Palaeobiodiversity and Palaeoenvironments (2020) 100:705–718
https://doi.org/10.1007/s12549-020-00417-4

SENCKENBERG

ORIGINAL PAPER

Early Famennian bryozoan fauna from the Baqer-abad section, northeast Isfahan, central Iran

Andrej Ernst[1] · Ali Bahrami[2] · Ayesheh Parast[2]

Received: 15 April 2019 / Revised: 2 July 2019 / Accepted: 16 January 2020 / Published online: 3 April 2020

Abstract

A bryozoan fauna from the Upper Devonian (lower Famennian) of the Bahram Formation of the Baqer-abad section in central Iran contains four species: three trepostomes and one rhabdomesine cryptostome. Two trepostome species and one genus are new: *Anomalotoechus parvus* sp. nov. and *Zefrehopora asynithis* gen. nov. et sp. nov. The trepostome *Coeloclemis zefrehensis* Ernst et al., 2017 and the rhabdomesine cryptostome *Euthyrhombopora tenuis* Ernst et al., 2017 were recorded previously from the Upper Devonian (Frasnian) of the Bahram Formation at the Zefreh section. The fauna is dominated by the erect ramose *Euthyrhombopora tenuis*, accompanied by relatively frequent *Zefrehopora asynithis*, which developed both the erect and encrusting colonies. The bryozoans indicate low to moderate water energy environment in a middle to outer ramp position. Low diversity and high abundance of one species indicate an environmental stress apparently caused by strong sediment deposition. No significant differences in the composition of the bryozoan assemblages of the Frasnian and lower Famennian of the Bahram Formation were observed mirroring global patterns.

Keywords Bryozoa · Taxonomy · Early Famennian · Northeast Isfahan · Central Iran

Introduction

The late Middle and Late Devonian represents a relatively warm period with an acme in diversity, size and latitudinal distribution of reefs and associated shallow-water sediments in the Middle Devonian (Flügel and Kiessling 2002; Joachimski et al. 2009). On the other hand, the mid-Palaeozoic underwent dramatic change in Earth's climate systems which resulted in changes in ocean chemistry and sea level. As a consequence of this, palaeoecosystems were impacted by several mass extinctions and ecological perturbations spanning millions of years (e.g. Talent et al. 1993). Fluctuations in physical palaeoenvironments and resultant mass extinctions were recorded in the sedimentological record by lithological changes and geochemical excursions which are also dependent on the depositional setting (Mottequin et al. 2017). Middle to Late Devonian strata are mainly composed of shallow-water facies and occur in isolated units in central Iran (e.g. Zahedi 1973; Soffel and Förster 1984; Wendt et al. 2005). The distribution of the upper Palaeozoic sediments around Isfahan (Fig. 1) is mostly limited to the northern Isfahan basin (Soh and Natanz regions Najhf, Negheleh, Varkamar, Northern Tar and Western Kesheh sections; (Zahedi 1973; Adhamian 2003; Ghobadipour et al. 2013; Bahrami et al. 2015), northeastern Isfahan basin (Zefreh, Chahriseh and Dizlu sections; Brice et al. 2006; Gholamalian 2003; Habibi et al. 2013; Königshof et al. 2017; Ernst et al. 2017; Bahrami et al. 2018) and southern Isfahan basin (Darchaleh and Ramsheh (in Shahreza region) sections; Boncheva et al. 2007; Leven and Gorgij 2008, 2011; Bahrami et al. 2014). The main objectives of this paper are to describe and interpret the bryozoan fauna from bryozoan-

This article is registered in Zoobank under urn:lsid:zoobank.org:pub:DAD5D022-364E-4E12-938E-FC2434767ABC

✉ Ali Bahrami
Bahrami_geo@yahoo.com

Andrej Ernst
Andrej.Ernst@uni-hamburg.de

Ayesheh Parast
hp400875@gmail.com

[1] Institut für Geologie, Universität Hamburg, 20146 Hamburg, Germany

[2] Department of Geology, Faculty of Sciences, University of Isfahan, Isfahan, Iran

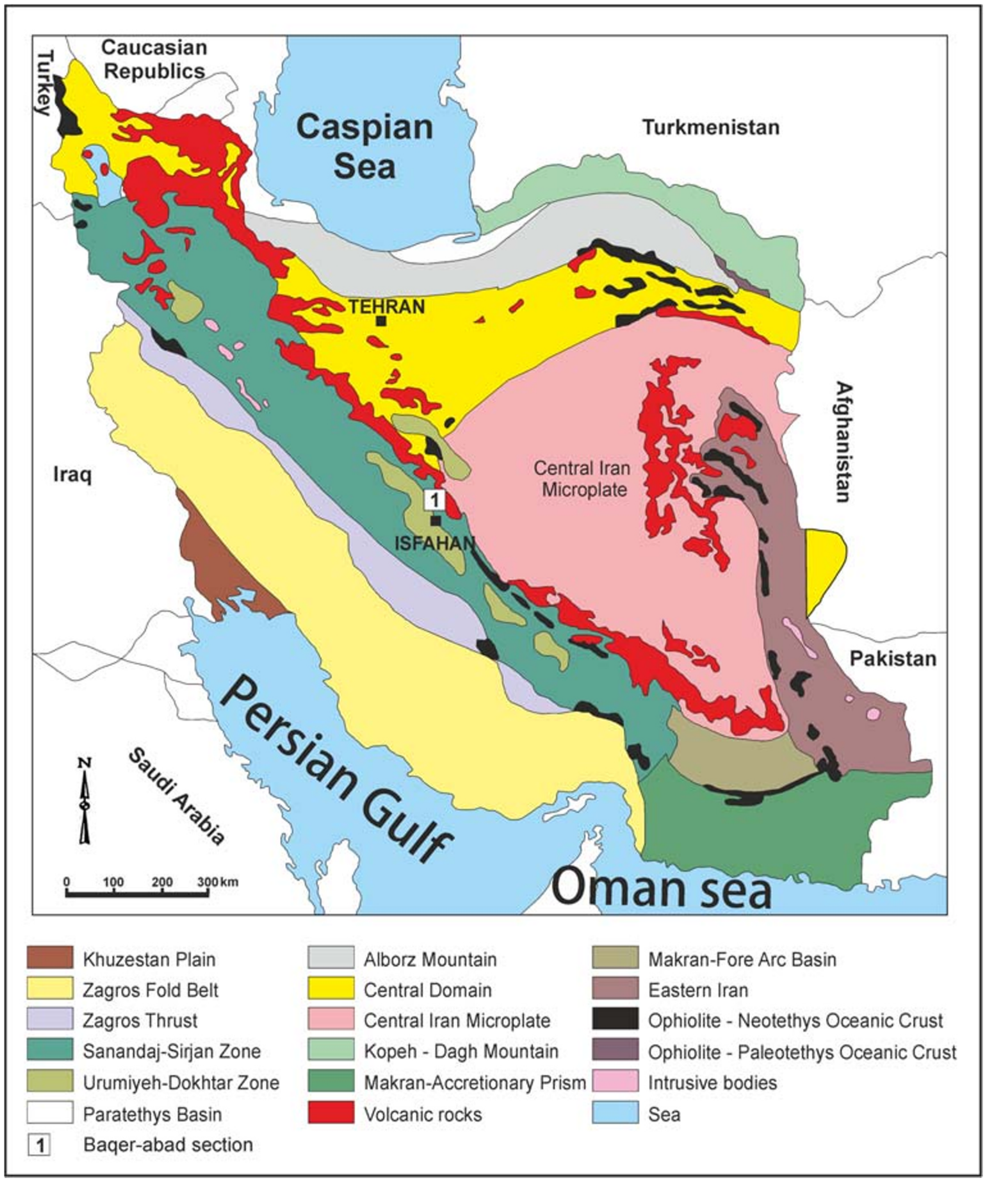


Fig. 1 Structural map of the central Iran (the star marks the position of the investigated section; after Königshof et al. 2017)

bearing horizons at the lower part of the Bahram Formation in the study area (Baqer-abad section, NE Isfahan).

Geological setting and material

The Baqer-abad section is located 46 km to the northeast of Isfahan (N 33° 2′ 38″, E 51° 57′ 91″ WGS coordinates; Fig. 2) in the area where most Devonian outcrops of Iran are exposed; the sequence includes some hiatuses due to erosion and/or tectonic activity. The entire section has a thickness of approximately 1000 m, ranging stratigraphically from the Devonian (Bahram Formation) to the Cretaceous (Aptian-Albian), whereas the studied section of the Bahram Formation has a thickness of 220 m representing mainly shallow-water palaeoenvironments. The section has been grouped in 13 units which include fossiliferous carbonate units with brachiopods, tentaculitids, corals, gastropods, crinoid remains and bryozoans, with a few shale (grey to black) and sandstone interbeddings. Bryozoans occur in distinct layers mainly in the lower part (*triangularis* to *crepida* conodont zones) of the section in unit 1 (samples P1–P6; Figs. 3, 4). Twenty-seven rock samples were taken from this part of the section from which 54 thin sections of different size were made.

