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# The revised Permian genus *Dagmarita* Reitlinger, 1965 (Dagmaritinae, Foraminifera) and its phylogenetic relationships

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**Abstract.**—Among Permian smaller foraminifers, the genus *Dagmarita* is one of the most studied due to its worldwide distribution. The detailed study of the Zal (NW Iran) and Abadeh (Central Iran) stratigraphic sections led to redescription of the genus *Dagmarita* and its taxonomic composition. In *Dagmarita*, a peculiar generic morphological character, represented by a secondary valvular projection, has been detected for the first time among globivalvulinid foraminifers. The phylogeny of *Dagmarita*, and in particular its ancestor *Sengoerina*, is discussed and the new species, *D. ghorbanii* n. sp. and *D. zalensis* n. sp., are introduced. Analogies and differences among all the species belonging to *Dagmarita* are highlighted and morphological features of the new taxa are shown in 3D reconstructions, useful for understanding differently oriented sections of the specimens in thin section.

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## Introduction

Reitlinger (1965) described *Dagmarita* (type species *Dagmarita chanakchiensis* Reitlinger, 1965) from the middle–late Permian of Transcaucasia, as a new genus characterized by a biserial test with lateral spines, simple aperture, and thin calcareous wall. Subsequently, Bozorgnia (1973) specified in the description of *Dagmarita chanakchiensis*, from Central Alborz (Iran), that the wall is double-layered (inner layer microgranular and outer hyaline layer radiate and thin). From the late 1970s to early 1990s, the introduction of several new species, such as *Dagmarita elegans* Sosnina and Nikitina, 1977 and *Dagmarita simplex* Wang in Zhao et al., 1981, led to the increase in species diversity of the genus (Sosnina in Sosnina and Nikitina, 1977; Wang in Zhao et al., 1981; Hao and Lin, 1982; Vuks in Kotlyar et al., 1984; Lin, 1984; Lin et al., 1990). In the meantime, Altıner (1981) and Loeblich and Tappan (1987) described *Dagmarita* as having a possible short enrolled biserial earliest stage. Mohtat-Aghai and Vachard (2003) erected *Dagmarita shahrezaensis* from the Hambast Formation of the Shahreza area (Central Iran), introducing it as a biserial taxon, without thorn-like projections and with a unilayered microgranular wall. Finally, Gaillot and Vachard (2007) and Ebrahim Nejad et al. (2015) further modified the description of *Dagmarita*, defining this genus as doubtfully characterized by three initial pairs of chambers, more or less globivalvulinid in coiling, and by a mono-, double- or trilayered wall.

Concerning its suprageneric position, *Dagmarita* was initially placed among the Biseriamminidae Chernysheva, 1941 (Reitlinger, 1965). Bozorgnia (1973) later introduced the monogeneric family Dagmaritidae. Successively, Zaninetti and Altıner (1981) synonymized the Dagmaritidae with the family Biseriamminidae and divided the latter into subfamilies Biseriammininae Chernysheva, 1941 and Dagmaritinae Bozorgnia, 1973. Several later authors continued to retain the subfamily Dagmaritinae as valid, even if they revised its systematic status (Loeblich and Tappan, 1987; Mohtat-Aghai and Vachard, 2003; Gaillot and Vachard, 2007; Gaillot et al., 2009; Altıner and Özkan-Altıner, 2010; Hance et al., 2011; Vachard, 2016). The latest taxonomical rearrangement has been proposed by Gennari et al. (2018a).

Based on material from Zal (NW Iran) and Abadeh (Central Iran) stratigraphic sections, the present study aims to introduce two new species of the genus *Dagmarita*. We redescribe the genus and discuss its taxonomic composition and phylogeny. In addition, the 3D reconstructions of the new species *Dagmarita ghorbanii* n. sp. and *Dagmarita zalensis* n. sp. are presented in order to better understand their complex shapes and transects in different orientations in thin sections. This paper also represents a methodological contribution, which could serve as a starting point for similar studies on other groups of fossil Foraminifera.

## Geological setting

The analyzed stratigraphic sections (Zal and Abadeh C-D) are well known in the literature and extensively studied as containing the Permian-Triassic boundary (Iranian-Japanese Research Group, 1981; Heydari et al., 2003; Korte et al., 2004; Kozur, 2007; Shen and Mei, 2010; Angiolini et al., 2013; Leda et al., 2013; Liu et al., 2013; Gennari et al., 2018b). The Zal section is located 26.5 km SSW of Julfa and 1.6 km WNW of the Zal village, NW Iran (38°43′9.1″N, 45°34′37.5″E), whereas the Abadeh C-D section is situated in the Hambast Valley, ~60 km SE of Abadeh, Central Iran (30°53′56.1″N, 53°12′29.8″E) (Fig. 1). This latter stratigraphic section corresponds to the entire Section C and part of Section D studied by Iranian-Japanese Research Group (1981).


**Figure 1.** Map of Iran showing the locations of studied sections.

Iran has been structurally subdivided into ten structural provinces, some of which are separated by suture zones (Stöcklin, 1968; Alavi, 1991; Nezafati, 2006). These provinces are: (1) Khuzestan plain, (2) Zagros fold and thrust belt, (3) Sanandaj-Sirjan zone, (4) Makran, (5) Eastern Iran, (6) Lut Block, (7) Central Iran Block, (8) Kopet Dagh, (9) Urumieh-Dokhtar zone, and (10) Alborz Mountains (Fig. 2). The final structural setting of Iran is the result of tectonic processes that affected all the provinces during the Alpine-Himalayan orogeny in the Oligo-Miocene (Stöcklin, 1968, 1977; Alavi, 1991; Gaetani et al., 2009; Zanchi et al., 2009; Spina et al., 2018). The studied sections are located in two different structural provinces: the Abadeh C-D section belongs to the Sanandaj-Sirjan thrust belt; the Zal section is located within the Central Iran Block (Fig. 2).

The Permian–Triassic Abadeh C-D section is composed from bottom to top by the Abadeh (380.5 m), Hambast (36 m), and Elikah (8 m) formations (Fig. 3). The Capitanian–early Wuchiapingian Abadeh Formation (Liu et al., 2013, with references therein) consists of two units (Unit 4 and Unit 5). The Unit 4 is mainly composed of thick-bedded bioclastic limestones and thin- to medium-bedded limestones alternating with black shales. The upper part of Unit 4 consists of thick-bedded limestones with abundant stratified and nodular chert. Unit 5 is dominated by dark thick-bedded bioclastic limestones. The overlying Lopingian Hambast Formation (Unit 6 and Unit 7) (Liu et al., 2013, with references therein) is characterized by thick black shales interbedded with dark-gray thin-bedded limestones, which become reddish and nodular in the upper part (*Paratirolites* Bed, Unit 7). The only investigated basal part of the latest Changhsingian–Induan Elikah Formation (Unit a) is marked by stromatolitic limestones (thrombolites) (Iranian-Japanese Research Group, 1981; Richoz et al., 2010; Liu et al., 2013).

The Permian–Triassic Zal section is characterized from bottom to top by the Gnishik (350 m), Arpa (320 m), Khachik (360 m), Julfa (33 m), Ali Bashi (16 m), and Elikah (10.5 m) formations (Fig. 3). The Wordian Gnishik Formation (Leven, 1998) consists of dark-gray thin-bedded limestones and massive limestones alternating with marly limestones and black shales. The upper part of the formation shows an increase of marly limestones and black shales. The Wordian–Capitanian Arpa Formation (Leven, 1998) is mostly represented by light-gray thin-bedded and massive bioclastic limestones. The occurrence of nodular chert in the lower part of the Formation is characteristic. The overlying Capitanian–early Wuchiapingian Khachik Formation (Ghaderi et al., 2016) consists of thin- and thick-bedded limestones passing upward into marly limestones and limestones with chert nodules interbedded with shales. The topmost unit of the Khachik Formation is characterized by dark-gray limestones, forming a unit named the *Codonofusiella* Limestone. The Lopingian Julfa Formation (Julfa Beds sensu Stepanov et al., 1969) (Schobben et al., 2015; Ghaderi et al., 2016) is composed of nodular limestones and marly limestones with intercalations of gray to red shales. The Lopingian Ali Bashi Formation (Teichert et al., 1973; Schobben et al., 2015; Korn et al., 2016) comprises the unnamed shaly unit (Ghaderi et al., 2014) mostly characterized by red shales and the *Paratirolites* Limestone represented by red, nodular, marly limestones that are rich in ammonoids. The Ali Bashi Formation is successively overlain by the the latest Changhsingian–Induan Elikah Formation (Schobben et al., 2015; Zhang et al., 2018) in the studied part, which is composed of red and gray shales ('Boundary Clay') and yellow-gray, marly thin-bedded limestones.

