong to *Cribrosphaeroides permirus* (Antropov).
I. angulata Konoplina, 1959	1	Frasnian of Western Ukraine	Specimen might belong to *Cribrosphaeroides permirus* (Antropov). Considered not an *Irregularina*.
I. quadrata Poyarkov, 1969	1	Upper Famennian, around Kazakhstan/Uzbekistan/Kyrgyzstan tripoint	Bilateral symmetric, no irregular form. Considered not a representative of *Irregularina*! Genus unknown
I. angulata Poyarkov, 1969	2	Givetian and Frasnian of South Fergana, Kyrgyzstan	considered as falling into the variability of *Irregularina karlensis*
I.? rugosa Kotlyar, 1982	2	Frasnian to Famennian in Poltava and adjacent regions, NE Ukraine	The elongate-lobate and wrinckled outline is considered as falling into the variability of *Irregularina karlensis*

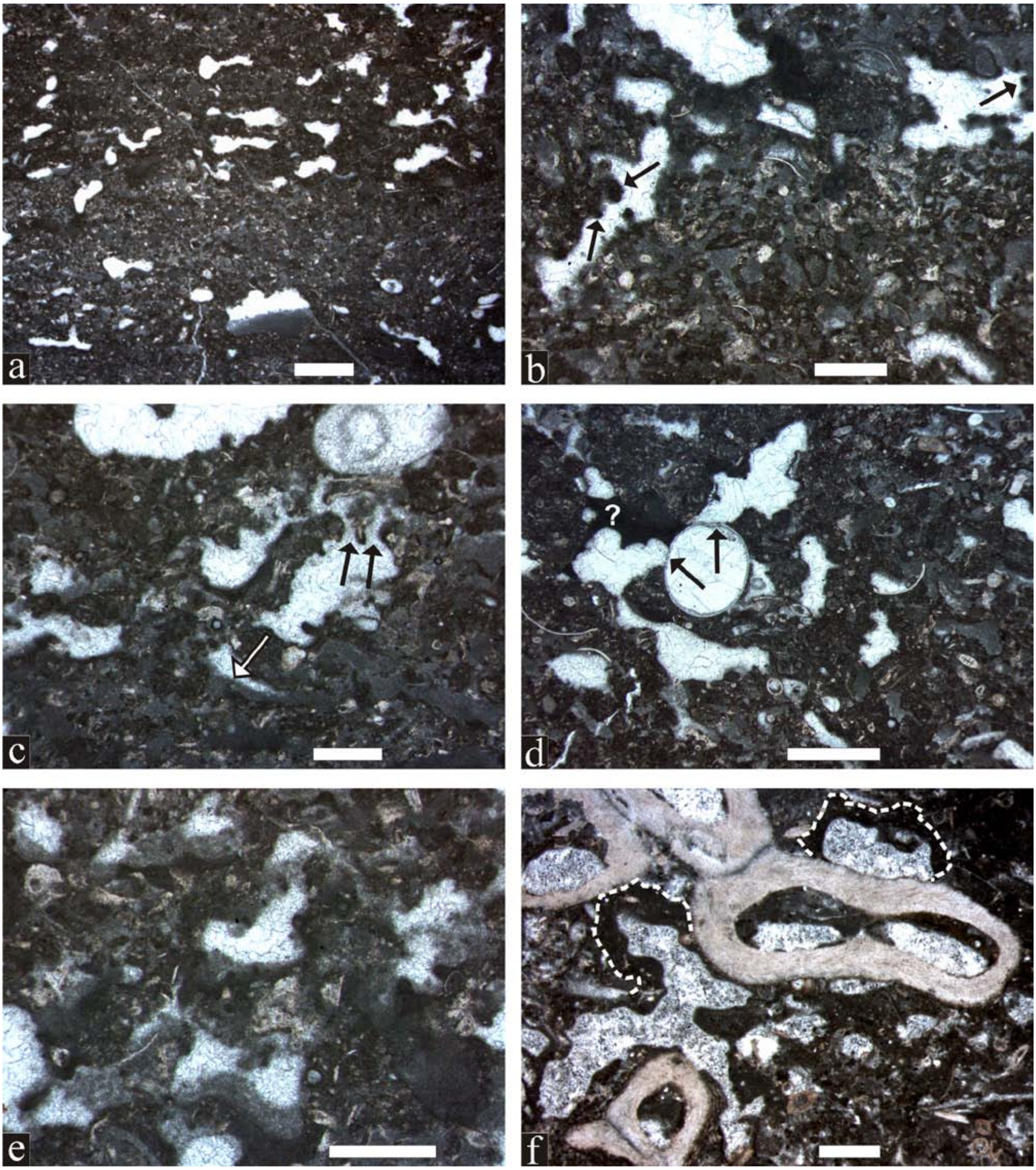

Fig. 5 - *Irregularina* microfacies from the Givetian of the Sötenich (e) and Hillesheim Synclines (all others), Eifel, Germany. **a** Wacke-packstone with abundant specimens of *Irregularina*, partly showing a subparallel orientation. This configuration compares to the LF-B I subtype of laminoid-fenestral fabrics (Flügel, 2004: fig. 5.5). **b-c** Close-up views showing the irregular rugose outline caused by the impression of individual sediment particles (arrows in b) revealing flexible response of the outer membrane. Note also the irregular bending protuberances spreading into the surrounding sediment (black arrows in c). Note the irregular canal network, interpreted as burrowing galleries (= ichnofabric), filled mainly with homogenous microsparite, in parts with clear sparite (white arrow). **d** Some specimens with flattened parts attaching a bioclast (arrows). The dark micritic zones (?) are not interpreted as parts of the organisms (e.g., wall), but transformation (? dissolution) of surrounding matrix. **e** Close-up view showing the dense overall penetration of the fine-grained sediment without orientation and the transformation of the sparitic filling into microsparite. **f** Specimens of *Irregularina* within a bioclastic wacke-/packstone. The specimens attach on the outer and inner side of the hollow bioclasts, calical tubes of cf. *Roemerolites tenuis*. Note the flattened and elongated attached sides (arrows) and the irregularly branching specimen in the centre. Some specimens exhibit an outer zone of dark micritized sediment (dotted lines). Thin-section Ko 1a, except f = thin-section SB 16.Scale bars 1mm for **a,d**; 0.5mm for **b-c, e-f**