Systematic palaeontology

Bryozoans were studied in thin sections using a binocular microscope. Morphological character terminology is partly adopted from Anstey and Perry (1970) for trepostomes and from Hageman (1993) for cryptostomes. The spacing of structures is measured as the distance between their centres. Statistics are

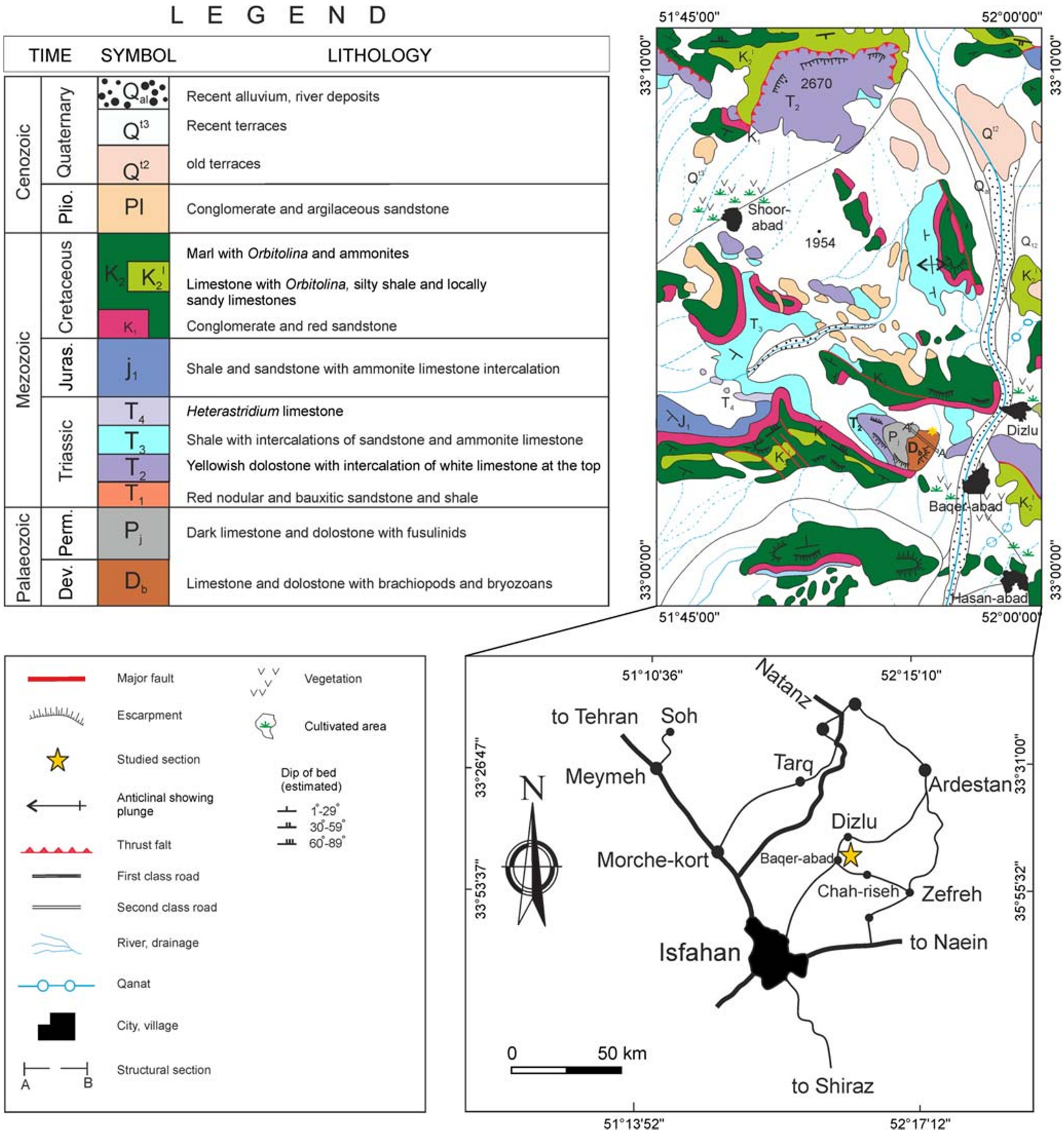


Fig. 2 Geological map of the studied area with indication to accessible road to the studied section. (After Zahedi (1973), slightly modified)

summarised using number of measurements (*N*), arithmetic mean (*X*), sample standard deviation (SD), coefficient of variation (CV) and minimum (MIN) and maximum (MAX) values. All the studied material is housed at Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany (prefix SMF).

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Superorder Palaeostomata Ma, Buttler and Taylor, 2014
Order Trepostomata Ulrich, 1882
Suborder Amplexoporina Astrova, 1965
Family Stenoporidae Waagen and Wentzel, 1886
Genus *Coeloclemis* Girty, 1911

Type species: *Coeloclemis tumida* Girty, 1911. Fayetteville Shales (Upper Mississippian, Carboniferous); Westville, Oklahoma, USA.

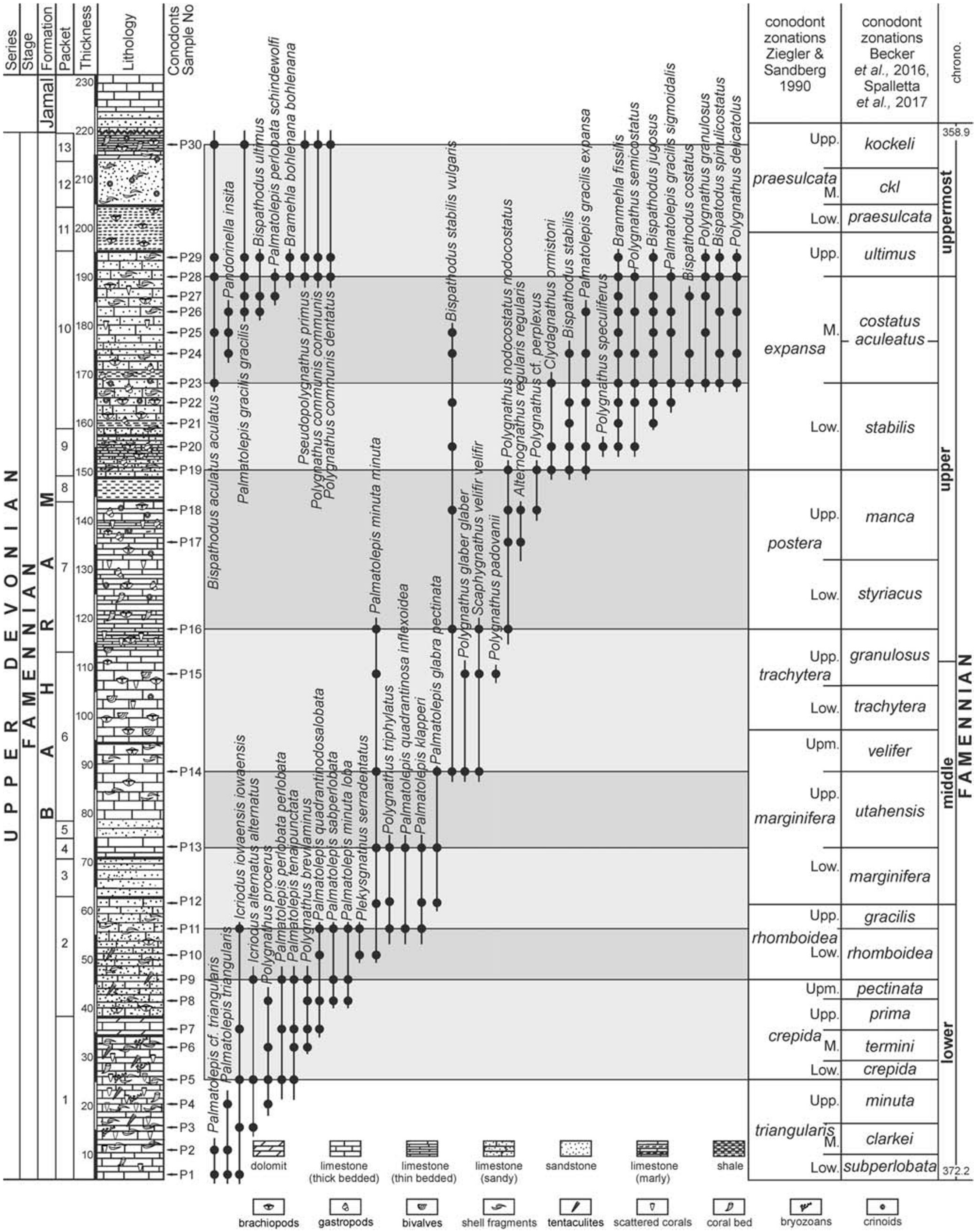


Fig. 3 Lithological characteristics and stratigraphy of the Baqer-abad section based on conodont fauna