## Material and methods

We studied a total of 553 limestone samples from the Zal and the Abadeh C-D sections, analyzing two thin sections per sample. *Dagmarita ghorbanii* n. sp. was recorded in 12 samples from the Zal section (Gnishik, Arpa, and Khachik formations) and in four samples from the Abadeh C-D section (Abadeh Formation), whereas *Dagmarita zalensis* n. sp. was recorded in two samples from the Zal section (Gnishik and Arpa formations). The images of the specimens were produced with different magnifications using Leica DM4500 P LED transmitted light microscope equipped with a Leica MC170 HD digital camera.

*3D modeling.*—In our study, the new species *Dagmarita ghorbanii* n. sp. and *Dagmarita zalensis* n. sp. were investigated in detail with the purpose to obtain, for each of them, a three-dimensional visualization. The resulting 3D models have been reconstructed taking into account some parameters and measurements acquired from available specimens of the new taxa. The measurement data subsequently were used to obtain an average value for each of the parameters on which the 3D reconstructions are based. For this purpose, the open-source software ImageJ (https://imagej.nih.gov/ij/) was used to measure 2D images. The 3D renderings of the new species were computed using the software Maxwell Studio 4.1 for Mac, whereas the virtual reconstructions were performed using Rhinoceros 5.3.2 for Mac.

*Repositories and institutional abbreviations.*—The studied material is stored at the paleontological laboratories of the

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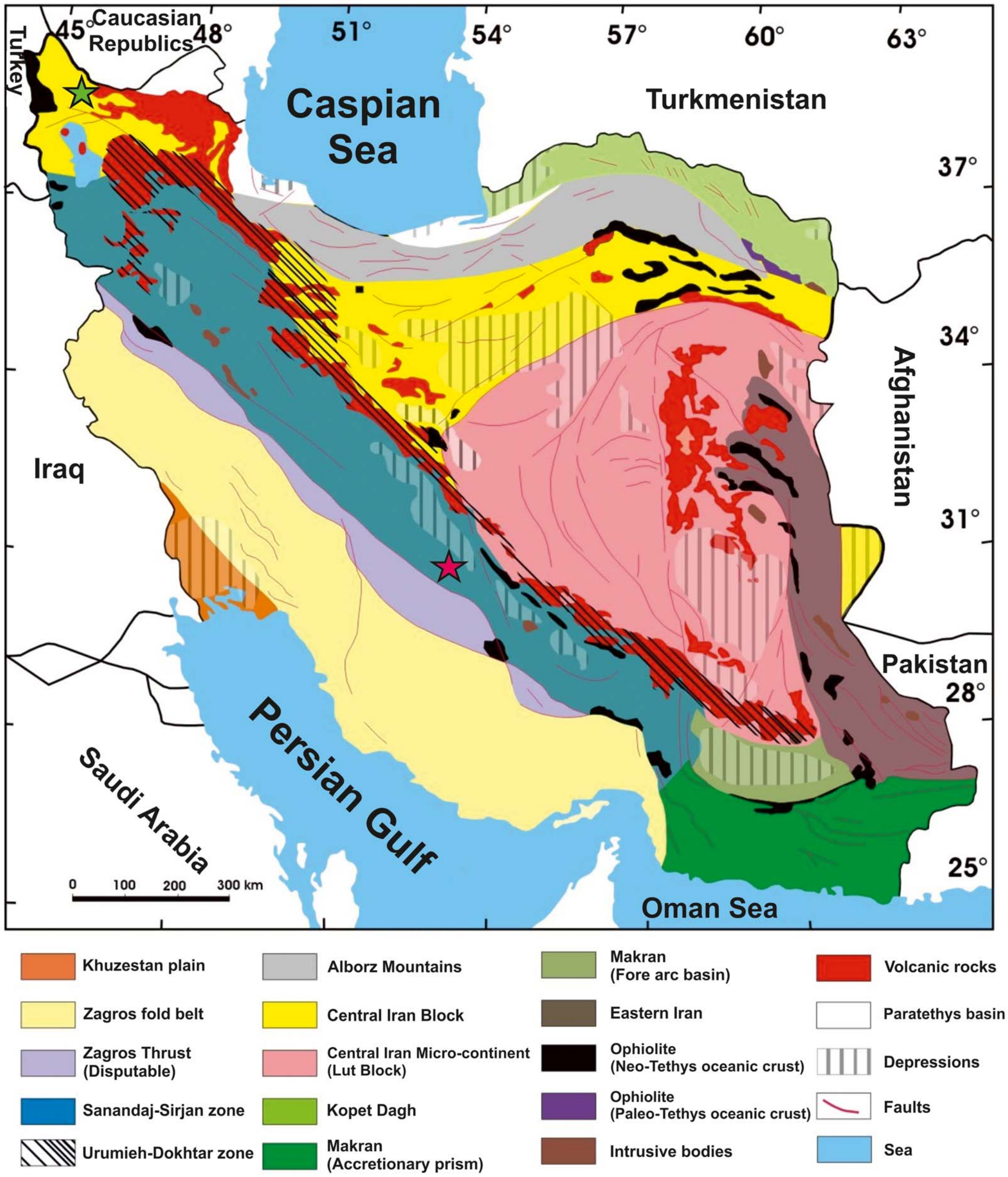


**Figure 2.** General geological map of Iran showing its structural provinces. The position of the Zal section is indicated by a green star, and the Abadeh C-D section by a pink star. Modified from Nezafati (2006).

National Iranian Oil Company (NIOC), Tehran, Iran, under the numbers MRAN 10103 to MRAN 10456 (Zal section) and in the micropaleontological collection of the Department of Physics and Geology of University of Perugia, Italy, under the numbers 1–200, corresponding to certain samples and thin sections in the collection of Abadeh (HB).

## Systematic paleontology

Phylum Foraminifera d'Orbigny, 1826
Class Fusulinata Maslakova, 1990 emend. Gaillot and Vachard, 2007
Subclass Fusulinana Maslakova, 1990 nom. correct. Vachard et al., 2010
Order Endothyrida Fursenko, 1958

*Remarks.*—Currently, the subclass assignment of the superfamily Biseriamminoidea Chernysheva, 1941 is doubtful. Herein, we have followed the macrotaxonomic classification suggested by Hance et al. (2011), Vachard (2016), Gennari et al. (2018a), and Gennari and Rettori (2019), who placed it in the subclass Fusulinana. However, the superfamily Biseriamminoidea could fall into the subclass Nodosariana Mikhalevich, 1992 due to the test morphology and the wall structure of the included genera (Mikhalevich, 2014). According to V.I. Mikhalevich (personal communication, 2019) fusulines rarely have a biserial test and never have a hyaline test wall. The continuity and evolution of the Paleozoic and Mesozoic nodosariats are marked by a gradual disappearance of the microgranular layer of the wall (Reitlinger, 1965; Kuznetzova and Basov, 1974; Grigyalis,