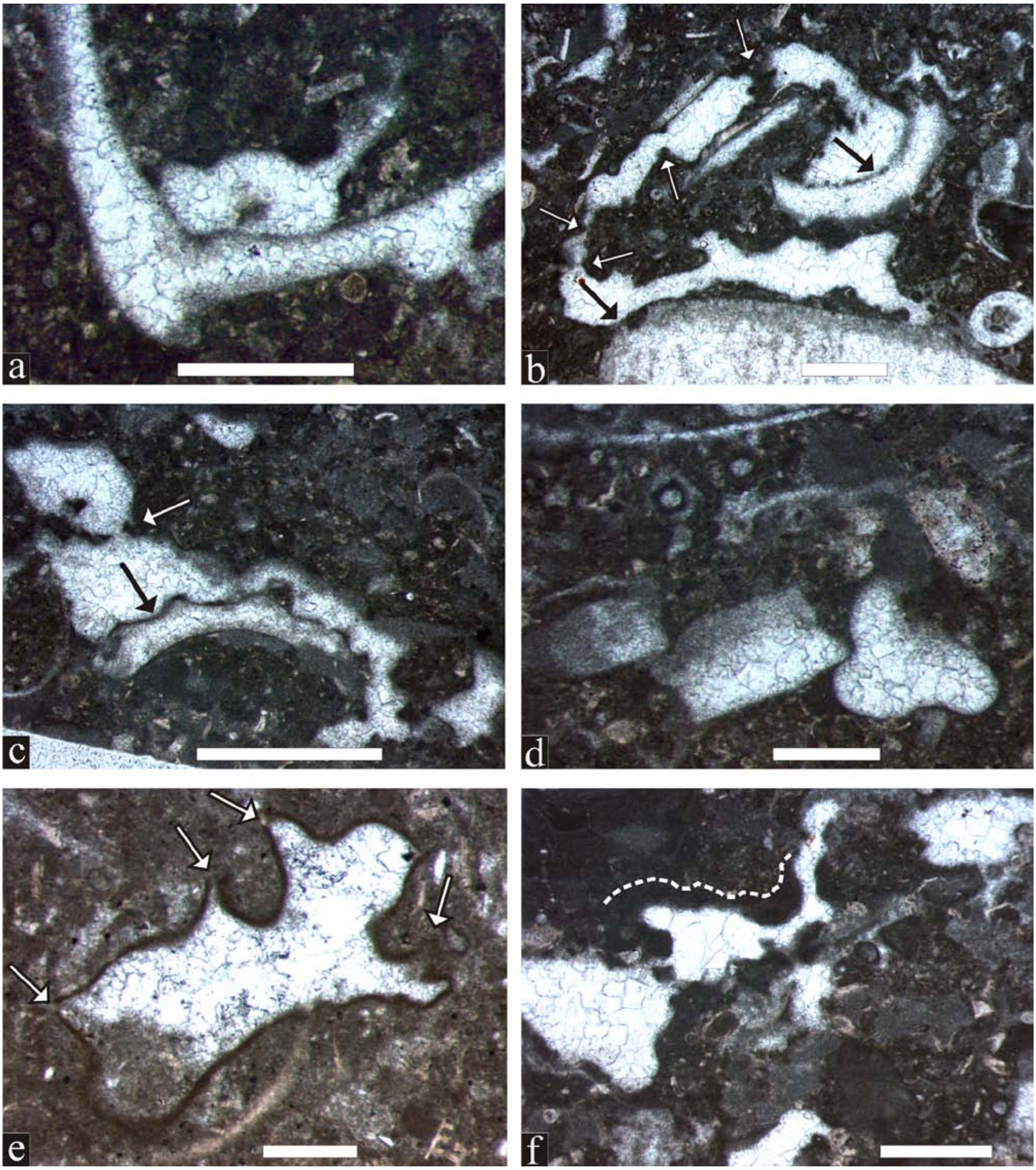

Fig. 6 - *Irregularina* specimens from the Givetian of the Hillesheim Syncline, Eifel, Germany. **a** Specimen attached to a bioclast. Detailed view from Fig. 9b. **b** Specimen exhibiting the shape of an irregular bending tube with several constrictions (white arrows) and attaching partly to bioclasts (black arrows). **c** Irregular constricted tubiform specimen attaching to a bioclast (black arrow). Note the formation of an individual chamber by a deep constriction of the tube (white arrow). **d** Three closely attaching bodies belonging either to one specimen connected by tubiferous protuberances (thus pretending plurilocularity) or referring to three individuals recalling *Irregularina lobata* Reitlinger (compare Fig. 11c). **e** Specimen of *Irregularina karlensis* Vissarionova closely resembling the original type-species illustration (compare Fig. 11a). Note the broken protuberances (“apertures”) (white arrows). **f** Specimen exhibiting irregular tubiform expansions between sediment particles and a thick dark micritic zone around some parts (dotted line). Thin-section Ko 1a, except e = thin-section SB 16. *Scale bars* 0.25 mm for **a, d-e**; 0.5 mm for **b-c, f**

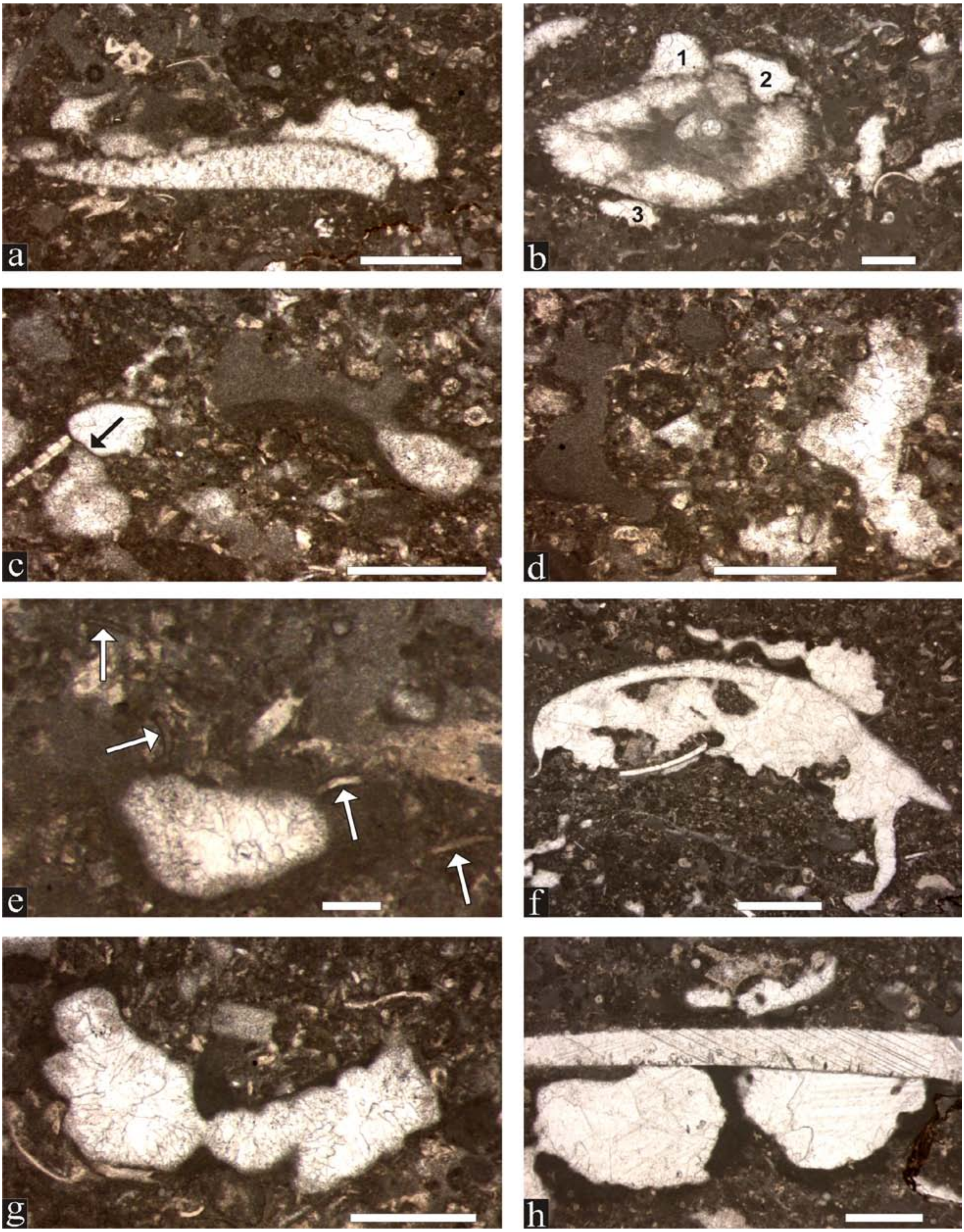

Fig. 7 - *Irregularina* specimens from the Givetian of the Hillesheim Syncline, Eifel, Germany. **a** Specimen attached on the margin of a bioclast (brachiopod shell?). **b** Several specimens within the matrix, and three specimens (*1-3*) attaching a bioclast (coral?) at various sides. **c** Irregular galleries (burrows?) filled with microsparite, partly with clear sparite. Sparite-filled *Irregularina* body recognizable by the preserved wall (arrow). **d** Irregular microsparite filled channels (burrows?). Note sparite-filled body of equivalent outline on the right (filled burrow or *Irregularina* without preserved wall). **e** Sparite-filled *Irregularina* body within microsparite-filled canals (burrow?). Note the tiny individual *Girvanella*-like tubes (arrows). **f** *Irregularina* specimens attached to a curved shell on both sides. Note the contemporaneous recrystallization (sparry calcite) of *Irregularina* bodies and shell. **g** *Irregularina* with several constrictions. Note the dark micritic halo of variable thickness. **h** Two inflated *Irregularina* specimens attaching the lower side of a shell bioclast. Note the microborings on the concave attaching side of the shell. Thin-section Ko 1b. Scale bars 0.5 mm for **a-d, f-h**; 0.2 mm for **e.**