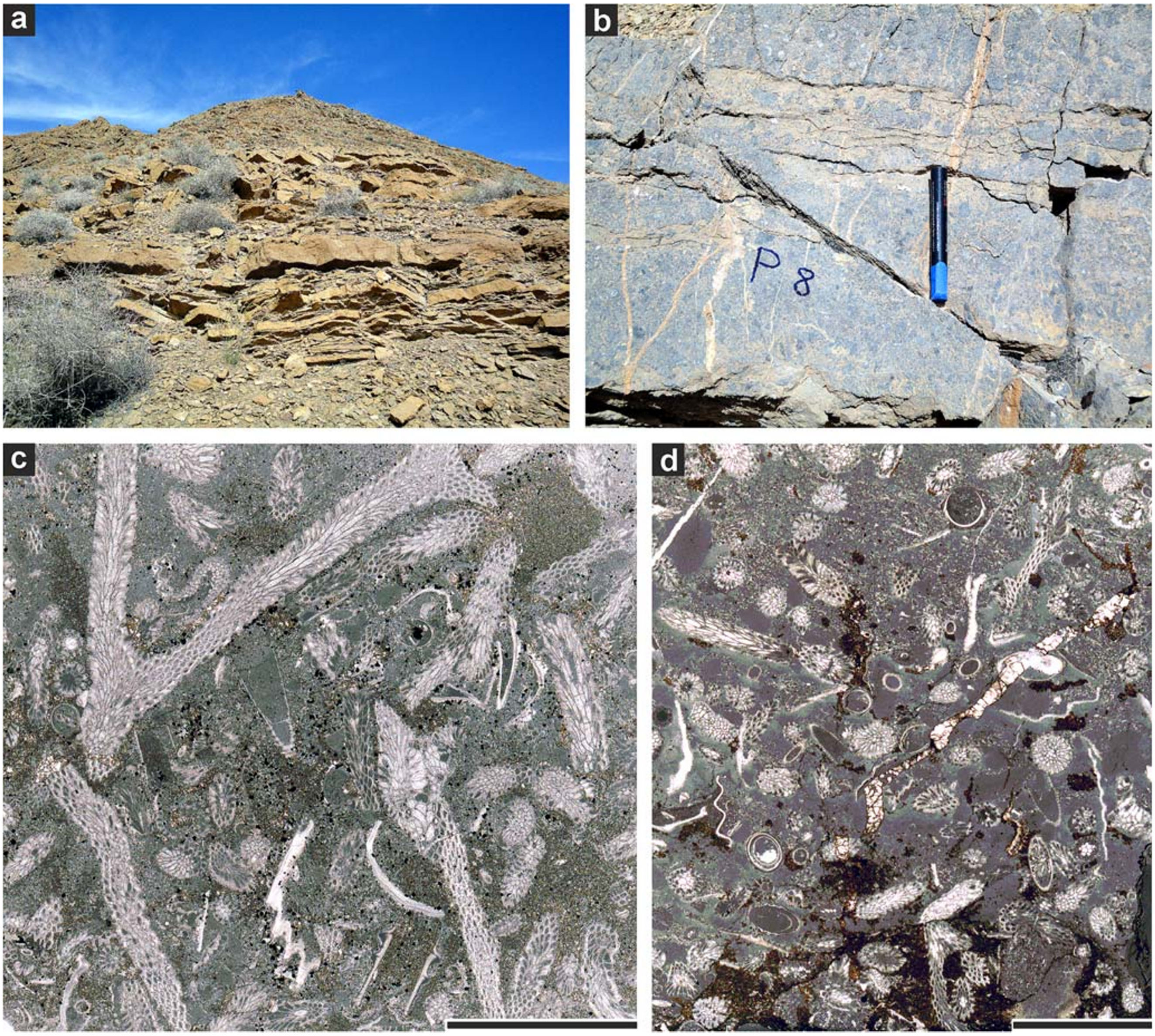
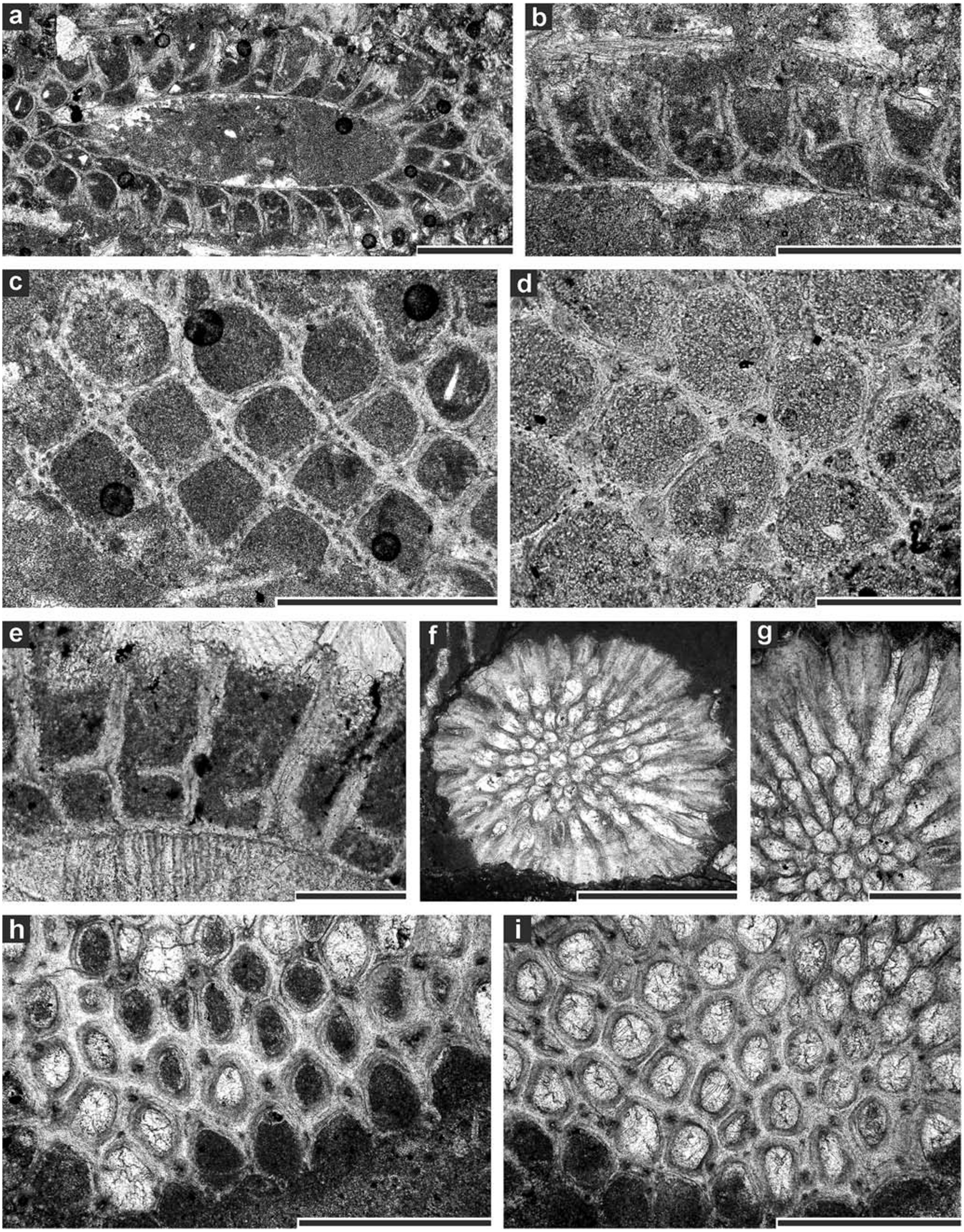


Fig. 4 **a**–**b** Field photographs of the Baqer-abad section. **a** Medium to thick-bedded sandy limestone just above the bryozoan bearing horizons (package 2). **b** Grey thick-bedded limestone with scattered bryozoan fauna (part of package 1). **c**–**d** Thin sections parallel (**c**) and across (**d**) bedding plane showing lithological characteristic of limestones at the Zefreh section. **a** SMF 23.899, **b** SMF 23.914. Scale bars 5 mm (**c**–**d**)

Occurrence: Upper Devonian to Lower Carboniferous; Iran; USA.