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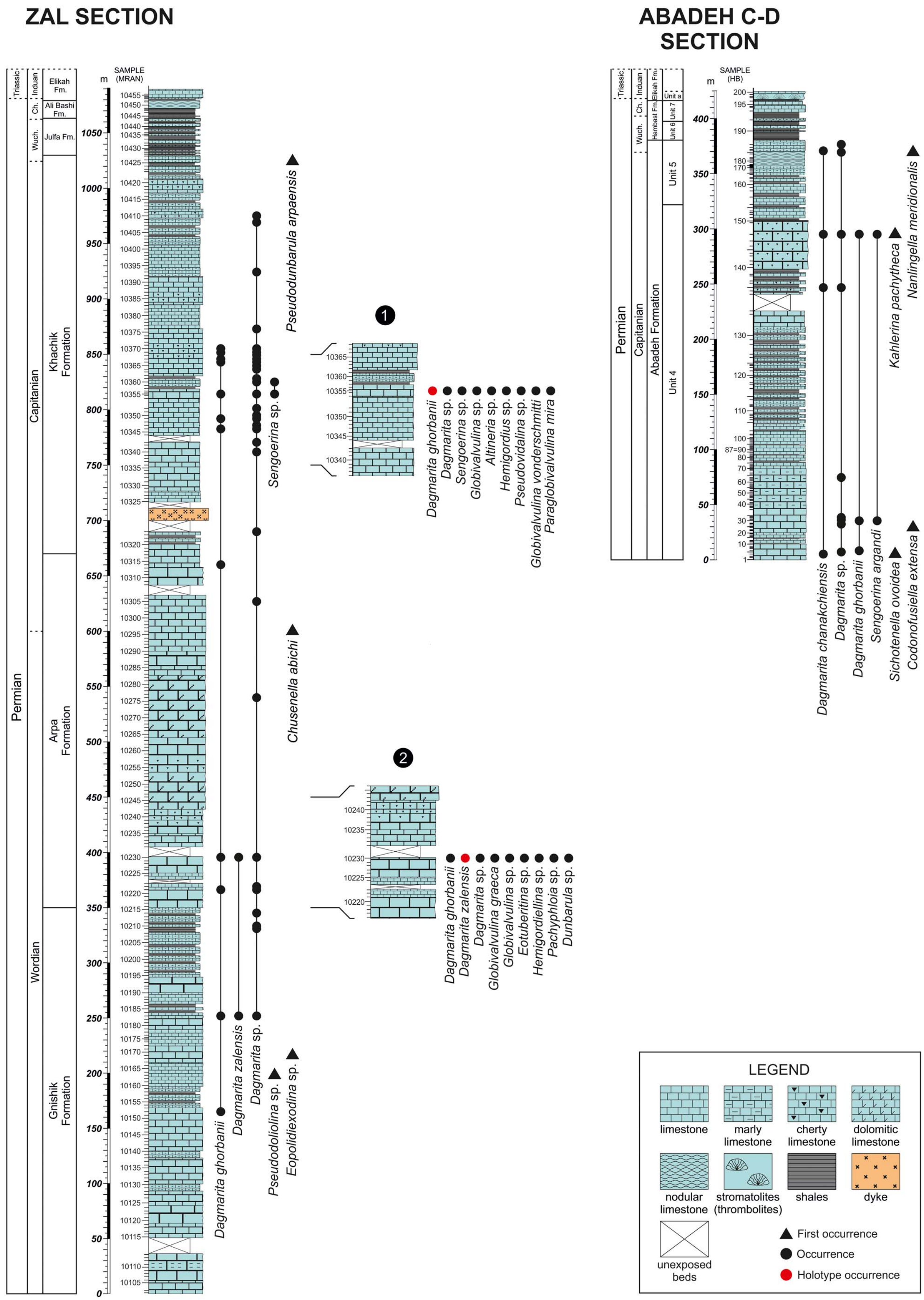


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**Figure 3.** Stratigraphic logs of the Zal and Abadeh C-D sections, with the stratigraphic ranges of the genus *Dagmarita* Reitlinger, 1965, including *Dagmarita ghorbanii* n. sp. and *Dagmarita zalensis* n. sp., and of the genus *Sengoerina* Altıner, 1999. (**1, 2**) Details of the type levels of the new species with the accompanying foraminiferal assemblages. Abbreviations: Ch.: Changhsingian; Wuch.: Wuchiapingian.

1978; Mikhalevich, 2000; Karavaeva and Nestell, 2007), so that Nodosariata Mikhalevich, 1992 becomes the unique group with a hyaline wall in the Paleozoic (Vachard et al., 2010). Furthermore, Hohenegger (1997) and Groves et al. (2003, 2004, 2005) considered Paleozoic and Mesozoic Lagenida as a monophyletic group. The macrotaxonomic position of the Biseriamminoidea will be the subject of a future research.

Superfamily Biseriamminoidea Chernysheva, 1941 emend. Gennari et al., 2018a
Family Globivalvulinidae Reitlinger, 1950 emend. Gennari et al., 2018a
Subfamily Dagmaritinae Bozorgnia, 1973 emend. Gennari et al., 2018a

*Diagnosis.*—Test free, elongated in shape, biserial, uncoiled with rounded peripheral outline. Subspheric chambers, semi-circular to semi-ellipsoidal in axial section. Presence of outer thornlike projections of the test wall. Endoskeletal septal partitions (peripheral chamberlets) are present in *Louisettita*. Test wall plurilayered, composed of dark microgranular and white median or outer hyaline layer. The microgranular layer described with perforations (in *Danielita*). Aperture depressed at the base of the final chamber and protected by a single or double valvular projection.

*Occurrence.*—Roadian (Guadalupian, Permian) (Zheng, 1986) to latest Changhsingian (Lopingian, Permian) of the Paleotethys, the Neotethys, and the Panthalassa (Japan and North America) (Gennari et al., 2018a).

*Remarks.*—Diagnosis emended from Gennari et al. (2018a) due to the double valvular projection observed in the material from Abadeh C-D section (Central Iran). The subfamily Dagmaritinae is composed of the following genera: *Dagmarita* Reitlinger, 1965; *Louisettita* Altıner and Brönnimann, 1980; *Danielita* Altıner and Özkan-Altıner, 2010.

Genus *Dagmarita* Reitlinger, 1965

*Type species.*—*Dagmarita chanakchiensis* Reitlinger, 1965.

*Other species.*—*Dagmarita altilis* Wang in Zhao et al., 1981; *Dagmarita ghorbanii* n. sp.; *Dagmarita zalensis* n. sp. The species *Dagmarita elegans* Sosnina in Sosnina and Nikitina, 1977, *Dagmarita cuneata* Sosnina in Sosnina and Nikitina, 1977, *Dagmarita exilis* Sosnina in Sosnina and Nikitina, 1977, *Dagmarita oblonga* Sosnina in Sosnina and Nikitina, 1977, *Dagmarita simplex* Wang in Zhao et al., 1981, *Dagmarita minuscula* Wang in Zhao et al., 1981, *Dagmarita liantanensis* Hao and Lin, 1982, and *Dagmarita elongata* Lin et al., 1990 are herein considered as synonyms of *Dagmarita chanakchiensis* Reitlinger, 1965.

*Diagnosis.*—Test free, biserial, uncoiled, rectilinear. Subspheric chambers with a rounded periphery of the roof. Thornlike projections of the test wall are present at the peripheral edge of the chambers producing an external angular profile. Aperture depressed at the base of the final chamber. The apertural connection between one chamber and the other is marked by a thickened end of the slightly curved septa with a hooklike shape, which becomes a valvular projection in the last chamber. A secondary valvular projection is present, but not always preserved. The test wall is calcareous, two-layered, with an inner microgranular dark layer and an outer hyaline, clear, translucent layer.

*Occurrence.*—Roadian (Guadalupian, Permian) to latest Changhsingian (Lopingian, Permian) of Paleotethys and Neotethys (Zheng, 1986; Gaillot et al., 2009; Ebrahim Nejad et al., 2015; Gennari et al., 2018a) (Fig. 4).