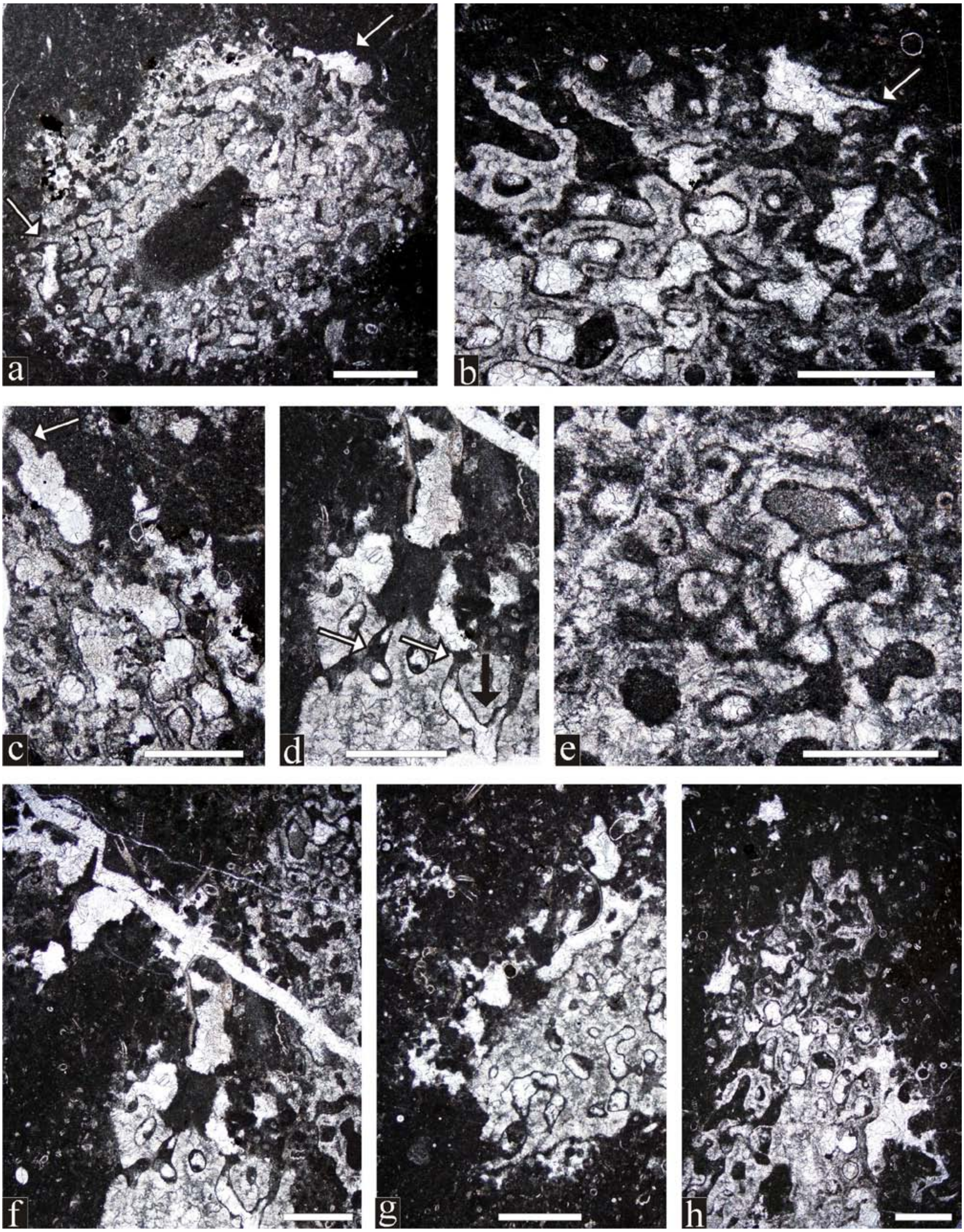

Fig. 8 - *Irregularina* sp. from the Middle Frasnian of the Mokrá Western quarry, Moravia, Czech Republic. **a, c** An amphiporid skeleton with attached (arrow above in a) and cryptoendolithic specimen (arrow left below in a) of *Irregularina*. The arrow in c shows an elongated extension. **b, d-e** Cryptoendolithic *Irregularina* showing swollen and constricted parts closely accommodating to the available spaces of the labryinthic amphiporid interior. The arrow in b shows an elongate extension (compare *Irregularina*? *horrida*, Fig. 10d). In tangential sections, the micritic wall of *Irregularina* is recognizable (arrows in d). **f-h** Cryptoendolithic and attached specimens of *Irregularina*. Thin-section MOK_42.5 m. Scale bars 1 mm.

probably formed by aggrading neomorphism of allomicritic sediment (Figs. 4a, e; cf. Morse & McKenzie, 1990, Flügel, 2004). The same type of sediment occurs within the interstices of peloidal (?microbial) clots or within an irregular network of canals.

Description of the Moravian specimens

The microfacies where the specimens of *Irregularina* occur is represented by an *Amphipora* wacke-/packstone (Fig. 8a). The stocky single-chambered specimens attach to the exterior of the cylindrical fragments of amphiporid skeletons which results in a more or less plano-convex outline in sections perpendicular to the substrate. The upper part may be also slightly rugose or lobate. From the base of the chamber, elongate protrusions may penetrate the labyrinthic skeletal galleries of amphiporids (Figs. 8c, 9a). Hereby they completely fill the available spaces attaching tightly to the side walls by means of a thin micritic wall (Fig. 8g). With this example, the internal micritic linings within amphiporid intraskeletal walls can without doubt be referred to the organism attaching to the exterior. With this behaviour, the externally attaching stocky single chambers transform into tubes that also may bifurcate thus following the labyrinthic skeletal voids. In the central axial canal, specimens of *Irregularina* were also observed. Due to its larger size or width (compared to the labyrinthic vesicles), the specimens do not completely fill this void but closely attach to the walls in the canal, in the same way as to the skeleton exterior. The spaces encompassed by the cryptoendolithic outbuildings show slightly different infillings and cements compared to untouched vesicles in the amphiporids (Fig. 8f – h). The clots inside the Moravian *Irregularina* chambers are present (Fig. 8e, Fig. 9c), but they are less abundant and also more intensely erased due to recystallization into the translucent sparry cements.

DISCUSSION

Way of life and biological nature of *Irregularina*

The specimens from the Devonian of the Eifel, forming *Irregularina* wacke-/packstones and described in the present paper, are here interpreted as being preserved in-situ within the sediment where their mass-occurrence forms a fenestral fabric or open-space structure, respectively the irregular laminoid type B-I (Flügel, 2004: Fig. 5.5) (Fig. 3b). In this context, irregular means with shapes that are so complex they cannot be defined exactly (see also Tebbutt et al., 1965). Generally, the term fenestral fabric is non-genetic referring to cement-filled voids that form characteristic fabrics usually in fine-grained carbonates, mostly of abiogenic origin (e.g., Flügel, 2004: p. 190). Fenestrae may result from shrinkage processes (“shrinkage-pore”), burrowing, molds of algal mats, or trapped gas bubbles (Boyd, 1975; Shin, 1983). In the present case, the cement-filled voids are referred to variously-shaped specimens of *Irregularina* in fabric-forming abundances. Many, but not all, of the sparitic fenestrae show good evidence for their biogenicity, e.g., attaching forms (including cryptoendoliths), preserved outer membrane, small-scale grain-body interactions. In cases, we also found reworked specimens of *Irregularina* washed-out from the sediment. Loeblich & Tappan (1987) defined the test of *Irregularina* as “free”, whereas already Vachard (1994: p. 30) put a question mark to it, remarking that the irregular deformations and constrictions might possibly result from a growth between individual sediment grains. Therefore, *Irregularina* might belong to an interpsammobiontic (or psammobiontic) small “invertebrate” as assumed by Vachard (1994). One indication is represented by small-scale grain-body interactions. Individual sediment grains that are pressed into the outer body membrane are discernible by concave to sack-like depressions revealing