Diagnosis: Colonies encrusting, maculae unknown. Autozooecia usually cylindrical or prismatic, with short recumbent parts, growing from exterior basal colony walls. Autozooecial apertures circular to oval, becoming polygonal in deeper sections. Hemiphragm, in type species, located at transition of exozone to endozone, on proximal side deflected towards base. Exilazooecia rare or absent. Exozonal styles present, usually located at autozooecial corners. Diaphragms absent. Walls thick and laminated in exozone, in tangential-section autozooecial boundary cross-sectional shape four to six sided in inner exozones becoming sub-polygonal to sub-circular in outer exozones, with disordered pattern on outer colony surface. Cortex thickness regular, no cingulum; weakly beaded in some species. Autozooecial cortex microstructure laminated, boundaries serrated. Cortex spherules and tubules common, generally located at zooecial boundaries in rows and occasionally in groups. Some tubulae project as spines into zooecial chambers (modified after Caroline Buttler, pers. comm., 2016).

Remarks: *Coeloclemis* is unique because of the presence of a single hemiseptum in the autozooecia. It differs from *Stenophragmidium* Bassler, 1952 in the presence of this single hemiseptum instead of hemiphragms in autozooecia. Records of *Coeloclemis* from the Upper Carboniferous and Permian do


a
b
c
d
e
f
g
h
i

◀ **Fig. 5** **a**–**e** *Coeloclemis zefrehensis* Ernst et al., 2017. **a**–**b** Longitudinal section of the colony showing autozooecial chambers with hemisepta, SMF 23.852. **c** Tangential section showing autozooecial apertures, acanthostyles and microacanthostyles, SMF 23.852. **d** Tangential section showing autozooecial apertures, acanthostyles and microacanthostyles, SMF 23.845. **e** Longitudinal section of the colony showing autozooecial chambers with hemisepta, SMF 23.840. **f**–**i** *Anomalotoechus parvus* sp. nov. **f**–**g** Branch transverse section, holotype SMF 23.864. **h**–**i** Tangential section showing autozooecial apertures and acanthostyles, holotype SMF 23.864. Scale bars 1 mm (**f**), 0.5 mm (**a**, **b**, **c**, **g**, **h**, **i**), 0.2 mm (**d**, **e**)

not belong to this genus because of the absence of a hemiseptum, which is a diagnostic feature of *Coeloclemis*.

Coeloclemis zefrehensis Ernst et al., 2017
(Fig. 5a–e; Table 1)

2017 *Coeloclemis zefrehensis* Ernst et al., p. 543, fig. 3a–f

Material: SMF 23.840–SMF 23.863.
Description: Thin encrusting colonies, 0.20–0.36 mm thick. Autozooecia growing from a thin epitheca, bending gently in their deeper portion and intersecting the colony surface at angles of 80–90°. Epitheca 0.008–0.010 mm thick. Typically single long hemiphragm in each autozooecium on its proximal wall, curved proximally. Autozooecial diaphragms rare, straight. Autozooecial apertures polygonal. Exilazooecia few to absent. Acanthostyles large, abundant, 3–5 surrounding each autozooecial aperture. Microacanthostyles abundant, arranged irregularly in the exozonal wall between autozooecia, 0.010–0.025 mm in diameter. Autozooecial walls granular, 0.005–0.010 mm thick in endozone; laminated, 0.030–0.055 mm thick in exozone.
Remarks: *Coeloclemis zefrehensis* Ernst et al., 2017 differs from *C. tumida* in the smaller distances between autozooecial apertures (0.13–0.23 mm vs. 0.29–0.40 mm in *C. tumida*). The species *Eostenopora unica* Yang, Hu and Xia, 1988 described from the Frasnian of China may belong to the genus *Coeleclemis*. Singular hemisepta typical for *Coeloclemis* are visible in longitudinal sections of this species (Yang, Hu and Xia. 1988, p. 155, pl. 19, Figs. 4–5). This species has larger autozooecial apertures (aperture width 0.15–0.21 mm vs. 0.09–0.19 mm in *Coeloclemis zefrehensis*).
Occurrence: Zefreh section, central Iran; Bahram Formation, Upper Devonian (Frasnian). Baqer-abad section, central Iran; Bahram Formation, Upper Devonian (lower Famennian).

Family Atactotoechidae Duncan, 1939
Genus *Anomalotoechus* Duncan, 1939
(= *Stereotoechus* Duncan, 1939; see Boardman 1960; Astrova 1978)

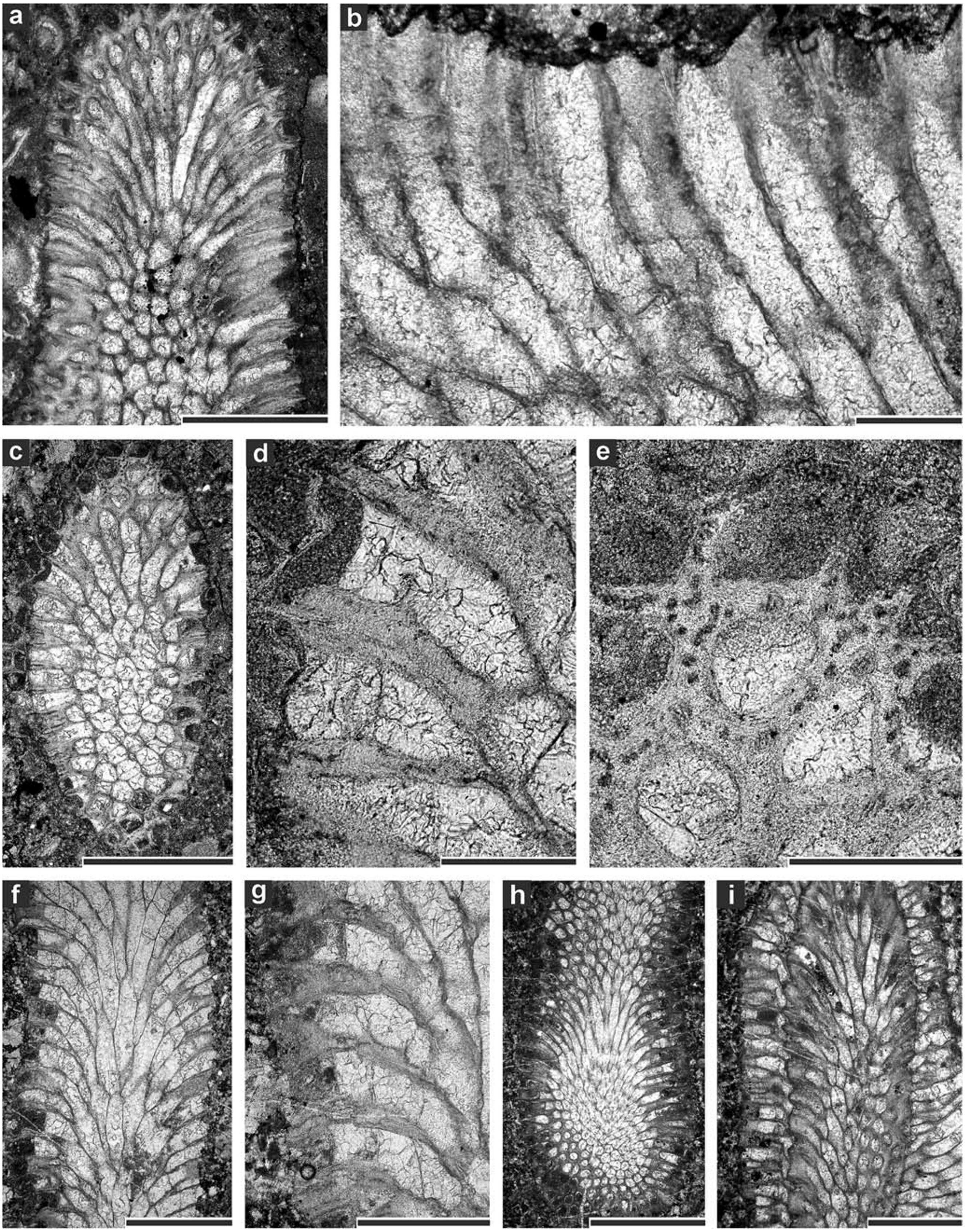
Type species: *Anomalotoechus typicus* Duncan, 1939. Traverse Group (Middle Devonian); Michigan, USA.
Diagnosis: Encrusting, massive, less commonly branched colonies. Autozooecia with polygonal to rounded-polygonal apertures. Diaphragms abundant in exozones, straight or inclined. Exilazooecia rare, short. Acanthostyles abundant. Autozooecial walls thin in the endozone; merged, without visible zooecial boundaries, strongly and irregularly thickened in the exozone, often with monilae-shaped thickenings.
Remarks: *Anomalotoechus* Duncan, 1939 differs from *Leptotrypa* Ulrich, 1883 in having massive and branched colonies, thickened walls and abundant diaphragms, and from *Atactotoechus* Duncan, 1939 in having abundant acanthostyles.
Occurrence: Upper Silurian–Upper Devonian; North America, Eurasia.