*Remarks.*—Diagnosis emended from Reitlinger (1965). Reitlinger (1965) described the transverse section of *Dagmarita* as flat, angular as figured (Reitlinger, 1965, pl. 1, fig. 11) for the type species *Dagmarita chanakchiensis*. In our opinion, the cross section figured by Reitlinger (1965) is not

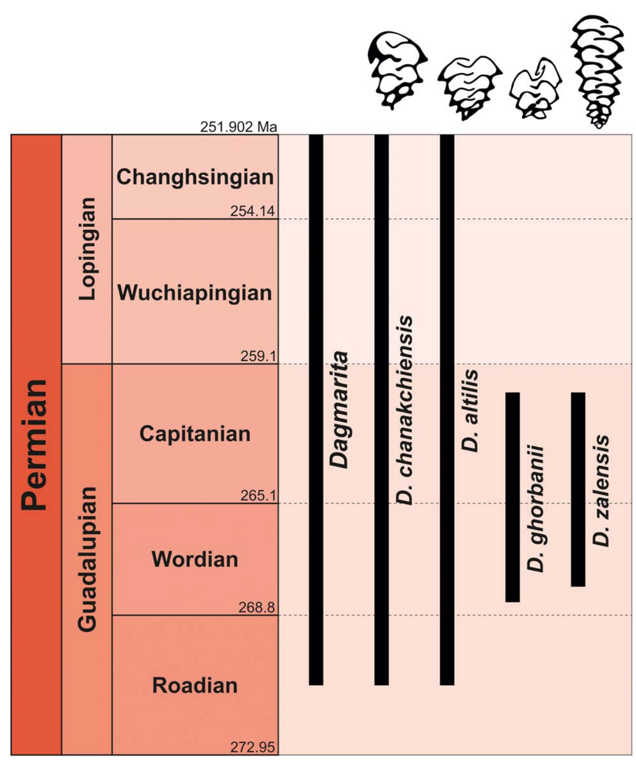


**Figure 4.** Stratigraphic range (thick line) of the genus *Dagmarita* and its species, including *Dagmarita ghorbanii* n. sp. and *Dagmarita zalensis* n. sp. The chronostratigraphic scale used is the last version published by International Commission on Stratigraphy (International Chronostratigraphic Chart 2019/05; http://www.stratigraphy.org/index.php/ics-chart-timescale).

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perpendicular to the growth axes, but it is an oblique transverse section, passing through a corner of the chamber and showing a degree of compression, which is greater than the uncompressed specimens. On the basis of a huge number of observed specimens from our samples and from the literature, we consider the genus *Dagmarita* as uncoiled and biserial from the beginning (Fig. 5), as originally described by Reitlinger (1965, p. 62), even if some authors report a probable biserial coiled earliest stage (Altıner, 1981; Zaninetti and Altıner, 1981; Loeblich and Tappan, 1987; Gaillot and Vachard, 2007; Ebrahim Nejad et al., 2015). The specimen assigned to *Dagmarita* aff. *D. chanakchiensis* by Lys et al. (1980, p. 99, pl. 3, fig. 13) shows an enrolled juvenile stage. On the basis of this character, Ciarapica et al. (1986, p. 208) considered the specimen figured by Lys et al. (1980) as belonging to *Crescentia vertebralis* Ciarapica, et al., 1986. Thornlike projections are always present in the genus *Dagmarita*, but their development and protrusion are herein considered to have taxonomic value at the species level. Observation of species populations highlights that the more the suture intersections are perpendicular, the less the thornlike projections are developed and protruding. Moreover, the depth of the septal depression increases when the angle of the intersection of the septum with the previous chamber is equal to or less than 90° and is further marked if the chambers have a hemispherical to semi-ellipsoidal shape as in *Dagmarita chanakchiensis*. The wall of *Dagmarita* is two-layered, as defined by Altıner and Özkan-Altıner (2010), and there is no evidence of three-layered, as cited by Gaillot et al. (2009) and Ebrahim Nejad et al. (2015).

*Dagmarita* differs from the genera *Paradagmarita* Lys in Lys and Marcoux, 1978, *Paradagmacrusta* Gaillot and Vachard, 2007, *Sengoerina* Altıner, 1999, and *Crescentia* Ciarapica et al., 1986 by having completely uncoiled biserial test (Fig. 5), thornlike projections of the test wall, and a secondary valvular projection (Fig. 5). It also differs from the biserial, uncoiled genera *Danielita* and *Louisettita* because the former is characterized by a perforated inner, microgranular layer of the wall, whereas the latter has endoskeletal septal partitions. Based on the absence of thornlike projections, and in agreement with Gaillot et al. (2009), we assert that *Dagmarita shahrezaensis* Mohtat-Aghai and Vachard, 2003 might belong to another genus yet to be described and should be classified, according to Altıner and Özkan-Altıner (2010), in a suprageneric taxon possibly related to Palaeotextulariidae. Furthermore, the morphological features of the population of *Dagmarita shahrezaensis*, illustrated by Mohtat-Aghai and Vachard (2003), do not seem to be congeneric with the genus *Dagmarita*. Gaillot et al. (2009) doubtfully referred the species *Dagmarita caucasica* Vuks in Kotlyar et al., 1984 to the genus *Bidagmarita* Gaillot and Vachard in Gaillot et al., 2009, which has been recently kept outside the subfamily Dagmaritinae by Gennari et al. (2018a).

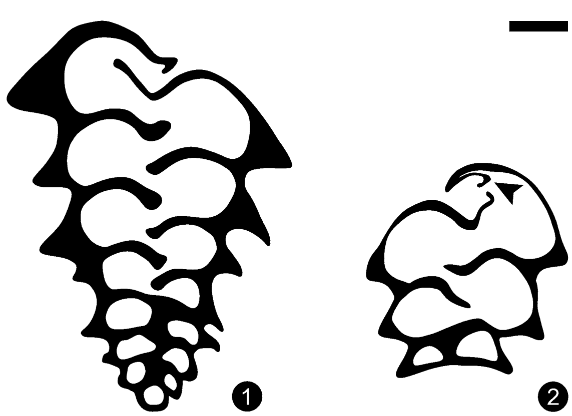

**Figure 5.** Cartoon showing the biserial test, completely uncoiled (**1**) and the secondary valvular projection (**2**). (**1**) *Dagmarita* sp. (modified from Gennari et al., 2018a, fig. 1). (**2**) *Dagmarita chanakchiensis* Reitlinger, 1965 (sample HB 148; Abadeh C-D section). Scale bar = 100 µm.

*Dagmarita chanakchiensis* Reitlinger, 1965

1965 *Dagmarita chanakchiensis* Reitlinger, p. 63, pl. 1, figs. 10–12.
1977 *Dagmarita elegans* Sosnina in Sosnina and Nikitina, p. 50, pl. 2, fig. 8.
1977 *Dagmarita cuneata* Sosnina in Sosnina and Nikitina, p. 50, pl. 2, figs. 5, 6.
1977 *Dagmarita exilis* Sosnina in Sosnina and Nikitina, p. 51, pl. 2, fig. 7.
1977 *Dagmarita oblonga* Sosnina in Sosnina and Nikitina, p. 52, pl. 2, fig. 4.
1981 *Dagmarita simplex* Wang in Zhao et al., p. 74, pl. 1, fig. 24.
1981 *Dagmarita minuscula* Wang in Zhao et al., p. 74, pl. 1, fig. 26.
1982 *Dagmarita liantanensis* Hao and Lin, p. 27, pl. 3, figs. 1, 13.
1990 *Dagmarita elongata* Lin et al., p. 122, pl. 2, figs. 23–26.

*Holotype.*—Longitudinal frontal section (No. 3470/10) from the Khachik Formation of Chanakhchi area, Transcaucasia (Reitlinger, 1965, p. 63, pl. 1, fig. 10).

*Occurrence.*—Roadian (Guadalupian, Permian) to latest Changhsingian (Lopingian, Permian) of Paleotethys and Neotethys (Lin et al., 1990; Kobayashi, 2004; Gaillot and Vachard, 2007; Song et al., 2009) (Fig. 4).

