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Abstract

Several dozen specimens of *Rotularia leptostoma*, *Rotularia spirulaea*, and a few individuals of *Ditrupa strangulata* were collected from Soh and Zefreh localities in Isfahan province of central Iran. Serpulid tubes of *R. leptostoma* and *R. spirulaea* are well known from Eocene deposits across the Neo-Tethyan realm and North America. Both *R. leptostoma* and *D. strangulata* are reported from Iran for the first time. This study provides new insights into the microstructure of *R. leptostoma* and *D. strangulata* and discusses their mode of life, palaeoecology, and palaeogeographic distribution, contributing to a better understanding of Eocene palaeocurrents linking Europe and North America. In the Soh and Zefreh regions, *Rotularia* occurs abundantly within Eocene limestone deposits and represents the dominant component of a rich fossil assemblage that includes *Nummulites*, bivalves, gastropods, echinoids, and brachyuran crabs. This study also discusses the palaeoecological and sedimentological conditions of the Isfahan province and provides additional palaeogeographic interpretations related to the Eocene marine environment.

Keywords *Rotularia*, *Ditrupa*, tube-dwelling polychaetes, tube microstructure, palaeogeography, Isfahan province

Introduction

Serpulid polychaetes, commonly known as serpulids, are suspension feeders belonging to the family Serpulidae Rafinesque, 1815, within the order Sabellida Levinsen, 1883 (Capa et al. 2021). These tube-dwelling invertebrates are characterised by their calcareous or calcitic/aragonitic tubes (Vinn et al., 2008a; ten Hove & Kupriyanova, 2009; Kupriyanova et al., 2009; Ippolitov et al., 2014; Rouse et al., 2022; Kupriyanova et al., 2023). Serpulids are important invertebrates in marine benthic ecosystems, where they colonise various hard and soft substrates (e.g. Schlögl et al., 2008; Zatoń et al., 2011; Ferrández-Cañadell, 2018; Kočová

Veselská et al., 2021). Their fossil record extends back to the Permian (Sanfilippo et al., 2017, 2018; Ramsdale, 2021), with a main diversification from the Jurassic to Recent (e.g. Jäger et al., 2001; Radwańska, 2004; Ippolitov, 2007a, 2007b, 2010, 2011; Vinn, 2007; Jäger & Schubert, 2008; ten Hove & Kupriyanova, 2009; Ippolitov et al., 2014; Vinn et al., 2013; Jäger & Lang, 2017; Kočí 2012; Luci et al., 2013; Sanfilippo et al., 2013; Rosso et al., 2015; Kočí et al., 2017, 2019, 2022a, 2022b; Breton et al., 2020; Kupriyanova et al., 2014, 2020; Rouse et al., 2022).

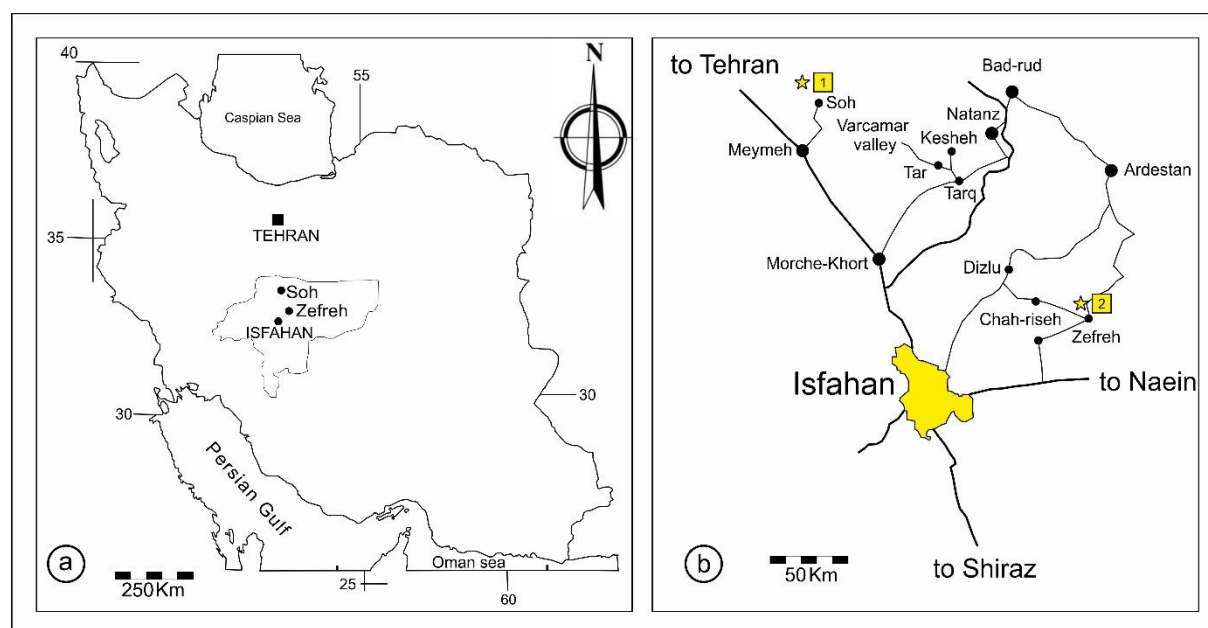
Although most serpulids are sessile and firmly attached to hard substrates, a few genera, including *Ditrupa*, *Nogrobs*, *Rotularia* and *Spirodiscus*, represent free-living forms that rest loosely on or stick in soft ground (ten Hove & Smith, 1990; Jäger, 2005; Seilacher et al., 2008; Morton & Salvador, 2009; Hartley, 2014; Ippolitov et al., 2014; Kupriyanova & Ippolitov, 2015; Kupriyanova & Flaxman, 2023). The vast majority of serpulids inhabit marine environments from shallow coastal waters to deep bathyal and hadal zones, including hydrothermal vents and hydrocarbon seeps (ten Hove & Kupriyanova, 2009; Vinn et al., 2013; Kupriyanova et al., 2020; Rouse & Kupriyanova, 2021). Exceptions are rare, but include *Ficopomatus enigmaticus* (Fauvel, 1923), which occurs in brackish waters, and *Marifugia cavatica* (Absolon & Hrabě, 1930), the only known freshwater serpulid, restricted to cave environments (Bosák et al., 2004; Kupriyanova et al., 2009; ten Hove & Kupriyanova, 2009; Kočí et al., 2026).

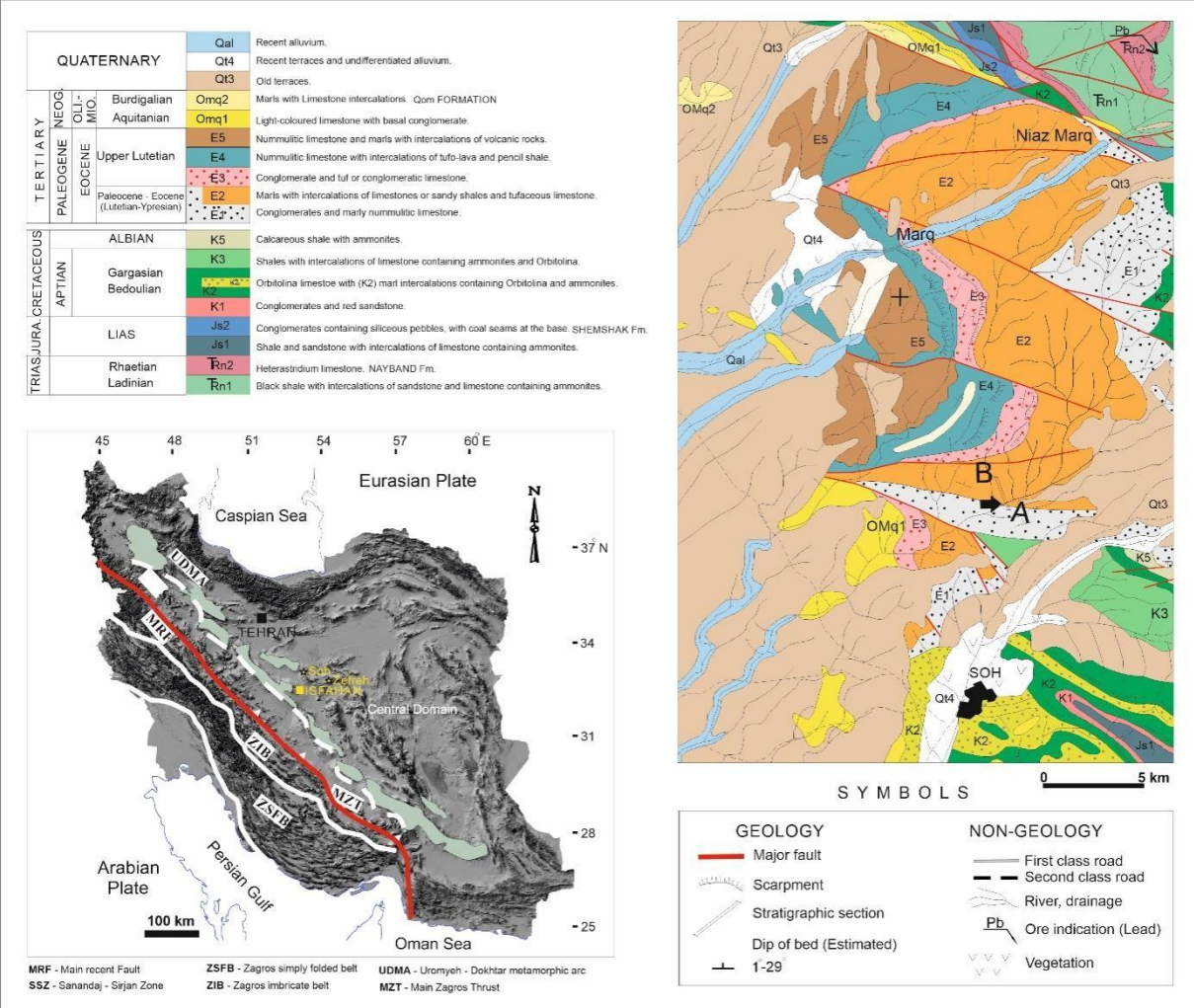
This study focuses on Eocene serpulid polychaetes from Iran. Until 2025, the only serpulid genus reported from Iran was *Rotularia* Defrance, 1827 (Bahrami et al., 2018; Hassan-Vand et al., 2018). Jäger et al. (in press) were the first to describe an assemblage of serpulid and sabellid polychaetes from Iran, based on material from the vicinity of Birjand in the eastern part of the country. Here, we build on their work by documenting a polychaete assemblage from Central Iran, specifically from Isfahan Province. This paper aims to: 1. Document and systematically describe the serpulid polychaetes from the Eocene deposits of the Soh and Zefreh areas in Central Iran; 2. Investigate the tube-wall microstructure of these serpulids and evaluate its taxonomic significance for species-level determination; 3. Assess the mode of life and palaeoecology of the studied taxa, with particular emphasis on their adaptations to soft-substrate environments and their relationship to sedimentological and hydrodynamic conditions; 4. Characterise the associated fossil assemblages and depositional settings of the Eocene successions at Soh and Zefreh; 5. Evaluate the palaeogeographical distribution of the genus *Rotularia* and discuss its migration pathways during the Paleocene and Eocene.

Geological and geographical setting

The Soh and Zefreh regions expose a diverse range of geological formations, including widely distributed Paleozoic (Zahedi, 1973; Adhamian, 2003; Wendt et al., 2005; Ghobadipour et al., 2013; Bahrami et al., 2015) and Mesozoic strata (Berberian et al. 1982; Mannani & Yazdi, 2009; Yazdi et al., 2010), as well as stratigraphically younger marine sequences ranging from the Paleocene to the Oligo-Miocene. The Soh section is located north of Soh village, approximately 90 km northwest of Isfahan, while the Zefreh section is situated east of Zefreh village, about 75 km northeast of Isfahan (Figs. 1, 2). Their respective WGS coordinates are N 33°28'36", E 51°27'6" (Soh), and N 32°55'3.85", E 52°11'23.91" (Zefreh). Both localities belong to the Central Iran microplate, bordered by the NW-SE Sanandaj–Sirjan metamorphic belt to the west and the Great Kavir fault to the east. Paleocene deposits begin with a terrigenous succession of red to white conglomerates and sandstones, overlain by fossiliferous Eocene carbonates and marls with intercalations of thin-bedded tuffaceous siltstones and sandstones of early Eocene. The sedimentary cycle concludes with Sabkha deposits that cap the Oligo-Miocene Qom Formation.