Anomalotoechus parvus sp. nov.
(Figs. 5f–i and 6a–b; Table 2)

Derivation of name: The species name refers to the small colony (from Latin *parvus*—small)
Holotype: SMF 23.864.
Paratypes: SMF 23.865–SMF 23.870.
Type locality: Baqer-abad section, central Iran.
Type level: Bahram Formation, Upper Devonian (lower Famennian).
Measurements: See Table 2.
Diagnosis: Thin-branched colonies with distinct exozones; diaphragms rare; autozooecial walls thick, monilae-shaped in early exozone; exilazooecia few, small; acanthostyles abundant, 3–5 surrounding each autozooecial aperture; maculae absent.
Description: Branched colonies, 0.94–2.10 mm in diameter, with 0.19–0.65 mm wide exozones and 0.43–1.15 mm wide endozones. Autozooecia long in endozones, bending abruptly in exozones. Autozooecial

Table 1 Summary of descriptive statistics for *Coeloclemis zefrehensis* Ernst et al., 2017. Abbreviations: *N*, number of measurements; *X*, mean; *SD*, sample standard deviation; *CV*, coefficient of variation; *MIN*, minimal value; *MAX*, maximal value

	N	*X*	SD	CV	MIN	MAX
Autozooecial aperture width, mm	50	0.14	0.021	15.38	0.09	0.19
Autozooecial aperture spacing, mm	50	0.18	0.020	11.40	0.13	0.23
Acanthostyle diameter, mm	40	0.036	0.007	19.45	0.025	0.050
Acanthostyles per aperture	22	3.6	0.727	19.99	3.0	5.0
Autozooecial wall thickness, mm	10	0.040	0.007	16.97	0.030	0.055


a
b
c
d
e
f
g
h
i

◀ **Fig. 6** **a**–**b** *Anomalotoechus parvus* sp. nov. **a** Branch longitudinal section showing autozooecial chambers, holotype SMF 23.864. **b** Branch longitudinal section showing autozooecial chambers and monilae-shaped autozooecial walls, holotype SMF 23.864. **c**–**i** *Zefrehopora asynithis* gen. nov. et sp. nov. **c** Oblique section of a branched colony, holotype SMF 23.871. **d** Longitudinal section showing autozooecial chambers with diaphragms and hemiphragms (arrow), holotype SMF 23.871. **e** Tangential section showing autozooecial apertures, acanthostyles and tubules, holotype SMF 23.871. **f**–**g** Longitudinal section of the colony showing autozooecial chambers with hemiphragms, paratype SMF 23.880. **h** Oblique section of a branched colony showing autozooecial chambers in endozone and exozone, paratype SMF 23.887. **i** Longitudinal section showing secondary overgrowth, paratype SMF 23.887. Scale bars 2 mm (**h**), 1 mm (**a**, **c**, **f**, **i**), 0.5 mm (**g**), 0.2 mm (**b**, **d**, **e**)

apertures rounded-polygonal. Autozooecial diaphragms rare in exozone, straight, thin; absent in endozone. Autozooecial walls laminated, 0.005–0.008 mm thick in endozone; merged without visible zooecial boundaries, locally monilae-shaped in early exozone, 0.05–0.12 mm thick in exozone. Exilazooecia few, polygonal in shape, 0.03–0.05 mm in diameter. Acanthostyles abundant, 3–5 surrounding each autozooecial aperture. Maculae absent.

Remarks: *Anomalotoechus parvus* sp. nov. differs from *A. insuetus* (Morozova, 1959) from the Frasnian of Kuznets Basin in having rare autozooecial diaphragms, and from *A. ramosus* (Morozova, 1959) from the same locality in having rare autozooecial diaphragms and abundant acanthostyles. *Anomalotoechus parvus* differs from *A. pervulgatus* Lavrentjeva, 2001 from the lower Famennian of Transcaucasia in having branched colony and in smaller autozooecial apertures (aperture width 0.09–0.16 mm vs. 0.12–0.22 mm in *A. pervulgatus*).

Occurrence: *Anomalotoechus parvus* sp. nov. is currently only known from the Bahram Formation, Upper Devonian (Frasnian) at the Baqer-abad section, central Iran.

Family Eridotrypellidae Morozova, 1960

Genus *Zefrehopora* gen. nov.

Type species: *Zefrehopora asynithis* gen. nov. et sp. nov., by monotype.

Derivation of name: The genus name refers to the Zefreh section in the vicinity of which it was found.

Occurrence: Central Iran; Bahram Formation, Upper Devonian (Frasnian).

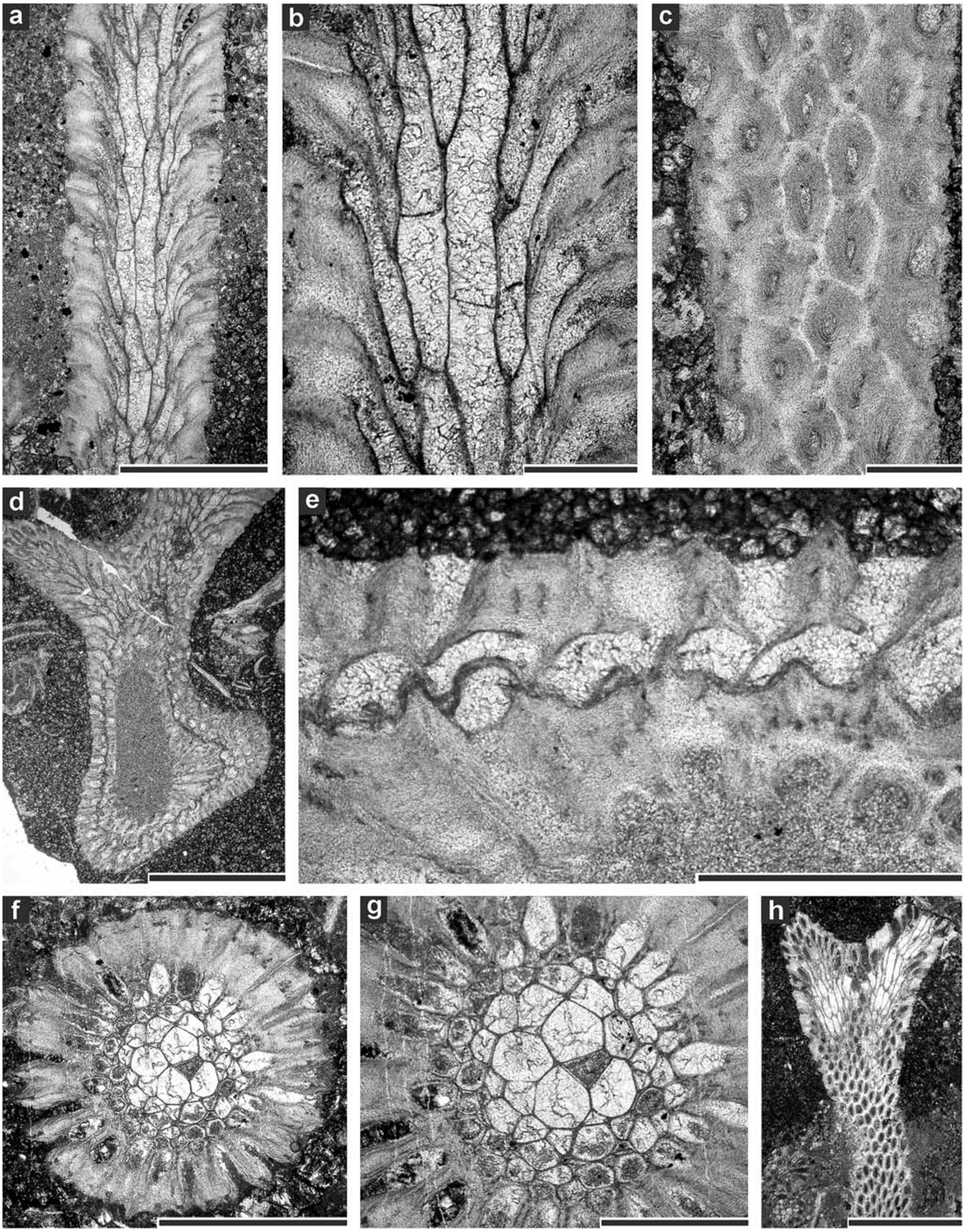
Diagnosis: Branched and encrusting colonies; autozooecial apertures rounded-polygonal; autozooecial diaphragms rare to common, concentrated in the exozone, straight, thin; hemiphragms rare, straight; exilazooecia few; acanthostyles abundant, 2–5 surrounding each autozooecial aperture; tubules between acanthostyles abundant; autozooecial walls laminated, merged without visible zooecial boundaries; indistinct maculae of macrozooecia.