*Description.*—Test free, rectilinear, elongated in shape, biserially arranged. The test is made up by seven to nine pairs of chambers rapidly increasing in the last two/three pairs of chambers. The chambers are hemispherical to semi-ellipsoidal in outline, with a rounded periphery of the roof. Sutures deeply depressed with an intersection angle never greater than 90° as observable in longitudinal frontal section. Nipple-shaped projections of the test wall are present at the peripheral edge of the chambers. The two growth axes in the final stage are close, coplanar, and parallel. The aperture is as described for the genus, even if the secondary valvular projection is not clearly visible. The apertural connection between one chamber and the other is placed at half of the height of the following chamber. The test wall is calcareous, two-layered, with an inner microgranular dark layer and an outer hyaline, clear, translucent layer.

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*Remarks*.—*Dagmarita chanakchiensis* differs from *D. altilis* by a greater height of the test, the shape of the test, the higher number of pairs of chambers, and the shape of the chambers (Table 1). We agree with Altıner (1981), Jenny-Deshusses (1983), and Mohtat-Aghai and Vachard (2003) that all the species from Middle–Late Permian of Russia described by Sosnina in Sosnina and Nikitina (1977) (*D. elegans*, *D. cuneata*, *D. exilis*, and *D. oblonga*) are synonyms of *Dagmarita chanakchiensis.* We also assert that *D. simplex* Wang in Zhao et al., 1981, *D. minuscula* Wang in Zhao et al., 1981, *D. liantanensis* Hao and Lin, 1982, and *D. elongata* Lin et al., 1990, from Maokouan (∼Guadalupian) to Changhsingian of southern China, are synonyms of the type species of the genus *Dagmarita*. The only distinctive features are the dimensional parameters, which however are gradual and change from specimen to specimen as well as with the orientation of thin sections. In addition, the type material is often poorly illustrated and sometimes (as for *D. simplex*, pl. 1, fig. 24) represented only by the holotype. This lack of information makes it difficult to achieve a clear understanding of the diagnostic criteria.

*Dagmarita altilis* Wang in Zhao et al., 1981

1981 *Dagmarita altilis* Wang in Zhao et al., p. 74, pl. 1, fig. 21.
1984 *Dagmarita minima* Lin, p. 112, pl. 1, figs. 18, 19.

*Holotype*.—Longitudinal frontal section (ACT 29) from the upper part of Changhsing Formation of Changxing, Zhejiang, South China (Wang in Zhao et al., 1981, pl. 1, fig. 21).

*Occurrence*.—Roadian (Guadalupian, Permian) to latest Changhsingian (Lopingian, Permian) of southern China (Wang in Zhao et al., 1981; Lin et al., 1990; Gaillot et al., 2009), Changhsingian of Transcaucasia (Pronina, 1988, 1989; Pronina-Nestell and Nestell, 2001), Lopingian of Zagros and Fars (Iran) and Hazro (Turkey) (Gaillot et al., 2009) (Fig. 4).

*Description*.—Test free, rectilinear, conic shaped, biserially arranged. The test is made up by six to seven pairs of chambers, increasing in width rather than in height, making the test assume the typical low flared cone shape. The chambers are hemispherical elongated in outline, with a rounded periphery of the roof. Sutures slightly depressed, with an intersection angle greater than 90°. Pronounced and protruding thornlike projections of the test wall are present at the peripheral edge of the chambers. The two growth axes are coplanar and strongly divergent. The aperture is as described for the genus, even if the secondary valvular projection is not clearly visible. The apertural connection between one chamber and the other is close to the base of the following chamber. The test wall is calcareous, two-layered, with an inner microgranular dark layer and an outer hyaline, clear, translucent layer.

*Remarks*.—The species *Dagmarita minima* Lin, 1984 from early Maokouan of southern China, is herein considered as synonymous with *D. altilis*, as already proposed by Lin et al. (1990), Gaillot and Vachard (2007), and Gaillot et al. (2009).

*Dagmarita ghorbanii* new species
Figures 6, 7

1981 *Dagmarita* sp.; Okimura and Ishii, p. 20, pl. 1, fig. 10.

*Holotype*.—The specimen in oblique longitudinal lateral section in Figure 6.1, from sample MRAN 10355; Capitanian (Guadalupian, Permian); Khachik Formation; Zal section (NW Iran) (Fig. 3). The type material is stored at the National Iranian Oil Company, Department of Paleontology, Geochemistry and Researches (Tehran, Iran).

*Diagnosis*.—Species of the genus *Dagmarita* characterized by two non-coplanar and divergent growth axes. The biserial test is made up by three to five pairs of trapezoidal chambers. Small thornlike projections of the test wall are present.

*Occurrence*.—Middle Permian (=Guadalupian), Wordian to Capitanian, Iran (Fig. 4).

*Description*.—Test free, rectilinear, cuneiform in shape, biserially arranged. The test is made up by three to five pairs of chambers increasing in width rather than in height. The chambers are trapezoidal in outline with a rounded periphery of the roof. Sutures depressed with perpendicular intersection. Small thornlike projections of the test wall are present at the peripheral edge of the chambers. The two growth axes of the adult stage are close, non-coplanar, and slightly divergent in the last two pairs of chambers. The aperture is as described for the genus, even if the secondary valvular projection is not clearly visible. The apertural connection between one chamber and the other is close to the base of the following chamber. The test wall is calcareous, two-layered, with an inner microgranular dark layer and an outer hyaline, clear, translucent layer.

*Etymology*.—The new species is dedicated to Prof. Mansour Ghorbani (Department of Geology, Faculty of Geoscience, Shahid Beheshti University and Arian Zamin Co., Tehran, Iran) for his great contribution to the knowledge of geology of Iran.

**Table 1.** Comparative table of measurements of all the species of the genus *Dagmarita*.

| Species | Height of the test (μm) | Width of the test (μm) | Number of pairs of chambers | Thickness of the wall (μm) |
|---|---|---|---|---|
| *Dagmarita chanakchiensis* Reitlinger, 1965 | 420–710 | 210–480 | 6–9 | 10–20 |
| *Dagmarita altilis* Wang in Zhao et al., 1981 | 390 | 400 | 6–7 | — |
| *Dagmarita ghorbanii* n. sp. | 280–500 | 270–410 | 3–5 | 6–12 |
| *Dagmarita zalensis* n. sp. | 450–800 | 180–280 | 8–11 | 7–12 |