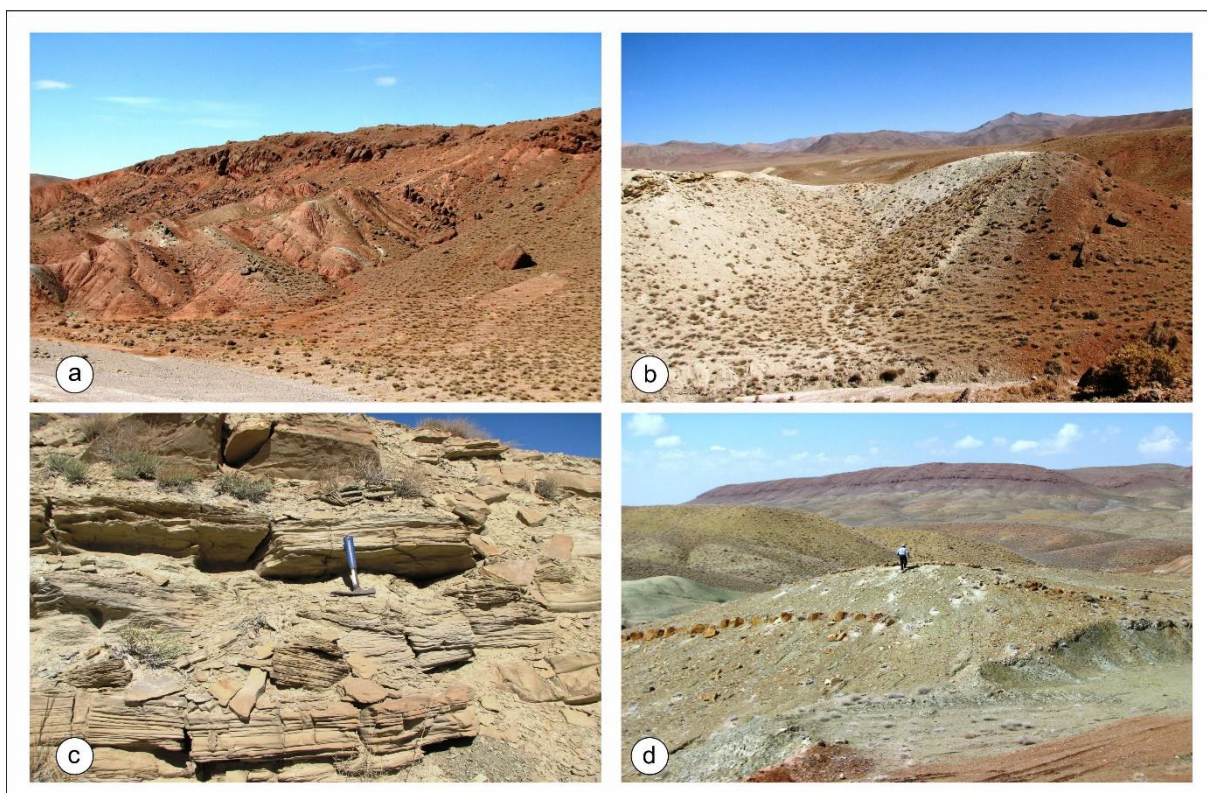
Fig. 1



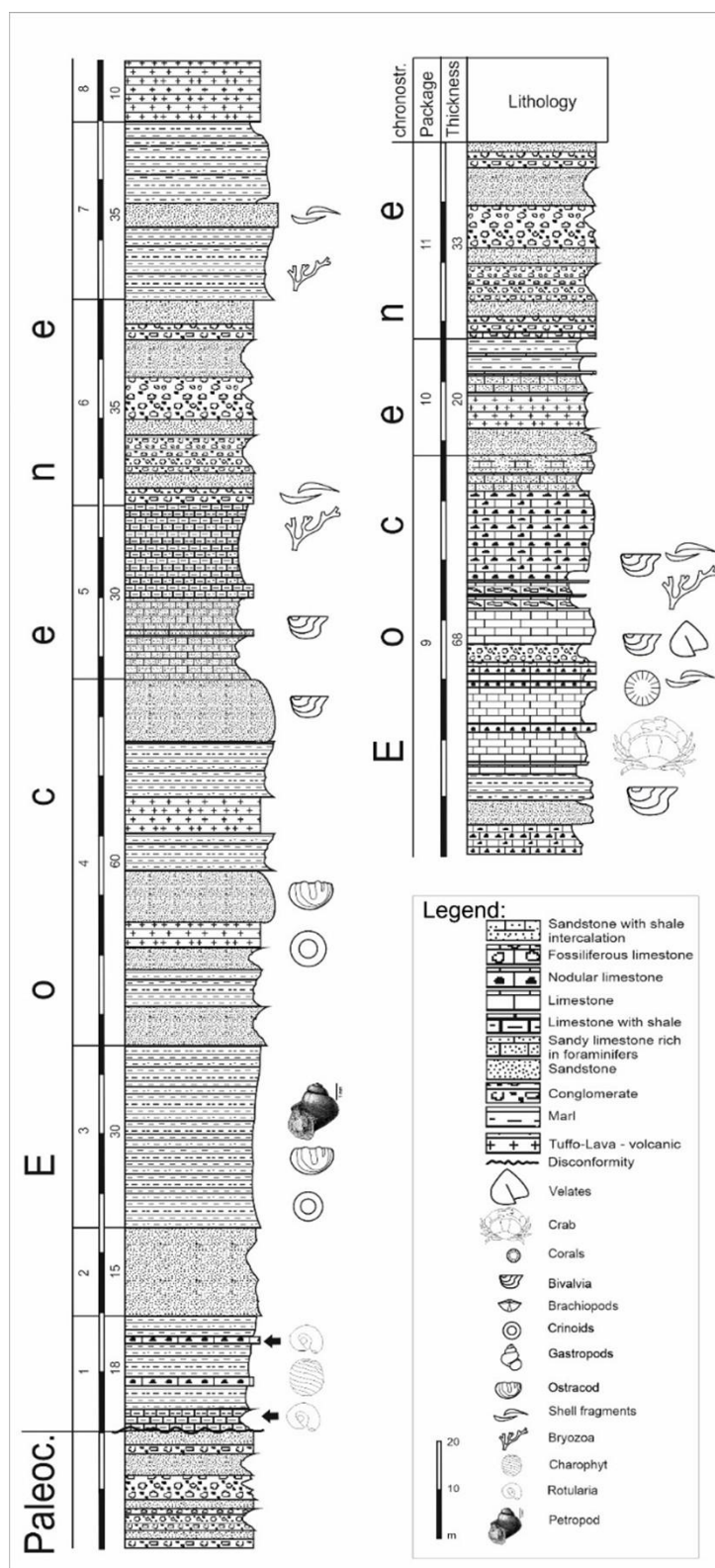


Two thick Eocene successions are widely exposed in the studied areas (Sadri, 2011; Janssen et al., 2013; Hassan-Vand et al., 2018; Ossó et al., 2023).

The studied Eocene section at Soh is about 354 meters thick and consists of 11 lithological units. These units primarily comprise alternating layers of white to light green marl, sandy limestone, and thin beds of marly limestone rich in silicified bivalves and gastropods (*Conus* sp., *Glycymeris* sp., *Natica* sp., *Oliva* sp., *Pinna* sp., *Velates* sp.), solitary corals, condensed oyster layers, crustacean *Retrocypoda almelaiare*, and igneous intrusions of trachy-andesite and basalt (Figs. 2, 3). Detailed descriptions are provided in the lithological column (Fig. 4). Of particular interest are two horizons at the base of the section (unit 1), which include grey to yellowish marls and interbedded brown to yellow limestones containing abundant serpulid polychaetes, charophyte algae, ostracods, oysters, and foraminifera, e.g. *Coskinolina* sp., *Elphidium* sp., *Marginulina* sp., *Nodosaria catesbi*, *N. scalaris*, *Nummulites globulus* (Hassan-Vand et al., 2018). Unit 1 is a key focus of this study.



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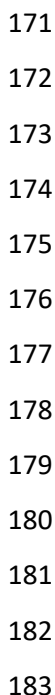


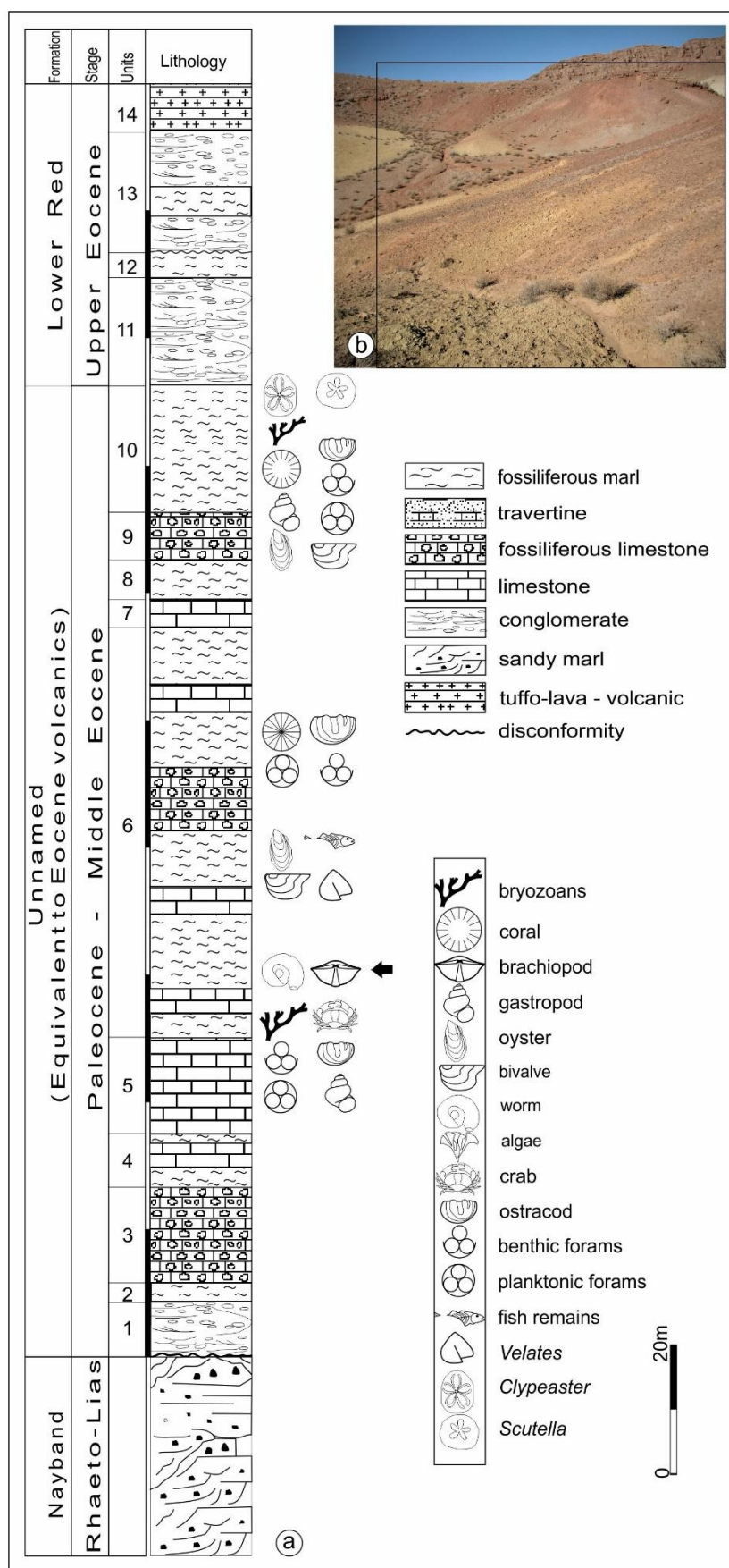
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161 The Zefreh section is 160 meters thick and comprises the lower to middle Eocene
 162 fossiliferous limestones and marls, overlain by the upper Eocene sandstones and conglomerates
 163 of the Lower Red Formation (Fig. 5). Ten lithological units are given in detail in Fig. 6. The

Fig. 5





Material and methods

The studied serpulid specimens were collected from the lower Eocene deposits of the Soh outcrop and from the Paleocene to the Middle Eocene strata of the Zefreh section, both located in the Isfahan region of central Iran. Sampling was conducted by surface collection and through sediment sieving. A total of 249 specimens from the Soh and Zefreh sections were examined and identified as serpulid polychaete tube remains. Specimens were prepared using a pneumatic air scribe under magnification and then photographed using a digital microscope, Keyence VHX-E20, at the Geological Institute of the Czech Academy of Sciences and a Hitachi S-3700N scanning electron microscope (SEM) at the Paleontological Department of the National Museum in Prague. Selected specimens were measured with a calliper, embedded in plastic resin, dried for 48 hours, and subsequently polished using Microlite powder and carborundum abrasive papers of increasing grit size (200, 400, 600, 800, 1000, 1500, 2000). Before SEM imaging, the cleaned tubes were treated in a 1% acetic acid solution for three minutes. Gastropods and a single echinoderm specimen from associated fauna were photographed using a digital microscope, Keyence VHX-E20, at the Geological Institute of the Czech Academy of Sciences. All figures of serpulid tubes and associated fauna were prepared in CorelDRAW 20. All figures of geological, geographical, and stratigraphical settings were prepared in Photoshop CS6.

Repository and abbreviations

University of Isfahan, Geology Museum, Isfahan, Iran (UIGM). Inventory numbers: IUMC 40021–IUMC 40269 (serpulid polychaetes); IUMC 40070–IUMC 40272 (gastropods); and IUMC 40073 (echinoderm).