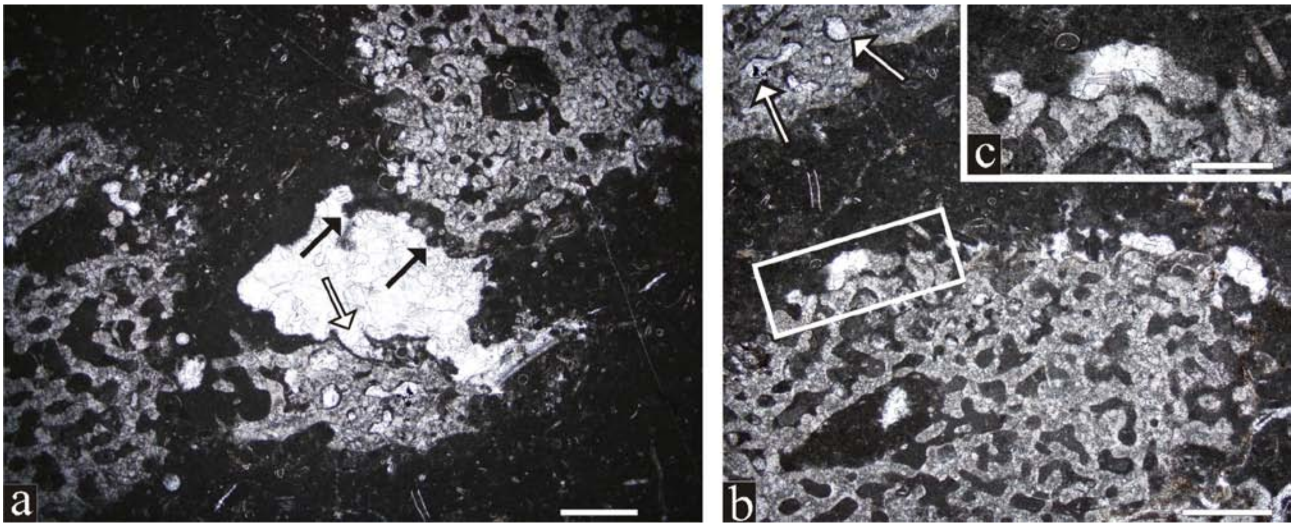

Fig. 9 - *Irregularina* sp. from the Middle Frasnian of the Mokrá Western quarry, Moravia, Czech Republic. **a** Largest observed specimen (diameter ~ 3.5 mm) attaching to an amphiporid skeleton. Note the single basal extension (white arrow) protruding downwards in the amphiporid skeleton and the concave depressions at the top as a flexible response to individual grain pressure (black arrows). **b** Several specimens attached to the external surface of an amphiporid (the white rectangle marks the detail shown in c). Note cryptoendolithic specimen(s) in the skeleton above (arrows). **c** Detail from b showing an attached specimen. Note how the basal part closely follows the substrate morphology. Thin-section MOK_42.5 m. Scale bars 1 mm for **a-b**; 0.5 mm for **c.**

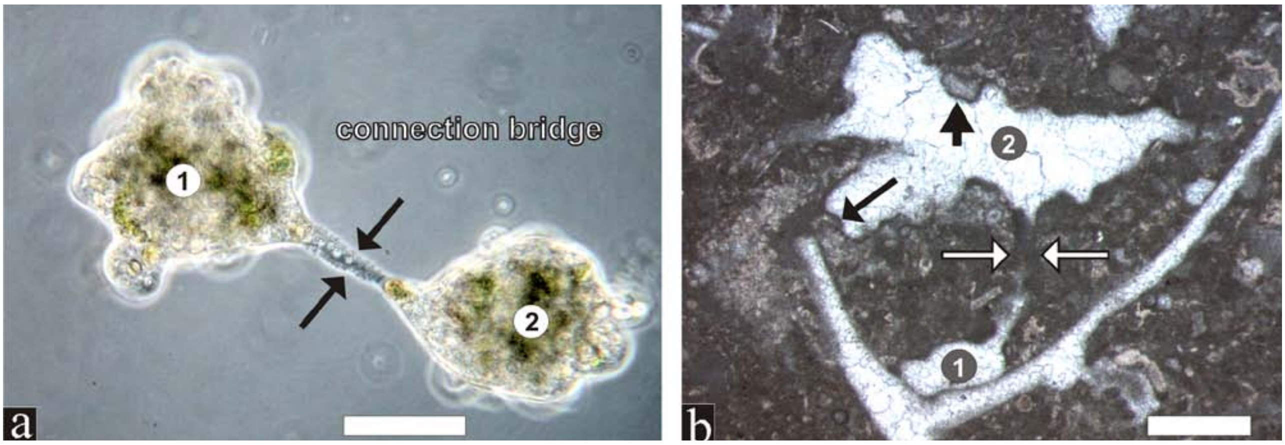

Fig. 10 - a Final stage of the sexual reproduction of a modern amoeba by binary fission (by courtesy of Ron Neumayer, microimaging.ca). Note the connection bridge (white arrows in **b**) between two cells (1-2), which later will be broken. **b** Thin-section of a Devonian *Irregularina* caught in a possible stage of division comparable to the modern example in **a**. The shape of the lower attaching form (1, detail shown in Fig. 6a) resembles to some extent *Irregularina*? *horrida* Reitlinger (Fig. 12d). The upper shape (2) with long prolongations exhibits a rather uneven, wavy outline recalling somehow the type-species *Irregularina karlensis* Vissarionova (Fig. 11a). Note the thin micritic wall (slim black arrow) and the concave depressions resulting from the pressure of individual sediment grains (fat black arrow). Givetian of the Hillesheim Syncline, Eifel, Germany, thin-section Ko 1. Scale bars 0.05 mm for **a**; 0.25 mm for **b.**

a flexible response (Fig. 5b). The shape with convex bulges may signify active pushing the mud away, and the shape with concave bent margins, inwards, may signify a passive reaction to pressure of the surrounding mud, when the organism loses its "turgor" (hydrostatic pressure), for any reason. Astonishingly, the *Irregularina* specimens are never observed completely collapsed. This implies that lithification started before pressure became strong enough to cause compaction. One might speculate that early cementation (formation of hardground?) and/or stiffening of micrite around occurred that prevented compaction.

It can be assumed that the different sediment grain-size and interstitial pore width account for the various morphologies and dimensions. The inferred motility of *Irregularina* on a limited scale, indicated by local compression and loosening in the host matrix, requires a flexible and elastic outer wall or membrane allowing *Irregularina* to change its shape. As the name already implies, *Irregularina* is so variable that it has no definite form, appearing almost as a shapeless bizarre mass. Based on these considerations, the outer envelope could originally not have been a rigid calcareous wall during the whole life-time (or life cycle) (see also remarks below concerning thaumatoporellaceans). Maybe we are dealing with an organic membrane that was calcified (impregnated) during rock lithification that today is preserved as a thin dark micritic envelope. Therefore we refrain from using words like shell or wall that implies its rigid construction.

Concerning the specimens that are in contact to bioclasts (Figs. 5f, 6a-c), these are considered not being fixed permanently by some kind of organic or inorganic cement. It is assumed that the bioclasts represent natural obstacles within the sediment where *Irregularina* simply presses against in a loose manner (Fig. 7h). The basal side of *Irregularina* may be completely attaching thereby following existing substrate surface structures (Fig. 6c), or touching the latter only at some parts (Fig. 6b). Animals with a potential or exclusive psammobiontic way of life usually belong to the meiofauna (e.g.,McIntyre, 1969; Pollock, 1971; Giere, 2009) and are actually known from the protozoan group of the Ciliates (class Ciliata or phylum Ciliophora, e.g., Carey, 1991; Al-Rasheid, 2001; Burkovsky & Mazei, 2010), rotifers (or Rotatoria, e.g., Ricci, 1983; Herzig et al., 2005), gastrotrichs (phylum Gastrotricha, e.g., Swedmark, 1964; Strayer et al., 2010), Archianellida (belonging to the order Polychaeta, e.g., Hermans, 1969; Jouin, 1971), nematodes (phylum Nematoda, e.g., Hope, 1971; Hugot et al., 2001), copepods (a subclass of crustaceans, e.g., Noodt, 1971; Boxshall & Defaye, 2008), or sponges (e.g., Rützler, 1997; Cerrano et al., 2002). Psammobiontic protists are usually concentrated in the upper 1-5 cm of the bottom water interface (e.g., Fenchel, 1969; Rundell & Leander, 2010). Among the metazoans, for example, the marine Acoela (a group of flatworms) are inhabitants of the interstitial eulitoral zone. These may exhibit characteristic adaptations to their environment within the sandy sediment. Usually long and slim forms dominate, whereas mud preferring specimens often are characterized by a clumsy compact habitus (Dörjes, 1968). Moreover, many of them exhibit various types of vacuoles inside their epidermis in order to support elasticity, which counteracts mechanical deformations of the surrounding sediment. The shape of amoebozoa also depends on the surrounding litho-hydrostatic pressure depending on the burial depths in the sediment and the height of the water column above. In these conditions, the amoebozoan movements (or cytoplasma flows) come to an end and the shape changes from a “random, multipseudopodial organism to a sphere” (Landau, 1965: sphering under pressure).