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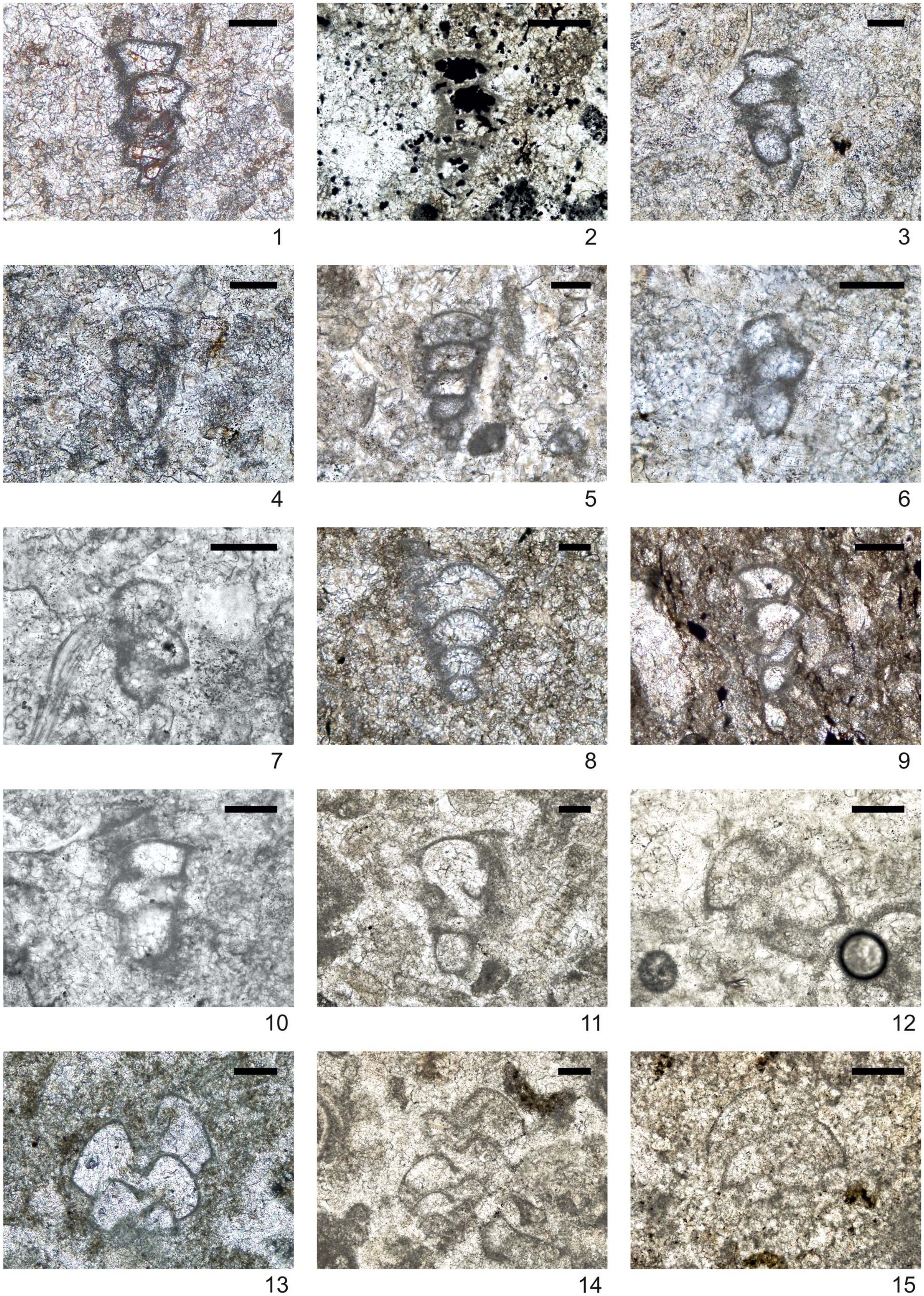


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**Figure 6.** *Dagmarita ghorbanii* n. sp. from Zal (NW Iran) and Abadeh (Central Iran) stratigraphic sections: (**1**) holotype, oblique longitudinal lateral section, sample MRAN 10355; (**2**) oblique longitudinal lateral section, sample MRAN 10319; (**3**) oblique transversal section, sample MRAN 10230; (**4**) oblique longitudinal lateral section, sample MRAN 10367; (**5**) longitudinal lateral section, sample MRAN 10183; (**6**) oblique longitudinal lateral section, sample MRAN 10230; (**7**) oblique longitudinal lateral section, sample MRAN 10230; (**8**) longitudinal lateral section, sample MRAN 10355; (**9**) oblique longitudinal lateral section, sample MRAN 10349; (**10**) oblique longitudinal section, sample MRAN 10230; (**11**) oblique longitudinal section, sample HB 148; (**12**) oblique longitudinal frontal section, sample MRAN 10367; (**13**) oblique longitudinal frontal section, sample HB 30; (**14**) oblique longitudinal frontal section, sample HB 148; (**15**) oblique longitudinal frontal section, sample HB 148. Scale bars = 100 μm.

*Dimensions.*—Height of the test 280–500 μm; width of the test 270–410 μm; number of pairs of chambers 3–5; thickness of the wall 6–12 μm.

*Remarks.*—*Dagmarita ghorbanii* n. sp. can be distinguished from *Dagmarita chanakchiensis* by the number of pairs of chambers (6–9 in *D. chanakchiensis*) and the smaller height of

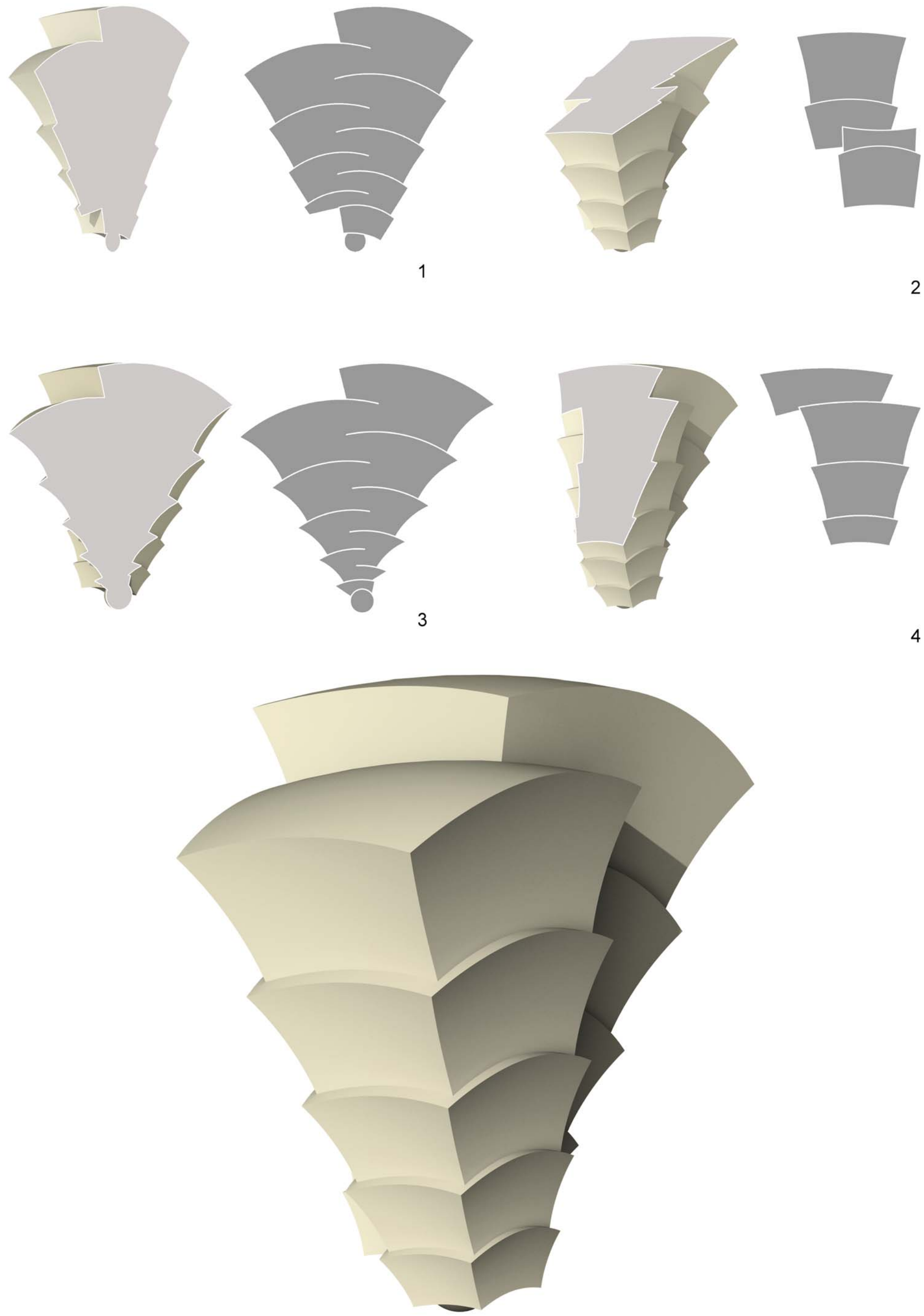


**Figure 7.** Three-dimensional reconstruction of *Dagmarita ghorbanii* n. sp.: (**1**) oblique longitudinal frontal section; (**2**) oblique transversal section; (**3**) oblique longitudinal frontal section; (**4**) oblique longitudinal lateral section.