Systematic palaeontology

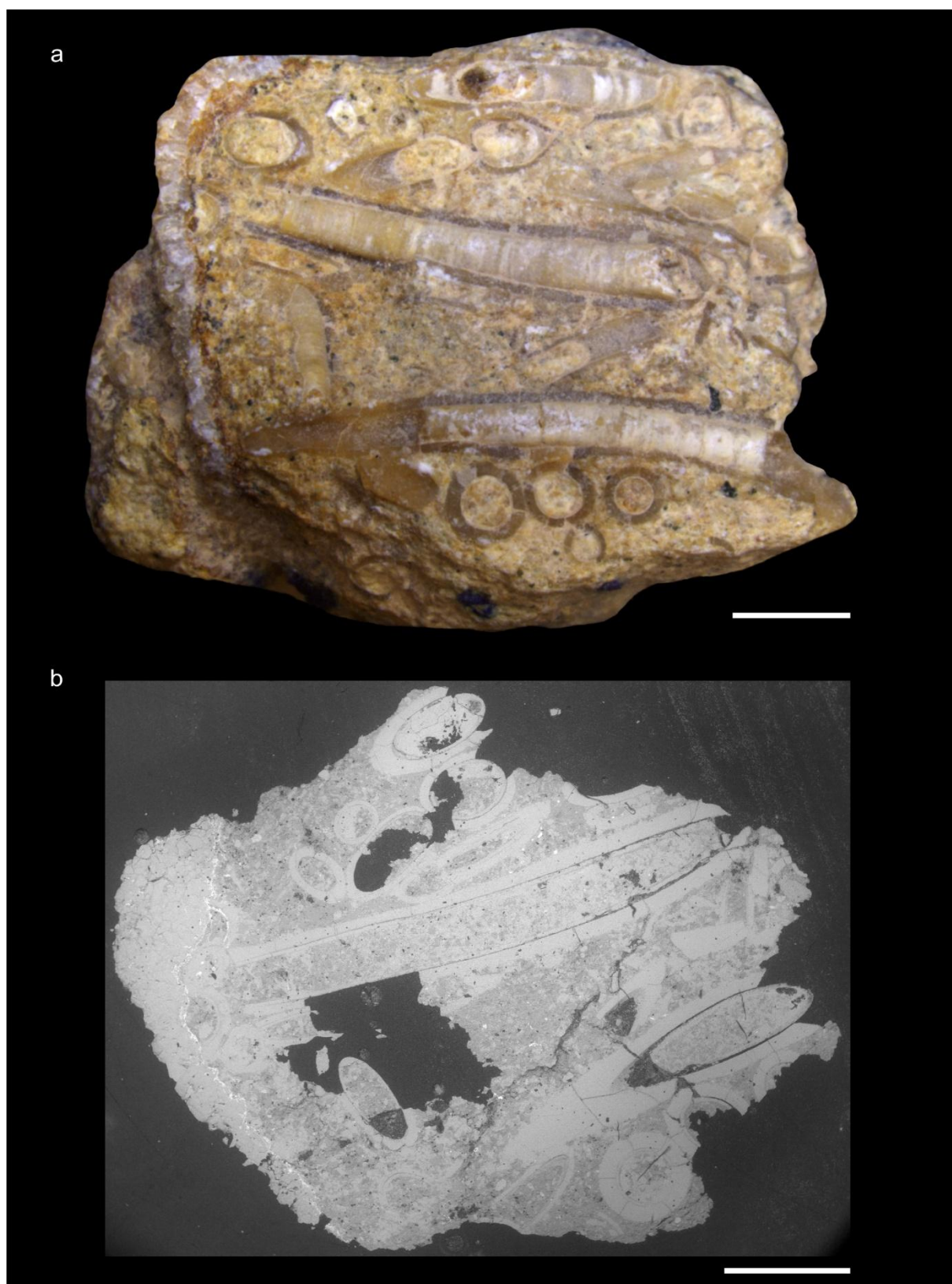
The systematic classification of tube-dwelling polychaetes *Ditrupa* and *Rotularia* follows that of Rovereto (1904), Gardner (1939), Wrigley (1951), Schmidt (1955a, 1955b), Ball (1960), Regenhardt (1961), Howell (1962), Chiplonkar and Tapaswi (1973), Ware (1975), Lommerzheim (1979), Jäger (1983, 1993), Macellari (1984), Savazzi (1995), Vinn (2007, 2008), Ippolitov et al. (2014), McNamara (2023), and many other papers cited here.

Class Polychaeta Grube, 1850

Subclass Sedentaria Lamarck, 1818

Infraclass Canalipalpata Rouse & Fauchald, 1997

221 Order Sabellida Levinsen, 1883
 222 Family Serpulidae Rafinesque, 1815
 223
 224 *Ditrupa* Berkeley, 1835
 225 *Type species. Dentalium subulatum* Deshayes, 1825 = *Dentalium arietinum* O. F. Müller, 1776;
 226 designated by Bush, 1905 (following synonymy of Saint-Joseph, 1898).
 227
 228 *Ditrupa strangulata* (Deshayes, 1825)
 229 Figs. 7, 8
 230
 231 1814 *Dentalium coarctatum* — Brocchi: p. 264, pl. 1, fig. 4
 232 1815 *Dentalium incrassatum* — Sowerby: p. 180, pl. 79, figs. 3–4
 233 1825 *Dentalium strangulatum* — Deshayes: p. 372, pl. 16, fig. 28
 234 1842–1854 *Dentalium incrassatum* Sowerby — Chenu: Livr. 7, pl. 7, fig. 19
 235 1898 *Dentalium coarctatum* Brocchi — Pilsbry & Sharp: p. 242
 236
 237 *Material.* The bulk of several tubes preserved in a rock sample; housed in the Geology Museum
 238 of the University of Isfahan, no. IUMC 40021, Soh locality. The sample was embedded in
 239 plastic resin, subsequently polished and thereby destroyed.
 240
 241 *Description.* Two-layered, tusk-shaped tube; the outer parable layer is thick (see Fig. 7a), the
 242 inner layer is thin; lumen is circular (for the description of the tube microstructure, see the
 243 chapter on tube-wall microstructures below).
 244
 245 *Remarks and relationship.* *Ditrupa strangulata* is known from Eocene deposits in France and
 246 was originally described by Deshayes (1825) as *Dentalium strangulatum*. Subsequent studies,
 247 particularly by ten Hove and Smith (1990, p. 114), have highlighted the taxonomic challenges
 248 associated with this species, noting its frequent and often ambiguous application to various
 249 European fossils. This taxonomic uncertainty was later resolved by Vinn et al. (2008b), who
 250 identified distinct microstructural differences between *D. arietina* and *D. strangulata*. These
 251 findings highlight the important role of tube microstructure in accurately taxonomic
 252 distinguishing fossil *Ditrupa* species.
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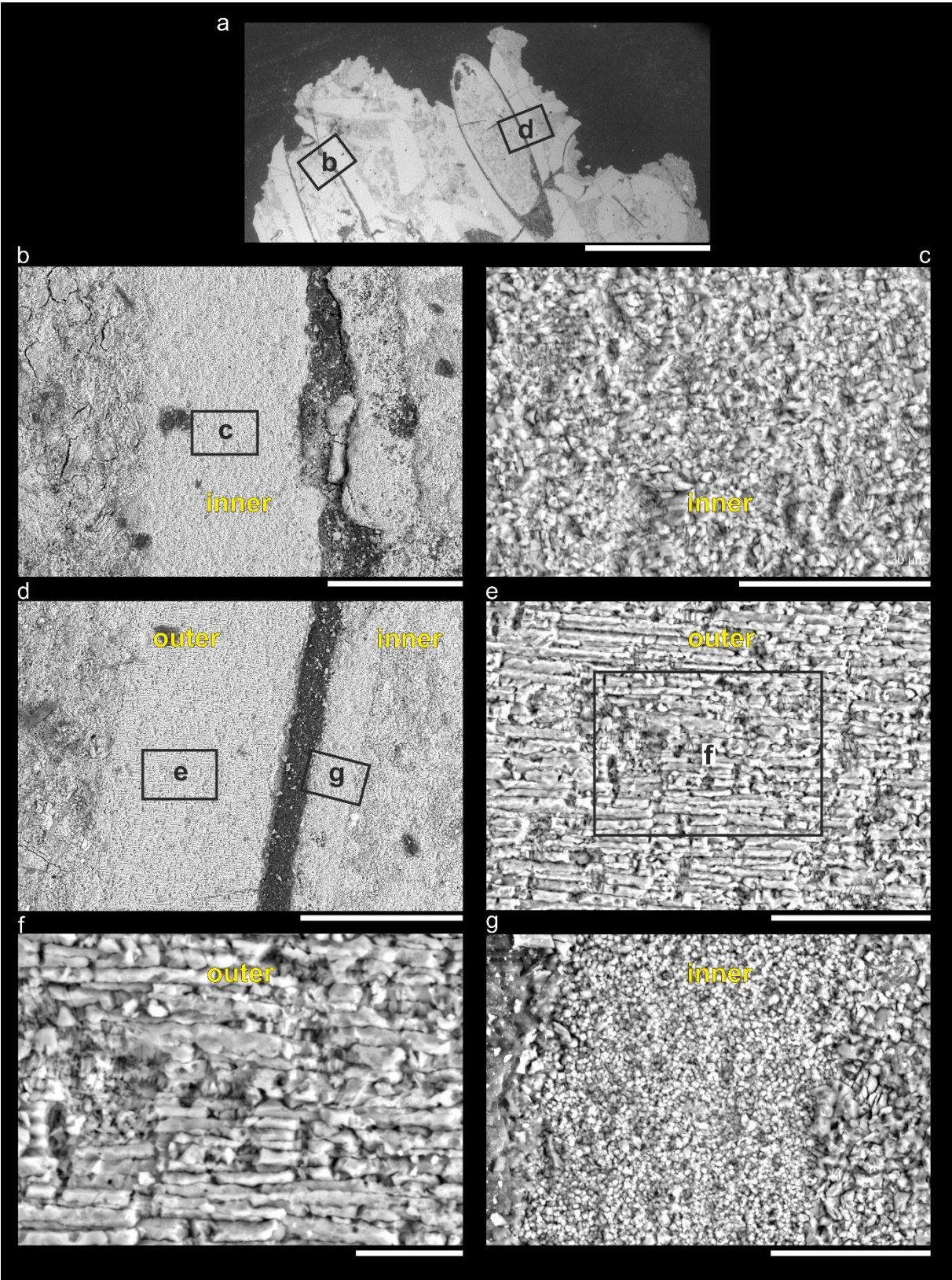


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Rotularia Defrance, 1827

Type species. Rotularia spirulaea (Lamarck, 1818, p. 366) (by subsequent designation Wrigley, 1951, p. 184)

Rotularia spirulaea Lamarck, 1818

Fig. 9

2018 *Rotularia spirulaea* (Lamarck, 1818) — Hassan-Vand et al.: p. 128–133, figs. 6–12 (with additional synonymy)

Non 2018 *Rotularia spirulaea* (Lamarck, 1818) — Bahrami : p. 6–10; Pl. 1, 1–35; Pl. 2, 1–30

Material. 21 tubes; housed in the Geology Museum of the University of Isfahan, no. IUMC 40022–IUMC 40042, Soh locality. All morphological parameters, including the tube diameter and coiling direction of the specimens, are given in Tab. 1.

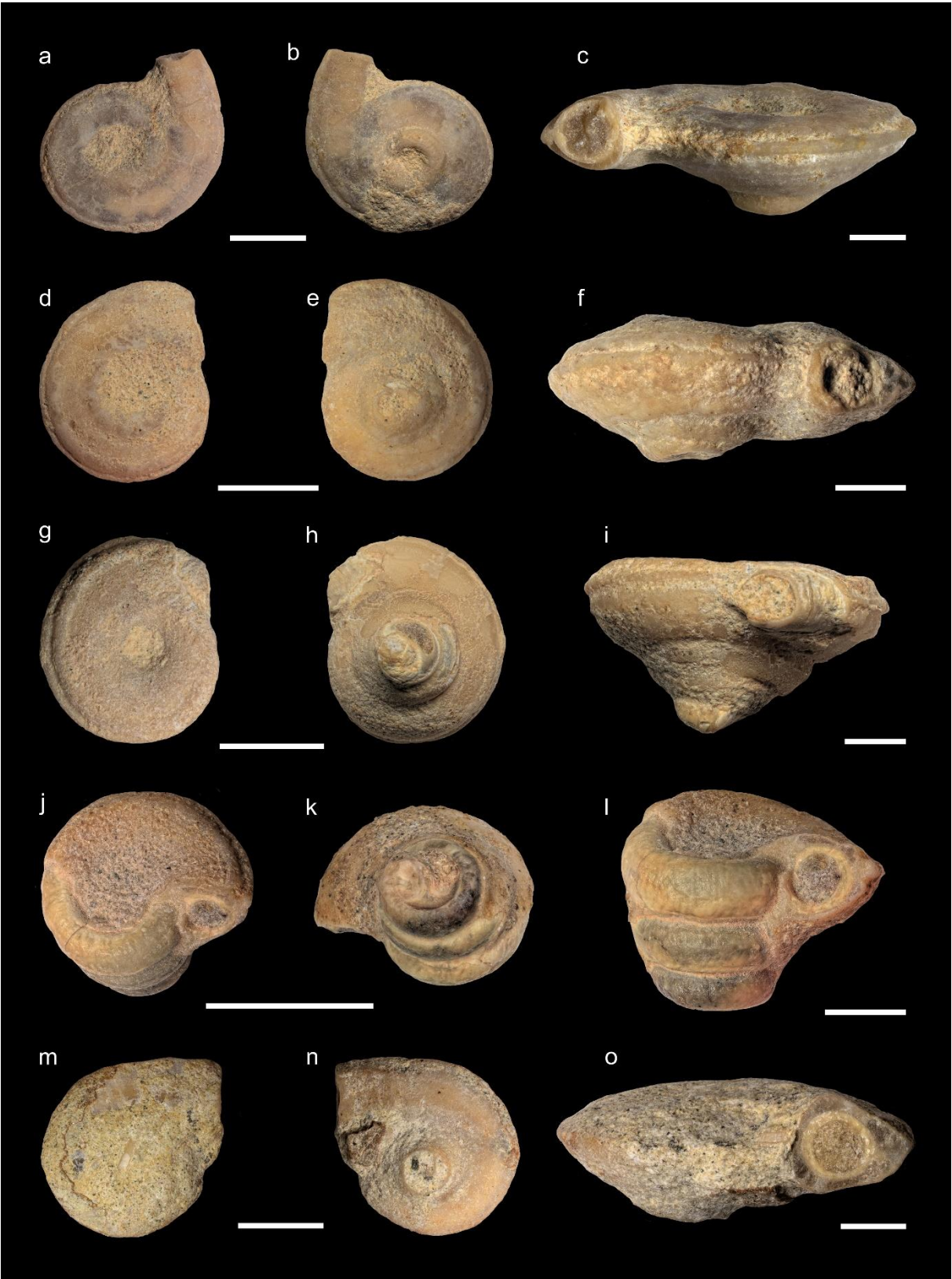
Tab. 1

specimen	diameter (mm)	diameter of the tube (mm)	high (mm)	direction of coiling	notes
1	11.6	3.1	4.7	sinistrally	trochospiral
2	10.7	3.1	4.2	sinistrally	planispiral
3	12.8	2.7	4.1	dextrally	planispiral
4	10.0	2.4	4.0	sinistrally	planispiral
5	10.4	2.8	2.9	sinistrally	planispiral
6	10.2	3.2	4.0	sinistrally	planispiral
7	10.0	2.2	3.2	sinistrally	planispiral
8	7.9	2.6	2.9	sinistrally	planispiral
9	10.9	2.7	3.1	sinistrally	planispiral
10	10.2	2.0	5.7	dextrally	trochospiral
11	9.4	2.6	3.2	dextrally	planispiral
12	9.5	2.3	3.1	dextrally	planispiral
13	8.0	2.8	5.1	sinistrally	planispiral
14	7.9	2.9	3.3	sinistrally	planispiral
15	10.1	3.1	3.7	sinistrally	planispiral