Marine psammobiontic (or interstitial) organisms are usually reported from the supratidal sands (e.g., Golemansky & Côuteaux, 1982) whereas the Devonian *Irregularina*-bearing samples can be attributed to shallow-subtidal calcium carbonate muds. Compared to modern psammobiontic organisms, *Irregularina* shows some affinities to lobose amoebozoans, animal-like

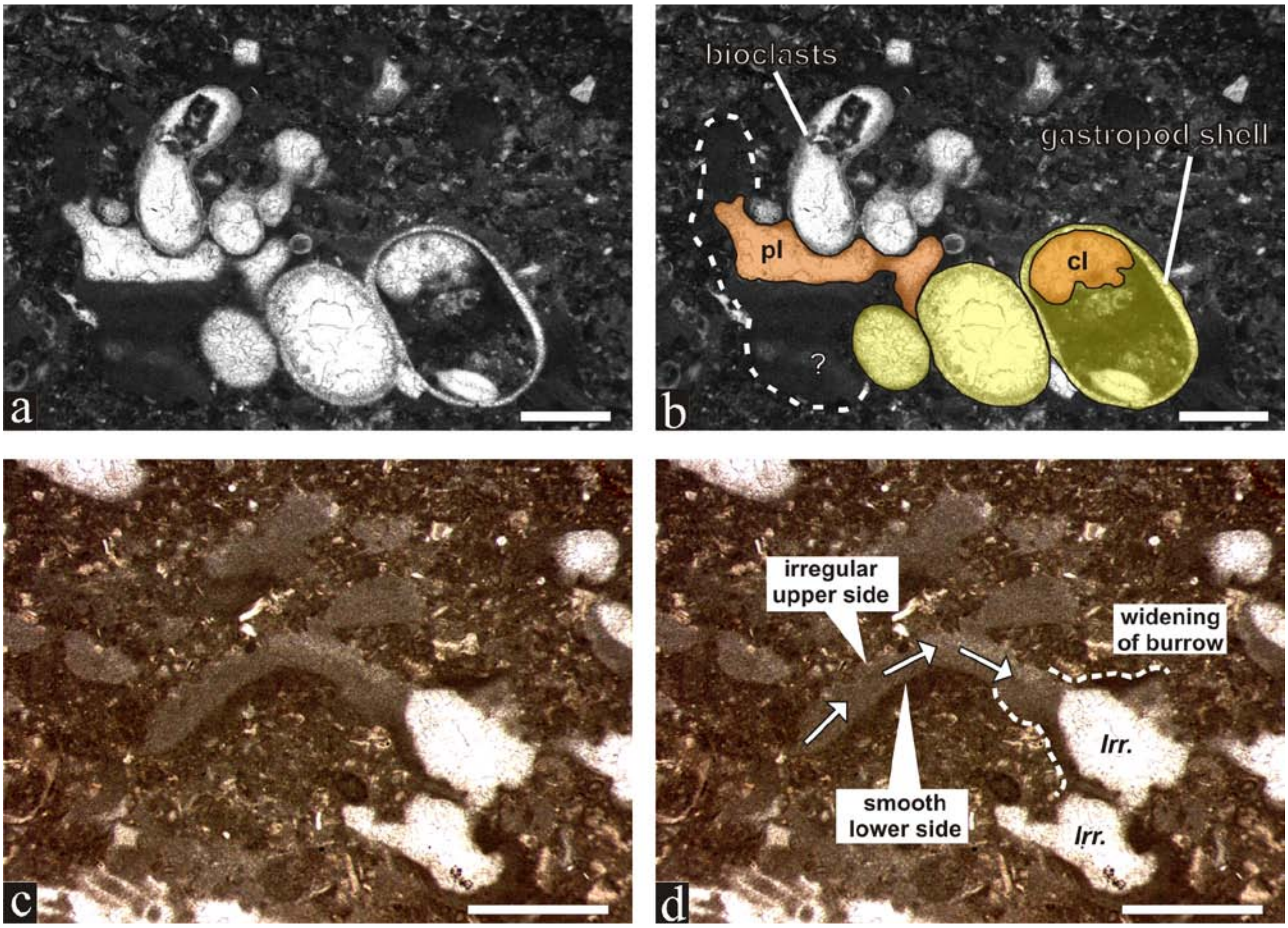

Fig. 11 - *Irregularina* from the Givetian of the Hillesheim Syncline, Eifel, Germany (left: thin-section appearance, right: interpretation) **a-b** Psammobiontic *Irregularina* (pI) stretching between bioclastic obstacles and a cryptoendolithic specimen (cI) inside a gastropod shell. Note the dark coloured micritic sediment (white dotted line) around the body of *Irregularina*. The question mark indicates a possible ghost of another specimen, only dimly recognizable. The dotted line surrounds an area of dense homogeneous microsparite (burrowed area?). Thin-section Ko 1b, scale bar 0.5 mm. **c-d** *Irregularina* (*Irr.*) inside a microsparite-filled canal interpreted as burrow. During locomotion through the sediment, *Irregularina* might adapt a barrel to cylindrical shape, the resting stage might be highly irregular, thicker, thus, leading to a widening of the burrow. Thin-section Ko 1b, scale bar 0.5 mm.

protists. Let us remember that the ability to change its morphology and to move together with an assumed heterotrophic nutrition mode (ingestion of food) are typical characteristics of animals (Whittaker & Margulis, 1978; Hickman et al., 2010). The name amoeba itself comes from the Greek word amoibe, meaning transformation (or change). It refers to the changing shape/morphology by the development of locomotive pseudopodia (e.g., Grebecki, 1990; Smirnov, 2008). Amoebae use the pseudopodial protuberances also for feeding by incorporating food particles (e.g., bacteria, algae). Psammobiontic animal-like protists are heterotrophs that are forced to move through the sediment in order to catch their food. Due to the overall microbial aspect of the sediment, where *Irregularina* was dwelling (Fig. 7f), a feeding on cyanobacteria, microalgae is most likely. This would be an explanation for the irregular network of rather cylindrical canals interpreted as burrows that exhibit a smooth lower part (gliding pressure of *Irregularina*!) and finely denticulated upper side. This ichnofabric, i.e. a feeding trace or fodichnion (Seilacher, 2007), differs from the surrounding sediment by its filling of homogeneous dense and grey microsparite. It can be speculated that during directional locomotion, *Irregularina* adapted a barrel to cylindrical shape whereas the assumed resting stage should then be represented by thicker, irregular morphologies resulting also in a widening of the burrow (Fig. 11c-d). Most likely, the burrowed substrate was represented by a consolidated softground so that the galleries were not compacted or collapsed.