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the test (up to 710 µm in *D. chanakchiensis*) (Table 1). The axes of *D. ghorbanii* n. sp. are non-coplanar and slightly divergent in the final part of the test, whereas in *D. chanakchiensis* the axes are coplanar and not divergent. In *Dagmarita altilis*, the axes are coplanar and highly divergent in the final part. The width/height ratio of the chambers in *D. ghorbanii* n. sp. is less than in *D. altilis*. The latter also has more pairs of chambers (6–7). *Dagmarita ghorbanii* n. sp. can be distinguished from *Dagmarita zalensis* n. sp. by its reduced number of pairs of chambers, smaller height of the test, and by the different shape of chambers (Table 1). The axes in *D. zalensis* n. sp. are coplanar and parallel. The development and protrusion of thornlike projections of *Dagmarita ghorbanii* n. sp. are less pronounced than in all the other species of *Dagmarita*.

*Dagmarita zalensis* new species
Figures 8, 9

2012 *Dagmarita chanakchiensis* Reitlinger; Şahin et al., p. 295, pl. 1, fig. 15.
2015 *Dagmarita* aff. *elegans* Sosnina; Ebrahim Nejad et al., fig. 12.1–12.5. [online publication]
2016 *Dagmarita chanakchiensis*; Zhang et al., p. 102, fig. 4.9–4.11.

*Holotype*.—The specimen in oblique longitudinal frontal section in Figure 8.1, from sample MRAN 10230; Wordian (Guadalupian, Permian); Arpa Formation; Zal section (NW Iran) (Fig. 3). The type material is deposited at the National Iranian Oil Company, Department of Paleontology, Geochemistry and Researches (Tehran, Iran).

*Diagnosis*.—Species of the genus *Dagmarita* characterized by two close, coplanar, and parallel growth axes. The biserial test is made up by eight to eleven pairs of subquadrate chambers. Pronounced thornlike projections of the test wall are present.

*Occurrence*.—Middle Permian (=Guadalupian), Wordian to Capitanian, Iran, Turkey, and Tibet (Fig. 4).

*Description*.—Test free, rectilinear, elongated in shape, biserially arranged. The test is made up by 8–11 pairs of chambers slowly increasing, so that the width/height ratio is approximately one, both in the juvenile and in the adult stages. The chambers are subquadrate in outline with a rounded periphery of the roof. Sutures markedly depressed with non-perpendicular intersection. Pronounced thornlike projections of the test wall are present at the peripheral edge of the chambers. The two growth axes of the adult stage are close, coplanar, and parallel, giving a skyscraper silhouette. The aperture is as described for the genus, even if the secondary valvular projection is not clearly visible. The apertural connection between one chamber and the other is placed at half of the height of the following chamber. The test wall is calcareous, two-layered, with an inner microgranular dark layer and an outer hyaline, clear, translucent layer.

*Etymology*.—After the name of the Zal section (NW Iran), where the new species has been recorded.

*Dimensions*.—Height of the test 450–800 µm; width of the test 180–280 µm; number of pairs of chambers 8–11; thickness of the wall 7–12 µm.

*Remarks*.—Although the height range of the test of *Dagmarita zalensis* n. sp. and *Dagmarita chanakchiensis* partly overlaps, the former has the maximum height (Table 1). *Dagmarita zalensis* n. sp. can be more reliably distinguished from *D. chanakchiensis* by the higher number of chambers (maximum 22). Furthermore, the width of the final part of the test moderately increases in *D. zalensis* n. sp. and strongly in *D. chanakchiensis*, so that the maximum width of the latter is almost double that of the former. This is the reason why *D. zalensis* n. sp. shows the typical skyscraper silhouette. The thornlike projections in *D. zalensis* n. sp. are smaller and less protruding than in *D. chanakchiensis*. *Dagmarita zalensis* n. sp. also can be distinguished from *Dagmarita altilis* by the height (390 µm in *D. altilis*) and width (400 µm in *D. altilis*) of the test and the number of pairs of chambers (6–7 in *D. altilis*). Moreover, in *D. zalensis* n. sp., the axes are close and less divergent in the final part and the thornlike projections are less protruding.

## Phylogenetic remarks of the genus *Dagmarita*

In the original description, Reitlinger (1965) stated the uncertain status of the phylogenetic origin of the genus *Dagmarita*. Based on stratigraphic and morphological reasons, Zaninetti and Altıner (1981) reconstructed the possible phylogeny of *Dagmarita*, showing that it evolved from a biserially coiled ancestor belonging to the *Globivalvulina* stock. In particular, they supported this lineage asserting that some specimens of *Dagmarita chanakchiens* show a coiled initial stage. According to this evolutionary trend, Altıner (1997, 1999) identified *Globivalvulina cyprica* Reichel, 1946 as a possible ancestor within the *Globivalvulina* stock. Moreover, Altıner (1999) established the genus *Sengoerina* ('genus A' in Altıner, 1997) as having morphological features both of globivalvulinin and dagmaritin stages. According to Altıner, this genus represents the ancestor of biseriamminids having angular chambers (Dagmaritinae). Mohtat-Aghai and Vachard (2003) objected to this phylogenetic interpretation, claiming that the genus *Sengoerina* is younger (Midian = Capitanian) than *Dagmarita* (early Murgabian = late Roadian), so that *Sengoerina* cannot represent the ancestor of *Dagmarita*. Subsequently, for chronostratigraphic reasons Gaillot and Vachard (2007), Altıner and Özkan-Altıner (2010), and Vachard (2016) considered the appereance of *Dagmarita* to be later than that of *Sengoerina*, acknowledging the lineage *Globivalvulina cyprica*-*Sengoerina*-*Dagmarita*.

In this study, we follow the most recent phylogenetic reconstruction of the family Globivalvulinidae and its subfamilies (Globivalvulininae, Paraglobivalvulininae, Dagmaritinae, and Paradagmaritinae) (Gennari et al., 2018a), in which Dagmaritinae is sister taxon to Paradagmaritinae. In the phylogenetic reconstruction proposed by Gennari et al. (2018a), the Globivalvulininae would represent the most primitive clade within the family Globivalvuninidae, whereas the pair formed by Dagmaritinae and Paradagmaritinae occupy the most derived position in the phylogenetic tree. Gennari et al. (2018a) included

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**Figure 8.** *Dagmarita zalensis* n. sp. from Zal (NW Iran) stratigraphic section: (**1**) holotype, oblique longitudinal frontal section, sample MRAN 10230; (**2**) longitudinal frontal section, sample MRAN 10183; (**3**) longitudinal frontal section, sample MRAN 10230; (**4**) oblique longitudinal frontal section, sample MRAN 10230; (**5**) oblique longitudinal frontal section, sample MRAN 10183; (**6**) longitudinal lateral section, sample MRAN 10183; (**7**) longitudinal lateral section, sample MRAN 10230; (**8**) oblique longitudinal lateral section, sample MRAN 10183; (**9**) longitudinal lateral section, sample MRAN 10183. Scale bars = 100 µm.