16	8.2	2.6	3.1	sinistrally	planispiral
17	7.0	2.6	3.1	sinistrally	planispiral
18	9.3	2.2	2.8	dextrally	planispiral
19	7.8	2.8	3.7	sinistrally	planispiral
20	9.8	2.4	4.3	sinistrally	planispiral
21	6.5	2.0	4.4	sinistrally	planispiral

Description. The tubes are small to moderate in size; the diameters of the coiled tubes range from 6.5 mm to 12.8 mm, and the tube diameter varies from 2 mm to 3.2 mm. Tube is planispirally (e.g. Fig. 9a–c) or trochospirally (conically) coiled (e.g. Fig. 9j–l). Sinistral coiling predominates (Fig. 9d–o), dextrally coiled forms are less common (Fig. 9a–c). The concave umbilical side represents the upper surface, the lower side is slightly convex. At or near the centre of the lower side, the first whorl is sometimes visible, along with remains of the tiny initial tube segment that was originally attached to a substrate. The broken mouth part indicates that these specimens died before constructing this straight, anteriormost mouth part of the tube. A longitudinal carina (keel) is developed along the margin of the whorl, giving a lenticular shape to the coiled tubes. This sharp, carinated keel is slightly shifted toward the lower attached side. Excluding the keel, the tube is nearly circular in cross-section. The lumen is also circular.

Remarks and relationships. *R. spirulaea* resembles *R. pseudospirulaea* Oppenheim, 1901 from the Eocene of Austria (see Savazzi 1995: 76, figs. 9–12). However, in *R. pseudospirulaea* the peripheral carina (keel) is absent or only weakly developed, two spiral threads are present on each side, and the spiral remains slightly conical in the adult stage. Another *Rotularia* species with a single longitudinal keel is *R. clymenioides* (Guppy, 1866) from the Eocene of the Caribbean and Austria, but its keel is usually more rounded than that of *R. spirulaea*. Morphologically, *R. spirulaea* is closest to *R. nummularia* (Schlotheim, 1820) from the Eocene of Italy, as both species possess a single sharp keel. However, as Vinn (2008) shows, these two taxa differ in the microstructure of their tube layers (see below).



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Rotularia leptostoma (Gabb, 1860)

Figs. 10–13

1860 *Spirorbis leptostoma* — Gabb: p. 385, pi. 67, fig. 36 (erroneous reference in the text to "fig. 41")

1931 *Spirorbis (Tubulostium) leptostoma* Gabb — Renick & Stenzel, Texas Univ. Bull. 3101, p. 105, pi. 7, fig. 29. Referred to "Annelida-Chaetopoda."

2018 *Rotularia spirulaea* (Lamarck, 1818) — Bahrami, p. 6–10; Pl. 1, 1–35; Pl. 2, 1–30.

Material. 227 specimens; housed in the Geology Museum of the University of Isfahan, no. IUMC 40043–IUMC 40269, Zefreh area. Five specimens (IUMC 40265–IUMC 40269) were embedded in plastic resin, subsequently polished and thereby destroyed. All morphological parameters, including the tube diameter and coiling direction of the specimens, are given in Tab. 2.

Tab. 2

number	diameter (mm)	tube diameter (mm)	high (mm)	coiling
1	9.6	2.6	4.8	sinistrally
2	10.3	2.3	2.6	sinistrally
3	8.9	2.7	7.1	sinistrally
4	6.2	2.2	6.9	sinistrally
5	4.7	1.4	3.5	sinistrally
6	9.1	2.1	4.4	dextrally
7	9.3	2.2	5.2	sinistrally
8	10.4	3.3	3.4	sinistrally
9	5.1	2.1	5.9	sinistrally
10	8.2	2.2	9.4	sinistrally
11	9.0	2.2	9.0	sinistrally
12	10.2	2.2	5.1	sinistrally
13	5.6	2.0	8.8	sinistrally
14	5.8	1.5	5.6	sinistrally

15	7.3	2.7	10.4	sinistrally
16	7.3	2.0	5.7	sinistrally
17	5.8	1.8	7.0	sinistrally
18	5.8	2.3	4.5	sinistrally
19	8.4	2.4	7.6	sinistrally
20	5.0	1.9	6.6	sinistrally
21	5.3	2.2	5.5	sinistrally
22	6.6	2.4	4.7	sinistrally
23	5.7	2.0	5.0	dextrally
24	9.4	2.0	2.8	sinistrally
25	12.5	3.4	4.1	sinistrally
26	11.8	3.1	3.5	sinistrally
27	12.1	2.9	2.9	dextrally
28	9.6	2.6	4.5	sinistrally
29	11.1	2.7	3.3	sinistrally
30	11.8	3.2	5.0	sinistrally
31	9.1	1.9	3.4	sinistrally
32	9.9	1.7	4.0	sinistrally
33	10.8	2.4	3.7	dextrally
34	10.9	2.2	3.4	sinistrally
35	8.4	2.3	3.3	dextrally
36	9.6	2.9	3.4	sinistrally
37	8.2	2.4	3.8	sinistrally
38	10.1	2.2	3.5	sinistrally
39	8.8	2.6	3.8	sinistrally
40	11.0	2.4	3.5	sinistrally
41	8.5	2.5	3.3	sinistrally
42	10.4	2.6	4.3	sinistrally
43	9.6	2.1	2.8	sinistrally
44	9.7	2.6	3.5	sinistrally
45	7.7	2.3	2.5	sinistrally
46	10.0	2.0	3.2	sinistrally
47	8.2	2.1	3.2	sinistrally

48	8.1	2.0	2.9	sinistrally
49	9.7	2.2	2.9	sinistrally
50	7.4	1.8	5.5	sinistrally
51	8.7	1.45	2.5	sinistrally
52	8.3	1.5	2.4	sinistrally
53	8.1	2.5	2.8	sinistrally
54	9.0	2.8	4.2	sinistrally
55	9.4	2.1	3.1	sinistrally
56	10.2	2.4	3.9	sinistrally
57	8.8	2.0	3.0	dextrally
58	9.3	2.6	3.8	dextrally
59	9.5	2.4	4.8	dextrally
60	9.6	2.0	3.1	dextrally
61	8.6	2.5	5.5	sinistrally
62	10.2	2.9	4.8	sinistrally
63	10.1	2.3	2.9	dextrally
64	9.6	2.4	3.9	sinistrally
65	9.9	2.3	3.7	sinistrally
66	9.7	2.4	3.2	sinistrally
67	8.1	2.2	3.4	sinistrally
68	9.0	1.9	4.3	sinistrally
69	7.6	1.3	2.4	sinistrally
70	8.0	2.1	3.4	dextrally
71	7.1	1.6	2.8	sinistrally
72	8.8	2.3	3.5	sinistrally
73	7.6	2.0	3.1	sinistrally
74	8.6	2.0	2.2	dextrally
75	9.7	1.9	3.2	sinistrally
76	7.8	2.1	3.1	sinistrally
77	8.4	2.2	3.6	dextrally
78	8.7	2.2	2.9	sinistrally
79	7.7	1.8	2.9	sinistrally
80	7.7	2.1	3.6	sinistrally

81	8.1	1.6	4.6	sinistrally
82	8.4	2.0	4.3	dextrally
83	7.9	2.0	3.7	sinistrally
84	8.0	2.1	3.1	sinistrally
85	9.1	2.4	2.8	sinistrally
86	8.4	1.6	3.3	sinistrally
87	7.4	1.9	2.3	sinistrally
88	6.8	1.4	2.8	sinistrally
89	7.4	2.2	4.0	sinistrally
90	7.2	2.2	2.8	sinistrally
91	7.9	2.1	3.2	sinistrally
92	7.7	1.8	2.4	sinistrally
93	7.4	2.2	3.8	sinistrally
94	7.5	1.8	2.2	sinistrally
95	4.1	1.5	2.0	sinistrally
96	8.7	2.4	5.5	sinistrally
97	7.8	2.2	4.2	sinistrally
98	7.9	2.3	4.8	sinistrally
99	7.9	1.7	3.9	dextrally
100	8.1	2.4	3.9	sinistrally
101	7.5	1.9	4.8	sinistrally
102	9.9	2.8	4.2	sinistrally
103	8.8	2.3	6.9	sinistrally
104	9.9	2.9	5.4	sinistrally
105	7.5	2.4	4.8	sinistrally
106	8.5	1.9	3.8	sinistrally
107	8.0	2.5	4.3	sinistrally
108	8.8	2.1	3.8	sinistrally
109	9.4	3.1	4.6	sinistrally
110	8.9	1.8	5.0	sinistrally
111	8.9	2.7	5.6	sinistrally
112	5.8	2.0	7.9	sinistrally
113	5.9	2.2	6.1	sinistrally

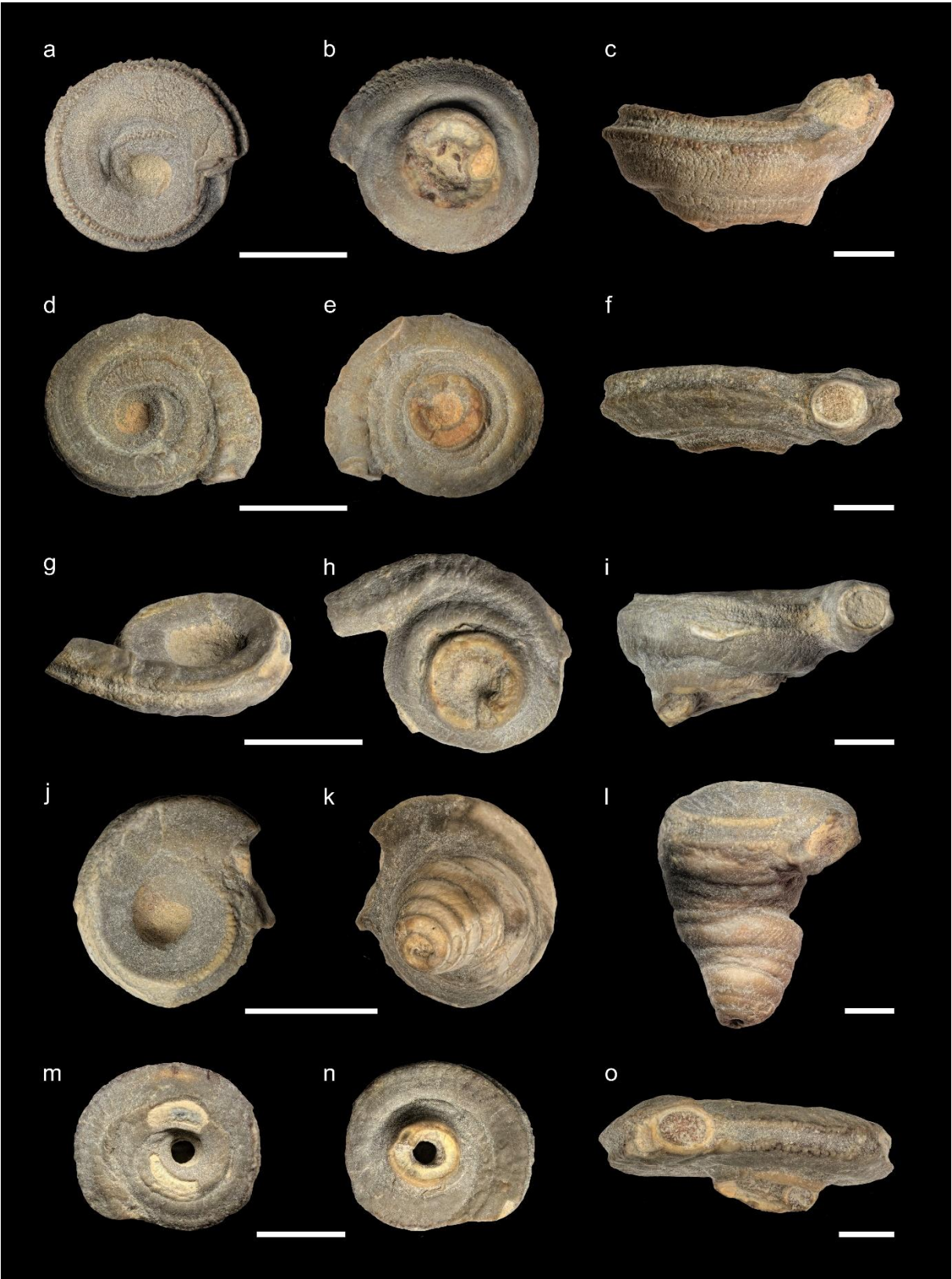
114	8.8	2.4	8.0	sinistrally
115	7.1	2.0	6.8	sinistrally
116	5.6	1.7	5.9	sinistrally
117	6.9	2.1	5.6	sinistrally
118	9.6	1.7	3.9	sinistrally
119	8.6	2.9	5.3	sinistrally
120	9.5	1.8	4.2	sinistrally
121	8.2	2.7	7.2	sinistrally
122	9.6	1.7	4.1	sinistrally
123	7.8	1.9	5.0	sinistrally
124	8.8	2.6	7.2	sinistrally
125	8.8	2.1	4.9	sinistrally
126	8.3	2.2	4.9	sinistrally
127	9.3	1.9	5.9	sinistrally
128	7.9	2.7	5.3	sinistrally
129	8.5	2.5	4.7	sinistrally
130	8.8	2.5	6.3	sinistrally
131	10.7	2.4	4.6	dextrally
132	7.5	3.1	8.1	sinistrally
133	7.2	2.2	4.8	sinistrally
134	7.6	2.7	4.2	sinistrally
135	7.8	1.8	4.7	sinistrally
136	9.3	2.0	5.0	sinistrally
137	7.2	2.4	8.0	sinistrally
138	6.9	1.7	4.8	sinistrally
139	9.2	2.4	6.4	sinistrally
140	8.6	2.4	6.3	sinistrally
141	7.3	2.3	5.3	sinistrally
142	8.2	2.2	4.2	sinistrally
143	7.1	2.1	5.2	sinistrally
144	6.6	3.4	6.0	sinistrally
145	7.7	2.3	3.1	sinistrally
146	9.2	2.4	6.2	dextrally