Generally, the high morphological variability of lobose amoebozoans is given by three different basic shapes: (i) stationary or resting, (ii) during non-directed movement and (iii) during directional locomotion (Smirnov et al., 2005: Fig. 2 and with more details therein). During so-called non-directed (= random) movement, the shape changes rapidly and continuously so that the form cannot be indicated precisely. In the case when the amoeba adapts to a continuous and directed locomotion, the shape becomes more stable. The irregular extensions that in the description of several *Irregularina* species (see Tab. 2) were ascribed to foraminiferan apertures are here – in morphological ananlogy to amoebae – referred to these motile protrusive cytoplasmic structures, i.e. pseudopodia (= “false feet”, here: finger-like, cylindrical lobopodia with rounded tips). Besides pure morphological accordance, this interpretation is also deduced from the assumed motility and ability to form such body extensions. In the case where specimens were washed-out from non- to semi-consolidated sediment, for example by strong tides or storms, the formerly closed tips may break off then looking like openings (or apertures) as in the type-species *Irregularina karlensis* (Figs. 6e, 12e). In one exceptional case, two bodies are preserved connected by a thin connecting bridge (Fig. 10). This example can be compared to the amoebozoa, when assuming a specimen caught in a stage of binary division. Dividing amoebae first produce a furrow that successively becomes deeper and finally forms a daughter cell still connected to the mother cell by a connecting bridge (Fig. 10a) (e.g., Grębecka et al., 2002). In the last stage of the division process, the bridge breaks up. Another possibility would be that we are dealing with a syzygia (conjunction or association) of two specimens. In any case, if this fragile *Irregularina* "construction" would not be preserved in an in-situ position (within the sediment), it would most likely have been broken. This observation can be taken as further indication for the inferred psammobiontic way of life. Between individual bioclasts, *Irregularina* was observed stretching closely into the available interstices, also in opposite directions (upwards and downwards) (Fig. 11a-b). Concerning the wall structure of *Irregularina*, it is said to be "perforate" by Loeblich & Tappan (1987) *versus* "homogeneous" as stated by Vissarionova (1950) and Vachard (1994). In addition, Vissarionova mentions the occasional occurrence of an outer bright layer. Reitlinger (1954) described the wall of *Irregularina lobata* as fine granulated, sometimes with foreign particles embedded into the wall from their outer sides.

This latter interpretation corresponds to observations that the thickness and continuity of calcified walls seems to be variable, and moreover, even a well discernible wall can disappear in some parts of the specimens. In reworked specimens, micritic host-sediment sticked to the outer membrane can be mistaken as corresponding to the wall of *Irregularina*. Such an irregular wall of highly variable thickness is for example visible in the holotype specimen of *Irregularina*? *horrida* (Fig. 12d), *Irregularina lobata* Reitlinger (Fig. 12c), or "*Uslonia permira*" Antropov illustrated by Zadorozhnyy & Yuferev (1984) (Fig. 12e-f) and *Irregularina nodosa* (Antropov) (Fig. 12g). In this context, Antropov (1950) remarked that the wall thickness is unstable, fluctuating in a wide range from 10 to 40 µm. Another possibility would be that the foreign particles (sand grains) are not incorporated (agglutinated) into the thin membrane but simply glued to the external surface. Such a behaviour observed in some naked amoebae (Hall, 1953), serves as a simple protection of their body. In testate amoebae (or Thecamoebians) that exhibit a rigid test agglutination is a common feature (e.g., Ogden, 1988; Van Hengstum et al., 2007). In benthic foraminifera, cement is used to fix and incorporate agglutinated particles to the wall (e.g., Bender & Hemleben, 1988; Roberts & Murray, 1995). As another possibility, these sediment remains might result from the reworking of *Irregularina* specimens already enclosed in semi-lithified carbonate mud. The dense micritic zone or halo observed around some specimens (Fig. 6f, 7g) might be a carbonate precipitation in fine micropores due to influencing of the physical-chemical microenvironment (saturation/precipitation) by the metabolism of *Irregularina*. In any case, it does not correspond to its outer body membrane. Such a mechanism could be additionally be enforced by the microbial communities (see Fig. 7e), respectively their activities in the sediment (Dupraz & Vischer, 2005). Perhaps these processes lead to the hardening of the sediment that prevented later compaction as discussed before.

Besides the forms interpreted as psammobionts, the specimens attached to amphiporids and invading their skeletal tissue need another explanation. As a direct analogy of the Devonian specimens of *Irregularina* that were stretching into the labyrinthic interior spaces of *Amphipora*, specimens of *Thaumatoporella*, so far interpreted as an alga incertae sedis (De Castro 1990, for details) occur as cryptobionts inside the Upper Jurassic stromatoporoid *Cladocoropsis mirabilis* Felix (Fig. 13). Also in this case, thaumatoporellaceans occur dispersed in the micritic matrix, attached to the stromatoporoid skeletons and completely lining the interior mimicking with its shape 1:1 its canal system. Whether, in these cases, *Irregularina* and *Thaumatoporella* were invading the metazoan skeletons parasitically or as predators during life time of the host or just used the dead skeletons as protection site is unknown. Another cross linkage to thaumatoporellaceans is given by multilobate irregular-shaped forms homeomorphic to *Irregularina*. From the Lower Cretaceous of Romania such morphotypes were described as *Vermiporella crisiae* by Dragastan et al. (1989). Examples of *Irregularina*-shaped thaumatoporellaceans from the Liassic and Upper Cretaceous of Albania, some clearly exhibiting the finely perforated outer membrane (or wall), are illustrated in Figure 14. Also thaumatoporellacens obviously possessed a non-rigidly calcified wall during life-time as evidenced by flexible responses to pressure. This would require that the organism body itself was under pressure as discussed by Flügel (1983: p. 276). A nice example was shown by Cherchi & Schroeder (2005: fig. 7) from Early Jurassic crust-forming thaumatoporellaceans. Here several larger grains pressing to the outer wall lead to a distinct reduction in thickness of the encrusting specimen only at the contact zone, a reaction that would not be possible with a rigid skeleton. The next crust layer simply overgrows these large grains that then become switched between them. Whether this process can be termed trapping, "retention of particles on a microbial substrate and their subsequent incorporation" by vertical growth of the organism (Riding 1991: p. 24), however, remains debatable. The same holds true also for the deduced re-interpretation of thaumatoporellaceans as calcified colonial cyanobacteria (see also Carannante et al. 2007: p. 264). Worth to mention, that already Radoičić (1960: p. 138) remarked (without giving arguments) that the dark skeletons of *Thaumatoporella* "probably primarily had not been calcareous". Morphologically, some of the Liassic thaumatoporellaceans (without detectable pores) can directly be compared with Devonian forms like *Irregularina*? *horrida*, *I. nodosa* or I. *lobata*. This analogy of Devonian *Irregularina* and some representatives of Mesozoic thaumatoporellaceans might be interpreted in terms of a convergent morphological