Table 2 Summary of descriptive statistics for *Anomalotoechus parvus* sp. nov. Abbreviations as for Table 1

	N	*X*	SD	CV	MIN	MAX
Autozooecial aperture width, mm	20	0.09	0.027	28.46	0.06	0.16
Autozooecial aperture spacing, mm	20	0.17	0.030	17.95	0.12	0.24
Acanthostyle diameter, mm	20	0.05	0.008	17.72	0.03	0.06
Acanthostyles per aperture	10	3.7	0.823	22.25	3.0	5.0
Branch diameter, mm	10	1.63	0.373	22.90	0.94	2.10
Exozone width, mm	10	0.45	0.156	34.50	0.19	0.65
Endozone width, mm	10	0.72	0.216	29.94	0.43	1.15
Autozooecial wall thickness, mm	10	0.08	0.022	28.22	0.05	0.12

Table 3 Summary of descriptive statistics for *Zefrehopora asynithis* gen. nov. et sp. nov. Abbreviations as for Table 1

	N	*X*	SD	CV	MIN	MAX
Autozooecial aperture width, mm	70	0.12	0.017	14.68	0.08	0.15
Autozooecial aperture spacing, mm	70	0.17	0.023	13.32	0.13	0.22
Acanthostyle diameter, mm	45	0.03	0.016	48.84	0.013	0.060
Acanthostyles per aperture	25	3.1	0.862	27.99	2.0	5.0
Exilazooecia width, mm	20	0.04	0.009	24.50	0.02	0.05
Branch diameter, mm	5	1.59	0.410	25.79	1.08	2.10
Exozone width, mm	5	0.36	0.108	29.71	0.25	0.50
Endozone width, mm	5	0.87	0.224	25.84	0.58	1.20
Autozooecial wall thickness, mm	45	0.05	0.010	19.92	0.028	0.070


a
b
c
d
e
f
g
h

◀ **Fig. 7** **a**–**h** *Euthyrhombopora tenuis* Ernst et al., 2017. **a**–**b** Longitudinal section of the colony showing autozooecial chambers with hemisepta and axial zooecia, SMF 23.899. **c** Tangential section showing autozooecial apertures, acanthostyles and paurostyles, SMF 23.903. **d** Branched colonies with secondary overgrowth producing ramose branches, SMF 23.903. **e** Secondary overgrowth on the branched colony, SMF 23.903. **f**–**g** Branch transverse section autozooecial chambers and axial zooecia, SMF 23.910. **h** Oblique section of a branched colony with dichotomy, SMF 23.930. Scale bars 2 mm (**d**, **h**), 1 mm (**a**, **f**), 0.5 mm (**b**, **e**, **g**), 0.2 mm (**c**)

Remarks: *Zefrehopora* gen. nov. differs from *Eridocampylus* Duncan, 1939 in possessing straight hemiphragms instead of hook-shaped heterophragms. *Zefrehopora asynithis* differs from *Dyoidophragma* Duncan, 1939 in having fewer hemiphragms and in the occurrence of tubules between acanthostyles. Moreover, *Dyoidophragma* is known to develop only encrusting colonies, whereas the new genus developed both encrusting and ramose, branched colonies.

Zefrehopora asynithis gen. nov. et sp. nov.
(Fig. 6c–i; Table 3)

Derivation of name: The species name refers to the unusual morphology of this bryozoan expressed in combination of tubules, acanthostyles and hemiphragms (from Greek *asynithis*—unusual).
Holotype: SMF 23.871.
Paratypes: SMF 23.872– SMF 23.889.
Type locality: Baqer-abad section, central Iran.
Type level: Bahram Formation, Upper Devonian (lower Famennian).
Measurements: See Table 3.
Diagnosis: Branched and encrusting colonies; diaphragms rare; hemiphragms straight, 1–2 per autozooecium; autozooecial walls thick, merged in exozone; exilazooecia few, small; acanthostyles abundant, 2–5 surrounding each autozooecial aperture; tubules between acanthostyles abundant; indistinct maculae of macrozooecia.
Description: Branched and encrusting colonies. Branched colonies 1.08–2.10 mm in diameter, with 0.25–0.50 mm wide exozones and 0.58–1.20 mm wide endozones. Autozooecia long in endozones, bending abruptly in exozones. Autozooecial apertures rounded-polygonal. Autozooecial diaphragms rare to common, concentrated in the exozone, straight, thin. Locally 1–2 short straight hemiphragms in autozooecia present. Autozooecial walls laminated, 0.005–0.010 mm thick in endozone; merged without visible zooecial boundaries, 0.028–0.070 mm thick in exozone. Exilazooecia few, rounded-polygonal in shape, 0.02–0.05 mm in diameter. Acanthostyles abundant, 2–5 surrounding each autozooecial aperture, originating in endozone. Tubules between acanthostyles abundant, 0.010–0.015 mm in diameter. Indistinct maculae of macrozooecia present. Macrozooecial apertures 0.16–0.20 mm in width.
Remarks: As for genus.
Occurrence: *Zefrehopora asynithis* gen. nov. et sp. nov. is currently known only from the Bahram Formation, Upper Devonian (lower Famennian) of the Baqer-abad section, central Iran.

Order Cryptostomata Vine, 1884
Suborder Rhabdomesina Astrova and Morozova, 1956
Family Rhabdomesidae Vine, 1884
Genus *Euthyrhombopora* Yang, Hu and Xia, 1988

Type species: *Euthyrhombopora hunanensis* Yang, Hu and Xia, 1988. Mississippian, Tournaisian; China.
Diagnosis: Colonies branched. Autozooecia radially diverging in a broad endozone and forming more or less distinct bundle. Autozooecial apertures oval or circular, regularly spaced. Acanthostyles of two sizes: macroacanthostyles in junctions of autozooecial walls and paurostyles surrounding autozooecial apertures. Diaphragms and hemisepta few or absent in most species (modified after Yang, Hu and Xia. 1988).
Remark: *Euthyrhombopora* differs from *Rhombopora* Meek, 1872 in the radial budding pattern of autozooecia in endozone as against the radial or spiral pattern in *Rhombopora*, as well as in the presence of hemisepta. *Euthyrhombopora* differs from *Nicklesopora* in the arrangement of autozooecia in form of the

Table 4 Summary of descriptive statistics for *Euthyrhombopora tenuis* Ernst et al., 2017. Abbreviations as for Table 1

	N	*X*	SD	CV	MIN	MAX
Autozooecial aperture width, mm	50	0.05	0.008	15.43	0.04	0.08
Aperture spacing along branch, mm	50	0.30	0.034	11.19	0.23	0.38
Aperture spacing diagonally, mm	50	0.18	0.014	7.95	0.15	0.20
Acanthostyle diameter, mm	50	0.041	0.009	21.90	0.025	0.060
Paurostyle diameter, mm	30	0.021	0.005	21.72	0.015	0.030
Axial zooecia width, mm	20	0.15	0.024	15.64	0.11	0.20
Branch diameter, mm	25	0.95	0.217	22.84	0.62	1.63
Exozone width, mm	25	0.26	0.082	31.68	0.13	0.50
Endozone width, mm	25	0.44	0.109	24.95	0.23	0.68

axial bundle and in arrangement of larger and smaller acanthostyles around autozooecial apertures (only paurostyles in *Nicklesopora*).

Occurrence: Upper Devonian–Lower Carboniferous (Mississippian); China, Iran, Siberia, Caucasus, Malaysia, USA.

Euthyrhombopora tenuis Ernst et al., 2017
(Figs. 4a–b, 7a–h; Table 4)

2017 *Euthyrhombopora tenuis* Ernst et al., p. 548, figs. 6a–f

Material: SMF 23.890–SMF 23.943.

Description: Branched colonies, branch diameter 0.62–1.63 mm, with 0.23–0.68 mm wide endozones and 0.13–0.50 mm wide exozones. Secondary overgrowths and encrusting sheets occurring, 0.2–0.3 mm in thickness. Axial region often formed by few irregular and large axial zooecia; locally axial zooecia are not developed. Autozooecia tubular, bending sharply in exozone. Single massive superior hemiseptum occurring at the base of exozone; inferior hemiseptum is absent. Autozooecial apertures are oval, arranged in regular rhombic pattern on the colony surface. Acanthostyles large, with distinct hyaline cores and laminated sheath, 1–2 regularly arranged between autozooecial apertures. Abundant paurostyles arranged in single row between acanthostyles surrounding apertures, in a regular rhombic to hexagonal pattern. Metazooecia absent.