147	9.2	2.9	5.6	dextrally
148	7.1	2.0	5.2	dextrally
149	7.3	2.0	5.5	sinistrally
150	5.6	2.4	5.3	sinistrally
151	6.5	3.3	4.6	sinistrally
152	6.4	2.0	5.1	sinistrally
153	5.6	1.8	5.8	sinistrally
154	7.7	1.7	3.3	sinistrally
155	8.1	2.5	7.1	sinistrally
156	5.9	2.1	5.9	sinistrally
157	6.9	1.8	8.0	sinistrally
158	8.9	1.6	3.4	sinistrally
159	6.7	2.1	7.2	sinistrally
160	6.1	1.9	5.7	sinistrally
161	7.4	1.9	3.4	sinistrally
162	7.2	1.8	3.7	sinistrally
163	6.0	2.2	7.7	sinistrally
164	5.9	2.3	6.1	sinistrally
165	7.0	2.8	4.0	dextrally
166	6.3	2.1	4.3	sinistrally
167	6.4	2.0	4.3	sinistrally
168	5.6	2.5	4.2	sinistrally
169	6.9	2.0	4.1	sinistrally
170	4.7	2.5	4.9	sinistrally
171	5.7	2.1	3.6	sinistrally
172	7.1	2.2	3.8	sinistrally
173	7.5	2.0	3.2	sinistrally
174	7.6	1.3	3.2	sinistrally
175	6.2	1.7	5.0	dextrally
176	6.1	1.7	6.8	dextrally
177	5.4	2.3	6.8	dextrally
178	4.6	1.7	6.0	dextrally
179	4.0	1.0	2.8	dextrally

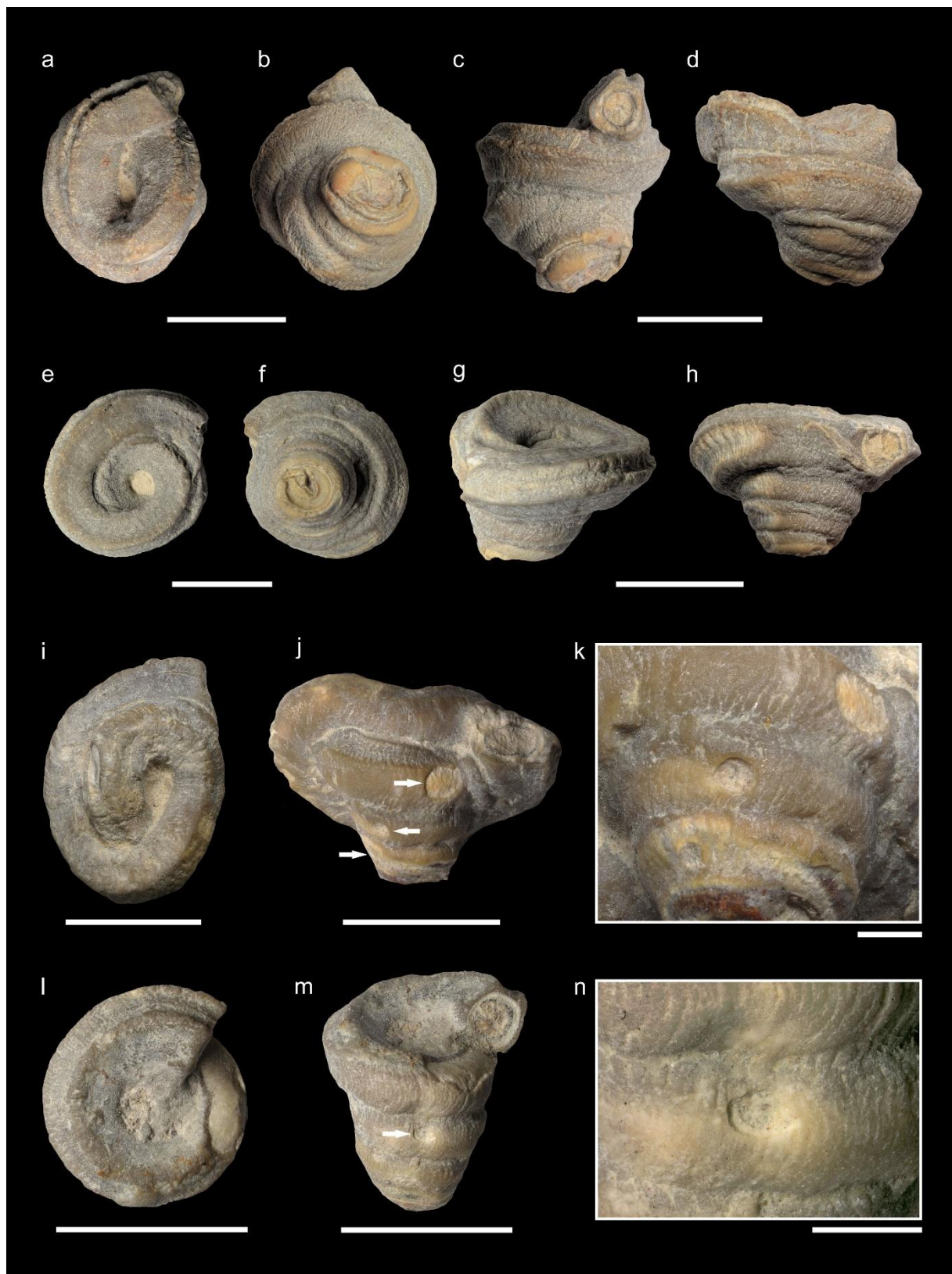
180	3.0	2.0	2.2	dextrally
181	3.4	1.0	3.1	dextrally
182	6.1	2.2	3.2	sinistrally
183	4.8	2.4	6.6	sinistrally
184	6.2	2.2	4.2	sinistrally
185	7.3	2.1	4.1	sinistrally
186	5.5	2.5	6.6	sinistrally
187	5.8	1.9	3.6	sinistrally
188	7.1	2.0	9.1	sinistrally
189	5.3	2.3	5.9	sinistrally
190	5.5	1.9	5.3	sinistrally
191	6.0	2.2	4.2	sinistrally
192	5.5	1.8	5.9	sinistrally
193	4.3	1.2	2.6	sinistrally
194	4.4	1.7	4.5	sinistrally
195	5.9	1.9	4.1	sinistrally
196	4.9	1.8	4.6	sinistrally
197	5.1	1.7	5.7	sinistrally
198	5.3	1.7	5.5	sinistrally
199	4.8	1.5	3.4	sinistrally
200	6.1	2.1	4.9	sinistrally
201	6.6	2.8	4.5	sinistrally
202	6.5	2.1	6.4	sinistrally
203	7.2	2.2	7.2	sinistrally
204	4.8	2.0	5.3	sinistrally
205	7.3	2.2	4.1	sinistrally
206	5.7	2.4	5.5	sinistrally
207	6.2	1.8	5.0	sinistrally
208	4.8	1.8	6.9	sinistrally
209	4.8	2.1	6.5	sinistrally
210	5.9	2.2	5.9	sinistrally
211	5.1	1.6	5.0	sinistrally
212	4.9	1.9	5.6	sinistrally

213	5.4	2.2	6.2	sinistrally
214	6.6	1.9	3.8	sinistrally
215	4.9	2.3	4.3	sinistrally
216	5.0	1.9	4.9	sinistrally
217	4.7	1.7	4.9	sinistrally
218	3.9	1.4	3.9	sinistrally
219	4.9	2.0	5.3	sinistrally
220	4.1	2.0	5.0	sinistrally
221	3.8	1.6	5.9	sinistrally
222	4.5	1.6	4.1	sinistrally
223	4.2	1.6	5.2	sinistrally
224	5.2	1.9	4.0	sinistrally
225	3.8	1.2	2.9	sinistrally
226	3.4	1.4	4.5	sinistrally
227	7.4	1.3	5.4	sinistrally

Description. The tubes are small to moderate in size; diameters of the coiled tubes range from 3 mm to 12.5 mm; the tube diameter varies from 1 mm to 3.4 mm. Most specimens are planispiral (e.g. Fig. 10d–f); however, some display trochospiral (conical) coiling (e.g. Fig. 10j–l). 201 specimens (88,55%) are sinistrally coiled (Figs. 10a–l, 11), while only 26 (11,45%) specimens are dextrally coiled (Fig. 10m–o). The umbilical upper side is concave, whereas the lower side is slightly convex (Fig. 10 c, f, i). The dorsal bicarinate keel is composed of two distinct, sharply rounded keels separated by a well-defined concave furrow. This double-keeled carina (=keel) extends along the margin of the whorl. Aside from the keel, the tube is circular in cross-section, as is the lumen. The surface bears very weak transverse wrinkles, which develop into more prominent convex transverse striations (e.g. Fig. 11k, n).



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356 *Remarks and relationships.* *Rotularia leptostoma* is readily distinguished from all other
 357 rotulariid species by the presence of two sharp, closely spaced keels (bicarinate keel). In this

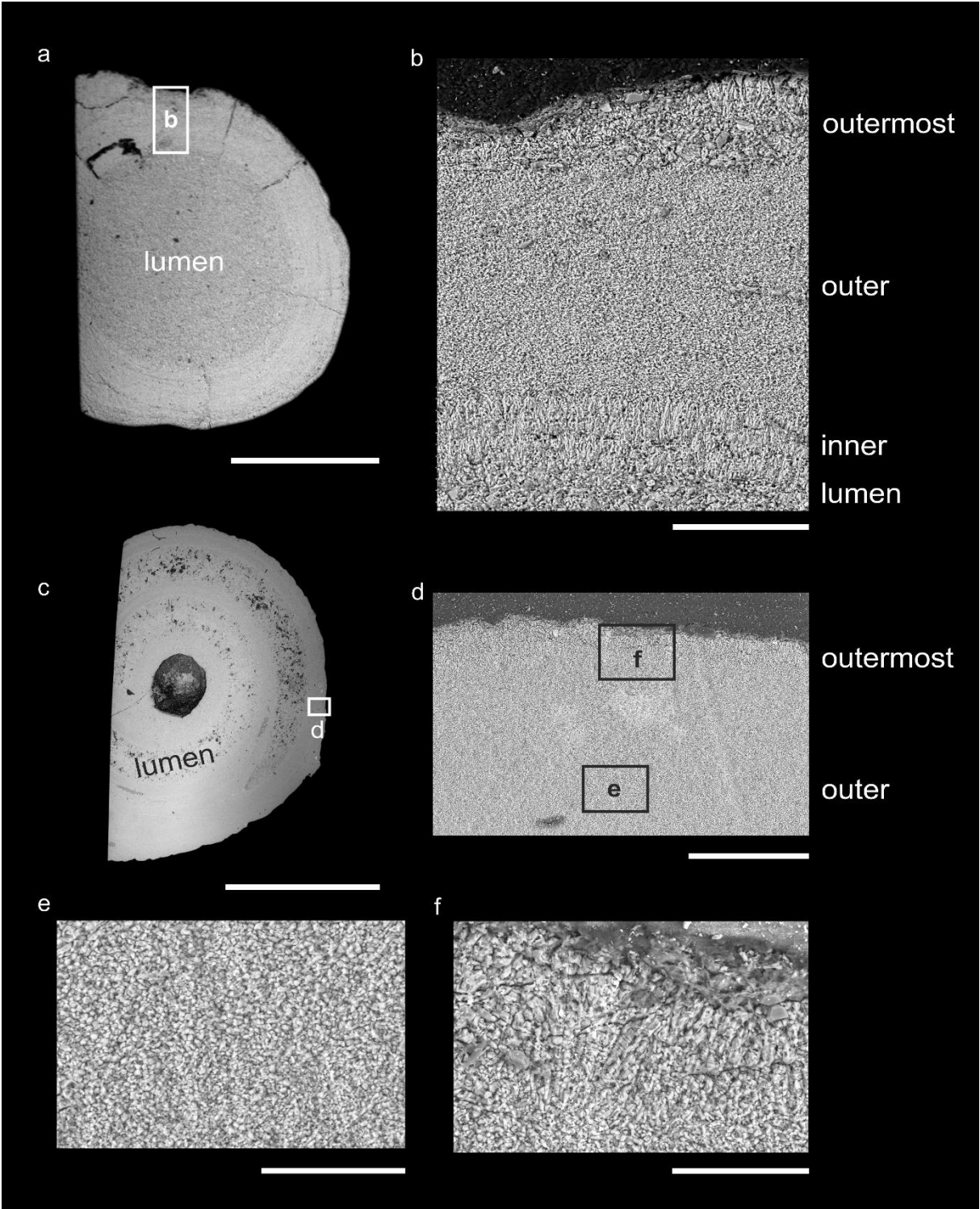
respect, it is most similar to *Rotularia angulosa* var. *crassa* (Doncieux, 1926) from the Eocene of southern France, which also bears two carinate keels but differs in the considerably wider spacing between them. *R. leptostoma* is known from the Eocene of Texas (USA), Austria, southern Germany, and Iran. The palaeogeographic distributions of Paleocene and Eocene *Rotularia* are shown in Figs. 14 and 15, respectively.