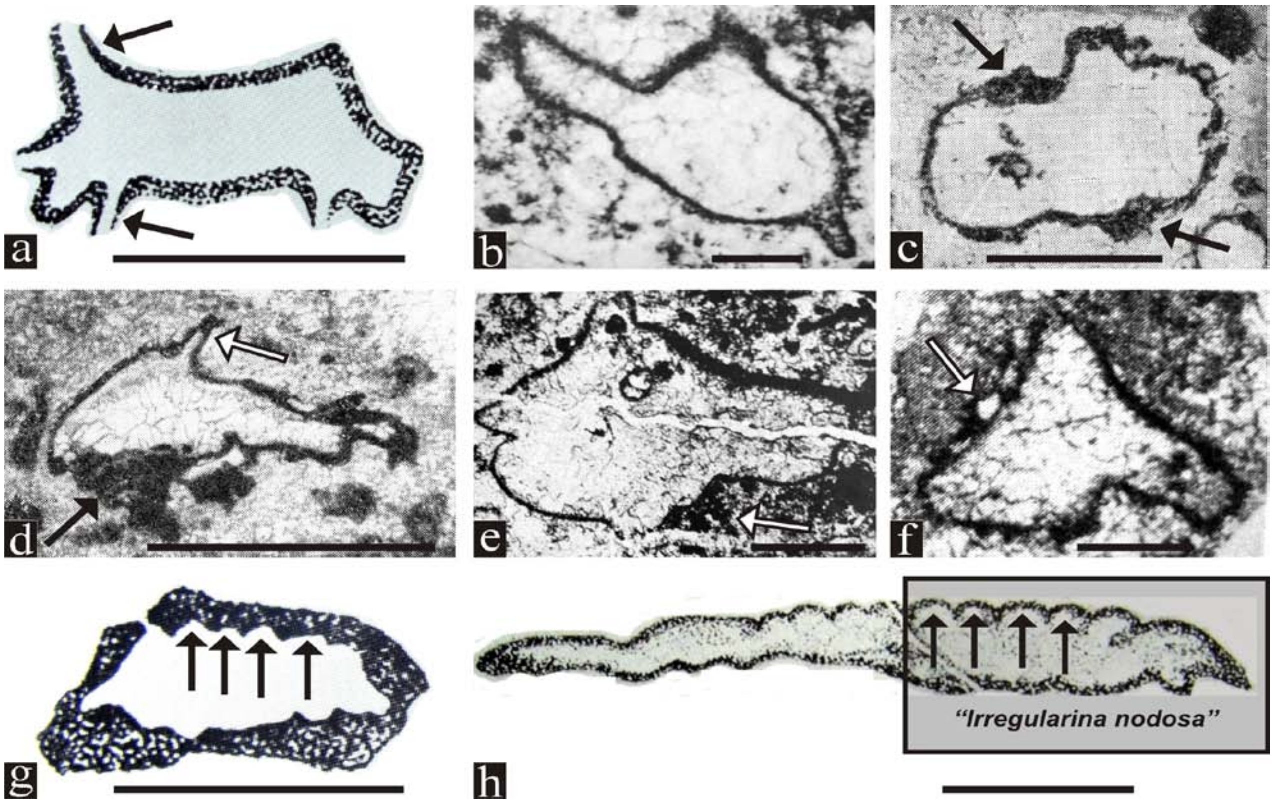

Fig. 12 - Examples of thin-section appearance of some representatives of *Irregularina* (**a-d**) and problematic algae (**e-f**) according to their original descriptions. **a** *Irregularina karlensis* Vissarionova, Givetian of Russia (from Vissarionova, 1950, fig. 1). Arrows show the so-called apertural nozzles. **b** *Irregularina* sp., Devonian of France (from Vachard 1994: pl. 3, fig. 12 " relatively typical specimen of the genus with its irregular shape")**. c** *Irregularina lobata* Reitlinger, Devonian of Russia (from Reitlinger, 1954: pl. 18, fig. 8). Arrows show sediment particles attaching to the external side of the wall. **d** *Irregularina*? *horrida* Reitlinger, holotype, Devonian of Russia (from Reitlinger 1954: pl. 17, fig. 6). Note attached sediment particles (black arrow) and "apertural nozzle" (white arrow). **e-f** *Uslonia permira* Antropov, Devonian of Russia (from Zadorozhnyy & Yuferev, 1984: pl. 4, figs. 11-12). **g** *Irregularina nodosa* (Antropov), Frasnian of Tatarstan (from Rauzer-Chernousova & Fursenko, 1959). Note the rugose outline (arrows). **h** *Irregularina*? *rugosa* Kotlyar, holotype, Frasnian of Ukraine (from Kotlyar, 1982: fig. 3a). This form with its rugose outline (arrows) can be considered a more compressed and elongated morphotype of *I. nodosa* (Fig. g). Scale bars 0.2 mm

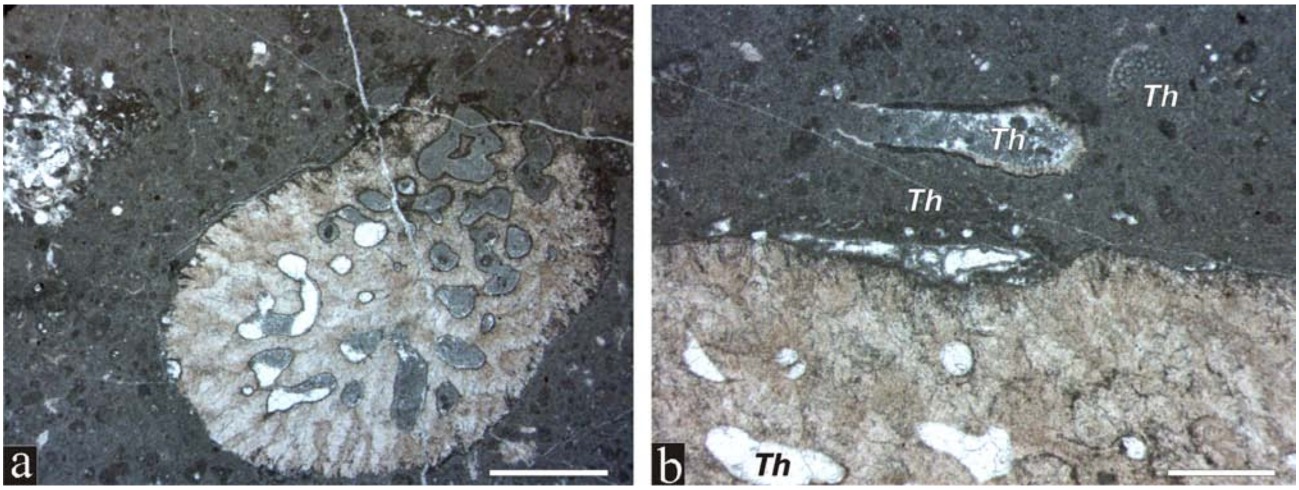

Fig. 13 - Cryptoendolithic thaumatoporellaceans entering the stromatoporoid *Cladocoropsis mirabilis* Felix from the Oxfordian-Kimmeridgian of Serbia. Thaumatoporellaceans are also attaching the skeletons and simultaneously occur free inside the micritic matrix (Th in b). This cryptoendolithic behaviour is directly comparable to Devonian *Irregularina* specimens (see Figs. 8-9). Thin section RR 2618. Scale bar 1mm for **a**; 0.5 mm for **b**