Remarks: *Euthyrhombopora tenuis* Ernst et al., 2017 differs from *E. carnosa* (Trizna, 1958) from the Mississippian (Tournaisian) of the Kuznets Basin in possessing thinner branches (0.62–1.63 mm vs. 1.90–2.00 mm in *E. carnosa*). It differs from *E. diaphragmata* Yang, Hu and Xia, 1988 from the Mississippian (Tournaisian) of China in possessing thinner branches and in smaller autozooecia (autozooecial width 0.04–0.08 mm vs. 0.12–0.14 mm in *E. diaphragmata*).

Occurrence: Zefreh section, Central Iran; Bahram Formation, Upper Devonian (Frasnian). Baqer-abad section, central Iran; Bahram Formation, Upper Devonian (lower Famennian).

Discussion

The studied fauna contains four species: three trepostomes—*Coeloclemis zefrehensis* Ernst et al., 2017, *Anomalotoechus parvus* sp. nov. and *Zefrehopora asynithis* gen. nov. et sp. nov.—and one rhabdomesine cryptostome *Euthyrhombopora tenuis* Ernst et al., 2017. The trepostome *Coeloclemis zefrehensis* and the rhabdomesine cryptostome *Euthyrhombopora tenuis* were recorded previously from the Upper Devonian (Frasnian) of the Bahram Formation of the Zefreh section (Ernst et al. 2017).

The bryozoan assemblage is represented by encrusting and erect branched growth forms with the latter dominating the fauna numerically (66.7%). Encrusting colonies occur in form of hollow erect tubes, which are apparently cavariiform, i.e. encrusting ephemeral cylindrical objects (*Coeloclemis zefrehensis*) and as secondary overgrowths of erect branched species (*Zefrehopora asynithis*, *Euthyrhombopora tenuis*). *Anomalotoechus parvus* developed exclusively erect branched colonies. *Euthyrhombopora tenuis* is clearly the dominant species represented by numerous fragments (Fig. 4c–d). *Zefrehopora asynithis* and *Coeloclemis zefrehensis* are less abundant, whereas *Anomalotoechus parvus* occurs in a few thin sections. Fenestrate and cystoporate bryozoans are completely absent in the Bahram Formation.

The studied bryozoan fauna shows low diversity and high abundance of one species (*Euthyrhombopora tenuis*). The same pattern has been observed in the Frasnian of the Bahram Formation (Ernst et al. 2017). Low diversity and high abundance one or few species are usually signs of an environmental stress (e.g. Bone and Wass 1990; Bone 1991; Butler and Cuffey 1996). The position of the studied fauna within the middle to outer ramp setting (Königshof et al. 2017; Ernst et al. 2017) implies a soft and unstable substrate with relatively high rates of fine sedimentation. Erect colonies of the dominant species *Euthyrhombopora tenuis* are relatively immune to such sediment influx, and can tolerate wide range of water energy (e.g. Nelson et al. 1988; Amini et al. 2004). In contrast, encrusting species are strongly affected by strong sediment precipitation.

Bryozoans do not show significant extinctions during the bioevents at the Frasnian-Famennian transition (Bigey 1988; Morozova et al. 2002). During these bioevents, bryozoan faunas experience rather taxonomic shifts rather than reduction in diversity and abundance (Ernst 2013). Bryozoans from the Bahram Formation display a similar pattern. Both the Frasnian (Zefreh section) and lower Famennian (Baqer-abad section) assemblages are represented by four species, but two trepostome species (*Cyphotrypa definita* Morozova, 1960 and *Anomalotoechus ramosus* Morozova, 1960) of the Frasnian were replaced by the trepostomes *Anomalotoechus parvus* sp. nov. and *Zefrehopora asynithis* gen. nov. et sp. nov. in the Famennian assemblage. *Coeloclemis zefrehensis* and *Euthyrhombopora tenuis* occur in both assemblages.

Conclusions

The bryozoan fauna from the lower Famennian of the Bahram Formation at the Baqer-abad section, central Iran, contains four species: three trepostomes *Coeloclemis zefrehensis* Ernst et al., 2017, *Anomalotoechus parvus* sp. nov. and *Zefrehopora asynithis* gen. nov. et sp. nov., and one rhabdomesine cryptostome *Euthyrhombopora tenuis* Ernst et al., 2017. The latter species is numerically dominant. Two species are previously known from the Frasnian of the Bahram Formation at the Zefreh section. The studied assemblage shows lower diversity and high abundance of one species (*Euthyrhombopora tenuis*) existing apparently in stressful environment. Environmental stress was apparently caused by soft substrate and high sediment precipitation in the middle to outer ramp setting. Dominance of erect branched colonies against encrusting ones is explained as adaptation for an environment with high sediment influx. No difference in the diversity and abundance of bryozoans in the Frasnian and lower Famennian assemblages of the Bahram Formation was observed. The transition between Frasnian and Famennian is marked by a replacement of two trepostome taxa.

Acknowledgements We are grateful to Paul D. Taylor, London, Steve Hageman, Boone, and Patrick N. Wyse Jackson, Dublin, for their helpful and constructive reviews.

Funding information Open Access funding provided by Projekt DEAL. This study has been supported by the Deutsche Forschungsgemeinschaft (DFG), grant ER 278/6.1 (for Andrej Ernst), and by the Vice chancellor for Research and Technology of the University of Isfahan, Iran (for Ali Bahrami and Ayesheh Parast).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Adhamian, A. (2003). Middle Devonian (Givetian) conodont biostratigraphy in the Soh area north of Esfahan, Iran. *Courier Forschungsinstitut Senckenberg, 245*, 183–193.

Amini, Z. Z., Adabi, M. H., Burrett, C. F., & Quilty, P. G. (2004). Bryozoan distribution and growth form associations as a tool in environmental interpretation, Tasmania, Australia. *Sedimentary Geology, 167*(1–2), 1–15.

Anstey, R. L., & Perry, T. G. (1970). Biometric procedures in taxonomic studies of Paleozoic bryozoans. *Journal of Paleontology, 44*(3), 383–398.

Astrova, G. G. (1965). Morphologia, istoria razvitia i sistema ordovikskich i siluriiskikh mshanok [Morphology, history of development and system of the Ordovician and Silurian Bryozoa]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 106*, 1–432. [in Russian]

Astrova, G. G. (1978). Istoriya razvitiya, sistema i filogeniya mshanok: otryad Trepostomata [The history of development, system, and phylogeny of the Bryozoa: order Trepostomata]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 169*, 1–240 (in Russian).

Astrova, G. G., & Morozova, I. P. (1956). K sistematike mshanok otryada Cryptostomata [On systematics of the order Cryptostomata]. *Doklady Akademii Nauk SSSR, 110*(4), 661–664 (in Russian).

Bahrami, A., Boncheva, I., Königshof, P., Yazdi, M., & Ebrahimi Khan-Abadi, A. (2014). Mississippian/Pennsylvanian boundary interval in central Iran. *Journal of Asian Earth Sciences, 92*, 187–200.

Bahrami, A., Königshof, P., Boncheva, I., Tabatabaei, M. S., Yazdi, M., & Safari, Z. (2015). Middle Devonian (Givetian) conodonts from the northern margin of Gondwana (Soh and Natanz regions, north-west Isfahan, central Iran): biostratigraphy and palaeoenvironmental implications. *Palaeobiodiversity and Palaeoenvironments, 95*(4), 555–577.

Bahrami, A., Königshof, P., Boncheva, I., Yazdi, M., Ahmadi Nahre Khalaji, M., & Zarei, E. (2018). Conodont biostratigraphy of the Kesheh and Dizlu sections, and the age range of the Bahram Formation in central Iran. *Palaeobiodiversity and Palaeoenvironments, 98*, 315–329.

Bassler, R. S. (1952). Taxonomic notes on genera of fossil and recent Bryozoa. *Journal of the Washington Academy of Sciences, 42*, 381–385.

Bigey, F. P. (1988). Devonian Bryozoa and global events: the Frasnian–Famennian extinction. In N. J. Mc Millan, A. F. Embry, & D. J. Glass (Eds.) The Devonian of the World. *Proceedings of the Second International Symposium of the Devonian System. Canadian Society of Petroleum Geology, Calgary, Memoir, 14*, 53–62.

Boardman, R. S. (1960). Trepostomatous Bryozoa of the Hamilton Group of New York State. *U.S. Geological Survey, Professional Paper*, 340, 1–87.

Boncheva, I., Bahrami, A., Yazdi, M., & Torabi, H. (2007). Carboniferous conodont biostratigraphy and Late Paleozoic platform evolution in South central Iran (Asad-abad section in Ramsheh area-SE Isfahan). *Rivista Italiana di Paleontologia e Stratigrafia, 113*, 329–356.

Bone, Y. (1991). Population explosion of the bryozoan *Membranipora aciculata* in the Coorong lagoon in late 1989. *Australian Journal of Earth Science, 38*, 121–123.