Drill holes in tubes of Rotularia leptostoma. Two specimens of *R. leptostoma* from Zefreh locality display incomplete drill holes that are circular to slightly elliptical, perpendicular, and wider than deep. They are preserved as shallow, faintly parabolic depressions (Fig. 11k, n) and are attributable to the ichnogenus *Oichnus* Bromley, 1981 (see Wisshak et al., 2015). Specimen IUMC 40050 bears three drill holes arranged one above another, each occurring on a separate whorl of the tube (Fig. 11k). The largest and uppermost borehole is elliptical, measuring 2.0 mm in length and 1.3 mm in width. The middle, more circular borehole has a diameter of 0.6 mm. The smallest and lowermost borehole measures 0.4 mm in diameter. Specimen IUMC 40051 bears a single parabolic drill hole on the fourth tube whorl, measuring 1.9 mm in length and 0.7 mm in width (Fig. 11n).

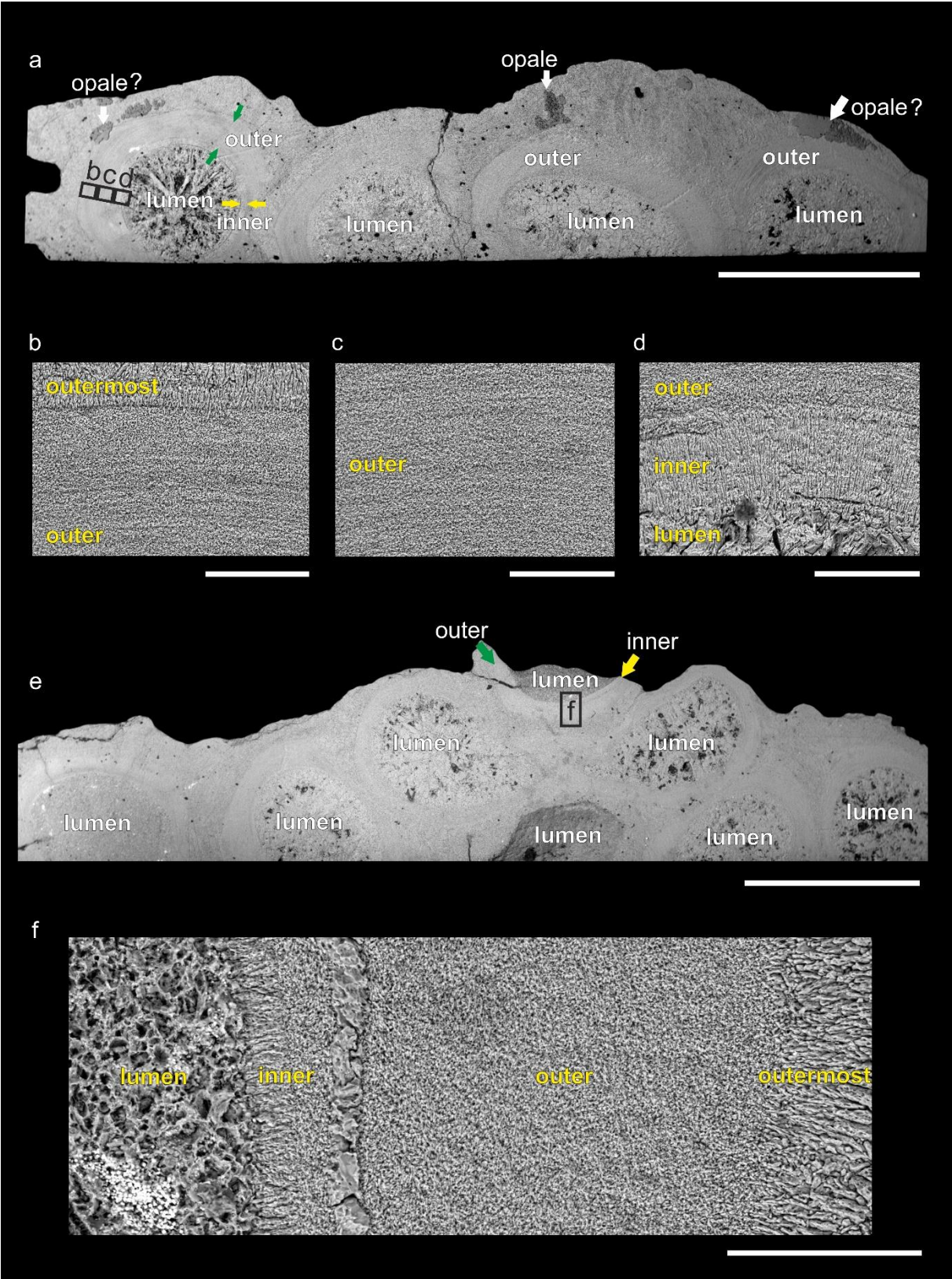
Tube-wall microstructures of tube-dwelling polychaetes from the Soh and Zefreh areas

The tube wall of *Ditrupa strangulata* (Deshayes, 1825) is two-layered. The outer layer is composed of a regularly ridged prismatic structure (RRP sensu Vinn et al., 2008b; Vinn & Kupriyanova, 2011; Vinn, 2020) and is illustrated in Fig. 8e and 8f herein. The inner layer consists of a fine-granular homogeneous structure (sensu Vinn et al., 2008b; Vinn, 2020) and is shown in Fig. 8c and 8g.

The tube wall of *Rotularia leptostoma* consists of three distinct layers, a thin inner layer (internal) and a thicker outer layer (external), the latter interpreted as being subdivided into outer-middle and outermost sublayers (Figs. 12–13). The inner layer is composed of several lamellae of spherulitic prismatic crystals, corresponding to a lamello-fibrillar structure (LFS sensu Vinn, 2007; 2008; 2020; Vinn et al., 2008a; Figs. 12b, 13d and 13f herein). The outer-middle, homogeneous layer consists of irregularly oriented spherulitic crystals (HAC sensu Vinn, 2007; 2008; 2020; Vinn et al., 2008a; Figs. 12b, 12e, 13c, 13f herein). The outermost layer is formed by short, semi-regularly oriented spherulitic prismatic crystals. These short crystals are less regularly oriented than the longer crystals in the inner lamello-fibrillar layer (Figs. 12b, 12f, 13b, 13f).



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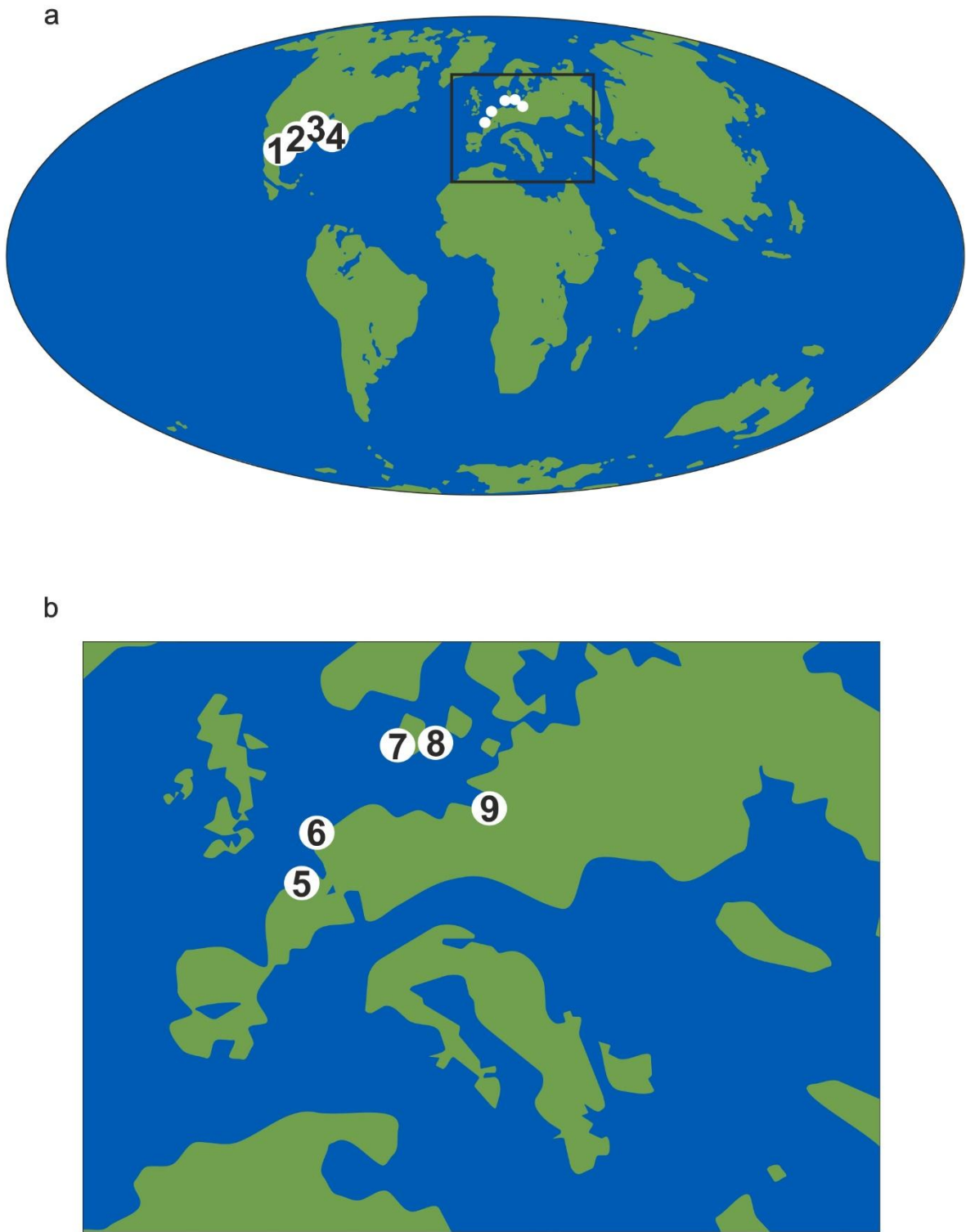
The tube microstructure of *R. spirulaea* has previously been studied by Vinn (2008), and the Iranian specimens were examined by Hassan-Vand et al. (2018, figs. 8–10). Its tube is composed of two distinct layers: a homogeneous outer layer of variably shaped angular calcium carbonate crystals (HAC) and an inner layer with a lamello-fibrillar structure (LFS). Although *R. spirulaea* is morphologically most similar to *R. nummularia*, the two species differ clearly in tube microstructure (Vinn, 2008). Vinn (2008) showed that they differ in the relative thickness of the inner tube layer, expressed as the ratio of inner-layer thickness to the lateral thickness of the outer layer, as well as in the size of crystals and crystal clusters within both tube layers. In this respect, the tube microstructure of *R. leptostoma* more closely resembles that of *R. spirulaea*. In *R. spirulaea*, the inner tube layer reaches 27% of the lateral thickness of the outer layer (Vinn, 2008), closely matching the value observed here for *R. leptostoma* (25%). By contrast, the inner tube layer of *R. nummularia* reaches 66.6% of the lateral thickness of the outer layer (Vinn, 2008). Thus, although the general microstructure of the tube layers appears broadly similar within the genus, species differ in the relative thickness of individual layers and in the size and orientation of their crystals. These differences support the use of tube microstructure as an important species-level diagnostic character in fossil serpulids, as proposed by Vinn (2007; 2008; 2020) and Vinn et al. (2008a; 2008b).

Stratigraphic and palaeogeographical distribution of *Rotularia*

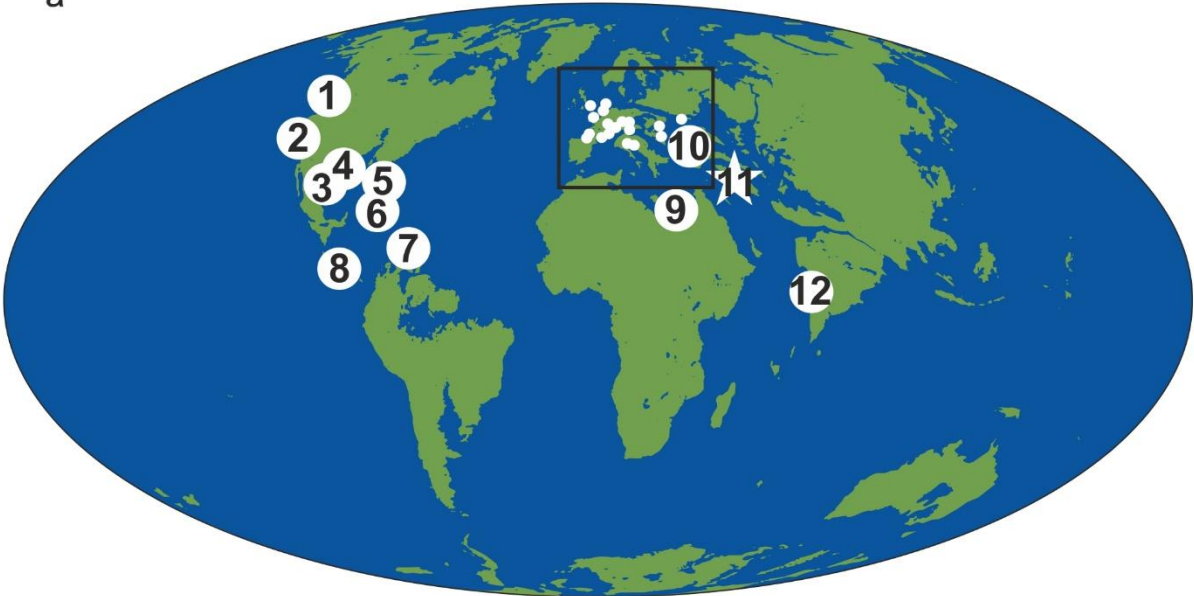
Rotularia sensu lato traditionally included four subgenera, namely *R. (Austrorotularia)*, *R. (Praerotularia)*, *R. (Rotularia)* and *R. (Tectorotularia)*, all of which were elevated to generic status (Jäger, 2005; Ippolitov et al., 2014; McNamara, 2023). McNamara (2023) pointed out that *Praerotularia* Lommerzheim, 1979 is a junior synonym of *Rotulispira* Chiplonkar & Tapaswi, 1973, and thus the latter has nomenclatural priority. Taxa traditionally included in *Rotularia sensu lato* show markedly different stratigraphic ranges. *Austrorotularia*, *Rotulispira* and *Tectorotularia* are restricted to the Mesozoic and are known from the fossil record up to the Maastrichtian (Ippolitov et al., 2014). McNamara (2023) further noted that the forms assigned to *Praerotularia* (= *Rotulispira*) probably comprise only Cretaceous species. In contrast, *Rotularia sensu stricto*, characterised by a general lack of transverse ornament, has a distinctly younger stratigraphic range and is confined to the Paleogene, extending from the Danian to the late Eocene (Ippolitov et al., 2014; McNamara, 2023).