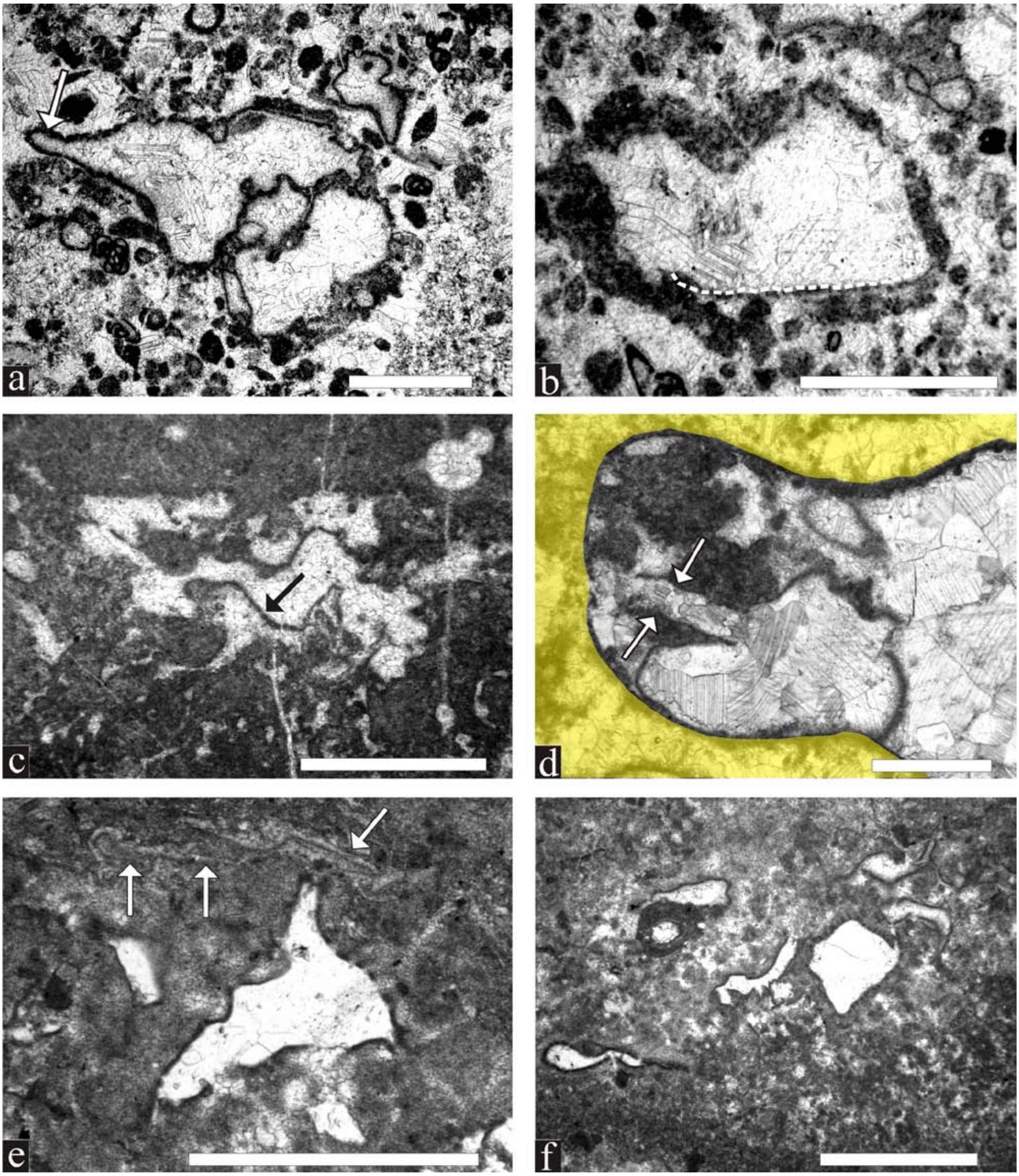

Fig. 14 - Examples of *Irregularina*-shaped thaumatoporellaceans from the Early Jurassic of Albania (**a-b**), the Early (**c**) and Middle Jurassic (**d**) of Croatia and the Upper Cretaceous of Albania (**e-f**). **a-b** The specimens occur in a grainstone most likely winnowed from a packstone deducable from the sediment particles fixed to the thin outer wall. Note the elongate test protrusions in the specimen left above in **a** (= "apertural nozzles" in Palaeozoic *Irregularina*). In **b,** the boundary between the wall and the sediment is partly accentuated by a dotted white line. Thin-section A 3644o. **c** Specimen exhibiting numerous irregular constrictions dwelling in a microbial crust. Late Aalenian-Early Bajocian, thin-section SL 2-3. **d** Specimen dwelling cryptoendolithically in a gastropod shell (accentuated in yellow). Note the protuberance on the left side (arrows) (= "apertural nozzles" of *Irregularina*). Pliensbachian, thin-section VE 514-13. **e** *Irregularina*-shaped *Thaumatoporella* showing perforated wall. Note the altered and compressed specimen above (arrows). "Senonian", thin-section Kru-1b. **f** Microbialite showing clotted texture (thrombolite) with several thin-walled polymorphic specimens of *Thaumatoporella*. "Senonian", thin-section Kru-3. Scale bars 0.5 mm.

evolution for interstitial modes of life (e.g., Rundell & Leander, 2010). Another additional explanation would be that both taxa belong to the same order of higher taxonomic rank. It is worth mentioning that according to Vachard (1994: p. 34) and Vachard & Clement (1994: p. 300), the Irregularinidae (e.g., genera *Irregularina*, *Bisphaera*, *Cribrosphaeroides*) and the Thaumatoporellaceae sensu De Castro (1988, 1990) share several common features. Psammobiontic thaumatoporellaceans may also exhibit sediment grains attaching to the outer membrane/wall (Fig. 14). Other morphotypes (or species?) of thaumatoporellaceans, however, are clearly encrusting forms, for instance in Late Triassic reefal carbonates (Sadati, 1981; De Castro, 1990; Cherchi & Schroeder, 2005; Schlagintweit & Bover-Arnal, 2013). In any case, the illustrated Liassic specimens, homeomorphic to *Irregularina*, are morphologically different from the Late Cretaceous type-material (Raineri, 1922; De Castro, 1990, 2002). Therefore we refrain from attributing them to the type-species *T. parvovesiculifera* (Raineri) but instead simply refer to them as thaumatoporellaceans. Further discussions about the interrelationships between certain representatives of the Irregularinidae and thaumatoporellaceans are beyond the scope of the present contribution and will be the topic of a separate contribution.

Apart from all the discussed similarities of *Irregularina* and amoebozoans, also the size of individual *Irregularina* specimens is in the range recorded from the latter, especially giant forms. Many amoebozoa are only 10 to 20 µm in size, but giant forms such as the amoeba *Chaos carolinense* exhibit sizes up to 5 mm (e.g., Tan et al., 2005). Summarizing, many characteristics that we observed from the investigated *Irregularina* specimens could be well explained assuming that we are dealing with a motile animal-like amoeboid protist possessing a psammobiontic way of life or alternatively occurring as cryptoendoliths (parasitically?) inside metazoan skeletons.

Taxonomic inventory of *Irregularina*

Based on variations in morphology (ouline) and size, 12 species of *Irregularina* were described as compiled by Vachard (1994: p. 34) (Fig. 12). In our compilation we note the establishment of all together 17 species (Tab. 2). Vachard noted gradual morphological transitions (“ecophenotypic modifications”) and difficulties in determinations of these species. Different “species” of *Irregularina* were distinguished by differences in the general outline, size, and the presence and number of both constrictions and “apertural nozzles”. When referring to differences in morphology, it is important to stress that these are related to the two-dimensional appearances in thin-sections as none of the created species is based on isolated material. This means, that we are not dealing with an objective criterion but random planes of sectioning that may or may not cut morphological characteristics. This problem was also shortly adressed to Middle-Late Devonian microfossils, i.e. parathuramminids, by Racki & Soboń-Podgórska (1993). Besides different planes of sections, the high morphological variability is directly related to the psammobiontic and cryptoendolithic way of life. *Irregularina* can be referred to flexible bodies that, like some thaumatoporellaceans, were able to adapt its morphology to available spaces. Lacking a fixed external morphology, differences in size and morphology (with all transitions) considered as adaptive characteristic in psammobiontic biota can therefore not be used to distinguish different species of *Irregularina*. In accordance with the adaptive approach, we find specimens with morphologies referable either to *I. karlensis*, *I. nodosa*, *I. lobata* or *I.*? *horrida* in the same samples studied. In one case for example, a specimen of *I.*? *horrida* is connected to a specimen of *I. karlensis* by means of an “apertural nozzle” (Fig. 10b) and interpreted as a specimen in state of possible binary division. As we do not see a comprehensible exact definition of individual species, all our specimens are tentatively referred to the type-species *I. karlensis*. Of course, we cannot exclude the possibility of more than one species but we are unable to clearly define separate taxa with characteristics that can unambiguously be applied by subsequent workers. Even monospecificy of *Irregularina* cannot be excluded at the current stage of knowledge. In order to increase the accuracy of such a rigorous taxonomic interpretation, however, it is considered necessary to examine the type material of the established species.

CONCLUSIONS

New observations and interpretations on the problematic microfossil *Irregularina* Bykova are provided. The high morphological variability (here: contour or outline in random thin-sections) is given by the inferred motility of *Irregularina* (due to a flexible, non-rigid outer body membrane) allowing to change its shape. This feature also permitted the adaptation to special microhabitats, e.g., availability of pore spaces, within the sediment or hollow bioclasts (cryptoendolith!). Therefore, the shape represents an insufficient characteristic for reliable discrimination of species and their determination in random thin-sections. The general diversity is challenged and a monotypy of the genus *Irregularina* cannot be excluded. Some of the described “species” are interpreted as not belonging to the genus *Irregularina*.

The evidenced characteristics of *Irregularina* are neither compatible with a foraminiferan nor algal origin. In fact, compared to the modern psammobiontic (or interstitial) organisms, *Irregularina* shows some affinities to lobose amoebozoans, animal-like phagotrophic protists. Details on the exact taxonomic position and way of life (motility, feeding behavior), however, must remain open for discussion.

Similar features as observed from *Irregularina*, may be attributed also to certain representatives of Mesozoic thaumatoporellaceans that exhibit *Irregularina*-type homeomorphic shapes with or without elongated protuberances (“apertural nozzles”).

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