*Sengoerina* within the subfamily Paradagmaritinae due to its biserially enrolled early stage and chambers that become angular in the uncoiled stage. Therefore, we cannot retain as valid the relationship between *Sengoerina* and *Dagmarita*. Our stratigraphic data (Fig. 3) support this hypothesis, indicating that the appearance of *Dagmarita* is earlier (Wordian) (Gennari et al., 2018a) than that of *Sengoerina* (Capitanian) (Fig. 10). Conversely to what has been previously suggested by Zaninetti and Altıner (1981), Altıner (1997, 1999), Gaillot and Vachard (2007), Altıner and Özkan-Altıner (2010), and Vachard

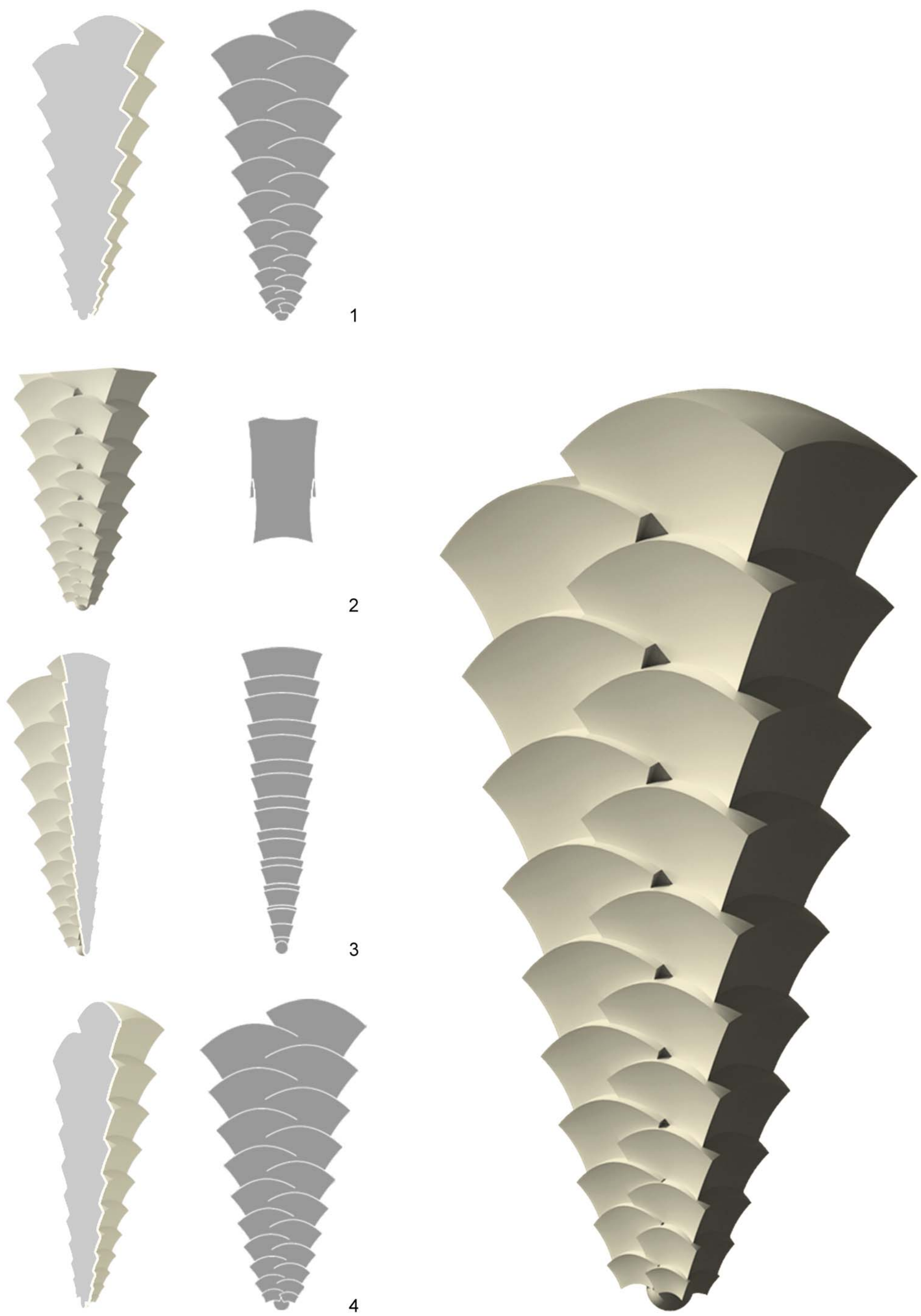


**Figure 9.** Three-dimensional reconstruction of *Dagmarita zalensis* n. sp.: (**1**) longitudinal frontal section; (**2**) transversal section; (**3**) longitudinal lateral section; (**4**) oblique longitudinal frontal section.

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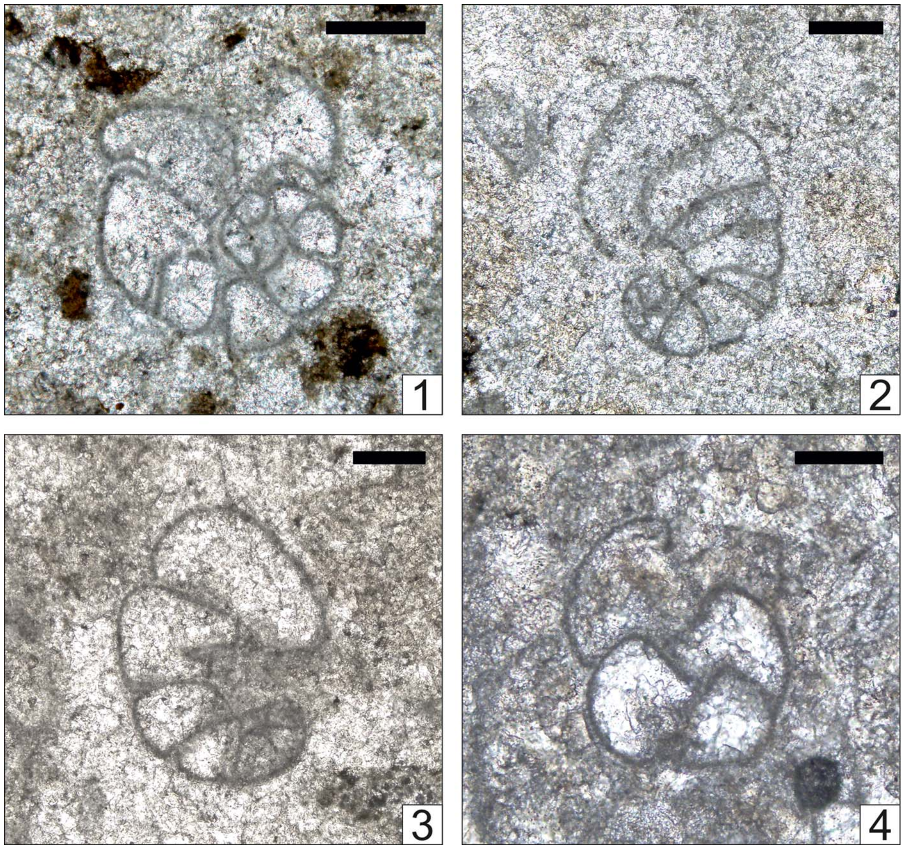


**Figure 10.** (**1–3**) *Sengoerina argandi* Altıner, 1999: (**1**) oblique lateral section, sample HB 30; (**2, 3**) oblique lateral section, sample HB 148. (**4**) *Sengoerina* sp., tangential section, sample MRAN 10360. Scale bars = 100 μm.

(2016), and in agreement with Gennari et al. (2018a), the only possible evidence for a phylogenetic relationship between Globivalvulininae, Paradagmaritinae, and Dagmaritinae would be a still unknown Carboniferous (?Mississippian) common ancestor.

## Conclusions

There are five main conclusions from this study summarized as follows: (1) the genus *Dagmarita* has been re-described on the basis of the type of chamber arrangement, apertural structures, and type of the test wall; (2) a secondary valvular projection has been defined for the first time, as a peculiar morphological feature of the genus *Dagmarita*; (3) two new species belonging to the genus *Dagmarita* (*Dagmarita ghorbanii* n. sp. and *Dagmarita zalensis* n. sp.) have been herein described from the Permian–Triassic successions of Zal (NW Iran) and Abadeh (Central Iran) (3D reconstructions allowed identification of the possible sections of the two new taxa, confirming those chosen to represent the populations); (4) on the basis of our taxonomic revision, the genus *Dagmarita* comprises *Dagmarita chanakchiensis* Reitlinger, 1965, *Dagmarita altilis* Wang in Zhao et al., 1981, *Dagmarita ghorbanii* n. sp., and *Dagmarita zalensis* n. sp.; and (5) finally, in our phylogenetic interpretation, the initially coiled genus *Sengoerina* should not be considered as the ancestor of *Dagmarita* and the ancestor of the subfamily Dagmaritinae would still be an unknown Carboniferous (?Mississippian) taxon.

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