Fossil occurrences of *Rotularia* are documented from Europe and Central Asia via the Tethyan seaway, and North America, indicating broad dispersal across shallow marine environments (Figs. 14, 15). The long temporal range and widespread palaeogeographical

distribution of *Rotularia* suggest a high ecological tolerance and effective dispersal capabilities, likely facilitated by larval stages and marine connections between palaeoceanic realms. In North America, *Rotularia* is reported from multiple localities along the Gulf of Mexico (Alabama, Arkansas, Florida, Mexico), and the Caribbean, as well as from the Pacific coast (California and Washington State). This distribution pattern may reflect a predominantly trans-Atlantic migration between North America and the Tethyan realm rather than direct trans-Pacific dispersal from the eastern Tethys. During the Mesozoic and the Cenozoic, trans-Atlantic dispersal pathways were likely more accessible than trans-Pacific routes, as the palaeogeographic configuration of continents and the presence of extensive shallow continental shelves in Europe and Africa facilitated marine dispersal, making the Atlantic route the most effective pathway (e.g. Fallaw, 1979; 1983). Fallaw (1983) also suggested that, even at present, the Atlantic route may provide the easiest pathway for organisms to achieve trans-Pacific dispersal. By the Eocene, the Western Interior Seaway, a shallow epicontinental sea formerly connecting the Arctic Ocean with the Gulf of Mexico, was already closed, thus precluding this dispersal pathway. *Rotularia* thus may have reached California and Washington State via the Caribbean region through an open seaway to the Pacific margin, followed by northward dispersal along the Pacific coast.



a



b



Palaeoecological remarks and associated fauna

Juveniles of rotulariid serpulids were cemented to small substrates, and later in ontogeny grew into secondary, reclining epifaunal soft-bottom dwellers in medium- to high-energy environments (Macellari, 1984; Savazzi, 1995; Seilacher et al., 2008; Astibia et al., 2016; Elorza & Astibia, 2018, McNamara, 2023). Seilacher et al. (2008, p. 363) described the evolution of this soft-bottom adaptation in *Rotularia*, emphasising morphological modifications related to stability on unconsolidated sediment: lenticular (disk-shaped), heavy tubes with thick walls, and spiral ribs or, in the Eocene forms, massive keels that shift ballast toward the disk margin. The growth plan includes a transition from trochospiral to involute planispiral coiling and, at adulthood, the formation of an uncoiled terminal chimney that is typically smooth, with a thinner wall and lacking ribs. These stabilising structures increased the effective area of contact with the substrate and were only exceptionally bent out of the coiling plane, a situation common in other sessile soft-bottom dwellers among polychaetes and gastropods. The morphology of the Soh and Zefreh serpulids matches this model. All examined specimens occur in soft substrates and are preserved with the apex oriented downward, while the adult free anterior part (terminal chimney) rests horizontally on the sediment surface (see, e.g. Fig. 10 g–i). In *Rotularia leptostoma* (Gabb, 1860), a massive bicarinate keel is developed, whereas *R. spirulaea* bears only a single massive keel; in both taxa, the keel effectively shifted additional ballast at the external margin of the coiled disc, thereby enhancing stability on soft substrates. The mode of life of *Rotularia* has, however, no recent counterparts for comparison, and it is difficult to speculate on its specific environmental requirements.

The fossil species *Ditrupa strangulata* (Deshayes, 1825) exhibited a free-lying mode of life on the soft seafloor (A. H. Müller, 1969), similarly to fossil *Ditrupa brevis* Sanfilippo, 1999, and to extant *Ditrupa* species, including the Atlantic–Mediterranean *D. arietina* (e.g. Morton & Salvador, 2009; Hartley, 2014) and the Indo-Pacific *D. gracillima* Grube, 1878 (see ten Hove & Smith, 1990). Larvae briefly attach to a pebble or shell but break free later, leaving no trace of an attachment scar even in the most posterior part of the calcareous tube (ten Hove and Kupriyanova, 2009; Kočová Veselská et al., 2021). *D. arietina* lives within the sediment or lies loosely at the sediment surface, with an anterior bulge exposed above the substratum. This anterior bulge accommodates the retracted feeding tentacles, and the aperture can be sealed by a further tentacle bearing an operculum (Morton and Harper, 2009; Morton & Salvador, 2009; Hartley, 2014). *D. arietina* is considered an indicator of unstable sea floors, tolerant of high quantities of suspended inorganic matter and able to flourish under turbid conditions (Guizien et al., 2010; Martinell et al., 2012). Although *Ditrupa* is most commonly reported from shallow

seas at depths of about 10–30 m (e.g. more turbid Mediterranean settings), it can occur much deeper (Morton & Salvador, 2009; Hartley, 2014). Hartley (2014) collected specimens of *D. arietina* at 75 m in the central North Sea and at 151–167 m in the northern North Sea. Off the Azores, *Ditrupa* has been reported from around 200 m (Morton & Salvador, 2009), and in the Celtic Sea, it was described as very abundant at multiple sites, including off SW Ireland at 102–305 m (Ellis et al., 2013). Morton & Salvador (2009) suggested that such depth differences may reflect variation in light conditions and food availability, potentially interacting with sediment grain size and disturbance.

Tube-dwelling polychaetes from Soh and Zefreh are associated with benthic foraminifera (listed in Tab. 3), gastropods (*Pleurotomaria*, *Conus*, *Natica*; Fig. 16a–f), bivalves (*Atrina*, *Glycymeris*), echinoids (*Schizaster*; Fig. 16g–h), and brachyuran cheliped remains (*Harpactocarcinus*, *Zanthopsis*; Ossó et al., 2023). The foraminiferal assemblage indicates rather warm and shallow marine conditions during the middle–late Lutetian, while the sandstone-tuffaceous siltstone alternation points to cyclic high-energy episodes capable of transporting coarse material. In the upper part of the section, increasing algal content further supports the persistence of warm and shallow water conditions through this interval.

Tab. 3

<i>Nummulites striatus</i> Bruguère
<i>Assilina exponens</i> Sowerby
<i>Nummulites perforatus</i> Montfort
<i>Alveolina</i> sp.
<i>Discocyclina</i> sp.
<i>Triloculina trigonula</i> Lamarck
<i>Miliola saxorum</i> Lamarck
<i>Nummulites variolarius-incrassatus</i> de la Harpe
<i>Sphaerogypsina</i> sp.
<i>Lockhartia</i> sp.

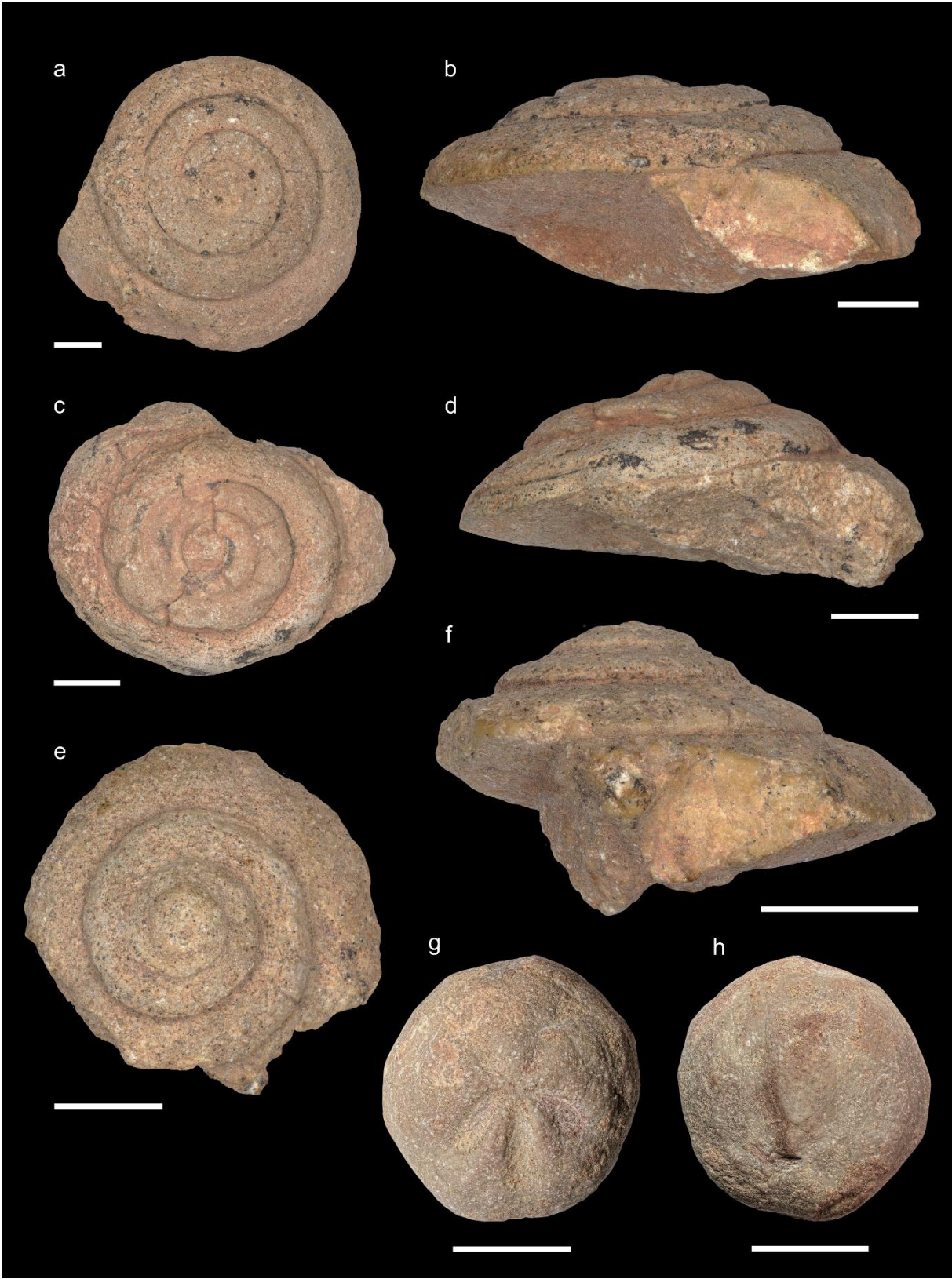
<i>Coskinolina</i> sp.
<i>Operculina</i> sp.
<i>Orbitolites complanatus</i> Lamarck
<i>Rotalia</i> sp.
<i>Valvolina</i> sp.
<i>Bolivina pulchra</i> Rhumbler
<i>Dentalina budensis</i> (Hantken)
<i>Siphonodosaria annulifera</i> (Cushman & Bermúdez)
<i>Trifarina wilcoxensis</i> (Cushman & Ponton)
<i>Dentalina consobrina</i> d'Orbigny
<i>Nodosaria latejugata</i> Gümbel
<i>Ellipsolingulina impressa</i> Terquem
<i>Nonionella hantkeni</i> var. <i>spissa</i> Cushman
<i>Eponides polygonus</i> Le Calvez
<i>Sphaerogypsina globulus</i> (Reuss)
<i>Lagena globosa</i> Sequenza
<i>Spiroplectinella roemeri</i> (Lalicker)
<i>Alveolina</i> sp.
<i>Reussella elongata</i> Terquem
<i>Assilina</i> sp.
<i>Quinqueloculina</i> sp.
<i>Marginulina wetherelli</i> Jones

<i>Spirorutilus carinatus</i> (d'Orbigny)
<i>Lenticulina excisa</i> (Bornemann)
<i>Elphidium</i> sp.

529

530 The polychaete assemblage from Soh and Zefreh appears less diverse than those
531 reported from other Eocene localities in Iran. For example, Jäger et al. (in press) described a
532 particularly diverse polychaete fauna from Rubiyat, including the sabellid *Glomerula*
533 *serpentina* attached to the foraminifer *Assilina* sp., as well as serpulids such as *Pyrgopolon*
534 (*Pyrgopolon*) sp., *Propomatoceros* sp., *Propomatoceros* sp. 2, *Mucroserpula* sp., and
535 *Josephella* sp. Soh a Zefreh localities notably lack serpulids preserved as epibionts, whereas
536 Rubiyat lacks soft-bottom rotulariids and *Ditrupa* tubes. This contrast may reflect
537 environmental differences, potentially including greater water depth at Rubiyat (estimated up
538 to 80 m based on *Assilina*) compared with Soh and Zefreh. The relatively low palaeodiversity
539 of the Eocene limestone in the Soh and Zefreh areas can be related to clastic influx linked to
540 submarine volcanism and associated environmental stress that affected benthic stability on or
541 within the substrate (e.g. through rapid shifts in seawater chemistry, including pH changes and
542 acidification). The Soh and Zefreh palaeoenvironment is comparable to the nearby Isfahan
543 locality, which also shows relatively low palaeodiversity (cf. Hassan-Vand et al., 2018). During
544 cyclic high-energy episodes of transporting coarse material, *Ditrupa* and *Rotularia*, which
545 tolerate high suspended inorganic loads and can thrive in high-energy conditions, were likely
546 less affected than epibiotic polychaetes.