Bone, Y., & Wass, R. E. (1990). Sub-recent bryozoan-serpulid buildups in the Coorong lagoon, South Australia. *Australian Journal of Earth Science, 37*, 207–214.

Borg, F. (1926). Studies on recent cyclostomatous Bryozoa. *Zoologiska Bidrag från Uppsala, 10*, 181–507.

Brice, D., Yazdi, M., Torabi, H., & Maleki, M. (2006). Devonian brachiopods from the Zefreh section (central Iran). *Annales Société Géologique du Nord, 13*, 141–155.

Butler, K., & Cuffey, R. J. (1996). Reduced bryozoan diversity and paleoenvironmental stress in the Saluda Dolomite (uppermost Ordovician, southeastern Indiana). In D. P. Gordon, A. M. Smith, & J. A. Grant-Mackie (Eds.) *Bryozoans in space and time* (pp. 55–61). Wellington: NIWA.

Duncan, H. (1939). Trepostomatous Bryozoa from the Traverse Group of Michigan. *University of Michigan Paleontology Contributions, 5*(10), 171–270.

Ehrenberg, C. G. (1831). *Symbolae Physicae, seu Icones et descptiones Corporum Naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegiptum, Nubiam, Dongalaam, Syriam, Arabiam et Habessiniam, studia annis 1820–25, redirent.* Pars Zoologica, 4, Animalia Evertebrata exclusis Insectis. Berolini, 10 pls.

Ernst, A. (2013). Diversity dynamics and evolutionary patterns of Devonian Bryozoa. *Palaeobiodiversity and Palaeoenvironments, 93*, 45–63.

Ernst, A., Königshof, P., Bahrami, A., Yazdi, M., & Boncheva, I. (2017). A Late Devonian (Frasnian) bryozoan fauna from the central Iran. In B. Mottequin, L. Slavik, & P. Königshof (Eds.) *Climate change and biodiversity patterns in the mid-Palaeozoic. Palaeobiodiversity and Palaeoenvironments, 97*(3), 541–552.

Flügel, E., & Kiessling, W. (2002). Patterns of Phanerozoic reef crises. In W. Kiessling, E. Flügel, & J. Golonka (Eds.) Phanerozoic reef patterns. *SEPM Special Publication, 72*, 691–733.

Ghobadipour, M., Popov, L. E., Hosseini, M., Adhamian, A., & Yazdi, M. (2013). Late Devonian (Frasnian) trilobites and brachiopods from Soh area, central Iran. *Memoirs of the Association of Australasian Palaeontologists, 44*, 149–158.

Gholamalian, H. (2003). Age-implication of Late Devonian conodonts from the Chahriseh area, northeast of Isfahan, central Iran. *Courier Forschungsinstitut Senckenberg, 24*, 201–207.

Girty, G. H. (1911). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences, 21*, 119–156.

Habibi, T., Yazdi, M., Zarepoor, S., & Parvanehnejad Shirazi, M. (2013). Late Devonian fish micro-remains from central Iran. *JGeope, 3*(1), 25–34.

Hageman, S. J. (1993). Effects of nonnormality on studies of the morphological variation of a rhabdomesine bryozoan, *Streblotrypa* (*Streblascopora*) *prisca* (Gabb and Horn). *The University of Kansas Paleontological Contributions, 4*, 1–13.

Joachimski, M. M., Breisig, S., Buggisch, W., Mawson, R., Gereke, M., Morrow, J. R., Day, J., & Weddige, K. (2009). Devonian climate and reef evolution: insights from oxygen isotopes in apatite. *Earth and Planet Science Letters, 284*, 599–609.

Königshof, P., Carmichael, S. K., Waters, J., Jansen, U., Bahrami, A., Boncheva, I., & Yazdi, M. (2017). Palaeoenvironmental study of the Palaeotethys Ocean: the Givetian-Frasnian boundary of a shallow-marine environment using combined facies analysis and geochemistry (Zefreh Section/Central Iran). In B. Mottequin, L. Slavik, & P. Königshof (Eds.) *Climate change and biodiversity patterns in the mid-Palaeozoic. Palaeobiodiversity and Palaeoenvironments, 97*(3), 517–540.

Leven, E. J., & Gorgij, M. N. (2008). Bolorian and Kubergandian stages of the Permian in the Sanandaj-Sirjan zone of Iran. *Stratigraphy and Geological Correlation, 16*, 455–466.

Leven, E. Y., & Gorgij, M. N. (2011). First occurrence of Gzhelian and Asselian fusulinids in Vajnan Formation; Sanandaj-Sirjan Zone, Iran. *Stratigrafiya Geologicheskaya Korrelyatsiya, 19*(5), 16–31.

Ma, J.-Y., Buttler, C. J., & Taylor, P. D. (2014). Cladistic analysis of the 'trepostome' Suborder Esthonioporina and the systematics of Palaeozoic bryozoans. In A. Rosso, P. N. W. Jackson, & J. S. Porter (Eds.), *Bryozoan Studies 2013* (Vol. 94, pp. 153–161). Studi Trentini di Scienze Naturali.

Meek, F. B. (1872). Report on the paleontology of eastern Nebraska. In F. V. Hayden (Ed.) *Final report on the United States Geological Survey of Nebraska and Portions of adjacent Territories* (pp. 81–239). Washington: U.S. Government Printing Office.

Morozova, I. P. (1959). On new species of the genus *Stereotoechus*. *Materiali k osnovam paleontologhii Akademii Nauk SSSR, 3*, 12–15. [in Russian]

Morozova, I. P. (1960). Devonskie mshanki Minusinskikh i Kuznetskoy kotlovin [Devonian Bryozoa of the Minusinsk and Kuznetsk Basins]. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR, 86*, 1–207. [in Russian]

Morozova, I. P., Weis, O. B., & Racki, G. (2002). Emergence and extinction of the Givetian to Frasnian bryozoan faunas in the Kostom oty facies zone, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica, 47*, 307–317.

Mottequin, L., Slavik, L. & Königshof, P. (2017). Increasing knowledge on biodiversity patterns and climate changes in Earth's history by international cooperation: introduction to the proceedings IGCP 596/SDS Meeting Brussels (2015). In B. Mottequin, L. Slavik, & P. Königshof (Eds*.) Climate change and biodiversity patterns in the mid-Paleozoic*. *Palaeobiodiversity and Palaeoenvironments, 97*(3), 367–374.

Nelson, C. S., Hyden, F. M., Keane, S. L., Leask, W. L., & Gordon, D. P. (1988). Application of bryozoan zoarial growth-form studies in facies analysis of non-tropical carbonate deposits in New Zealand. *Sedimentary Geology, 60*, 301–322.

Soffel, H. C., & Förster, H. G. (1984). Polar wander path of the central-East-Iran microplate including new results. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 168*(2/3), 165–172.

Talent, J. A., Mawson, R., Andrew, A. S., Hamilton, P. J., & Whitford, D. J. (1993). Middle Palaeozoic extinction events: faunal and isotopic data. *Palaeogeography, Palaeoclimatology, Palaeoecology, 104*, 139–152.

Trizna, V. B. (1958). Rannekamennougol'nye mshanki Kuznetzkoi kotloviny [Early Carboniferous bryozoans of the Kuznetzk depression]. *Trudy VNIGRI, Microfauna of the USSR, 122*, 1–433. [in Russian]

Ulrich, E. O. (1882). American Palaeozoic Bryozoa. *The Journal of the Cincinnati Society of Natural History, 5*(121–175), 233–257.

Ulrich, E. O. (1883). American Palaeozoic Bryozoa. *The Journal of the Cincinnati Society of Natural History, 6*, 82–92 148–168; 245–279.

Vine, G. R. (1884). Fourth report of the committee consisting of Dr. H. R. Sorby and Mr. G. R. Vine, appointed for the purpose of reporting on fossil Polyzoa. *Reports of the 53rd Meeting of the British Association for the Advancement in Sciences*, 161–209.

Waagen, W., & Wentzel, J. (1886). Salt–range fossils. *Productus*–limestone fossils: Coelenterata. *Memoirs of the Geological Survey of India, Paleontologica Indica, Series, 13*(1), 835–924.

Wendt, J., Kaufmann, B., Belka, Z., Farsan, N., & Karimi Bavandpur, A. (2005). Devonian/Lower Carboniferous stratigraphy, facies patterns and palaeogeography of Iran. Part II. Northern and central Iran. *Acta Geologica Polonica, 55*, 31–97.

Yang, J., Hu, Z., & Xia, F. (1988). Bryozoans from the Late Devonian and early Carboniferous of Central Hunan. *Palaeontologica Sinica, New Series B, 174*(23), 1–197.

Zahedi, M. (1973). Étude géologique de la région de la région de Soh (W de l'Iran central). *Geological Survey of Iran, 27*, 1–197.