547



Conclusions

The middle Eocene deposits of the Soh and Zefreh areas in central Iran yield a serpulid assemblage dominated by *Rotularia leptostoma*, accompanied by *Rotularia spirulaea* and *Ditrupa strangulata*. *R. leptostoma* and *D. strangulata* are reported from Iran for the first time.

The tube wall of *Ditrupa strangulata* is two-layered, consisting of an outer regularly ridged prismatic structure and an inner fine-granular homogeneous layer. In contrast, *Rotularia leptostoma* has a three-layered tube wall composed of a thin inner lamello-fibrillar layer and a thicker outer layer subdivided into a middle homogeneous layer with irregularly oriented spherulitic crystals and an outermost layer of short spherulitic prismatic crystals. The microstructure of *R. leptostoma* closely resembles that of *Rotularia spirulaea*, particularly in the relative thickness of the inner layer, which represents about one quarter of the outer-layer thickness. Differences in the relative thickness of individual layers and in the size and orientation of their crystals among *Rotularia* species support the value of tube microstructure as an important diagnostic character at the species level in fossil serpulids.

Drill holes assigned to *Oichnus* occur on two specimens of *Rotularia leptostoma*. Their shallow, faintly parabolic morphology and perpendicular orientation indicate unsuccessful or interrupted drilling attempts, likely reflecting predatory interactions. These traces document biotic interactions within the Eocene benthic communities of central Iran.

The stratigraphic distribution of the studied polychaetes is consistent with current concepts of rotulariid systematics, with *Rotularia* sensu stricto confined to the Paleogene.

The broad palaeogeographical distribution of Palaeocene and Eocene *Rotularia* across Europe, Central Asia and North America indicates effective dispersal in shallow-marine settings. Its North American occurrence is most consistent with dispersal via trans-Atlantic marine pathways than with direct trans-Pacific migration from the eastern Tethys.

The foraminiferal assemblage indicates warm and shallow marine conditions during the middle–late Lutetian in the Soh and Zefreh areas, further supported by increasing algal content in the upper part of the section.

Morphology of the studied polychaetes indicates that the studied taxa were free-lying soft-bottom dwellers. *Rotularia* shows a reclining epifaunal posture, with stability enhanced by massive keels. *Ditrupa* likewise reflects a free-lying soft-substrate habit within the sediment or loosely at the sediment surface, with an anterior bulge exposed above the substratum. Comparatively reduced polychaete diversity at Soh and Zefreh relative to other Iranian Eocene localities is best interpreted as a response to environmental stress associated with siliciclastic influx and submarine volcanism, with consequent impacts on benthic stability and seawater

chemistry. Sandstone and tuffaceous siltstone alternations indicate episodic high-energy disturbance and elevated suspended loads, conditions that *Rotularia* and *Ditrupea* likely tolerated better than epibiotic polychaetes.

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Captions

Tab. 1 Measurements of 21 specimens of *Rotularia spirulaea* used in this study

Tab. 2 Measurements of 227 specimens of *Rotularia leptostoma* used in this study

Tab. 3 Associated foraminifera

Fig. 1 a Map showing the two localities, Soh and Zefreh, in Iran. **b** Detailed view of the two localities, Soh and Zefreh, near Isfahan. The localities are indicated by small yellow asterisks.

Fig. 2 Left: Geographic map of Iran showing the position of the Soh and Zefreh outcrops and accessible road from Isfahan city to these studied localities (Bakhtiyari, 2018). Right: Geological map of the Soh area (modified from Zahedi, 1973).

Fig. 3 Close-up view of the outcrop located northwest of Soh village. **a** Intercalation of red clays with sandstone and conglomerates, Paleocene. **b** Transitional boundary between the Paleocene red-brown deposits and the early Eocene grey to white marls. **c** Intercalation of thin-bedded siltstones and sandstones of early Eocene. **d** Early Eocene green marls with minor sandstone interlayers; the green marls are rich in serpulid tube worms.

Fig. 4 Stratigraphic column of the studied outcrop northwest of Soh village, showing the serpulid tube-bearing levels.

Fig. 5 a Geological map of the Zefreh area (modified from Radfar & Kohansal, 2002).

Fig. 6 a Stratigraphic column of the studied outcrop northwest of Zefreh village; the black arrow indicates the serpulid tube-bearing level. **b** Close-up view of the studied outcrop located northwest of Zefreh village-

Fig. 7 *Ditrupa strangulata* (Deshayes, 1825), specimen IUMC 40021, Soh locality.

a Several tubes irregularly arranged in the sediment. Their chaotic orientation suggests reworking during sedimentation in a high-energy palaeoenvironment. **b** SEM image of the polished surface after treatment with 1% acetic acid for 3 minutes. Scale bars = 2 mm

Fig. 8 SEM images showing the tube microstructure of *Ditrupa strangulata* (Deshayes, 1825), specimen IUMC 40021, Soh locality. **a** Overall view of the polished surface after treatment with 1% acetic acid for 3 minutes. **b–c** Details of a fine granular homogeneous microstructure of the inner tube layer. **d** View of the outer and inner tube layers; black rectangles indicate the enlarged areas shown in e–g. **e–f** Details of the regularly ridged prismatic structure (RRP) of the outer tube layer. **g** Detail of the inner tube layer, composed of a fine granular homogeneous microstructure. Scale bars: a = 2 mm, (b, d) = 200 µm, (c, e, g) = 30 µm, f = 10 µm

Fig. 9 *Rotularia spirulaea* Lamarck, 1818, Soh locality; upper, lower and lateral views, respectively. **a–c** Specimen IUMC 40022. **d–f** Specimen IUMC 40023. **g–i** Specimen IUMC 40024. **j–l** Specimen IUMC 40025. **m–o** Specimen IUMC 40026. Scale bars: (a–b, d–e, g–h, j–k, m–n) = 5 mm, (c, f, i, l, o) = 2 mm

Fig. 10 *Rotularia leptostoma* (Gabb, 1860), Zefreh locality; upper, lower and lateral views, respectively. **a–c** Specimen IUMC 40043. **d–f** Specimen IUMC 40044. **g–i** Specimen IUMC 40045. **j–l** Specimen IUMC 40046. **m–o** Specimen IUMC 40047. Scale bars: (a–b, d–e, g–h, j–k, m–n) = 5 mm, (c, f, i, l, o) = 2 mm

Fig. 11 *Rotularia leptostoma* (Gabb, 1860), Zefreh locality. **a–d** Specimen IUMC 40048, upper, lower and lateral views, respectively. **e–h** Specimen IUMC 40049, upper, lower and lateral views, respectively. **i–k** Specimen IUMC 40050, upper and lateral views, respectively. **l–n** Specimen IUMC 40051, upper and lateral views, respectively. The white arrows indicate incomplete drill holes attributable to the ichnogenus *Oichnus* Bromley, 1981. **k, n** Detailed views of *Oichnus* boreholes. Scale bars: (a–j, l–m) = 5 mm, (k, n) = 1 mm

Fig. 12 SEM images showing the tube microstructure of *Rotularia leptostoma* (Gabb, 1860), Zefreh locality. **a** Overall view of the tube transverse section, specimen IUMC 40052. **b** Detail of the tube layers: the inner tube layer with a lamello-fibrillar structure, the outer-middle homogeneous layer composed of irregularly oriented spherulitic crystals, and the outermost layer composed of short, semi-regularly oriented spherulitic prismatic crystals. **c** Overall view of the tube longitudinal section, specimen IUMC 40053. **d** Detail of the outer-middle and the outermost layers. **e** The outer-middle homogeneous layer with irregularly oriented spherulitic crystals. **f** The outermost layer with short, semi-regularly oriented spherulitic prismatic crystals. Scale bars: a = 1 mm, b = 100 µm, c = 5 mm, d = 200 µm, e, f = 40

Fig. 13 SEM images showing the tube microstructure of *Rotularia leptostoma* (Gabb, 1860), Zefreh locality. **a** Overall view of a transverse section of the tube anterior portion, specimen IUMC 40054. The occurrence of opal was caused by terrigenous silica input. **b–d** Detailed views of the microstructure of the tube layers: the inner tube layer with a lamello-fibrillar structure, the outer-middle homogeneous layer composed of irregularly oriented spherulitic crystals, and the outermost layer composed of short, semi-regularly oriented spherulitic prismatic crystals. **e** Overall view of the transverse section of the tube anterior portion, specimen IUMC 40055. **f** Detailed view of the microstructure of the tube layers. Scale bars: a, e = 2 mm; b–d, f = 100 µm

Fig. 14 Palaeocene occurrences of *Rotularia* Defrance, 1827. Base maps from Scotese (2014) with data (circles) from Lundgren (1891); Rovereto (1904); Gardner (1935); Jäger (1993, 2005).

a Occurrences outside Europe. 1=Parras and La Popa basins (Mexico): *R. dickhauti*; 2=Maverick County in Texas (USA): */R. tobar/ tobar*; 3= Little Rock in Arkansas (USA): *R. dickhauti*; 4=Alabama (USA): */R. tobar/ mcglameryae*.

b Detailed view of occurrences in Europe. 5=Paris Basin (France): *R.? conulus*; 6= Albert Canal (Belgium/Netherlands): *R. hisingeri*, *R. spirintorta*, */R. tobar/ gracilis*, */R. tobar/ vroenhovens*; 7=Sjaelland (Denmark): *R. hisingeri*, *R.? conulus*; 8=southern Sweden: *R. hisingeri*, *R.? conulus*; 9=Nasiłów in eastern Poland: *R. hisingeri*

Fig. 15 Eocene occurrences of *Rotularia* Defrance, 1827. Base maps from Scotese (2014) with asterisk indicates the occurrence of *Rotularia* in Iran and data (circles) from Lamarck (1818), Schlotheim (1820); Mantell (1822); Defrance (1827); Goldfuss (1833); Galeotti (1837); Chenu (1842); Leymerie (1846); Gabb (1860); Guppy (1866); Mayer (1876); White (1881); Rovereto (1898); Oppenheim (1901); Doncieux (1926); Gardner (1939); Richards (1948); Wrigley (1951); Schmidt (1955b); Nicol & Jones (1982); Squires (1984); Benini et al. (1988, 1992); Jäger (1993, 2005); Squires & Goedert (1994); Vega & Del Carmen Perrilliat (1995); Aguilar & Arias (1998); Hoşgör & Okan (2006); Mikuž (2008); Vinn (2008); Astibia et al. (2016); Elorza & Astibia (2017, 2018); Bahrami et al. (2018); Hassan-Vand et al. (2018).

a Occurrences outside Europe. 1=Washington State (USA): *R. tejonense*; 2=California (USA): *R. tejonense*; 3=Nuevo León (NE Mexico): *R. cortezi*; 4=Texas (USA): *R. horatiana* (Sabine County), *R. leptostoma* (Caldwell County); 5= Florida (USA): *R. vernoni*; 6=Republic

1091 of Cuba (Caribbean): *R. clymenioides*; 7= Barbados, Country of Curaçao, Republic of Trinidad
1092 and Tobago (Caribbean): *R. clymenioides*; 8=Republic of Costa Rica: *R. clymenioides*; 9=
1093 Egypt: *R. pseudospirulaea*; 10= Turkey: *R. spirulaea*; 11=Iran: *R. leptostoma*, *R. spirulaea*;
1094 12=Hyderabad (India): *R. spirulaea*.

1095 **b** Detailed view of occurrences in Europe. 13=Navarra (NE Spain): *R. spirulaea*;
1096 14=Nouvelle-Aquitaine region (SW France): *R. angulosa*, *R. spirulaea*; 15=Occitane region
1097 (S France): *R. angulosa*, *R. angulosa* var. *crassa*; 16=Auvergne-Rhône-Alpes region (SE
1098 France): *R. cristata*?; 17=Bourgogne-Franche-Comté region (E France): *R. lituus*; 18= Pays de
1099 la Loire region (NW France): *R. lituus*; 19= northern France: *R. bogneriensis*; 20=southern
1100 England (UK): *R. bogneriensis*; 21=Belgium: *R. bogneriensis*; 22=the Netherlands: *R. nysti*;
1101 23=northern Switzerland: *R. bogneriensis*; 24= the area southeast of Munich in southern
1102 Germany and the Salzburg area in Austria: *R. clymenioides*, *R. leptostoma*, *R. spirulaea*, *R.*
1103 *subcarinata*? (one internal mould only); 25= Regensburg in southern Germany: *R. angulosa*;
1104 26=Lower Austria: *R. clymenioides*, *R. spirulaea*; 27= Carinthia province in southern Austria:
1105 *R. leptostoma*, *R. pseudospirulaea*, *R. spirulaea*; 28=northern Italy: *R. nummularia*, *R.*
1106 *spirulaea*; 29=northern Adriatic (the Istria-Rijeka-Krk area) in Croatia: *R. spirulaea*;
1107 30=Bulgaria: *R. spirulaea*; 31=northern Romania: *R. spirulaea*; 32=Ukraine: *R. spirulaea*

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1109 **Fig. 16** Associated fauna. **a–f** Gastropod *Pleurotomaria* sp., upper and lateral views. **a–b**
1110 Specimen IUMC 40270. **c–d** Specimen IUMC 40271. **e.–f.** Specimen IUMC 40272. **g–h**
1111 Echinoderm *Schizaster* sp., specimen IUMC 40273, upper and lower views, respectively. Scale
1112 bars = 5 mm